DISSERTATION

Ecomorphology of the European *Hyaenodon*

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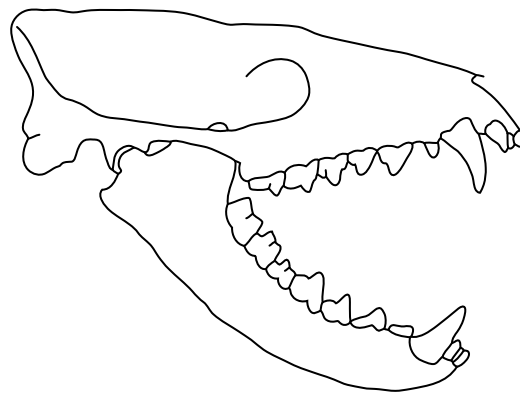
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Katharina Bastl

Dedicated to my beloved father,
Friedrich Bastl

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Abstract

Hyaenodon was a speciose genus in the late Eocene to early Miocene distributed over the Northern hemisphere (Europe, North America and Asia). Taking into account that carnivorous mammals are not as numerously preserved as others, certain Oligocene sites yield a considerable amount of material. This is true especially for North America (e.g. White River formation). In Europe, Quercy (France) is a complex of fissure fillings bearing a rich fossil record of many taxa including *Hyaenodon*. Concerning Asia the evidence is sparser and most findings come from Mongolia.

The focus of this thesis is on the ecomorphology of the European *Hyaenodon* with the aim to reconstruct diet, sensory capabilities and the locomotion pattern. However, facts of taxonomic value are discussed as well.

Hyaenodon has long been regarded as having been capable of processing bone. The enamel thickness, stereomicrowear results and the ultrastructure of the enamel were used as additional information to dental morphology and wear patterns to reconstruct the diet of this fossil predator. The ossiphagous tendencies can be confirmed. *Hyaenodon* occupies a broad dietary niche — overlapping with those of the recent lion and the spotted hyena. Different dietary tendencies were observed in the European and the North American taxa.

The sense of touch and hearing, as well as the brain were examined in detail. For the first time an auditory ossicle of *Hyaenodon* is described.

The infraorbital foramen is rather small. *Hyaenodon* did not possess as specialized whiskers as felids do. The sense of touch — concerning the whiskers — was equally developed as in canids.

Reviewing the hitherto knowledge of the brain — the following features were apparent: the neocortex is small, but folded; the olfactory lobes are largely developed. The sense of smell was compared to other senses important in *Hyaenodon*.

The hearing apparatus was examined including the bulla, an auditory ossicle (the incus) and the inner ear (cochlea and semicircular canals). The bulla is made up by a chambered entotympanic. The coiling of the cochlea is of the same degree as in dogs. The semicircular canals are extensive. The incus is showing the usual saddle-shaped facet, but with a large upper articulation surface and a small, circular lower articulation facet. Compared to recent carnivores it is most similar to cats. *Hyaenodon* was not adapted to low frequencies and most probably had a wide frequency range (as predators commonly do) with a possible adaptation to high frequencies (as in cats).

The skeletal remains, although by far less frequently preserved in Europe than in North America, were the basis for the inferences of locomotion pattern and predation style.

The nuchal ligament was assumed to support the proportionally oversized head (compared to recent Carnivora). If this ligament really was present, it did not insert on the epistropheus as it does in canine dogs. It is proposed here, that it inserted on the posterior aspect of the skull as in ungulates.

The skeleton of *Hyaenodon* exhibits terrestrial and cursorial features. Its general structure was robust with a strong musculature. The fibio-tarsal complex indicates progression over uneven surface. *Hyaenodon's* locomotion pattern is judged here as cursorial and interpreted in the sense that this predator was dwelling primarily on the ground with an adaptation to running.

The canines of *Hyaenodon* are mediolaterally compressed and like those in canids and not like the rounded canines in felids. This type of canines is ideal for slashing. Thus, *Hyaenodon* inflicted its prey with shallow wounds and not with a killing bite like recent felids do (additional evidence comes from the non-specialized whiskers). The predation style of *Hyaenodon* was ambushing, although it did not succumb in a chase with most contemporaneous prey animals. It was a powerful predator in the forests of the Eocene as well as in the more open landscape of the Oligocene.

Some taxonomic information can be provided as well:

The tooth eruption sequence is differing between the European and the North American forms: there are significant differences in the sequence of the lower jaw (concerning the p3, the p4, the m3 and the canine) and a difference in the sequence of the upper jaw (concerning the eruption of the P1).

The milk dentition in European *Hyaenodon* species shows different morphologies. For the first time differences are described concerning the morphology of the upper milk teeth DP3 and DP4 (development of the anterior cusp and the cutting blade) and the lower milk teeth dp3 and dp4 (development of the anterior cuspid and the talonid) in the Oligocene species *Hyaenodon exiguus* and *Hyaenodon filholi*. Compared with other known juvenile material from North America and Asia, the morphology of *Hyaenodon exiguus* appears to be a product of European evolution. The assumption that *Hyaenodon filholi* was an Asian immigrant is emphasized here.

Divergence within the genus was found. Some differences between the North American and the European *Hyaenodon* described in literature turned out to be not valid, e.g. the presence of a scapholunatum in the European taxa (based on misidentifications). However, the different tooth eruption pattern is a consistent difference, as well as the more plesiomorphic morphology of the M1 in North American forms. The root development (single- or double-rooted) of the p1 is varying, but does not give distinct clues: the oldest species show a single-rooted p1 and the Oligocene species in Europe possess a double-rooted p1. The skeleton of the European *Hyaenodon* shows differences between Eocene and Oligocene material. The evolution of the North American *Hyaenodon* is acknowledged as an own lineage.

Zusammenfassung

Hyaenodon war eine artenreiche Gattung im späten Eozän bis ins frühe Miozän der nördlichen Hemisphäre (Europa, Nordamerika und Asien). Unter Berücksichtigung der spärlichen Erhaltung von karnivoren Säugetieren, ist der Nachweis aus bestimmten oligozänen Fundstellen beachtlich. Das trifft besonders auf Nordamerika (z.B. White River Formation) zu. In Europa lieferten die Spaltenfüllungen von Quercy (Frankreich) einen reichhaltigen Fossilnachweis, darunter auch *Hyaenodon*. Das asiatische Material ist weit weniger umfangreich und die meisten Funde stammen aus der Mongolei.

Der Mittelpunkt dieser Arbeit ist die Ökomorphologie des europäischen *Hyaenodon* und verfolgt das Ziel Ernährung, sensorische Fähigkeiten und Fortbewegung zu rekonstruieren. Taxonomisch verwertbare Informationen werden ebenfalls diskutiert.

Hyaenodon wurde lange als Knochenbrecher gewertet. Die Zahnschmelzdicke, Ergebnisse aus der „stereomicrowear" Analyse und die Ultrastruktur des Zahnschmelzes wurden als Zusatzinformation zu der Zahnmorphologie und dem Kaumuster verwendet, um die Ernährung dieses fossilen Räubers zu rekonstruieren. *Hyaenodon* besetzte eine breite Nische, die mit der des rezenten Löwen und der Tüpfelhyäne überlappt. Unterschiedliche Tendenzen in der Nahrungspräferenz konnten zwischen europäischen und nordamerikanischen Taxa festgestellt werden.

Tast-, Gehörsinn und das Gehirn wurden je nach Möglichkeit untersucht. Erstmalig wird ein Gehörknöchelchen von *Hyaenodon* beschrieben.

Das Foramen infraorbitale ist relativ klein. *Hyaenodon* besaß keine spezialisierten Tasthaare wie Katzen. Der Tastsinn, hier eingeschränkt beurteilt an den Tasthaaren, war ähnlich wie in Hunden entwickelt.

Folgende Merkmale sind bei Betrachtung des bisherigen Wissens über das Gehirn zu erwähnen: Das Großhirn ist klein, aber gefurcht. Die olfaktorischen Loben sind groß. Der Geruchssinn war verglichen zu den anderen Sinnen sehr ausgeprägt.

Der Gehörapparat wurde untersucht, darunter die Bulla auditiva, ein Gehörknöchelchen (der Incus) und das Innenohr (die Gehörschnecke und die Bogengänge). Die Bulla ist aus einem gekammerten Entotympanicum aufgebaut. Die Aufwickelung der Gehörschnecke ist von einem vergleichbaren Grad wie dem des Hundes. Die Bogengänge sind ausgedehnt. Der Incus zeigt die übliche sattelförmige Gelenksfläche. Sie ist in eine große superiore und eine kleine, runde, inferiore Fläche unterteilt. Verglichen mit modernen Raubtieren ist der Incus am ähnlichsten dem der Katze. *Hyaenodon* war nicht an geringe Frequenzen angepasst. Höchstwahrscheinlich verfügte es über ein weites Spektrum an Frequenzen (wie Raubtiere allgemein) und könnte an hohe Frequenzen angepasst gewesen sein (wie die Katze).

Die Skelettelemente, auch wenn weniger zahlreich erhalten in Europa, waren die Grundlage für Rückschlüsse auf das Bewegungsmuster und die Jagdstrategie.
Das Ligamentum nuchae unterstützte den proportional zum Körper übergroßen Kopf. Wenn dieses Ligament tatsächlich vorhanden war, dann setzte es nicht am Epistropheus an wie in Caninae. Stattdessen wird hier vorgeschlagen, dass es am Hinterhaupt wie in Huftieren ansetzte.
Das Skelett von *Hyaenodon* zeigt terrestrische und kursoriale Merkmale. Generell war es von robustem Bau und mit starker Muskulatur ausgestattet. Der Fibio-Tarsal-Komplex weist auf Bewegung über unebene Flächen hin. Das Fortbewegungsmuster wird hier als kursorial beurteilt und in dem Sinne ausgelegt, dass *Hyaenodon* ein primär am Boden lebender Räuber mit Laufanpassungen war.
Die Eckzähne waren mediolateral komprimiert und in diesem Aspekt ähnlich den Caniden und damit anders als die im Querschnitt runden Eckzähne der Feliden. Dieser Typ ist ideal für das Aufschlitzen der Beute. Daher fügte *Hyaenodon* dem Beutetier mehrere flache Wunden zu und tötete nicht mit einem einzigem Biss wie moderne Feliden (dafür spricht auch die Ausbildung der Schnurrhaare). Die primäre Jagdstrategie war der Angriff aus dem Hinterhalt, aber auch eine Verfolgungsjagd mit den meisten damaligen Beutetieren konnte erfolgreich ausgehen. *Hyaenodon* war ein gefährlicher Räuber in den Wäldern des Eozäns und der offeneren Landschaft des Oligozäns.

Taxonomisch verwertbare Ergebnisse wurden ebenfalls erzielt:
Der Zahnwechsel verläuft bei europäischen Formen anders als bei Nordamerikanischen: deutliche Unterschiede sind im Ablauf des Zahnwechsels im Unterkiefer (den p3, p4, m3 und den Eckzahn betreffend) und auch im Oberkiefer (den P1 betreffend) festzustellen.
Die Milchbezahnung ist in Europa je nach Art ausgeprägt. Interessanterweise zeigen die oligozänen Arten *Hyaenodon exiguus* und *Hyaenodon filholi* unterschiedliche Morphologien der Oberkiefermilchzähne DP3 und DP4 (Entwicklung des anterioren Höckers und der Schneidekante) und der Unterkiefermilchzähne dp3 und dp4 (Entwicklung des anterioren Höckers und des Talonids). Im Vergleich mit juvenilem Material aus Nordamerika und Asien, erscheint die Morphologie von *Hyaenodon exiguus* als europäische Entwicklung. Die Annahme, dass *Hyaenodon filholi* ein asiatischer Einwanderer war, wird hier betont.

Divergenz innerhalb der Gattung *Hyaenodon* wurde festgestellt. Manche Unterschiede zwischen den nordamerikanischen und den europäischen Formen, die schon in der Literatur beschrieben worden sind, erwiesen sich als ungültig, z.B. das Vorhandensein eines Scapholunare in den eruopäischen Arten (basierend auf falscher Zuordnung). Der unterschiedliche Zahnwechsel ist jedoch ein beständiger Unterschied, ebenso wie die plesiomorphe Morphologie des M1 in den nordamerikanischen Formen. Die Wurzelentwicklung (ein- oder zweiwurzelig) des p1 ist variabel, gibt aber keine deutlichen Hinweise: die älteste bekannte Art zeigt einen einwurzeligen p1 und die oligozänen Arten Europas besitzen einen zweiwurzeligen p1. Das Skelett des europäischen *Hyaenodon* weist Unterschiede zwischen eozänem und oligozänem Material auf. Die Evolution des nordamerikanischen *Hyaenodon* wird als eigene Linie anerkannt.

Chapter 1

1. Introduction

The genus *Hyaenodon* belongs to the order Creodonta. This taxon included formerly various groups, e.g. miacids and mesonychids. Today the families Hyaenodontidae and Oxyaenidae remained in that order (e.g. Gunnell and Gingerich, 1991; McKenna, 1975). However, monophyly is doubted and higher systematics are discussed (e.g. Morlo et al., 2009; Polly, 1996). Therefore, this group is always given in quotation marks in the following.

Four subfamilies are included in the Oxyaenidae: Tytthaeninae, Ambloctoninae (= Palaeonictinae), Oxyaeninae and Machaeroidinae (the latter with doubt; Solé et al., 2011). The oxyaenids are known from the whole northern hemisphere, but are best represented in North America (Gunnell and Gingerich, 1991): they appeared during the late Paleocene, diversified and disappeared in the middle Eocene (Gingerich, 1980; Solé et al., 2011). In Europe the oxyaenids are reported after the Paleocene/Eocene boundary (Smith and Smith, 2001). However, their remains are rare (Gunnell and Gingerich, 1991). Just recently Solé et al. (2011) could give more detailed information on European oxyaenids (from Le Quesnoy, MP 7, Early Eocene) and thus an insight in the evolution of this group in Europe. The European oxyaenids appear primitive, e.g. *Oxyaena woutersi* resembles of all North American species *O. gulo* most (which is the most primitive species of the genus) in showing a less shearing dentition and a narrower talonid on the m2. Furthermore, the European species of *Oxyaena woutersi* recalls *Dipsalidictis* in having a more mesiad shifted protocone on the P4 (also seen in *Tytthaena*; Gingerich, 1980), protocone on the M1 less reduced than in *O. gulo*, deep ectoflexus on the M1, developed parastyle on the M1 and less developed pre- and postcingula on the M1 than in other *Oxyaena* species (Solé et al., 2011). The European *Palaeonictis gigantea* was confirmed to be related to the North American species *Palaeonictis wingi*. The study of Solé et al. (2011) supports a North American origin and a single dispersal event from North America to Europe, followed by a short endemic local evolution. Oxyaenids disappeared rapidly from Europe and could support the distinction between the MP 7 and MP 8+9 reference levels. Fossil evidence from Asia indicates a survival of oxyaenids until the middle Eocene (Granger, 1938). North America was assumed as center of origin of oxyaenids before: *Tytthaena* is known from the late Paleocene (middle Tiffanian; Gingerich, 1980). Oxyaenids are characterised by (Morlo and Habersetzer, 1999): two upper and lower molars, no metastyle on the M2, single-rooted or absent p1 and talonid crests built by the fused entoconid and hypoconulid (instead of the hypoconid as in hyaenodontids; also De Muizon and Lange-Badré, 1997).

The family Hyaenodontidae is characterized by possessing three carnassials in the upper and lower jaw (M1-3 and m1-3 respectively; Gingerich and Deutsch, 1989). Gingerich and Deutsch (1989) studied North American hyaenodontids. Limnocyonines were studied by Morlo and Gunnell (2003). Gingerich and Deutsch (1989) already proposed Africa as center of origin of the Hyaenodontidae, because of their diversity and dominance there. Hyaenodontidae are represented in Africa by Proviverrinae, Koholiinae, Apterodontinae and Hyainailurinae (Gheerbrant et al., 2006). Gheerbrant et al. (2006) erected *Boualitomus marocanensis*. The authors found that *Boualitomus* is more primitive than *Prototomus* in its small size and its talonid of the p4 bearing at least two accessory cusps and a bulbous protostylid. Note that these features are more cimolestid-like. This morphology relates it to *Tinerhodon* and supports the proviverrine affinity of the latter (Gheerbrant et al., 2006). *Tinerhodon* now fills the gap between Hyaenodontidae and primitive insectivore-like ancestors. *Boualitomus* and *Tinerhodon* are identified as the most primitive hyaenodonts and support in conjunction with the presence of cimolestids in Morocco, the African origin of the family (Gheerbrant et al., 2006). They emphasize that *Tinerhodon* shares no peculiar relationship with the North American *Cimolestes* (striking difference in the talonid on the p4). The key features for the possible African cimolestid ancestor are: molarization of the p4 talonid, reduction of m1 and the development of the paraconid and paracristid (related to that of the postmetacrista of the upper molars; Gheerbrant et al., 2006).
However, despite the different assumed origin centers of Hyaenodontidae and Oxyaenidae, the possibility of a common ancestor older than the late Paleocene *Tytthaena* was not excluded (Gheerbrant et al., 2006;

Solé et al., 2011). Although a convergent development of oxyaenids and hyaenodontids was favoured in consequence, which leaves the phylogeny of the "creodonts" still enigmatic.

Hyaenodon was a dominant predator in the late middle Eocene to early Miocene of Europe, North America and Asia. The question of origin and descent remain unresolved. The genus appears earliest in the late middle Eocene of Asia (Lange-Badré and Dashzeveg, 1989; Wang et al., 2005). In Europe and North America the genus appears in the late Eocene (Lange-Badré, 1979; Mellett, 1977). In North America *Hyaenodon* appears represented by two species (*H. venturae* and *H. vetus*), supporting the hypothesis of immigration of the genus in the New World (Mellett, 1977). Asia was assumed as most likely center of origin of *Hyaenodon* (Bastl et al., 2011).

The most detailed and recent revision was performed by Mellett (1977) for the North American, by Lange-Badré (1979) for the European and by Tsubamoto et al. (2008) for the Asian taxa. Except for Mellett (1977) and Morlo (1999) and a few publications on special topics (e.g. Joeckel et al., 1997), the ecomorphology of *Hyaenodon* was not the main topic of research. Furthermore, there is no publication summarizing the European findings of skeletal remains.

The Eocene/Oligocene transition did not influence the different species of *Hyaenodon*. However, in Europe there is a morphological change in *Hyaenodon* observed: Asian taxa immigrated (Lange-Badré, 1979; Remy et al., 1987). Additionally, it is apparent that most Eocene European taxa were brachyrhynch with a single-rooted p1 and most Oligocene European taxa were longirhynch with a double-rooted p1. This trend is not apparent in North America or Asia. It should be noted, that after the immigration of the first forms, the taxa evolved in their own lineages in North America (Mellett, 1977).

Hyaenodon was named by Laizier and Parieu (1838) and was erected on the European species *Hyaenodon leptorhynchus*. Since then many species were defined and some of them synonymized with others (Lange-Badré, 1979). The lower-level taxonomy is not the only discussed topic: "creodonts" include two families, the oxyaenids and hyaenodontids and are assumed to arise from *Cimolestes* (Polly, 1996). The earliest occurrence of oxyaenids is known from North America. The earliest occurrence of hyaenodontids is known from Africa (Gheerbrant, 1990; Gheerbrant et al., 2006; Lewis and Morlo, 2010; Solé et al., 2009; see above). Biogeography is not resolved and different migration routes were proposed (Lange-Badré and Böhme, 2005). Monophyly of "Creodonta" is doubted and the high-level systematics are in flux (Morlo et al., 2009; Polly, 1996; Solé et al., 2009). Solé (2010) provided the most recent work on the systematics of hyaenodontids. Interestingly, a similar problem arose with the ancestry of Carnivora: viverravids were the only Palaeocene carnivorans (Hunt and Tedford, 1993). Their ancestry possibly rests in the Late Cretaceous *Cimolestes*. This genus first lost their terminal molars and then enlarged the P4/m1 carnassial pair. Miacids occur in the earlist Eocene and may arise of a *Cimolestes* group with M3/m3 — thus a diphyletic origin of Carnivora remains plausible (Hunt and Tedford, 1993).

The mesonychid/oxyaenid guild was replaced by the nimravid/hyaenodontid guild by the late Eocene (Van Valkenburgh, 1999). For most of the Oligocene a rare exchange between the Old and the New World is assumed (Van Valkenburgh, 1999). This confirms the trends in *Hyaenodon* (see above). The "creodonts" of the Eocene in Europe and North America show less diversity (in diet and locomotion) than recent Carnivora (Morlo, 1999).

Hyaenodon was a carnivorous mammal. There are four dietary types in Carnivora (Van Valkenburgh, 1995): meat specialists (felids), meat-bone type (hyaenids), meat-plant matter (in equal amount; generalists) and the weak carnivore type (<50% meat; ursids). In the middle Oligocene only meat specialists and generalists were present (e.g. "creodonts" and nimravids; Van Valkenburgh, 1995). Concerning *Hyaenodon* this is doubted (e.g. Mellett, 1977) — as most authors considered the genus to occupy a hyena-like niche (Mellett, 1977).

The topic of this thesis is the ecomorphology of the European *Hyaenodon*. My aim was to gain information on as many various aspects as possible. Usually the parameters diet, locomotion and body weight are used to represent the ecomorphology of a taxon (Morlo et al., 2011). The locomotion pattern is highly connected to the habitat: favouring or restricting different locomotion types e.g. in a forest or an open landscape (Morlo et al., 2011). The same authors found that diet can be as useful as the locomotion pattern in differentiating guilds, but is in general the least important parameter, because meat is available in all environments. A few publications on special topics concerning the paleoecology of *Hyaenodon* were published (e.g. Joeckel et al., 1997), but were never put together to throw light on this fossil predator as a whole. Herein, any relevant information available is discussed. The paleoecology of *Hyaenodon* is based on three main topics herein: diet, sensory capabilities and locomotion pattern in connection with all related fields (e.g. ontogeny, hearing apparatus, brain morphology or hunting strategy).

Chapter 2

2. Methods

Different methods were applied to get a most complete picture of the ecomorphology of *Hyaenodon*: measuring, x-ray, CT-scan, thin-slides, 3D-reconstruction, stereomicrowear and analysis of the ultrastructure of the enamel were applied. The proceeding and the tools used during the application of each method are described in the respective chapters and are mentioned here.

For the x-raying of specimens, a digital x-ray at the DZU (Donauzentrum Urania, a Vienna hospital) was used. Andrea Tietze and her team supervised the procedure and kindly supported me.
The thin sections of teeth were prepared at the Department of Palaeontology (University Vienna). Our preparators supported me during this procedure. Each tooth was embedded in resin, cut with a thin saw and applied on a glass slide. The slides were grinded by hand with grinding powder (grain size 600 and 1000). It was necessary to prepare casts for the stereomicrowear analysis: the specimens of the various collections were cleaned at the museum with a cotton stick and alcohol. Especially the slicing facet of the carnassial was properly cleaned. Then the molding substance (President Jet Regular Body; coltène whaledent, article no. 4605) was applied with a gun (mixed with the hardener in its single-use tip) directly on the tooth of interest. This mold was further processed at the Department of Palaeontology (University Vienna). First a wall of Lab Putty (coltène whaledent; article no. 8805) was formed around the mold. With the help of the preparators, especially Roland Mayer, transparent resin was mixed and centrifuged. The molds were filled with the resin. This laboratory work was performed on a part of the material also at the BayPath College together with Jelena Hasjanova and Gina Semprebon. After a day the resin was hard enough to take the tooth casts out of the molds. These casts were then examined under the light microscope at low magnification (after Solounias and Semprebon, 2002). External oblique illumination was used to direct a fiberoptic light source across the surface of toothcasts at a shallow angle to the occlusal surface to visualize microwear scar topography. A standard 0.4 × 0.4 = 0.16 mm^2 ocular reticle was employed at 35× magnification to quantify the number of small and large pits (round scars), scratches (elongated scars with parallel sides), and gouges (large scars with irregular borders). I had the honor to be trained by Gina Semprebon personally at the BayPath College (Longmeadow, USA) in 2010.

To analyse the ultrastructure of enamel, the following procedure was performed (supervised by Daniela Kalthoff at the Department of Palaeontology, University Vienna): a fragment of the enamel of a tooth was embedded in polyester resin and sectioned (herein tangentially and transversally). Afterwards the specimen was grinded with grinding powder (grain size of 500, 1000 followed by polishing powder). The specimen was etched with 2N HCl for four seconds. Afterwards it was cleaned in an ultrasonic bed and dried. To analyse the specimen it was coated with gold and studied under the scanning electron microscope. The fragment was regularly studied under the binocular microscope during the procedure.

The computer tomography of a skull fragment with a bulla auditiva was performed together with Gerhard Weber and Martin Dockner on the microCT-device Viscom X8060 (tube: X9225-XD) at the Department of Anthropology (Universtiy Vienna). 696 slices with a resolution of 696 x 843 x 792 voxels with a voxel size of 20 x 20 x 20 μm were produced. The reconstruction of the CT-data on the bulla was performed together with Gerhard Withalm at his working station with the software Osirix. The same micro CT-scan was used for the reconstruction of the cochlea and the labyrinth. The software Amira 5.3 was available at the Department of Anthropology as well as a working station. Due to preservation simple tools, which automatically mark the area of interest (e.g. working with the threshold, greyscales) could not be used. Instead the label field was marked with the lasso-tool on a drawing panel in each slice of interest in two cutting planes. The surface generation was created with the option unconstrained smoothing. Measurements were performed directly in Amira with the 2D measurement tool.

The photos of the auditory ossicles, the thin-sections and the cat bulla were made with the digital microscope Keyence VHX-1000 D (connected to a profile measurement unit, the Keyence VHX-S15). Rica Stepanek introduced me to this microscope and Jürgen Kriwet (both Department of Paleontology) gave me the possibility to work on it.

Measurements were taken with a caliper to the nearest 0.1 mm (if not indicated differently). Tooth nomenclature follows Van Valen (1994). Concerning dental material the maximum length and width of a tooth was measured. The measurements of postcranial material are listed in the following. Except for the indication of the element, the proceeding of Fostowicz-Frelik (2007) was applied. The first two letters refer to the respective element (e.g. Hu for humerus) and is followed by the first letters of a specific region on the element (e.g. Tr for trochlea) and the general measurement (e.g. L for length).

Used abbreviations for postcranial material:

HuL	maximal length of the humerus
HuWl	lateral width of the humerus from anterior to posterior aspect
HuWm	medial width of the humerus from internal to external
HuWd	distal width of the humerus, measured medially
HuTrH	height of the humeral trochlea, measured from proximal to distal
HuTrW	width of the humeral trochlea, lateral extension
HuTrD	depth of humeral trochlea, from anterior to posterior aspect measured at the narrowest point
HuEpcW	width of the humeral epicondyle
HuCaW	width of the humeral caput, lateral extension
HuCaH	height of the humeral caput, from proximal to distal

RaprDiamin	minimal proximal cross-section of the radius, measured medial
RaprDia	maximal proximal extension, measured medial
RadisDia	maximal distal extension, measured medial
RaL	maximal length of the radius
RaWl	maximal width of the radius, measured lateral
RaWm	maximal width at the middle of the radial shaft, measured medial
RaApL	length of the proximal articulation surface on the radius
RaApW	width of the proximal articulation surface on the radius
RaAdL	length of the distal articulation surface on the radius
RaAdW	width of the distal articulation surface on the radius

UlL	maximal length of the ulna
UlWl	lateral width of the ulna
UlWm	medial width of the ulna
UlWp	proximal width of the ulna, measured medial
UlOlL	length of the olcranon
UlApL	width of the olcranon
UlInraW	width of the incisura radialis
UlprOlDia	width of the proximal olecranon from internal to external

ScL	length of the scaphoid
ScW	width of the scaphoid

Mc"L	length of the metacarpal
Mc"Wm	medial width of the metacarpal
Mc"Wl	lateral width of the metacarpal
Mc"Wmd	distal width, measured medial
Mt...	the same is valid for the metatarsal, see Mc-measurements above
FeL	maximal length of the femur
FeWm	medial width of the femur, measured at the half of the length of the shaft
FeWl	lateral width of the femur
FeWd	maximal distal width of the femur, measured anterior
FemCH	height of the medial condyles, dorso-ventrally measured
FemCL	length of the medial condyle, anterio-posterior extension measured laterally
FemCW	width of medial condyle, lateral extension measured in posterior aspect
FelCH	height of the lateral condyle
FelCL	length of lateral condyle
FelCW	width of lateral condyle
FeCW	width of the caput femori, internal-external extension measured
FeCF	distance from the external border of caput to the fovea capitis
FeCH	height of the caput femori, laterally measured
FeNeW	width of the neck, measured in anterior aspect
FeNeW2	width of the neck, measured in lateral aspect
FePagH	height of the patella groove, minimal extension
FePagHl	height of the patella groove, maximal extension
FePagW	width of the patella groove, anterio-posterior extension measured in lateral aspect
FeWpr	maximal lateral extension, measured proximally
FeWinf	width of the intercondylar fossa, lateral extension measured in posterior aspect
FedisH	distal height of the femur
TiPrDia	maximal antero-posterior extension of the proximal tibial surface
TiPrW	maximal lateral extension of the proximal tibial surface
TiL	length of the tibia
TiWm	medial width of the tibia
TiWl	lateral width of the tibia
TiCrH	height of the tibial crest, antero-posterior extension measured in lateral aspect
TiDiH	distal width of the tibia, measured medially
TidisL	length of the distal articulation surface of the tibia
TidisW	width of the distal articulation surface of the tibia
FiL	length of the fibula
CalL	length of the calcaneus
CalW	width of the calcaneus
CalCol	length of the neck of the calcaneus
CaluFaL	length of the upper facet (for the astragalus)
CaluFaW	width of the upper facet (for the astragalus)
CallFaL	length of lower facet (sustentaculum tali)
CallFaW	width of lower facet (sustentaculum tali)
CalTuW	width of the tuber, measured medially

CalTuWlat   width of the tuber, measured laterally

AstL   length of the astragalus
AstW   width of the astragalus
AstTrW   width of the astragalar trochlea, measured medially
AstTrH   height of the astragalar trochlea, in lateral aspect
AstTrL   length of the astragalar trochlea, antero-posterior extension in medial aspect
AstNeL   length of the neck

Chapter 3

3. Material

As this thesis focused on European remains of the genus *Hyaenodon*, the main part of the material examined came from Quercy collections from the major museums of Europe: the Musée d´Histoire Naturelle in Paris (France), the British Museum of Natural History in London (United Kingdom) and the Naturhistorisches Museum Wien in Vienna (Austria).

For comparison to the North American taxa, the following museums of the United States were visited: the American Museum of Natural History in New York and the Yale Peabody Museum in New Haven.

An important source for comparative material and samples of recent Carnivora was the collection of the Department of Palaeontology (Institut für Paläontologie, Universität Wien) in Vienna as well as the Naturhistorisches Museum Wien and the American Museum of Natural History in New York.

Abbreviations
For abbreviations for measurements see Chapter 2 (Methods).

Institutional Abbreviations
AMNH: American Museum of Natural History (New York, USA);
Au: Aubrelong collection at the MNHN;
BMNH: British Museum of Natural History (London, UK);
BSPG: Bayerische Staatssammlung für Geologie und Paläontologie (München, Germany);
FAM: Frick Collection at the American Museum of Natural History (New York, USA);
GMM: Geomuseum, Westfälische Wilhelms-Universität (Münster, Germany);
IUPW: Institute of Paleontology (University Vienna, Austria);
IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China;
LDB: La Débruge collection at the MNHN;
M: Collection of the BMNH;
MNHN: Musée d´Histoire Naturelle (Paris, France);
Mo: collection of the MNHN;
NMW: Recent Mammal Collection, Naturhistorisches Museum Wien (Vienna, Austria);
NMHW: Fossil Vertebrate Collection, Naturhistorisches Museum Wien (Vienna, Austria);
PD: Peche Desse collection at the MNHN;
PIN: Paleontological Institute, Russian Academy of Sciences, Moscow, Russia;
PST: assumingly a collection at GI: Institute of Geological Sciences, Mongolian Academy of Sciences, Ulan Bator, Mongolia;
PU: Princeton University (Princeton, New York, USA);
Qu: Quercy collection at the MNHN;
SDSMT: South Dakota School of Mines and Technology (Rapid City, South Dakota, USA);
SMNS: Staatliches Museum für Naturkunde (Stuttgart, Germany);
SNB: Sainte-Néboule collection at the MNHN;
YPM: Yale Peabody Museum (New Haven, USA);
YPM-PU: Princeton Collection moved to Yale Peabody Museum (New Haven, USA);

Anatomical Abbreviations of the dentition
C/c: upper/lower canine; D/d: upper/lower deciduous/milk tooth; HSB: Hunter-Schreger-Bands; I/i: upper/lower incisive; M/m: upper/lower molar; P/p: upper/lower premolar;

Chapter 4

4. Quercy

4.1 Introduction to the fissure fillings of the Quercy

A main part of the material examined for this study comes from phosphatic fissure fillings of the province Quercy (south-western France). The simple term "Quercy" refers to a complex of exceptional rich sites of main importance in the Paleogene of Europe. Therefore, a short overview of these deposits, their history, dating and fossil record shall be given.

Since 1965, paleontological investigations were undertaken in the famous Quercy phosphorites in south-western France (e.g. Lange-Badré, 1979). The Quercy fissure fillings are karstic fillings (Legendre et al., 1997). Evidence for the karstic nature of other phosphorites — the phosphorites of Bas-Languedoc — was found by Nègre (1908). Legendre et al. (1997) gave a good summary of the Quercy. These sites yield fossils of amphibians, reptiles, birds and mammals (Legendre et al., 1997). The time span of the phosphorites ranges from the latest middle Eocene to the beginning of the late Oligocene (MP 16 to MP 28; Legendre et al., 1997). Although some older and younger deposits were described too (Marandat et al. 1993; Sigé et al. 1991) and the total span was extended to early Miocene. For example, the filling of Cuzal (Quercy, Southern France) is of Late Lutetian age (MP 13-14) and additionally enlarges the faunal list of the Quercy (Marandat et al. 1993). The recent paleontological investigations of the Quercy phosphorites were carried out by the Laboratoire de Paléontologie de l´Université de Montpellier (Lange-Badré, 1979).
Due to extensive mining activity, especially during the first years of the exploitation, no professional personnel supervised the recovering of fossils. As a consequence information about exact location and stratigraphic data and thus exact dating is missing for many specimens. Filhol (1976) gave a first synthesis on the fissure fillings of the Quercy and their faunas. Large parts of the Quercy collection were collected by Filhol, Rossignol and Javal (Lange-Badré 1979). Their collections are distributed around the world (Lange-Badré, 1979), which complicates a comprehensive study on the Quercy.
Geographically, the phosphorites of the Quercy are situated in the north between the valleys of Lot and Célé, as far as Villeneuve d´Aveyron in the northeast and in the south up to the banks left of l´Aveyron (Legendre et al. 1997): In the east the Villefranche borders the Quercy and in the south and east lacustrine deposits of the aquitane basin are the borderline.
Sudre et al. (1992) gave a summary of mammal biochronology of the Paleogene north and south of the Pyrénées mountain range including the Quercy plateau. The biochronological scale of the Oligocene is mainly based on theridomyid rodents — abundant in the Quercy fillings. Therefore, several Quercy sites have been chosen as reference level: e.g. Itardies for MP 23, Garouillas for MP 25, Mas de Pauffié for MP 26, Pech du Fraysse for MP 28. Sudre et al. (1992) list numerous sites of the Quercy with Eocene, Oligocene and Miocene faunas. Correlation and chronology of localities from the North and South of the Pyrenees is given too (Sudre et al. 1992).
Maitre et al. (2006b) studied recently discovered localities in the Quercy paleokarst in geomorphological, faunistic and biochronological aspect. A species of *Hyaenodon* found in Bouziès — *Hyaenodon requieni* — was seen as characteristic element of the reference level MP 17a (Maitre et al., 2006b). The sediments of the paleokarst were transported by a large river and thus the fossils are often eroded and fragmented. In these new localities *Hyaenodon* is present at Bouziès — an Eocene site as mentioned above. The holotype of *Hyaenodon requieni* comes from d´Euzet (Gard, MP 17a; Maitre et al., 2006b). Most of the Quercy localities provide no paleoenvironmental indication for running water. An exception is the site of Monteils with fossils of the groups Urodelia, Anura and the occurrence of Charophyta. Concluding, strong precipitation is assumed for this locality (Maitre et al., 2006b).

4.2 The insect fauna of the Quercy and inferences on the paleoecology

Handschin (1944) was the first author who examined the insect fauna of the Quercy in a broad sense and in detail providing figures. This section follows him. The bodies of the insects were embedded in fine marly phosphatic sediments. The preservation is exquisite: the insects can be viewed from all sides and are three-dimensionally preserved. Handschin (1944) used the collection of the Natural History Museum in Basel (Switzerland). He emphasized that the insects of the Teritary are not much different from the recent insects and that stratigraphic work based on this group is impossible. Furthermore, the Quercy insects are an ecological specialised part of the whole insect fauna (Handschin, 1944).

Handschin (1944) erected new genera (e.g. *Protosilvestria sculpta, Euphora* sp.) or species (e.g. *Gryllotalpa aveyronensis, Onthophilus intermedius*). An overview of the identified taxa is given in Table 4/1.

Subphyllum	Family	determination	from
Myriapoda	Dorypetalidae	*Protosylvestria sculpta*	Bach; Caylux
Hexapoda	Blattidae	*Blatta* sp.	Bach
Hexapoda	Achetidae	*Gryllotalpa aveyronensis*	Villeneuve d´Aveyron
Lepidoptera	Tineidae	Tineidae indet.	Bach
Coleoptera	Silphidae	*Ptomascopus aveyronensis*	Mouillac; Bach
Coleoptera	Silphidae	*Thanatophilus* sp.	Bach
Coleoptera	Silphidae	*Silphidarium* sp.	Bach
Coleoptera	Histeridae	*Onthophilus intermedius*	Larnagol
Coleoptera	Lamellicornia	*Aphodius sp.*	Caylux
Coleoptera	Cerambycidae	*Dorcadion bachense*	Bach
Diptera	Phoridae	*Megaselia* sp.	Bach; Caylux
Diptera	Phoridae	*Euphora* sp.	Bach
Diptera	Phoridae	*Spiniphora* sp.	Bach
Hymenoptera		*Braconidarium* sp.	Bach

Tab. 4/1: The insect fauna of the Quercy (mostly from Bach). Especially beetles (Coleoptera) and flies (Diptera) are numerously preserved. Data taken from Handschin (1944).

Most insect fossils come from Bach. Not always were the adults (= imago) preserved (Handschin, 1944): there are cocoons (*Blatta* sp., Tineidae, Phoridae), caterpillars (Tineidae) and larvae (*Silphidarium* sp.). Beetles (Coleoptera) are the most numerous insects in the fossil record of the Quercy. *Ptomascopus aveyronensis* is the most frequent Quercy insect. Flies (Phoridae) are prevalent too. Particularly the smaller flies that indicate ammoniacal carcass decay. The cocoons are the most fragile ones, but still all the details of the morphology as in recent specimens could be observed. Even a parasite (parasitizing on phorids) — *Braconidarium* — was found in the fossil record (Handschin, 1944).

The insects were found in the fissure fillings together with the bones of the vertebrates (Handschin, 1944). They were interpreted as cadavericol and obscuricol. Handschin (1944) confirmed that a part of the insect fauna (namely *Euphora, Megaselia, Spiniphora, Ptomascopus, Onthophilus, Thanatophilus, Silphidarium* and Tineidae indet.) is cadavericol, but he refuted the obscuricol character of the insect fauna. The presence of carrion beetles (*Ptomascopus, Thanatophilus* and *Silphidarium*) indicates the first phases of carcass decomposition, because both the larvae and the adults feed on the flesh. The phorids indicate the next step

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of decomposition: they appear when a black, ammonical liquidation of meat and fat occurs. After this step of decomposition, the tineiids appear on the hair and horn substance. The blattids and *Gryllotalpa* prefer heat and humidity. *Aphodius* is a dung beetle and indicates presence of dung of ungulates or decomposition of the stomach contents. Even today *Dorcadion, Gryllotalpa, Blatta* and *Silvestria* are living on the ground in Southern France and characterise the arid climate.

Handschin (1944) described the exquisite preservation as follows. The metamorphosis of flies in warm climates is fast. It takes 10-14 days from egg to the imago and 5-8 days are needed for the cocoon phase. Due to the fine details preserved, Handschin (1944) concluded that those cocoons were soaked in hot liquid thus conserved due to fixation of the proteins. Then salts hardened the body. The expansion of the air in the tapetum of the compound eye of the fly cocoons is an evidence for hot liquid. The same is true for the beetles and the preservation of parasites, organs and cocoons. The fauna of the Quercy was a thanatocoenosisi: Animal carcasses sank in the mud, then insects were attracted and surprised by hot water invasions. Waterholes for amphibians and snails developed. Thus, the sites of the Quercy were affected by intervals of development and conservation periods (Handschin, 1944).

4.3 The vertebrate fauna of the Quercy with focus on mammals

The "Grande Coupure" — the Eocene/Oligocene border — is also marked in the Quercy phosphorites by extinction of 60% of the local fauna (Legendre et al. 1997).

Exploitation of the Quercy fissure fillings since 1965 has yielded more than 70 fossil mammal faunas (Remy et al. 1987). Concerning the fauna of the Quercy sites a short summary shall be given divided in two parts — the first describing the fauna before and the second after the "Grande Coupure" following Remy et al. (1987). See Table 4/2 for a summary. Note that the following paragraphs refer to Remy et al. (1987), if not indicated differently.

Eocene localities bear marsupials (*Peratherium, Amphiperatherium*). Archaic insectivores like apatemyids and amphilemurids are rare. *Pseudorhyncocyon* (Order Lepticitida) is present. Certain lineages of nyctitheres are common. Some late Eocene sites e.g. Pécarel are characteristic for Amphidozotheriinae (Nyctitheriidae, Lipotyphla). Chiroptera are present, but it is difficult to follow specific lineages. However, several families are identified. The archaic megadermatid *Necromantis adichaster* shall be mentioned as an example. Carnivorans ("creodonts" and fissipeds) are present, but the specimens give just a small picture of their diversity. *Simamphicyon* (Amphicyonidae) disappears at the nivaeu of Robiac. Hyaenodontids, miacids and proviverrines are well represented. *Quercygale* (Miacidae) is present in Perrière and hyaenodontids diversify there. On a local level the evolution of *Hyaenodon brachyrhynchus* and *Hyaenodon requieni* can be observed. There is no doubt that *Hyaenodon gervaisi* is a morphocline of *Hyaenodon requieni*. Primates have diversified in many forms, like *Leptadapis, Adapis, Microchoerus, Necrolemur* and *Pseudoloris*. *Cryptadapis* is only known from one locality: Sainte-Néboule. *Nannopithex* from Laprade is more primitive than the same genus from Egerkingen. Among the rodents issiodoromyines (Theridomyidae, Rodentia) provided biochronological information (*Elfomys, Pseudoltinomys*) as well as hypsodont theridomyines (*Theridomys, Patriotheridomys, Blainvillimys*). Glirids are present in some localities and the forms of *Paradelomys, Estellomys, Oltinomys* and *Remys* improved the biochronological data. *Suevosciurus* cf. *romani* — more primitive than the holotype — indicates the likely more ancient date of Laprade. Artiodactyla are well represented. The niveau of Robiac corresponds to the maximum of their diversity: *Cebochoerus* (Cebochoeridae), *Catodontherium* (Anoplotheriinae?), *Robiatherium* (Anoplotheriinae) — to mention some of them. The border of lower and upper Ludien was associated with the occurrence of anoplotherines and oxacronines (Cainotheriidae; Sudre, 1977). *Xiphia* and *Robiacina* (Anoplotheriidae; Sudre, 1977) show that Robiac is older than the phosphorites. *Pseudamphimeryx* (Amphimerycidae) and *Mixtotherium* (Mixtotheriidae) from Laprade show connections with taxa known from Egerkingen, although older than Robiac. Most artiodactyle faunas are known from the niveau of Euzet and Perrière and consist of the genera *Mouillacitherium* (Dichobunidae), *Dacrytherium* (Dacrytheriidae),

Leptotheridium (Cebochoeridae), *Tapirulus* (Anoplotheriidae), *Dichodon* (Xiphodontidae), *Haplomeryx* (Xiphodontidae), *Pseudamphimeryx* (Amphimerycidae), *Anoplotherium* (Anoplotheriidae) and *Dichobune* (Dichobunidae). Among the Perissodactyla paleotherids are rare. However, they constantly occur in certain Quercy sites of same date as sites without findings of paleotherids. This might be a product of paleoecological circumstances or disturbance of the thanatocoenosisi. In the oldest sites of the Quercy the diversity is great on species-level and the pachynolophines are dominant as well as characterised with the genera *Propalaeotherium* (Paleotheridae), *Anchilophus* (Palaeotheriidae) and *Leptolophus* (Pachynolophidae). Later (at the niveau of Escamps) *Palaeotherium* (Palaeotheriidae) and *Plagiolophus* (Pachynolophidae) are of significance. Oligocene localities bear marsupials too. Some survive the boundary like *Amphiperatherium* (Herpetotheriidae), others are represented with new evolved species as *Peratherium* (Herpetotheriidae). Clear differences in the insectivoran fauna between localities can be noted. In older localities nyctitherids are diverse, whereas they are rare in younger sites. Latter bear *Neurogymnurus* (Erinaceidae), a taxa important for the niveaus of Heimersheim, Garouillas and Mas de Pauffie and never occurs together with *Tetracus*, a genus associated with the nyctitherids. Soricids and talpids are rare. Chiroptera show slow evolution, especially in the dominant groups hipposiderids (Rhinolophidae) and Emballonuridae. Younger faunas show important changes: Vespertilionidae occur (especially myodontid forms) e.g. in Pech du Fraysse. Evolved emballonurids indicate younger age too — e.g. *Taphozous* in Pech Desse. Both in Pech du Fraysse and Pech Desse new forms of rhinolophids occur. Within the Carnivora the "Grande Coupure" is marked by clear changes: *Cynodictis* (Amphicyonidae) — abundant in Eocene sites — disappears. New forms appear: *Eusmilus* (Nimravidae), *Amphicynodon* (Ursidae), *Mustelictis* (Musteloida), *Pachycynodon* (Amphicyonidae), *Cephalogale* (Ursidae), *Stenoplesictis* (Aeluroidea) and *Palaeogale* (Musteloidea). In the youngest sites Carnivora are best represented, both in number and diversity. More modern taxa appear like *Plesictis* (Mustelidae) announcing the Carnivora of the Aquitanian. Hyaenodontids indicate the faunal turnover of the "Grande Coupure": *Pterodon* disappears. Species of *Hyaenodon* of assumed Asiatic origin arrive: *Hyaenodon dubius*, *leptorhynchus* and *filholi*. The species of the Ludien were brachyrhynch — in contrast to the immigrating (?) younger taxa with elongation of the muzzle and their smaller size. It seems there have been two waves of immigration: the first in the time of Soumailles with *Hyaenodon dubius* and *Hyaenodon exiguus* (they lasted until Pech du Fraysse) and *Hyaenodon leptorhynchus*. The second with *Hyaenodon filholi* (Mounayne) and *Thereutherium thylacoides* at the niveau Itardies. Nevertheless, *Hyaenodon brachyrhynchus* is found too. No primates are found in the phosphorites after the Eocene/Oligocene boundary. Primitive lagomorphs (*Shamolagus*) arrive (for example in Ravet) and are for a certain time very abundant. The rodents face extinction in the groups of Pseudosciuridae, Sciuroidae and Ischyrmyidae, whereas the Theridomyidae diversify and provide good biochronological indicators. Other groups also show evolutive change and are of importance: aplodontids, dipodids, cricetids, eomyids and glirids. The artiodactyle fauna consists of archaic families (*Dichobune*, *Tapirulus*, *Diplobune*), cainotheres (*Plesiomeryx*, *Caenomeryx*) and rare asiatic immigrants of entelodontids, suids, anthrocotherids and gelocids. The smallest forms are belonging to the cainotherids and they are found in all localities of the Quercy and in some localities in great number. Large sized artiodactyls are rare. *Entelodon* (Entelodontidae) is known from Aubrelong 1 with isolated findings. The largest anthracothere is also the youngest one: *Anthracotherium* cf. *valdense* from Pech Desse. Isolated teeth signal the presence of suids: typical taxa for this time are *Palaeochoerus* (Palaeochoeridae) and *Doliochoerus* (Palaeochoeridae). Ruminants are present, but show no great diversity on genus level. They are asiatic immigrants and were not very abundant except for *Bachytherium* (Itardies, Pech Desse) and *Lophiomeryx* (Hypertragulidae, Garouillas). In general, not much is known about the evolution of ruminants because of their sparse findings. *Iberomeryx* (Moschidae) is another taxa that shall be noted. Amoung the perissodactyls the decline of the paleotherids is significant. The last *Plagiolophus* (Pachynolophidae) disappears at the niveau Itardies-Montalban. Isolated findings of *Ronzotherium* (Rhinoceratidae) and *Cadurcotherium* (Amynodontidae) are the evidence for presence of rhinoceratids. Chalicotherids are represented by *Schizotherium* (Garouillas, Mas de Gaston).

Exhaustive faunal lists are provided in Remy et al. (1987).

Additional information concerning a special group was recently provided by Maitre et al. (2006): Amphilemuridae are erinaceomorph Lipotyphla and part of the fauna of the Quercy. Two new species were described by Maitre et al. (2006a): *Echinolestes quercyi* from the Quercy phosphorites and with an occurrence in MP 17a or b. *Echinolestes neboulensis* comes from Sainte-Néboule (Lot, Quercy) and occurs in MP 18. Thus, they are part of the Eocene fauna of the Quercy.

affiliation	Eocene	Oligocene
Didelphidae	*Peratherium* *Amphiperatherium*	*Peratherium* new species! *Amphiperatherium* survived
Pseudorhyncocyonidae (Leptictida)	*Pseudorhyncocyon*	no findings of Leptictida!
Apatemyidae	*Heterohyus*	
Nyctitheridae	*Saturnia*	*Saturnia*
Amphilemuridae	cf. *Gesneropithex* *Echinolestes* (Maitre et al. 2006a)	
Erinaceidae		*Neurogymnurus* *Tetrarcus*
Lagomorpha		*Shamolagus*
Chiroptera	megadermatid *Necromantis* Rhinolophidae, Emballonuridae, Natalidae, Molossidae etc.	No megadermatid! Slow evolution in Rhinolophidae and Emballonuridae (*Taphozous*); Myodontid Verspertilionidae
Amphicyonidae	*Cynodictis* *Simamphicyon*	*Cynodictis* † *Pachycynodon* *Cynelos* *Ysengrinia* *Brachycyon*
Miacidae	*Quercygale* *Miacis*	
Felidae		*Eusmilus* *Nimravus*
Ursidae		*Amphicynodon* *Cephalogale*
Musteloidea		*Mustelictis* *Palaeogale* *Plesictis*
Hyaenodontidae	*Pterodon* *Hyaenodon*: brachyrhynch!	*Pterodon* † *Hyaenodon*: longirhynch! *Thereutherium thylacoides*
Primates (Adapidae, Microchoeridae)	*Leptadapis* *Adapis* *Microchoerus* *Necrolemur* *Pseudoloris* *Cryptadapis* *Nannopithex*	no findings of primates!
Ischyromyidae (Rodentia)	*Plesiarctomys*	†

Theridomyidae	*Elfomys* *Pseudoltinomys* *Theridomys* *Patriotheridomys* *Blainvillimys*	diversification!
Gliridae	*Paradelomys* *Estellomys* *Oltinomys* *Remys* *Gliravus*	evolutionary change!
Pseudosciuridae	*Suevosciurus*	†
Anoplotheridae	*Robiatherium* *Robiacina* *Tapirulus* *Anoplotherium* *Catodontherium*	primitive artiodactyls last e.g. *Tapirulus*
Cainotheridae	Oxacroninae	*Plesiomeryx* *Cainomeryx*
Amphimerycidae	*Pseudamphimeryx*	
Mixtotheridae	*Mixtotherium*	
Dichobunidae	*Mouillacitherium* *Dichobune*	primitive artiodactyls last *Dichobune*
Dacrytheridae	*Dacrytherium*	
Cebochoeridae	*Cebochoerus* *Leptotheridium*	
Xiphodontidae	*Dichodon* *Haplomeryx*	
Palaeochoeridae		*Palaeochoerus* *Doliochoerus*
Moschidae		*Iberomeryx*
Entelodontidae		*Entelodon*
Chalicotheridae		*Schizotherium*
Palaeotheridae	*Anchilophus* *Propalaeotherium* *Palaeotherium*	
Pachynolophidae	*Plagiolophus* *Leptolophus*	
Rhinoceratidae	no findings	*Rhonzotherium*

Table 4/2: Summary of taxa occurring before and after the "Grande Coupure" (after Remy et al. 1987).

4.4 Comparable sites

Phosphatic fissure fillings have been mined not only in the province Quercy. Other polyphased karstic fillings near St.-Maximin were studied by Remy et al. (1997): these phosphorites, also called Gard phosphorites, date from early middle Eocene to Late Pliocene and yield a rich vertebrate fauna. The filling processes took place during the Middle Eocene up to the Quartenary with a break during the Miocene (uprising of hydrostatic levels). The authors concluded that most paleokarstic systems are polyphased in structure and that the faunas are usually not mixed — although filling units have to be recognised and samplings have to be carried out carefully (Remy et al., 1997). The reptile fauna is diversified (e.g. in "Grand Chantier", middle Eocene). Amphibians are represented by urodels and anurs. Marsupials are found — *Amphiperatherium* and *Peratherium* like in the Quercy. Apatemyid *Heterohyus*, amphilemurid *Macrocranion*, emballonurid chiroptera, nyctitherids, rodents *Masillamys*, *Eogliravus*, *Protadelomys*, plesiadapiform Paromomyidae *Arcius*, adapiformes *Microadapis*, hyaenodont *Proviverra*, perissodactyle *Pachynolophus* and *Lophiodon*, artiodactyle *Dichobune*, *Haplobunodon* and *Cebochoerus* are important elements of the mammalian fauna. The complete faunal list is given in Remy et al. (1997).

The fissure fillings of Liptingen (northern Hegau, around Sigmaringen, western Swabian Alb, Germany) are also a good example for comparison with the Quercy fillings (Scherzinger et al., 2005). The fissure fillings Liptingen 1 A-C are dated to be MP 21 and the faunal list is given in Scherzinger et al. (2005) and shows a similar composition of taxa as in Quercy sites: marsupials (*Peratherium*, *Amphiperatherium*), nyctitherids, erinaceids (*Tetrarcus*), talpids, dimylids, heterosoricids, soricids, hipposiderid Chiroptera, theridomyids, pseudosciurids, sciurids, glirids, cricetids, hyaenodontids (*Hyaenodon*), Carnivora (*Amphicynodon*, *Nimravus*), gelocids, Lophiomerycidae, cainotherids, palaeotherids, anoplotherids, helaletids and remains of Testudinata.

4.5 Correlation of the sites of the Quercy

Biochronology and correlation of localities has always been important. Lange-Badré (1979) gave in her thesis a correlation of European paleogene localities, including the Quercy localities. Table 1 (p. 14 in Lange-Badré, 1979) shows the used stratigraphy from the upper Eocene to the upper Oligocene and correlates sites of the Phosphorites of Quercy as well as those of the Auvergne, the Aquitaine Provence-Pyrénées, the Bassin of Paris, of Spain and Switzerland, Germany and Great Britain with the reference levels (horizons). Mouillac and Bach are not mentioned therein — see below for a separate discussion on those two sites. A correlation chart of most important European mammal localities is given in Schmidt-Kittler (1987). A first synthesis of correlated Quercy localities was given by Remy et al. (1987). Establishing of reference levels and determining of MP zones are important for comparison of the faunas. BiochroM´97 (1997) provides another important synthesis on this topic. Table 4/3 gives an overview of the European localities yielding *Hyaenodon* and Table 4/4 gives correlated Quercy localities yielding *Hyaenodon* exclusively. These lists are not exhaustive.

Zone	Epoch	Locality	Country	species
MP 17a	Eocene	Fons 4	France	*H. minor, requieni*
MP 17a	Eocene	Hordle Mammal Bed	Great Britain (England)	*H. minor*
MP 17a	Eocene	Roc de Santa	Spain	*H. requieni, minor*
MP 17a	Eocene	Aubrelong 2	France	*H.* sp.
MP 17a	Eocene	Euzet	France	*H. requieni, brachyrhynchus*
MP 17b	Eocene	Perrière	France	*H.requieni, brachyrhynchus, minor*
MP 18	Eocene	La Débruge	France	*H. requieni, brachyrhynchus*
MP 18	Eocene	St. Néboule	France	*H. brachyrhynchus*
MP 18	Eocene	Gösgen Kanal	Switzerland	*H. requieni, minor*
MP 19	Eocene	Escamps	France	*H.* sp.
MP 19	Eocene	Memerlin	France	*H. rossignoli*
MP 19	Eocene	Montmartre	France	*H. brachyrhynchus*
MP 19	Eocene	Obergösgen	Switzerland	*H. requieni*
MP 19	Eocene	Möhren 6	Germany	*H.* sp.
MP 21	Oligocene	Ronzon	France	*H. dubius*
MP 21	Oligocene	Aubrelong 1	France	*H. dubius*
MP 21	Oligocene	Liptingen 1A-C	Germany	*H. dubius*
MP 22	Oligocene	Villebramar	France	*H. dubius, leptorhynchus*
MP 22	Oligocene	Mas de Got	France	*H. dubius, leptorhynchus*
MP 23	Oligocene	Itardies	France	*H. dubius*
MP 23	Oligocene	Pendaré	France	*H.* sp.
MP 28	Oligocene	Pech du Fraysse	France	*H. exiguus, leptorhynchus*
MP 28	Oligocene	Pech Desse	France	*H. exiguus*
MP 29	Oligocene	Rickenbach	Switzerland	*H. filholi, exiguus*
MP 30	Oligocene	Coderet	France	*H. exiguus*

Table 4/3: Following BiochroM´97 (1997) this table provides the dating of most important European localities bearing *Hyaenodon*. Additional information from Lange-Badré (1979) and Scherzinger et al. (2005) were included.

Zone	Epoch	Locality	Country	species
MP 17a	Eocene	Fons 4	France	*H. minor, requieni*
MP 17a	Eocene	Aubrelong 2	France	*H.* sp.
MP 17a	Eocene	Euzet	France	*H. requieni, brachyrhynchus*
MP 17b	Eocene	Perrière	France	*H.requieni, brachyrhynchus, minor*
MP 18	Eocene	La Débruge	France	*H. requieni, brachyrhynchus*
MP 18	Eocene	St. Néboule	France	*H. brachyrhynchus*
MP 19	Eocene	Escamps	France	*H.* sp.
MP 19	Eocene	Memerlin	France	*H. rossignoli*
MP 19	Eocene	Montmartre	France	*H. brachyrhynchus*
MP 21	Oligocene	Ronzon	France	*H. dubius*
MP 21	Oligocene	Aubrelong 1	France	*H. dubius*
MP 22	Oligocene	Villebramar	France	*H. dubius, leptorhynchus*
MP 22	Oligocene	Mas de Got	France	*H. dubius, leptorhynchus*
MP 23	Oligocene	Itardies	France	*H. dubius*
MP 23	Oligocene	Pendaré	France	*H.* sp.
MP 28	Oligocene	Pech du Fraysse	France	*H. exiguus, leptorhynchus*
MP 28	Oligocene	Pech Desse	France	*H. exiguus*
MP 30	Oligocene	Coderet	France	*H. exiguus*

Table 4/4: List of the correlated Quercy localities yielding *Hyaenodon* (following BiochroM´97 1997; Lange-Badré 1979; Legendre et al. 1997; Remy et al. 1987).

In La Débruge (Quercy, France, MP 18) *Hyaenodon requieni* occurs together with *Pterodon dasyuroides* and the carnivore *Cynodictis lacustris* (BiochroM´97, 1997). In Escamps (MP 19) *Pterodon dasyuroides* is also found with *Hyaenodon* (BiochroM´97, 1997). The holotype of *Hyaenodon cayluxi* was found around Bach (Lot).

Material from Quercy housed in the NHMW comes mostly from "Mouillac" (near Caylux, Tarn-et-Garonne) and "Bach" (at Lalbenque, Lot). Both are no designations for localities and the following was learned through personal communication with Sébastien Couette: Mouillac is the name of the part of a forest, which is near Caylus. Caylus (= Caylux) is the name of a city and probably the name of a military camp. Bach is the name of a village, but there are a lot of localities around it. In Lange-Badré (1979) "Mouillac" and "Bach" are found (Fig. 1, p. 10.; Fig. 4/1 herein). Both are not dated — unlike the fissure fillings and are probably figured for orientation (Lange-Badré, 1979). Mouillac is near Pech-Desse and Itardies and Bach is near Mas de Got (see Fig. 4/1). Thus, Mouillac and Bach give no indication of precise location and date (pers. comm., Sébastien Couette, MNHN).

Fig. 1. — Localisation géographique et stratigraphique des principaux gisements de Créodontes dans les Phosphorites du Quercy.

— Ludien inférieur (Horizon d'Euzet-les-Bains)
+ Ludien moyen (Horizon de La Débruge)
● Ludien supérieur (Horizon de Montmartre)
X Stampien inférieur (Horizon de Ronzon)
□ Stampien moyen (Horizon de Montalban)
O Fin Stampien moyen.

Fig. 4/1: Map of important sites of the Quercy. Reproduced from Lange-Badré (1979: Fig. 1, p. 10). Most fissure fillings of the Quercy are old sites and for many of them the exact location is unknown. Note that Mouillac and Bach are sketched in. Expecially these two sites have yielded a great amount of fossils. Their exact location remains unclear, as well as a datation is missing (see the symbol in the map). However, Lange-Badré (1979) provided this map and the relative position of the sites. Ludien is late Eocene and Stampien is lower Oligocene.

Chapter 5

5. On *Hyaenodon*

5.1 Definition of the genus *Hyaenodon*

The tooth formula and/or the dental morphology was always included in the definition of *Hyaenodon* by various authors (Dashzeveg, 1985; Lange-Badré, 1979; Matthew, 1909; Mellett, 1977; Savage, 1965). The hitherto definitions for the genus are given in their temporal order:

"Hyaenodontinae: Molars sectorial, metaconids absent, carnassials more specialized. Body more compact, limbs and feet cursorial.
Hyaenodon: Molars $^2_3$ Protocones and talonids absent." (p. 465-466 in Matthew, 1909)

"Dental formula 3142/3143; M^2 with shallow groove on completely connate paracone and metacone; molars without protocone; metastyle strongly elongated, especially on M^2. Main carnassial pair M^2_3, with M^1_2 as accessory carnassials. M_3 without talonid, M_{1+2} with or without vestigial talonid." (p. 278 in Savage, 1965)

"Diagnosis: small to large hypercarnivorous placental mammals with dental formula 3-1-4-2/3-1-4-3. Distinguished from all other known hyaenodontids by the absence of M^3 and by the extreme development of carnassial teeth. Carnassials sequentially DP^3/DP_4; DP^4/M_1; M^{1-2}/M_{2-3}. M^{1-2} subjected to rotation along proximodistal axis. Brain small. Auditory bulla consisting of ectotympanic ring, with entotympanic and petrosal components. Mesaxonic feet, fissured unguals, digitigrade stance." (p. 13 in Mellett, 1977)

"Diagnose. – Hyaenodontinae de formule dentaire 3/3 I, 1/1 C, 4/4 P, 2/3 M; série dentaire présentant un fort dimorphisme sexuel; alvéole de I_2 repousée derriére celles de I_1 et de I_3. Molaires supérieures à pseudamphicone formant avec les métastyle un angle de 160°; M_3 à cingulum vestigial, vestibulaire, formant butée, et dont la longueur du paraconide représente 50 à 60 % de celle du protoconide. Crane à region otique courte et forte constriction postorbitaire; long canal naso-palatin avec ou sans fusion de ptérygoïdes; absence de canal de l´alisphenoide; symphyse s´étendant jusqu´à P_3; usure dentaire accompagnée de rotation vestibulo-linguale de 5° environ et d´extrusion partielle." (p. 93 in Lange-Badré, 1979)

"Diagnose: Formule dentaire: 3/3I, 1/1C, 4/4P, 2/3M. Carnassières en M^2/M_3. M^3 a disparu. Crane long et etroit avec une région faciale longue. Paracone et métacone encore un peu séparés sur la M^1, complètement fusionées sur M^2 (sauf chez les formes primitives). Le métastyle est allongé et le protocone réduit sur M^1 et M^2. Molaires inférieures sans métaconide; paraconide plus court que protoconide. Talonide de M_1 et M_2 petit; talonide rudimentaire ou absent à M_3." (p. 18 in Dashzeveg, 1985)

"Characteristics: Dental formula I3/3, C1/1, P4/4, M2/3; M3 absent; carnassial shearing extremely well developed, with shearing (in adults) occurring in M1-2 and m2-3; brain small; feet digitigrade. Average length of m1: 7.3-15.0 mm." (p. 98 in Gunnell, 1998)

Some diagnoses are based on North American material (e.g. Matthew, 1909; Mellett, 1977) and others on European material (e.g. Lange-Badré, 1979). The following diagnosis is an attempt to summarize the most important features of the taxon, using parts of earlier diagnoses.

Diagnosis of *Hyaenodon*: small to large sized hypercarnivorous hyaenodontid mammals, tooth formula 3142/3143 (M3 absent) with M1-2 and m1-3 being the carnassials in the adult and DP3-4, dp4 as well as the m1 as carnassials in the juvenile, morphology of the molars emphasizing the carnassial blade (reduced protocone, enlarged metastyle in the upper molars, reduced metaconid, small or absent talonids in the lower molars), shearing of the carnassials maintained during life due to rotation of the teeth, mandibular symphsysis

reaching up to the p3, small, but inflated entotympanic bulla, small neocortex, large and angled sagittal crest, long naso-palatinal canal, robust long bones, humerus with anconeal and epicondyliar foramen, fissured unguals, digitigrade stance.

5.2 History of the genus *Hyaenodon*

The first part of the name *Hyaenodon* means 'hyena', the second 'tooth', because the robust premolars of *Hyaenodon* resemble the premolars of hyenas. The type species is *Hyaenodon leptorhynchus* — a European species — erected by Laizier and Parieu (1838). The genus is speciose and comprised of 10 European, 10 North American and 8 Asian species. For an overview see Table 5/1.

Europe	North America	Asia
H. leptorhynchus Laizier and Parieu, 1838 (including *H. cayluxi* Filhol, 1876)	*H./N. horridus* Leidy, 1853	*H. pervagus* Matthew and Granger, 1924 (including *H. neimongoliensis* (Huang and Zhu, 2002) after Morlo and Nagel, 2006)
H. brachyrhynchus Blainville, 1841	*H./P. crucians* Leidy, 1853	*H. eminus* Matthew and Granger, 1925
H. minor Gervais, 1848-1852	*H./P. mustelinus* Scott, 1895	*H. yuanchensis* Young, 1937
H. requieni Gervais, 1848-1852	*H./N. montanus* Douglass, 1901	*H. mongoliensis* Dashzeveg, 1964
H. dubius Filhol, 1873	*H./N. vetus* Stock, 1933	*H./N. incertus* Dashzeveg, 1985
H. exiguus Gervais, 1873	*H./P. brevirostrus* Macdonald, 1970	*H. chunkhtensis* Dashzeveg, 1985
H. heberti Filhol, 1876	*H./N. megaloides* Mellett, 1977	
H. filholi Schlosser, 1887	*H./P. venturae* Mellett, 1977	*H./N. gigas* Dashzeveg, 1985
H. gervaisi Martin, 1906	*H./P. microdon* Mellett, 1977	*H. weilini* Wang, Qiu and Wang, 2005
H. rossignoli Lange-Badré, 1979	*H. raineyi* Gustafson, 1986	

Table 5/1: List of species of *Hyaenodon*: Species are given in the temporal order of their erection. Follows mainly for Europe Lange-Badré (1979), for North America Mellett (1977), for Asia Wang et al. (2005) and Tsubamoto et al. (2008).
H., *Hyaenodon*; *N.*, *Neohyaenodon*; *P.*, *Protohyaenodon*;

Europe

History of the genus for the European species was described by Martin (1906) and later by Lange-Badré (1979): The first specimens were figured by Cuvier (1825, p. 269, Pl. 68/69, Fig. 3 and 2-4), but were not determined on the genus level. Cuvier assigned them to the family of Procyonidae. These findings were a maxilla fragment with a left tooth row and a mandible fragment holding c, p2, p3 and p4 found in Montmartre. The same specimens were again figured by Blainville (1841-1842, Pl. XVII) and described as *Taxotherium parisiense*. He erected the species *Hyaenodon brachyrhynchus* and *Taxotherium parisiense* was included in the former. Then a mandible of *Hyaenodon leptorhynchus* was found in Cournon and described by Laizier and Parieu (1838). This specimen is well preserved and was first figured by Blainville (1839) and later by Gervais (1848-1852). Blainville described for the first time *Hyaenodon brachyrhynchus*. This specimen, a skull with mandible, was found near Rabastens (France) and was already designated to *Hyaenodon* by Dujardin (1840, p. 134). Gervais (1848-1852) erected the species *Hyaenodon requieni* and *minor*. He further established distinction on genus-level and systematic position of *Hyaenodon* and *Pterodon* (1848-1852). Most species and individuals of European *Hyaenodon* come from the phosphorites of the Quercy. Filhol (1876, 1882) described in various publications at least six species, some of them hard to distinguish (Lange-Badré, 1979). Schlosser (1887) contributed to the knowledge of the genus with his research on material from the Quercy. A first synopsis was published by Martin (1906). The revision of the European species of *Hyaenodon* followed in 1979 by Lange-Badré. New findings were made in the cleft filling Liptingen (Germany, Scherzinger et. al, 2005). Time range of several European species is shown in Fig. 5/1 A (based on Lange-Badré, 1979).

North America

Neohyaenodon was proposed by Thorpe (1922) as a new genus. It included *Hyaenodon horridus* as type and only species. The diagnostic features were an external buttress-like ridge on the paraconid of m3 and the development of pediculate glenoids (Thorpe, 1922). The latter is the result of allometric growth of the skull and thus *Neohyaenodon* is rather used for a lineage within *Hyaenodon* than for a separate genus (Mellett, 1977). *Protohyaenodon* was created as a subgenus within *Hyaenodon* by Stock (1933). The subgeneric characters are a distinct inner cusp on the P4, a tiny protocone on the M1 and the bifurcation of the tip of the paracone of the M2 (Stock, 1933). Mellett (1977) regarded *Neohyaenodon* and *Protohyaenodon* as two divergent lineages, derived from *Hyaenodon vetus* and *Hyaenodon venturae*. These are the earliest species of *Hyaenodon* in North America (Mellett, 1977).

The following information on the history of some North American species follow Lavrov and Emry (1998): *Hyaenodon minutus* was established upon an isolated m1 (CM 737) by Douglass (1901). Matthew (1903) described another specimen (AMNH 9623), a maxilla fragment holding P3, P4 and a broken M1. He proposed *Pseudopterodon minutus* for the taxon he found together with Douglass, because he didn´t agree with Douglass´ generic determination and associated it with the genus erected by Schlosser (1887). Mellett (1977) designated the first specimen to *Hyaenodon crucians*. Thus, *Hyaenodon minutus* is a synonym of *Hyaenodon crucians* (Lavrov and Emry, 1998). Mellett (1977) also established a new species, *Hyaenodon microdon*, for Matthew´s specimen, because Matthew wrongly connected it with Douglass´ species.

Hyaenodon exiguus was created by Stock, 1933. This was a junior homonym of *Hyaenodon exiguus* Gervais, 1876, a valid European species. So Mellett (1977) replaced the species name with *venturae* to emphasize the independence from the European species. Another species, after Mellett´s revision, has been added: Gustafson (1986) described *Hyaenodon raineyi*.

Time range of several North American species is shown in Fig. 5/1 A (based on Mellett, 1977 and Lavrov and Emry, 1998).

Africa

Savage (1965) described *Isohyaenodon* as a new subgenus of *Hyaenodon* based on African material. The following species were identified: *Hyaenodon/Isohyaenodon andrewsi*, *H./I. matthewi* and *H./I. pilgrimi*. Savage (1965) also included *Hyaenodon brachycephalus* Osborn, 1909, in *Isohyaenodon*. The distinguishing

feature was the subequal protoconid and paraconid on the third lower molar (Savage, 1965). Mellett (1977) considered *Isohyaenodon* not as member of *Hyaenodon* but a '*Pterodon*'-like creodont. He stated that the prevallum-postvallid shear angle in *Isohyaenodon* is strongly oblique and not almost parallel as in *Hyaenodon* (Mellett, 1977). Furthermore, he assumed a third upper molar for the African taxon. Mellett (1977) additionally proposed that *Hyaenodon brachycephalus* was correctly designated to *Isohyaenodon* because this group may form a subgenus within *Pterodon*. The conclusion is that true *Hyaenodon* never entered Africa (Mellett, 1977). Morales et al. (1998) further clarified the situation: Only mandibles of *Isohyaenodon* and only maxillae of *Metapterodon*, both from East Africa, are known. Morales et al. (1998) stated that the lower dentition of *Isohyaenodon matthewi* corresponds to the upper dentition of *Metapterodon zadoki*. In fact, there are differences separating *Isohyaenodon* from *Hyaenodon* and these feature are: more robust molars, lower molars with subequal paraconid and protoconid, m2 less reduced in comparison to m3 and better developed protocone (upper molars). Furthermore, Morales et al. (1998) stated that *Isohyaenodon* is more related to *Pterodon* and *Metapterodon* than to *Hyaenodon*. However, they still accept *Isohyaenodon* as a valid genus with the following species: *Isohyaenodon andrewsi*, *I. zadoki* (= *I. matthewi*), *I. pilgrimi* and *Isohyaenodon* sp. indet. (figured by Savage, 1965 as *Metapterodon kaiseri*). For more information on African hyaenodontids see Holroyd (1999) and Lewis and Morlo (2010).

Asia
As recently discussed in Tsubamoto et al. (2008) the taxonomy of the Asian species of *Hyaenodon* is complicated: *Hyaenodon incertus* Dashzeveg (1985) was designated to the genus *Neohyaenodon* by Lavrov (1999). The term *Neohyaenodon* was originally created for the North American species *Hyaenodon horridus* by Thorpe (1922) to separate this species on genus level. Thus, according to other authors *Hyaenodon* is appropriate (Morlo and Nagel, 2006; Tsubamoto et al., 2008). A specimen (PIN 473-109-110) identified as the European species *H. dubius* (Gromova, 1952) was later added to *H. incertus* (Dashzeveg, 1985). Another finding (PST 27-35) was defined by Dashzeveg (1985) as a new species of '*Pterodon*' *exploratus*. This was a mandible fragment holding the first and second molar. Later it was clear, that it does belong to *Hyaenodon*, rather than to *Pterodon* (Polly, 1993; Egi et al., 2007). Furthermore, the teeth were identified as dp4 and m1 by Morlo and Nagel (2006) and '*Pterodon*' *exploratus* is now synonymizied with *Hyaenodon incertus*. Dashzeveg (1964) described *Hyaenodon mongoliensis* as new genus and species, namely as *Megalopterodon mongoliensis*. This species was designated as *Pterodon* by Van Valen (1967) and as *Hyaenodon* by Mellett (1977). Lange-Badré and Dashzeveg (1989) described more specimens and suggested that *Hyaenodon incertus* could be synonymous with *Hyaenodon mongoliensis*. Whereas Morlo and Nagel (2006) supposed that *Hyaenodon gigas* could be synonymous with *Hyaenodon mongoliensis*. Up to now, there is no agreement and Lavrov (1999) stated that the specimens belonging to *Hyaenodon mongoliensis* (Lange-Badré and Dashzeveg, 1989) should be designated as a new genus.
Hyaenodon gigas was described by Dashzeveg (1985) and identified as *Neohyaenodon* by Lavrov (1999), which should be rejected as declared above. *Macropterodon zelenovi* (Lavrov, 1999) could be a junior synonym of *Hyaenodon gigas* (Wang et al., 2005; Morlo and Nagel, 2006; Egi et al., 2007).
Some of the undetermined findings could later be identified: *Hyaenodon* sp. 2 and *H.* sp. 3 (Dashzeveg, 1985) belong to *Hyaenodon incertus* and *Hyaenodon pervagus* (Lange-Badré and Dashzeveg, 1989). '*Pterodon*' sp. (Dashzeveg, 1985) is similar to *Hyaenodon* (Egi et al., 2007) and could be assigned to *Hyaenodon pervagus* or *incertus* (Tsubamoto et al., 2008).
A new Asian species was described by Wang et al. (2005): *Hyaenodon weilini*. The holotype is IVPP V12186 and includes isolated left P4 and M2, right P3, P4 and M2 and a root of a left upper canine. Other isolated teeth were designated to this species (IVPP V12187, IVPP V12188, IVPP V12189).
Time range of several Asian species is shown in Fig. 5/1 A (based on Dashzeveg, 1985; Huang and Zhu, 2002; Lange-Badré and Dashzeveg, 1989; and Wang et al., 2005).

5.3 On the European species

As the taxonomy was not the focus of this thesis, this chapter refers to the revision of the European taxa by Lange Badré (1979). She dealt with this topic in detail and gave important information on synonymy (for references concerning this topic see Lange-Badré, 1979). As an example *Hyaenodon compressus* was included in *Hyaenodon exiguus* and the material assigned to *Hyaenodon vulpinus* had to be divided up into the species *Hyaenodon leptorhynchus*, *exiguus*, *filholi* and *brachyrhynchus* (Lange-Badré, 1979). As this is mainly a translation and summary of respective parts of her thesis, I follow mostly her terminology. Her "eocone" (Lange-Badré, 1979) is herein simply termed as main cusp. Furthermore, the term "pseudamphicone" (= fusion of paracone and metacone on the upper molars) is not used, but rather the state of fusion is described. Some terms usually not applied on premolars, but used by Lange-Badré (1979) for premolars too, e.g. talonid, are applied herein, because I wanted to stay close to the original in french.

I decided to include Figures of the most complete material that was available to me, to give further information besides the description and to contribute to an increase on visual material, because even Lange-Badré (1979) did not provide pictures of every species lower and upper dentition.

Besides the tooth morphology, the fronto-nasal suture shall be mentioned: the nasals are v-shaped in dorsal view when they meet the frontals (Lange-Badré, 1979). However, this v-shape can be rounded even to a curve. Both conditions (sharply v-shaped and rounded fronto-nasal suture) can be found within the same species (e.g. *Hyaenodon minor* and *exiguus*; see Fig. 18, p. 97 in Lange-Badré, 1979). Lange-Badré (1979) found that the sharply v-shaped suture occurs in Eocene forms and in juvenile specimens of Oligocene taxa and concluded that this feature is a plesiomorph character.

Synonymy for *Hyaenodon* (taken from Lange-Badré, 1979, p. 93):

Taxotherium Blainville 1841
pro parte *Pterodon* Pomel 1846
Eutemnodus Bravard 1858
Pseudopterodon Schlosser 1887
Neohyaenodon Thorpe 1922

Some characters, e.g. the development of a cingulum/id is variable within a species (Lange-Badré, 1979). Additionally it has to be noticed that certain features are convergences within hyaenodontids as a whole (Solé, 2010), for example: a double-rooted p1, mesial position of the paraconid, reduction of the metaconid and the development of cingulids. Although some of these features seem to be a characteristic for a certain taxon, the variability and the case of convergence should not be neglected. The species *H. rossignoli* demonstrates this fact: it possesses a double- or a single-rooted p1.

The following features are valued as plesiomorph (based on the oldest European species, e.g. *Hyaenodon requieni*; Lange Badré, 1979):

- subequal development of the row of premolars and molars
- importance of the cingulum
- short, high and hook-shaped P2/p2
- lingual expansion on the P3
- strong, low and angled protocone on the P4
- strong concavity of the metastyle on the superior molars
- not fully fused para- and metacone
- vestige of the metaconid on the m3

A character Lange-Badré (1979) used, was the angle between the upper third and the upper fourth premolar. The rotation of the P3 varies and thus different species gave different values (see Tab. 5/2).

SPECIES OF *HYAENODON*	ANGLE BETWEEN THE P3 AND THE P4
gervaisi	135-140°
brachyrhynchus	140-145°
requieni	145-150°
dubius	150°
rossignoli	145-150°
minor	150-155°
leptorhynchus	155-160°
exiguus	155-160°
filholi	160-165°

Table 5/2: Angle between the P3 and the P4 in different European species of *Hyaenodon* (from Lange-Badré, 1979).

All European species shall be shortly characterized by their dental morphology in the following — more information can be found in Lange-Badré (1979). Information found by myself is added and indicated by (personal observation).

SPECIES OF THE LATE EOCENE

Hyaenodon requieni Gervais 1848-1852 (Fig. 5/1 B and 5/2 A-C herein; synonymy taken from Lange-Badré, 1979, p. 126):

> *Pterodon requieni* Gervais 1846
> *Pterodon requieni* Gervais 1848
> pro parte *Hyaenodon requieni* Gervais 1848-1852
> *Hyaenodon requieni* Gervais in Filhol 1876
> *Hyaenodon heberti* sensu Lydekker 1885
> pro parte *Hyaenodon heberti* Filhol in Schlosser 1887
> pro parte *Hyaenodon requieni* Gervais in Martin 1906
> pro parte *Hyaenodon requieni* Gervais in Depéret 1917
> (pl. XXII, Fig. 3; pl. XXIII, Fig. 2)
> *Hyaenodon heberti* mut. *euzetensis* Depéret 1917
> (pl. XXII, Fig. 1-2; pl. XXIII, Fig. 1)
> pro parte *Hyaenodon requieni* Gervais in de Bonis 1964

This species is of lion size. The length of the lower molar row corresponds to the length of the lower premolar row. The premolars possess a strong cingulum/id, that runs around the whole basis of the tooth. A short diastem is present between the P1 and the P2. The p1 is single rooted. The p2 is short, high and hook-shaped. The p3 is low and long. The protocone on the P4 is angular. The upper molars show a reduced protocone and a strongly concave metastyle. The angle between the axes of the P3 and the P4 is ranging from 145-150° (Lange-Badré, 1979).

Lange-Badré (1979) considered the species *Hyaenodon gervaisi* and *brachyrhynchus* as closely related to *Hyaenodon requieni*, which probably gave rise to the other two.

The species is known from the following sites: Fons 4 (Gard, France), Roc de Santa (Spain), Euzet-les-Bains

(Gard, France), La Débruge (Vaucluse, France), Quercy (e.g. Perrière, France), Frohnstetten (possibly; Germany), Möhren 2 (Germany), Weissenburg 9 (Germany), Obergösgen (Switzerland), Gösgen Kanal (Switzerland).

P1: double-rooted.

P2: lingual expansion near the main cusp, followed by a crest with a small cuspid (buccolingually compressed).

P3: strong distal root due to the distinct lingual expansion, sharp-edged cingulum, compressed metastyle.

P4: central, low and angled protocone, bordered by a trenchant cingulum over the whole lingual side, posterior metastyle is about two thirds of the height of the main cusp.

M1-2: the M1 shows two small anterior tips and thus the unfused para- and metacon. They are fused on the M2. The metastyle is strongly concave and in its distal portion hook-shaped. The protocone is already reduced, but its root is present on the basis of the anterior cusp. The parastyle is small on the M1 and already developed as a distinct blade on the M2.

p1: single-rooted, low, short and lingually strongly convex.

p2: postero-lingual expansion and thus trapeziform.

p3: low talonid, in general conical and much longer than high, no parastylid, but a triangular expansion that assimilates the crest of the main cusp.

p4: the talonid is a wide horizontal crest, that is not compressed to the main cusp, the parastylid is rarely developed, but if it is present, than it is of equal height as the talonid.

m1-3: the talonid on the m1 is as wide as the protoconid. The m2-3 show vestiges of a lingual cingulid below the protoconid. A crest (vestige of the metaconid) is sometimes present on the m3, that merges into the cingulid. No vestige of a talonid is present on the m3.

A striking feature was seen in the specimen LDB 5 (Fig. 5/1 B): the lower incisors are in a perfect row (personal observation). Normally, the second lower incisor is pushed in a posterior position. This is evident in other European, North American and Asian species (pers. obs.). Thus, regarding this aspect and to hitherto knowledge (Lange-Badré, 1979), *H. requieni* is the most plesiomorphic species of *Hyaenodon*.

Hyaenodon gervaisi Martin 1906 (Fig. 5/3 A-B herein; synonymy taken from Lange-Badré, 1979, p. 130):

Hyaenodon heberti Filhol sensu Schlosser 1887
Hyaenodon ambiguus Martin 1906 (pl. XVIII, Fig. 3-4)
Hyaenodon requieni Gervais sensu Jehenne 1965

Hyaenodon gervaisi is larger than *H. requieni*. The teeth are partly slightly overlapping, especially the premolars, because the species is brachyrhynch. The protocrone on the P4 decreases. The parastylid on the p4 is becoming as voluminous as the talonid. Para- and metacone are still unfused on the M1. The angle between the P3 and the P4 ranges from 135-140° (Lange-Badré, 1979).

The species is known from the following sites: Quercy (e.g. Les Rosières, Rigal-Jouet; France), Saint-Capraise-d'Eymet (Dordogne, France), La Milloque (Lot-et-Garonne, France), Dieupentale (Tarn-et-Garonne, France), Möhren 19 (Germany).

P1: short, conical and robust, double-rooted (although the roots are not equally developed), but placed in one alveolus (a lingual spiny projection indicates the fusion of the two alveoli), shifted linguad due to the shortening of the snout.

P2: much higher than long, distally not much elongated, mesial crest (at two thirds height of the main cusp) present that merges into the cingulum, sometimes a distal, globular cuspid higher than the cingulum is present.

P3: is in a specific rotated position, mesial the tooth is covered by the P2, the cingulum is well-developed, the

lingual expansion is significant, the metastyle is robust, but clearly higher than the parastyle, distal a robust posterior cusp is present, that is compressed in a blade.

P4: no parastyle present, the protocone shifted distad and is not in a central position (at the half of the length of the tooth), the protocone is also not as voluminous as in *Hyaenodon requieni*, cingulum irregularely developed, but strongly developed mesiad.

M1-2: the para- and the metacon are not fused on the M1. A short buccal buldge seperates the two tips. On the M2 the fused condition is achieved. The parastyle is reduced and only present in form of a crenulated vestige at the basis of the crown. No protocone is present, but its root is still preserved.

p1: single-rooted with an alveolus much wider than long, bucco-lingually asymmetrical.

p2: distally shortened, position shifted due to shortening of the snout, robust and wide tooth of oval shape, small diastem between the p1 and the p2 and the p2 and the p3.

p3: lingual expansion at the border of the main cusp to the talonid, much wider and higher at same length (when compared to *Hyaenodon requieni*), parastyle mesiad present as triangular eminence, crenulated cingulid runs distad, the distal portion can overlap the mesial part of the p4.

p4: parastylid developed as horizontal blade of equal height as the talonid, the lingual expansion is moderately developed and weaker than on the other premolars, the talonid is of half the height of the main cusp, the cingulid is high and trenchant.

m1-3: are uniform. The talonid is shorter than in *Hyaenodon requieni*. Vestiges of the cingulid can be observed sometimes. Below the paraconid of the m3 there is a crenulation as last evidence for a vestige of a cingulid present.

This species is remarkable in the robustness of its dentition (personal observation).

Hyaenodon brachyrhynchus Blainville 1841 (Fig. 5/4 A-B herein; synonymy taken from Lange-Badré, 1979, p. 136):

> *Hyaenodon leptorhynchus* Laizier and Parieu sensu Dujardin
> 1840
> *Nasua parisiense* von Meyer in Blainville 1841
> *Taxotherium parisiense* Blainville 1841 (pl. XII)
> *Hyaenodon brachyrhynchus* Blainville 1841 (pl. XII)
> *Hyaenodon parisiensis* Laurillard 1845
> *Pterodon cuvieri* et *Pterodon brachyrhynchus* Pomel 1846
> pro parte *Pterodon requieni* Gervais 1846 et 1852
> *Hyaenodon brachyrhynchus* Pomel 1853
> *Hyaenodon parisiensis* Pomel 1853
> *Hyaenodon cuvieri* Pomel in Pictet 1853
> *Hyaenodon brachyrhynchus* Blainville in Pictet 1853
> *Hyaenodon vulpinus* Gervais 1873 (pl. XVI, Fig. 5)
> pro parte *Hyaenodon requieni* Filhol 1876
> *Hyaenodon brachyrhynchus* Blainville in Lydekker 1885
> *Hyaenodon brachyrhynchus* Blainville in Schlosser 1887
> pro parte *Hyaenodon requieni* Gervais in Martin 1906
> *Hyaenodon* aff. *brachyrhynchus* Martin 1906
> pro parte *Hyaenodon requieni* Gervais in Depéret 1917
> pro parte *Hyaenodon requieni* "petite race" in de Bonis 1965
> pro parte *Hyaenodon minor* Gervais in Cray 1973

This species is of the size of a cheetah. The dentition is characterized by the fact that neither overlap of the teeth nor diastemata are present. It is brachyrhynch. The premolars are high and short, with a disto-lingual expansion. The p1 shows two fused roots, placed in one alveolus. The parastyle of the P4/p4 is developed as a blade and is of equal height as the distal cuspid/talonid. The protocone is in a central position. The angle between the P3 and the P4 ranges from 140-145°. Metastyles of the molars are aligned with the anterior cusps and the main cusp of the P4. The protocone is vestigial on the molars. As in other species the development of diastemata and the parastyle/id is variable. The size diminuishes in course of its evolution, in contrast to the evolution seen in *Hyaenodon requieni* (Lange-Badré, 1979).

The species is known from the following sites: Euzet-les-Bains (Gardm, France), La Débruge (Vaucluse, France), Montmartre (France), Quercy (e.g. Perrière, Sainte Néboule, both Lot, France), Upper Headon beds (Great Britain), Frohnstetten (Germany).

P1: double-rooted and placed in two alveoli, as a whole lingually rotated, the lingual cingulum contributes to the widening of the tooth without forming a distal crest.

P2: hook-shaped and the hightest tooth of the upper dentition after the canine, distinct disto-lingual widening that gives the tooth from occlusal view a somewhat triangular shape.

P3: obliquely positioned to the mesial teeth and in an angle of 60° to the following teeth, disto-lingually widened, distinct and trenchant cingulum, the posterior root is the strongest and possesses a bulge in individuals from La Débruge, that is no more present in the Quercy material, the metastyle is present as a small and conical cuspid and is less trenchant than in *Hyaenodon requieni* and *gervaisi*.

P4: the main cusp is framed by the mesial parastyle and a trenchant talon, the parastyle is a short blade and isolated by a notch from the main cusp, the talon is two or third times larger than the parastyle, the protocone is in a central position and angled, even more angled than in *Hyaenodon requieni*, the cingulum is only mesially present.

M1-2: The para- and the metacone are completely fused. The protocone is more reduced than in *H. requieni*, but the root is still present. The parastyle persists on the M1.

p1: rarely preserved, small, conical and asymmetrical tooth, double-rooted, but placed in one alveolus, the roots undergo fusion.

p2: it is parallel to the p1 and much higher than long, hook-shaped, moderate disto-lingual expansion.

p3: not typical, the lingual cingulid meets a triangular parastylid at the mesial basis of the main cusp, a basal swelling is present between the main cusp and the talonid, the talonid itself is short, wide and not compressed to the main cusp.

p4: parastylid and talonid are blade-shaped (similar as on the P4, here also not equally developed), the lingual cingulid is strongly developed.

m1-3: not much difference to those in *Hyaenodon requieni*, but smaller in general. The molars are wide in respect for their length. The paraconid is lingually trenchant. Sometimes vestiges of the parastylid are preserved on the basis of the m2 and the m3. The cingulid is irregularely developed, interrupted, granular, but always present below the paraconid on the buccal aspect — and there it forms a thin column that reaches two thirds of the heigth of the crown.

Hyaenodon heberti Filhol 1876 (Fig. 5/5 A-B herein; synonymy taken from Lange-Badré, 1979, p. 141):

> pro parte *Hyaenodon heberti* Filhol in Lydekker 1885
> pro parte *Hyaenodon heberti* Filhol in Schlosser 1887
> *Hyaenodon* aff. *heberti* Martin 1906
> *Hyaenodon arnaudi* Landesque in Depéret 1917

This species is large-sized, comparable to *Hyaenodon requieni* and slightly larger than the North American species *Hyaenodon cruentus*. The large size is a significant feature (Filhol, 1876). The teeth are more overlapping than in *Hyaenodon requieni*, but the premolars are not rotated and still aligned. A diastem is present between the p2 and the p3. The P3 shows a strong disto-lingual expansion. The upper molars retained a protocone and show a long metastyle. The lower dentition anterior to the p3 is not known (Lange-Badré, 1979).

The species is known from the following sites: Quercy e.g. Saint-Antonin and Saint-Martin-de-Villeréal (France).

P1: double-rooted, asymmetrical, short and distally not much elongated, aligned with the tooth row.

P2: short, because the distal border is not elongated and not concave, large lingual cingulum, no disto-lingual expansion.

P3: long and asymmetrical, distal part is elongated in comparison to *Hyaenodon requieni*, distal to the main cusp is a blade present, the tooth shows a slightly obtuse angulation, the angle between the P3 and the P4 cannot be properly measured.

P4: shorter than the P3, the mesial part is not elongated and no crest anterior to the main cusp is present, the metastyle does not reach half of the height of the main cusp, the talon is lower than in *Hyaenodon requieni*, the protocone is high, although lower than the mesial and distal parts of the tooth, and possesses a trenchant cingulum.

M1-2: on the M1 a small, conspicuous cuspid is present, no hook-shaped metastyle as in *Hyaenodon requieni*, the metastyle is aligned with the tooth row, due to wear the state of fusion of para- and metacone cannot be judged.

p3: long and low, lingual cingulid, elongated and low talonid, no tendence to disto-lingual expansion (in contrast to *H. requieni*).

p4: different from the p3, because of its symmetry, parastylid present as a crest and of equal height as the talonid, talonid is about the half of the height of the main cusp.

m1: the talonid should be remarkably long (Martin, 1906), but due to heavy wear in most specimens (trigonid worn to the level of the talonid) it was not possible for Lange-Badré to make a statement comfirming/rejecting this hypothesis.

m2: less vestiges of the cingulid on the mesio-buccal aspect of the paraconid than in other species, but there are vestiges of the cingulid lingual below the protoconid.

m3: no traces of a talonid, a cingulid can be strongly developed (material from Saint-Martin-de-Villeréal).

The relatively longer talonid on the m1 in comparison to the other molars could be observed (see Fig. 5/5 A) and is confirmed herein.

Hyaenodon minor Gervais 1848-1852 (Fig. 5/5 C-D herein; synonymy taken from Lange-Badré, 1979, p. 144):

> *Hyaenodon minor* Gervais in Lydekker 1885
> *Hyaenodon minor* Gervais in Schlosser 1887
> *Hyaenodon aimi* Forster Cooper 1926
> *Hyaenodon* cf. *minor* Gervais in Cray 1973

This species is about the size of a fox. Its snout is short and brachyrhynch. However, there are diastemata between the P1 and the P2 and between the p2 and p3. The angle between the P3 and the P4 ranges from 150-155°. The P4 possesses a trenchant parastyle and the protocone is not reduced. The M1 still shows the unfused tip of the paracone and the metacone. The M2 shows the fused condition. The p4 variably possesses a

parastyle. Vestiges of the talonid are present on the m3. A distinct cingulum/id is developed on the premolars and molars (Lange-Badré, 1979).

Hyaenodon minor was a frequent element of the late Eocene faunas. For this species, sexual dimorphism was proved. Furthermore, Lange-Badré (1979) stated, that this species was not a predecessor of later species and that the species it resembled most — *H. rossignoli* — should be acknowledged as sister species.

The species is known from the following sites: Fons 4 (Gard, France), Quercy e.g. Malpérie and Perrière (France), Roc de Santa (Spain), Hordle (Lower and Upper Headon beds, Great Britain), Gösgen Kanal (Switzerland).

P1: double-rooted, small, short and conical, distal border neither concave nor elongated, mesio-lingual crest meets the cingulum in forming a parastylar relief, strong cingulum.

P2: similar to the P1, but distally concave, possesses distad a small cuspid, that vanishes quickly with wear, no parastyle, strong cingulum.

P3: obliquely angled, strong and robust cingulum, rudimentary parastyle.

P4: wide parastyle (observed constantly) of equal lenght as the metastyle, but not much lower than the latter, protocone on a rectangular or a triangular base (depending on the site, material of the Phosphorites of the Quercy mostly show a triangular base), the metastyle is bucco-lingually compressed and present as a high and wide crest, cingulum strongly developed except along the metastyle.

M1: The M1 is more plesiomorph than the M2. Para- and metacone stay separated of about a third of their height. The paracone is lower and possesses a small, conical cuspid on its basis. The metacone is voluminous. A strong cingulum is developed. A parastyle is frequently present and formed to a wide crest. The metastyle is aligned with the tooth row.

M2: The para- and the metacone are fused. The parastyle was absorbed by the mesio-buccally crest. The cingulum is strongly developed. The protocone is reduced to a bulge on the basis of the crown. The metastyle is long and buccally little concave.

p1: single-rooted, its root is distally curved, the tooth is asymmetrical, low and can be absent (unilateral presence of the p1 reported by Lange-Badré, 1979), strong lingual cingulid, diastem between the p1 and the c in material from the Phosphorites (Quercy).

p2: short and asymmetrical, distally slightly concave, slight disto-lingual expansion and two fine crest that connect with the strong cingulid.

p3: strong parastylid, in general voluminous, wide and triangular, a globular talonid is present, which is isolated from the main cusp, strong cingulid.

p4: usually longer than the p3, parastylid developed that forms a small crest, this crest is about the same height of the talonid, the talonid is compressed to the main cusp, strong cingulid developed.

m1-3: frequently worn. Small and angular relief present on the mesio-lingual basis of the paraconid on the m1. Vestiges of a parastylid can be observed on the m2. Neither m1, nor m2 show a reduction of the talonid. The m3 possesses plesiomorph features as well: the lingual cingulid absorbs vestiges of the talonid.

Hyaenodon rossignoli Lange-Badré 1979 (Fig. 5/6 A-B herein; synonymy taken from Lange-Badré, 1979, p. 149):

pro parte *Hyaenodon exiguus* and *Hyaenodon minor* Martin and Filhol

Concerning the size this species is between *Hyaenodon minor* and *filholi*. The angle between the P3 and the P4 ranges from 145-150°. A distinct lingual cingulum/id is present on the premolars. The protocone on the P4 is not reduced. The P3 is strongly obliquely angeled. The tips of the para- and the metacone are still separated.

No parastyle is present on the M1 and the M2. The protoconid is compared to the paraconid short on the m3. It is a brachyrhynch species (Lange-Badré, 1979).

The species resembles most *Hyaenodon minor*, but these resemblances are of plesiomorph character: robust premolars, a trenchant lingual cingulum/id, emphasized protocone on the P4 and unfused tips of the paracone and the metacone on the M1. However, the species undergoes a different evolution than *Hyaenodon minor*, observable in the following features: double-rooted p1, short length of the protoconid on the m3 and a more oblique angle between the P3 and the P4 (Lange-Badré, 1979).

The species is exclusively known from the phosphorites of the Quercy (e.g. Memerlin, France).

P1: double-rooted, lingual cingulum with a mesial and a distal crest, which originate from the main cusp, disto-lingual rotation.

P2: proportionally much longer than in *Hyaenodon minor*, distally widened, showing a small cuspid compressed to the main cusp.

P3: similar to the respective tooth in *Hyaenodon minor* due to the strong development of the cingulum, the lingual expansion and the metastyle, the parastyle is reduced, the tooth is more obliquely positioned than in *Hyaenodon minor*.

P4: also similar to the respective tooth in *Hyaenodon minor*, but the protocone is less developed and more triangular, the cingulum is trenchant and expanded in the meta- and the parastyle, the parastyle is less trenchant than in *minor* and rather a small tip, the metastyle reaches two thirds of the crown heigth.

M1: in unworn state the para- and the metacone are discernible. The parastyle is reduced to a crest, located mesio-buccally from the paracone. The metastylar blade is straight. The protocone is reduced und only a rugosity is present as its trace.

M2: No parastyle is present. The paracon and the metacone are fused. The protocone is completely reduced.

p1: the roots show a tendence to fusion, sometimes two alveoli are present, sometimes just one is present.

p2: possesses a talonid with a small cuspid, mesio-lingually widened, angular outline.

p3: buccally symmetrical, no parastylid, low and globular talonid.

p4: much shorter than the p3 (in contrast to the state in *Hyaenodon minor*), lingual cingulid nearly completely reduced, the talonid is formed as a short, robust crest and perpendicular to the main cusp.

m1-3: the m1-2 possess frequently a rudimentary parastylid on the base of the paraconid. The m3 has a lingual cingulid and often a rudimentary talonid. The protoconid is short on the m3.

SPECIES OF THE OLIGOCENE

Hyaenodon dubius Filhol 1873 (Fig. 5/7 A-B herein; synonymy taken from Lange-Badré, 1979, p. 151):

> *Hyaenodon leptorhynchus* Laizier and Parieu sensu Filhol 1876
> *Hyaenodon aymardi* Filhol 1882
> *Hyaenodon leptorhynchus* Laizier and Parieu sensu
>   Lydekker 1885
> *Hyaenodon aymardi* Filhol in Schlosser 1887
> *Hyaenodon aymardi* Filhol in Martin 1906
> *Hyaenodon aymardi* Filhol in Brunet 1975

This species is medium-sized, smaller than *heberti*, but larger than *exiguus*. The snout is elongated and it belongs to the longirhynch forms. The premolars are aligned and diastemata are present (between the P1 and the P2 and the p2 and the p3). The P1/p1 is double-rooted. The third premolars are longer than the fourth

premolars (in both the upper and the lower dentition). A trenchant anterior blade is developed on the P4. The angle between the P3 and the P4 is about 150°. An anterior accessory cusp on the p4 can be present. On the M1 a rudimentary protocone is present. The paracone and the metacone are fused on both molars.

In the course of evolution this species size increases (Lange-Badré, 1979). Concerning the size it is similar to *Hyaenodon leptorhynchus*. Regarding the morphology it is similar to *Hyaenodon heberti*. Its European descendence is questioned (Lange-Badré, 1979). The anterior accessory cusp on the p4 is of extreme variability (from being not present to a large cusp).

The species is known from the following sites: Ronzon (Haute-Loire, France), Quercy (France) e.g. Aubrelong 1, Itardios, Mas-de-Got (Lot), Villebramar (Lot-et-Garonne), Montalban (Spain). Additionally known from Liptingen (Germany; see Scherzinger et al., 2005 and Bastl et al., 2011).

P1: double-rooted, strong lingual cingulum, the main cusp is slightly asymmetrical due to the short and concave distal border.

P2: much longer than high, no parastyle, lingual cingulum, hemispherical cuspid on the distal part.

P3: a small, conspicuous parastyle is present, but exclusively visible from linguad, conical metastyle, moderate lingual expansion.

P4: always shorter than the P3, tendence to symmetry due to the development of the parastyle, but the parastyle never reaches the dimension of the metastyle, the protocone is a plateau with a trenchant cingulum and centrally located.

M1-2: the para- and the metacone are fused. The only trace can be observed in the height difference of the mesio-buccal crest, that is an expansion of a bulge. No trace is present on the M2. Both molars show no parastyle. On the M1 a small, lingual tip (that rapidly vanishes with wear) is present as a vestige oft he protocone.

p1 and p2: no peculiar features, double-rooted, distally not much concave, lingual cingulid, no disto-lingual expansion, the main cusp of the p2 is followed by a curved and emphasized talonid.

p3: similar to the P3, but more straight, parastylid — if present — is located on the lingual side anterior to the main cusp, talonid is wide and detached from the main cusp.

p4: much shorter than the p3, despite variable development of the parastylid, talonid is detached as in the p3 and much higher than the parastylid.

m1-3: the molars are about two thirds of the length of the premolars. The m1 and the m2 resemble those of *Hyaenodon brachyrhynchus*. The m3 possesses in comparison to the paraconid an elongated protoconid. The parastylid is strongly individualized. The lingual cingulid is frequently formed to a crest and no trace of a talonid is present on the m3.

Hyaenodon leptorhynchus Laizier and Parieu 1838 (Fig. 5/8 A-C and 5/9 A herein; synonymy taken from Lange-Badré, 1979, p. 154):

> *Hyaenodon leptorhynchus* Laizier and Parieu in Blainville 1839
> non *Hyaenodon letorhynchus* Laizier and Parieu in Filhol 1876
> pro parte *Hyaenodon vulpinus* Gervais in Filhol 1876
> *Hyaenodon vulpinus* sensu Filhol in Martin 1906
> *Hyaenodon milloquensis* Martin 1906
> (pl. 17, Fig. 2; pl. 19, Fig. 10)
> *Hyaenodon bavaricus* Dehm 1935 (pl. 1, Fig. 1-4)
> *Hyaenodon vulpinus* sensu Filhol in Crochet 1971

further synonymy (as *H.* aff. *leptorhynchus* in Lange-Badré, 1979, p. 157) herein:

Hyaenodon cayluxi Filhol 1876

Hyaenodon aff. *leptorhynchus* Laizier and Parieu in

Martin 1906 (pl. 19, Fig. 3)

Hyaenodon martini Depéret 1917

The species is of medium size, between the larger *Hyaenodon dubius* and the smaller *Hyaenodon exiguus*. The mandible is low and the snout is elongated — it belongs to the longirhynch forms. The p1 and the p2 are separated through a diastem. The p2 is asymmetrical due its long talonid. The p4 is much shorter than the p3. The molars show the apomorph state (fusion of para- and metacone). Parastyle and protocone are reduced on the molars. The P3 shows a strong disto-lingual expansion. The upper and lower premolars show a strong lingual cingulum. The angle between the P3 and the P4 ranges from 155-160°. The P4 is characterized in its rectangular protocone, that is bordered by a large and robust cingulum (Lange-Badré, 1979).

Hyaenodon leptorhynchus shows the same morphological features as *Hyaenodon dubius* and *exiguus*: elongated snout, diastemata between the premolars, regression of the protocone, completely fused para- and metocone on the molars. An asiatic origin is assumed for this species as well as for other Oligocene European species. However, the relationship between *Hyaenodon leptorhynchus* and *exiguus* is assumingly a very close one (Lange-Badré, 1979).

Concerning the former species *Hyaenodon cayluxi*, which was referred to as *Hyaenodon* aff. *leptorhynchus* by Lange-Badré (1979), the following is stated: Various other authors referred *Hyaenodon cayluxi* to the species *minor* or *dubius* (for discussion see Lange-Badré, 1979). *Hyaenodon cayluxi* is exclusively known from the Quercy. It is of medium size and shows no diastemata in its dentition. The holotype is a juvenile mandible. Only mandibular material has been attributed to that taxon. The p1 is double-rooted. The p2 shows an elongated talonid. The p3 and the p4 show no parastylid and are of equal length with a compressed main cusp and a strong cingulid. The only difference to *Hyaenodon leptorhynchus* is the lack of diastemata (Lange-Badré, 1979). As this feature is a variable one (see other species), it is herein now fully included in *Hyaenodon leptorhynchus*. Note that the holotype is a juvenile mandible and diastemata could have been present in the adult.

The species is known from the following sites: Quercy (France), e.g. Villebramar, Mas-de-Got, Pech du Fraysse, Cournon, Saint-Martin-de-Castelvi, La Milloqe, Dieupentale; Möhren 13 (Germany) and Gunzenheim (Germany).

P1: double-rooted, asymmetrical, distally elongated, short diatstem between the canine and the P1, strong lingual cingulum.

P2: diastem between the P1 and the P2 in the adult, strong lingual cingulum, similar to the P1 but much larger, shorter than the p2.

P3: longest tooth of the premolars and as well the lowest, parastyle is if present low, lingual cingulum strong and forms sometimes a cuspid between the main cusp and the metastyle, strong disto-lingual expansion.

P4: protocone strongly developed, its (= protocone) large and rectangular outline is emphasized by the cingulum, parastyle is well developed and robust.

M1-2: parastyle and protocone are reduced on both molars. The fusion of the para- and the metacone is complete. The metastyle is long and strongly concave from a buccal view.

p1: double-rooted with two equally developed roots, much shorter and wider than the P1, strong lingual cingulid.

p2: elongated due to the expanded talonid, which sometimes possesses a small, conspicuous cuspid, strong lingual cingulid.

p3: much longer than the p4, strong and large lingual cingulid, instead of a parastylid a thickening is present, conical cuspid is present on the talonid.

p4: short, distinct lingual cingulid, usually no parastylid (during the species´ evolution it is reduced).

m1-3: the length of all the molars is 50-60% of the length of the premolar row. The m1 and the m2 are low, taking their length into account: the protoconid hardly reaches the height of the main cusp of the p3. The m3 shows an elongated paraconid and its tip is hook-shaped.

Hyaenodon exiguus Gervais 1873 (Fig. 5/10 A-B herein; synonymy taken from Lange-Badré, 1979, p. 158):

> *Pterodon exiguum* Gervais 1873 (pl. XVI, Fig. 3)
> *Hyaenodon exiguus* Gervais 1876
> *Hyaenodon compressus* Filhol 1876 (Fig. 161-163)
> *Hyaenodon vulpinus* Gervais in Filhol 1876
>   (Fig. 168, 170, 173-175)
> pro parte *Hyaenodon compressus* Filhol in Martin 1906
> *Hyaenodon vulpinus* Filhol in Martin 1906
> *Hyaenodon* aff. *compressus* Filhol in Helbing 1928
> *Hyaenodon filholi* Schlosser in Helbing 1928
> *Hyaenodon vulpinus* Gervais in Lavocat 1951
> *Hyaenodon vulpinus* Gervais in Ginsburg 1969

It is a longirhynch species of the size of a fox and thus small-sized in comparison to other species. The mandible is slim and the dentition elongated and trenchant. The teeth are slim and the molars are narrow. The delicate dentition resembles that of a smaller species — *Hyaenodon filholi*. The premolars are aligned and show diastemata in the adult (between the P1 and the P2 and between the p2 and the p3). The P/p1 is double-rooted. The P/p3 are long and mesially elongated with a low and rounded crest (withoud parastyle/id). The angle between the P3 and the P4 ranges from 155-160°. The protocone of the P4 shows a triangular outline and is small. The p4 is short. The para- and the metacone are completely fused on the molars. The protocone is reduced on the M2. The m3 is long, taking the height of the mandible into account (Lange-Badré, 1979).

This species is quite different from other European Eocene species. Thus, Lange-Badré (1979) assumed an outer-European origin and a possible descent from the Asian *Hyaenodon eminus*.

The species is known from the following sites: Quercy (France) e.g. Saint-Antonin, La Plante, Rigal-Jouet, Pech Desse (Lot), La Combératière (Lot-et-Garonne), Antoingt (Puy-de-Dôme), Étampes (Essonne), Coderet-Branssat (Allier) and Montalban (Spain).

P1: double-rooted, the only cusp is the main cusp, distally short and not much concave.

P2: strongly concave distal border, lingual cingulum meets the crest of the main cusp without forming a parastyle.

P3: no parastyle, mesially curved border, on the distal half the lingual cingulum meets the crest of the main cusp and widens to a moderate crenulated lobe.

P4: shows the tendence to reduce the protocone, the base of the protocone is of triangular shape and possesses a small cuspid, sometimes a parastyle is present, but more frequently a plateau as on the P3 is formed, the metastyle reaches two thirds of the height of the main cusp, the mesial border of the tooth is short.

M1-2: the length of the molar row is less then half of the length of the premolar row. The para- and the metacone are fused. The angulation of a mesial crest on the M1 is the only indication for the duality of its origin. The parastyle on the M1 is very small and is sometimes present in an elongation of the cingulum. The protocone is strongly reduced — on its root is a small cuspid. The M2 is in buccal view concave, but the metastyle is aligned with the anterior cusp. The metastyle of the M1 is partly covered by the mesial part of the M2.

p1 and p2: double-rooted and similar to each other, no tendence to fusion of the roots, the main cusp is asymmetrical and elongates to a talonid, strong lingual cingulid, during ontogeny a diastem between the p2 and the p3 develops.

p3: similar to the P3, mesial plateau instead of a parastylid, small mesio-lingual cuspid present, talonid is low and curved.

p4: this tooth is the highest of the premolars and much shorter than the p3, a parastylid is rarely present, the mesial border is short, sometimes a small mesio-lingual cuspid is developed, talonid is formed to a crest and reaches half of the height of the main cusp, in buccal view the p3 and the p4 are of angled appearance.

m1 and m2: the height is significantly lower than the length, which is typical for a longirhynch Oligocene species.

m3: low for its length. The tip of the paraconid points linguad and gives the blade a hook-shape.

Hyaenodon filholi Schlosser 1887 (Fig. 5/9 B herein; synonymy taken from Lange-Badré, 1979, p. 161):

> pro parte *Hyaenodon vulpinus* Gervais in Filhol 1876
> pro parte *Hyaenodon filholi* Schlosser in Martin 1906
> non *Hyaenodon filholi* Schlosser in Helbing 1928 (frg. 8)
> *Hyaenodon compressus* Filhol in Gromova 1952

This species is small sized and the smallest European taxon of *Hyaenodon*. It is leptorhynch and has a very low mandible. The P2 is short. The P4 shows a reduced protocone. The angle between the P3 and the P4 ranges from 160-165°. The p3 and the p4 are similar to each other. The upper molars show the advanced, fused state. A vestigial protocone is present on the M1. The metastyle of the M2 covers partly the anterior cusp of the M2. The m1 and the m2 are small. The talonid of the m2 is short regarding its length.

The former holotype of this species is determined as *Hyaenodon rossignoli* and a paratype was proposed in the thesis of Lange-Badré (1979). For *Hyaenodon filholi* an asiatic origin is assumed. Its size is close to *Hyaenodon rossignoli*, but its morphology is most similar to *exiguus* (Lange-Badré, 1979).

The species is known from the following sites: exclusively from the Quercy (France) e.g. Caylux, Mouillac, Bach and Promilhanes.

P1: no specimen holding the P1 is up to now preserved.

P2: short, distal border short as well and possessing a small cuspid, small lingual expansion reminding of *minor*, although much smaller.

P3: conical, the mesial border is short, no parastyle present, distinct lingual cingulum, distad globular cusp is present.

P4: in contrast to the P3 a parastyle can be developed, the parastyle is further emphasized by the lingual cingulum, the cingulum does not reach the metastyle, the protocone is of triangular outline and small, the metastyle is a robust crest and not much higher than the parastyle.

M1-2: the para- and the metacone are completely fused. The protocone is visible as very small tip on the M1. The cingulum is interrupted on the M1 and not present on the M2. The parastyle is missing. However, the missing parastyle does not result in an elongation of the buccal basis of the anterior cusp as in *Hyaenodon exiguus*. In contrast, the distal part of the metastyle on the M1 is covering the anterior part of the M2. The total length of both molars is low and about the length of the premolar row.

p1: asymmetrical due to elongated distal part, the distal part is also slightly lingually widened, moderately developed cingulid.

p2: is like the p1, but the cingulid is more distinct, the disto-lingual widening is less developed in respect to the tooth´s length, distally a small cuspid is present.

p3: the main cusp possesses a parastylear region and is semi-circular as in *Hyaenodon exiguus*, a real conspicuous parastylid is rarely developed, the talonid is low, curved and compressed to the main cusp.
p4: the development of a parastylid is variable, it is frequently reduced to a short mesial border and sometimes developed as a short, wide crest of half the length of the talonid, the talonid is high and compressed to the main cusp.
m1 and m2: are about the same length. The talonid is distinct on the m1 and regressing on the m2.
m3: no trace of a vestige of the talonid. A lingual crest sometimes forms a bulge on the distal aspect of the protoconid.

5.4 Problems of the stratigraphy of the European *Hyaenodon*

The biggest problem for the understanding of the evolution of the European *Hyaenodon* is the incomplete data on the stratigraphy, caused by the early exploit of the Quercy fissure fillings (see Chapter 4). For the Oligocene species an outer-European origin is assumed (Lange-Badré, 1979).
Lange-Badré (1979) divided the European species in two "populations":

1) the late Eocene forms, that are brachyrhynch, possess an incompletely fused naso-palatinal channel, with a robust dentition and the tips of paracone and metacone not fused: *Hyaenodon minor, rossignoli, brachyrhynchus, requieni* and *gervaisi*.

2) the Oligocene forms, that are of assumed asiatic origin. They are different from the former species due to being longirhynch, presence of diastemata, closed naso-palatinal channel and fused paracone and metacone on the upper molars: *Hyaenodon exiguus, filholi, dubius* and *leptorhynchus*.

She concluded, that concurrence on species-level played an important role, although the large Eocene species had no competitor: the new species were middle to small-sized. Lange-Badré (1979) furthermore concluded, that the North American species are of Asian origin and that the European species did not evolve from the North American lineage.

I completely agree, that the European taxa cannot be derived from the North American forms (conforms with Mellett, 1977 too). The immigration of Asian elements is still not clarified and the Asian material is rare, which complicates a proper understanding of the evolution of the European taxa. However, in this study evidence for a European lineage — contradicting the hypothesis of the immigration of all European Oligocene species — is provided (see Chapter 7). The immigration of *Hyaenodon filholi* to Europe is confirmed, but the morphology of the milk dentition in *Hyaenodon exiguus* proposes a survival of a European lineage.

A

	EUROPE	NORTH AMERICA	ASIA
EARLY MIOCENE			*H. weilini*
LATE OLIGOCENE	*H. leptorhynchus, filholi* (latter not exactly dated - Oligocene) *H. exiguus*	*H. brevirostrus*	*H. chunkhtensis*
EARLY OLIGOCENE	*H. brachyrhynchus, gervaisi* *H. dubius* *H. requieni*	*H. horridus* *H. crucians* *H. mustelinus*	*H. pervagus, incertus, gigas, neimongoliensis*
LATE EOCENE	*H. heberti*	*H. montanus, megaloides, microdon, raineyi* *H. vetus*	*H. eminus, mongoliensis*
MIDDLE EOCENE	*H. minor* *H. rossignoli*	*H. venturae*	*H. yuanchensis*

B

Fig. 5/1: Summary of the temporal and geographical distribution of all species of *Hyaenodon* and morphology of the lower dentition in *Hyaenodon requieni*. Bar equals 1cm. A, distribution of all species, adapted from Bastl et al. (2011) and based on Lange-Badré, 1979 (for Europe), Mellett, 1977 and Lavrov and Emry, 1998 (for North America) and Huang and Zhu, 2002; Morlo and Nagel, 2006; Tsubamoto et al. 2008 and Wang et al., 2005 (for Asia); B, LDB 5: *H. requieni*, lower jaw in buccal (upper) and occlusal (lower) view. Note the straight arrangement of the incisors.
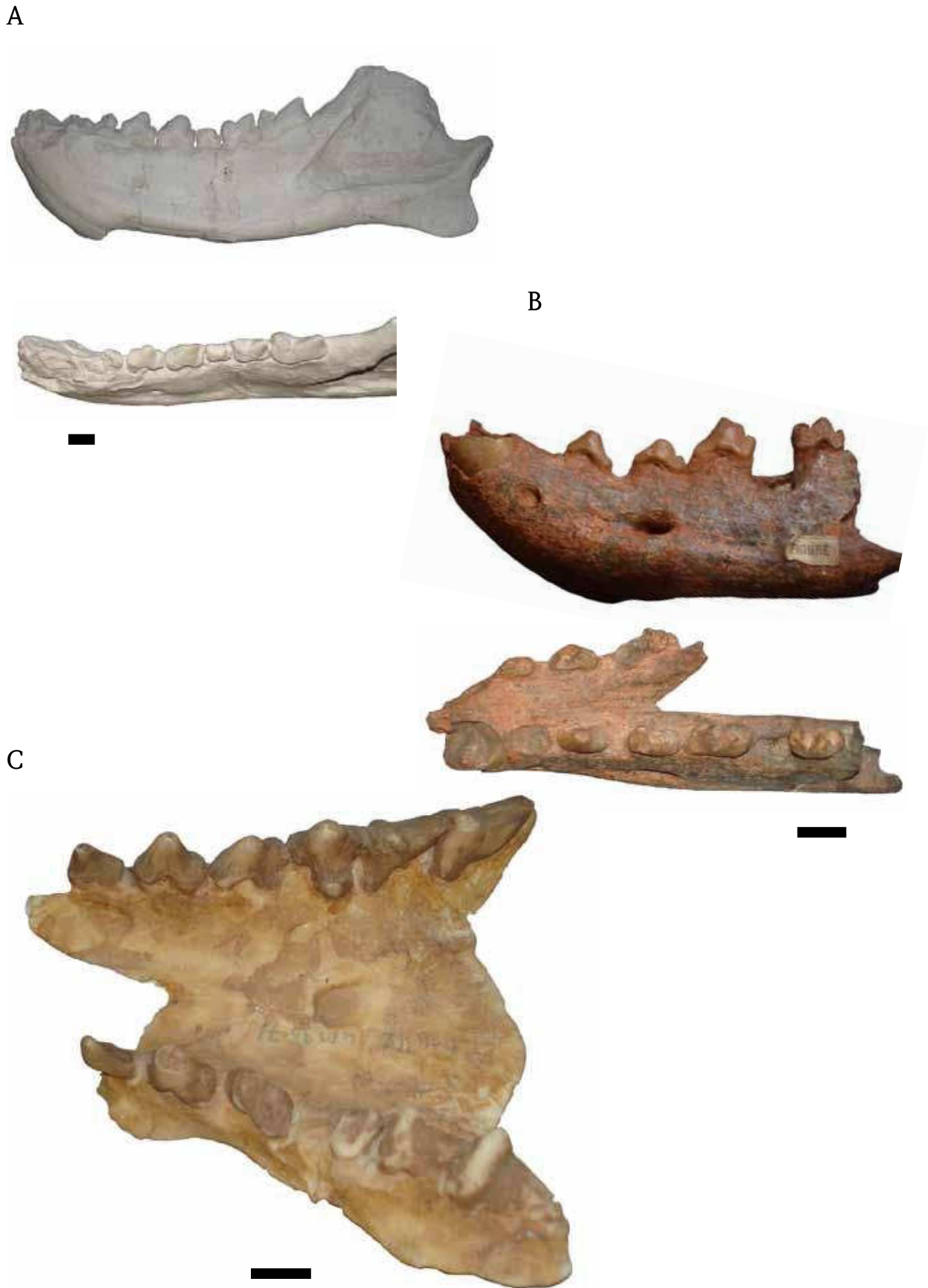
Fig. 5/2: Morphology of the upper and lower dentition in *H. requieni*. Bar equals 1cm. **A**, MNHN without number: cast of the lower jaw in buccal (upper) and occlusal (lower) view; **B**, Qu 8624: lower jaw from the Quercy in buccal (upper) and occlusal (lower) view; **C**, UM 957 from the MNHN: cast of the upper jaw in occlusal view.

Fig. 5/3: Morphology of the upper and lower dentition in *H. gervaisi*. Bar equals 1cm. **A**, MNHN without number: cast of the upper (upper) and lower (lower) dentition both in occlusal view; **B**, MNHN: So 6-1: lower jaw in buccal (left) and occlusal (right) view.
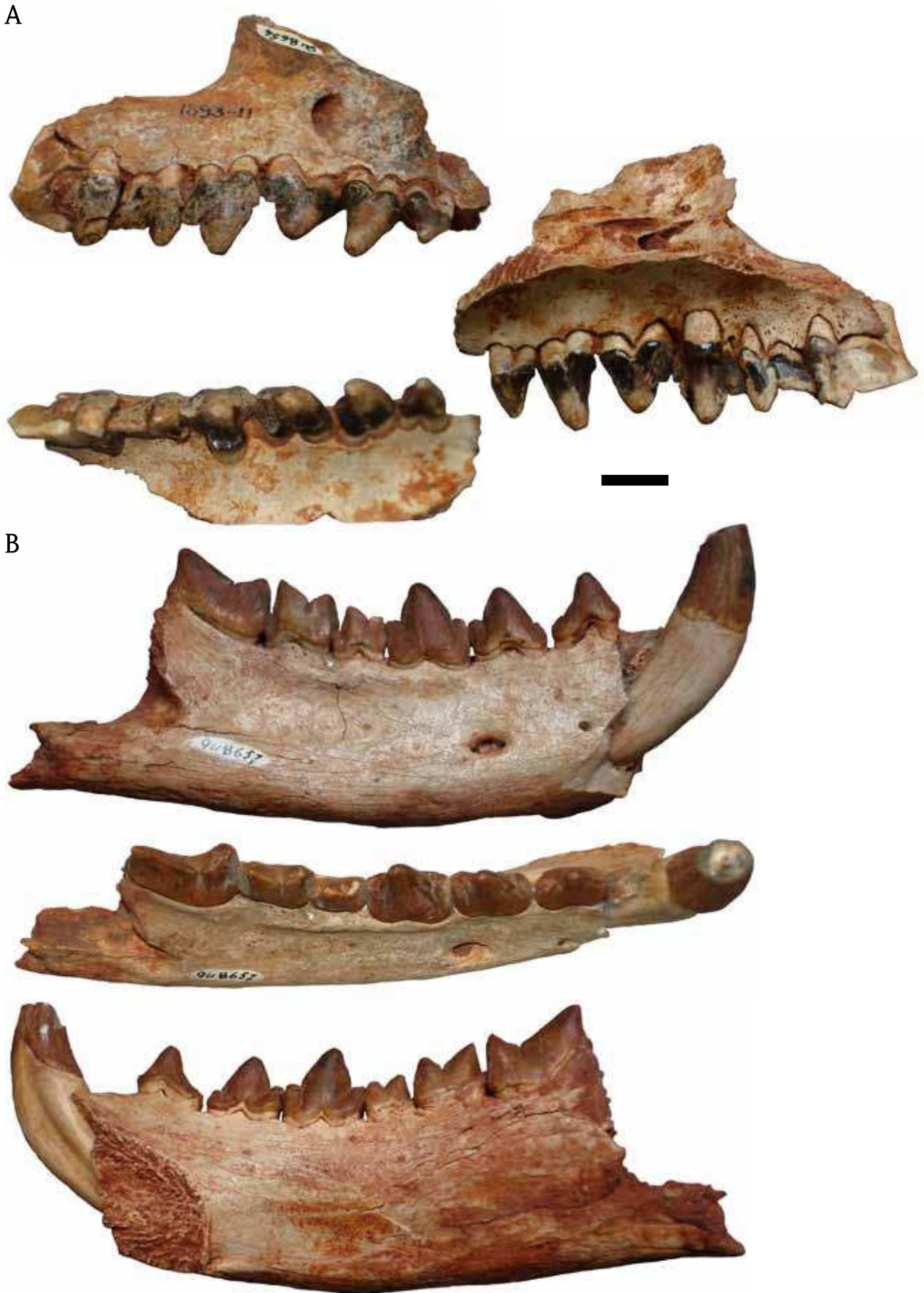
Fig. 5/4: Morphology of the upper and lower dentition in *H. brachyrhynchus*. Bar equals 1cm. **A**, Qu 8654: upper dentition from the Quercy (France), in buccal (upper left), lingual (upper right) and occlusal (lower left) view; **B**, Qu 8657: lower dentition from the Quercy (France), in buccal (upper), occlusal (middle) and lingual (lower) view.

Fig. 5/5: Morphology of the upper and lower dentition in *Hyaenodon heberti* and *minor*. Bar equals 1cm. **A,** Qu 8308: lower dentition of *H. heberti* in buccal (upper), occlusal (middle) and lingual (lower) view; **B,** Qu 8308: fragment of the upper jaw of *H. heberti* with M1-2 from the Quercy in occlusal view; **C,** Qu 8649: upper dentition of *H. minor* from the Quercy in occlusal view; **D,** Qu 8651: lower dentition of *H. minor* from the Quercy in buccal (upper), occlusal (middle) and lingual (lower) view.
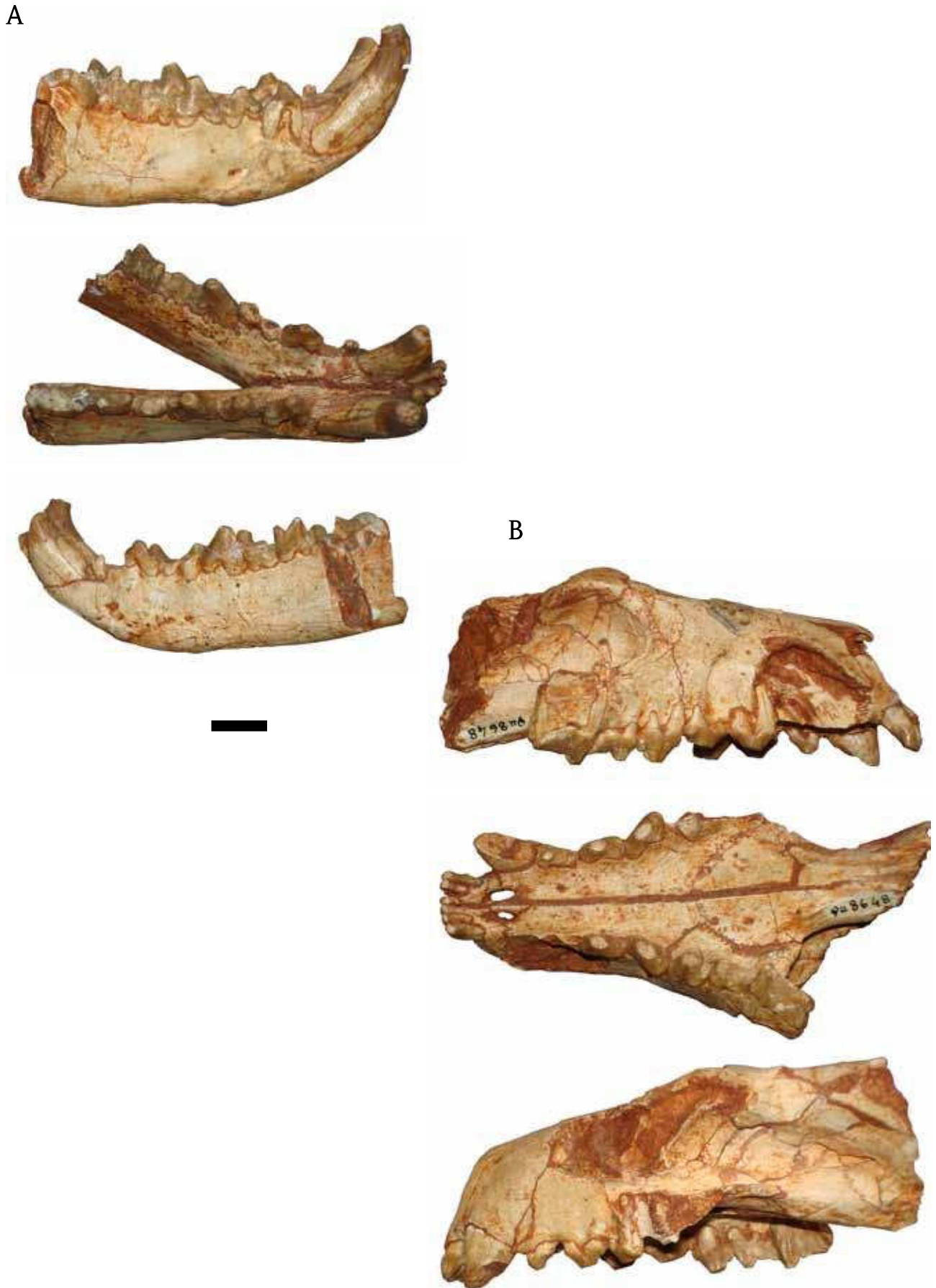
Fig. 5/6: Morphology of the upper and lower dentition in *H. rossignoli*. Bar equals 1cm. **A**, Qu 8306: lower dentition from the Quercy in buccal (upper), occlusal (middle) and lingual (lower) view; **B**, Qu 8648: upper jaw from the Quercy in buccal (upper), occlusal (middle) and lingual (lower) view; Note the brachyrhynch form of the snout and the small size of the species as well as the development of the p1.

Fig. 5/7: Morphology of the upper and lower dentition in *Hyaenodon dubius*. Bar equals 1cm. **A**, Au 732: lower dentition from Aubrelong in buccal (upper), occlusal (middle) and lingual (lower) view; **B**, Qu 8307: upper jaw from the Quercy in buccal (upper), occlusal (middle) and lingual (lower) view.

Fig. 5/8: Morphology of the upper and lower dentition in *H. leptorhynchus*. Bar equals 1cm. **A**, MNHN without number: upper dentition in buccal (upper), occlusal (middle) and lingual (lower) view; **B**, Qu 8464: lower dentition from the Quercy in buccal (upper), occlusal (middle) and lingual (lower) view; **C**, MNHN without number: cast of the holotyp in buccal view, unscaled; Note the leptorhynch form and the elongated premolar row.

Fig. 5/9: Morphology of the lower dentition in *Hyaenodon filholi* and in former *H. cayluxi* now included in *Hyaenodon leptorhynchus*. Bar equals 1cm. **A**, Qu 8622: former *H. cayluxi* (now *H. leptorhynchus*, see text) in buccal (upper), occlusal (middle) and lingual (lower) view; **B**, Qu 8662: *H. filholi* from the Quercy, lower dentition in buccal (upper), occlusal (middle) and lingual (lower) view. Note the delicateness of *H. filholi*.
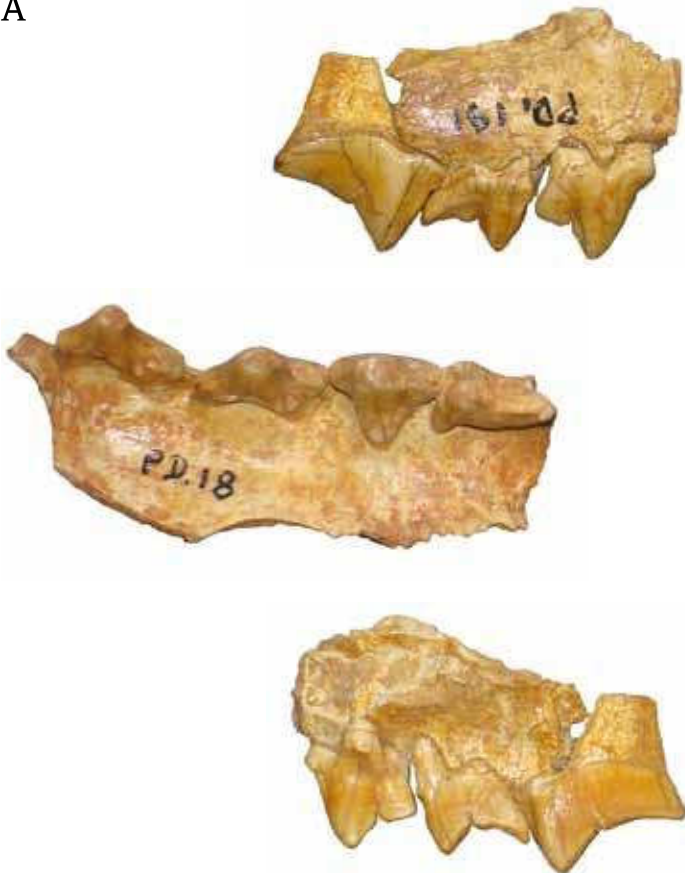
Fig. 5/10: Morphology of the upper and the lower dentition in *H. exiguus*. Bar equals 1cm. **A**, PD 18 and PD 181: upper dentition from Peche Desse in buccal (upper; PD 191), occlusal (middle; PD 18) and lingual (lower; PD 191) view; **B**, Qu 8328: upper dentition from the Quercy in buccal (upper), occlusal (middle) and lingual (lower) view.

Chapter 6

6. Dental Anatomy

The new described dental material herein is comprised of:

Hyaenodon exiguus
        Cranial material: PD 187, Qu 17662, NMHW 2010/0196/0003;
        Mandibular material: PD 487, M 4498, M 2353, M 2353a;

Hyaenodon filholi
        Cranial material: Qu 8664;
        Mandibular material: PD 510, MNHN 1875-931, M 2352, M 84866, M 84867,
        NMHW 2009z0084/0003;

Hyaenodon rossignoli
        Mandibular material: Qu 8356, Mo22;

Hyaenodon brachyrhynchus
        Qu 8632;

Hyaenodon minor
        Mandibular material: M 2348
        Cranial material: NMHW 2010/0196/0001, NMHW 2010/0196/0002;

Hyaenodon horridus
        M 5722;

6.1 New descriptions of dental material

6.1.1 *Hyaenodon exiguus*

The specimen **PD 187** (Fig. 6/1 A) was formerly designated to *Hyaenodon exiguus* and this determination can be confirmed here. The specimen comes from Peche Desse (Quercy, MP 28, Oligocene).

The fragment of a left maxilla shows the alveolus of the DC, the cavity for the germ of the C, the alveoli of the P1 (double-rooted), the alveoli of the DP2, the DP3, the DP4 and the M1. There is a mental foramen between the DP2 and the DP3. The tooth row is in line. No rotation of the milk teeth, especially concerning the DP3, is observed. Rotation is often displayed in the position of the P3 in adults. Small diastemata are present between the alveoli of the P1 and the alveoli of the DP2 and between the alveoli of the DP2 and the DP3.

The P1 is double-rooted. Two distinct alveoli are preserved with the anterior one being smaller.

The DP3 possesses a small anterior cuspid. The crest runs via this cuspid to the main cusp. The main cusp is pointing distally. The tooth is distally elongated and shows a posterior accessory cusp with a second minor cuspid distally. No cingula are present. The lingual root is slightly protruding linguad.

The DP4 shows two high, distinct and separated cusps (similar to the primitive condition in the M1 with not completely fused para- and metacone). They are subequal in heigth with the anterior one being slightly lower. Its cutting blade is elongated posteriorly and overlaps the M1 buccally. It already shows wear — the facet is weak, but present. The tips are dot-like worn. No cingula are present.

The M1 possesses anterior on its buccal aspect a small parastyl. The tooth in general is short. The anterior lingual root shows a weak cingulum.

The size falls into the range of *Hyaenodon exiguus* (Lange-Badré, 1979), especially concerning the DP4 and the M1.

	DP3	DP4	M1	P1 (estimated from the alveoli)	DP2 (estimated from the alveoli)
length	7.1 mm	8.8 mm	8.7 mm	6.6 mm	8.0 mm
width	2.8 mm	4.7 mm	5.5 mm		

The specimen **Qu 17662** (Fig. 6/1 B) was formerly designated to *Hyaenodon vulpinus* (invalid species, see Chapter 5) and can now be referred to *Hyaenodon exiguus*. This juvenile specimen was figured by Filhol as early as 1876. The only reliable information concerning site and time is "Quercy" (late Eocene/Oligocene). The skull fragment is compressed and crushed. On its left side bone was cut off to reveal the germs of the permanent dentition. The nasals show as expected an arrow-shape. The proximal part is strongly fragmented. Whether parts of cavities for incisors or relicts of the turbinalia can be seen is not clear. On the right side the alveoli of the P1, the erupting P2, the broken roots of the DP3, the broken roots of the DP4 with the tip of the P4 visible and the M1 (distal part broken) are preserved. The tip of the C is visible. On the left side the P1, the erupting P2 (DP2 fell out post mortem), the DP3, the DP4, the M1 and the M2 still in crypt are preserved. The germs of the P3 and the P4 are visible, because the bone was removed buccad. The germ of the P4 is more developed than the germ of the P3. On both sides diastemata are present between the P1 and the P2 and between the P2 and the DP3. The mental foramen is situated between the P2 and the DP3. The DP3 are not rotated. The tooth row is in line.

The P1 is a double-rooted tooth with two distinct alveoli. Its tip is broken and it is only slightly elongated distally. The anterior crest runs from the main cusp linguad to the base of the tooth. The posterior crest runs parallel to the length of the tooth. A buccal and a lingual cingulum are present with the lingual one being more developed.

The P2 is a high tooth and hook-shaped.

The DP3 possesses no anterior accessory cusp or cuspid. The posterior accessory cusp is building a short cutting crest together with another, smaller posterior accessory cuspid. The tooth is narrow. The tips of the cusps are flattened due to wear. Both, buccal and lingual cingula are present. The buccal one is very weak. The medial root is only slightly protruding linguad.

The DP4 shows a clear slicing facet on its cutting blade. The typical two-tipped main cusp is strongly worn. The cusps are subequal in height. A buccal cingulum is present, but weak. On the anterior lingual root there is a short lingual cingulum leading into a row of small tubercles. The cutting blade is short.

The M1 is derived — para- and metacone are completely fused. The slicing facet is more prominent than on the DP4. On both sides the cutting blade of the M1 is broken. The molar shows the same lingual cingulum on the anterior lingual root with the small tubercles like on the DP4.

The measurements fall into the size range of the species *Hyaenodon exiguus* (Lange-Badré, 1979).

	P1 sin.	DP2 sin.	P2 sin.	DP3 sin.	DP4 sin.
length	7.1 mm	7.8 mm	6.2 mm	8.8 mm	10.4 mm
width	3.7 mm			3.8 mm	4.6 mm

	P4 sin.	M1 sin. (distally broken)	M1 dex. (distally broken)	M2 sin. (distally broken)	germ of C sup. sin.
length	9.1 mm	8.9 mm	8.5 mm	11.0 mm	15.0 mm
width		5.5 mm	5.4 mm		

The specimen **NHMW 2010/0196/0003** (Fig. 6/1 C) was formerly designated to *Pseudaelurus*, but is in fact a juvenile individual of *Hyaenodon exiguus*. The specimen comes from Bach (Lot, France, late Eocene/ Oligocene).

The specimen is a juvenile right skull fragment with an erupting P1, the alveoli of the DP2, the alveoli of the DP3, the DP4 and the alveoli of the M1. There is a mental foramen between the alveoli of the DP2 and the alveoli of the DP3.

It is still connected with sediment and breaks easily. During preparation other specimens were found in the sediment: two incisivi of Rodentia indet., a vertebra of Serpentes indet. and a molar of Theridomyidae indet.

The DP4 is a tooth with three roots. The two highest cusps are still clearly separated and placed in the middle of the tooth. They are subequal in height. The blade elongates distad. It is quite high situated compared to the cusps. The buccal cingulum is weak. There is an anterior crest present that builds a mesial bulge on the buccal side. The anterior cusp of the two main cusps is less flattened than the more posterior one. A slicing facet is present.

The individual already processed food even in this ontogenetical young stage — the earliest stage of tooth replacement (see Chapter 7)!

The size falls into the range of the species *Hyaenodon exiguus*.

	DP4
length	10.3 mm
width	5.3 mm

The specimen **PD 487** (Fig. 6/2 A) was formerly identified as *Hyaenodon exiguus* and this can be confirmed here. The specimen comes from Peche Desse (Quercy, MP 28, Oligocene).

The fragment is a left mandible, reaching from the posterior alveolus of the p2 to the posterior alveolus of the m1. The bone is broken away on the buccal side, revealing the germs of the p3 and the p4. The symphysis reaches up to the p3. The mandible is slim and relatively delicate. Judging from the buccal view the following can be stated: the p4 is much shorter than the p3 and possesses a short cutting blade on its posterior aspect. There is no anterior accessory cusp present, nor a buccal cingulid. The p3 is similar to the p4 in possessing a short cutting blade on its posterior accessory cusp. In contrast to the p4 it is elongated — both anteriorly and posteriorly.

The size falls inbetween the ranges of the species *Hyaenodon filholi* and *exiguus* for the p4, but only into the range of *Hyaenodon exiguus* for the p3 (Lange-Badré, 1979). The fox-sized mandible and especially the long and anteriorly elongated p3 in relation to the short p4 argument for the latter, larger species.

	dp3	dp4	p3	p4	m1
length estimated from the alveoli	8.8 mm	7.6 mm			6.4 mm
length			10.7 mm	8.1 mm	

	under dp4	under m1
depth of the mandible	12.9 mm	13.0 mm

The specimen **M 4498** (Fig. 6/2 B) was formerly designated to *Hyaenodon leptorhynchus* and can now be determined as *Hyaenodon exiguus*. The mandible fragment comes from Pandaré (Caylux, France; MP 23, Oligocene).

The specimen is a fragment of a juvenile symphysis. The left ramus holds the dp4, the alveoli of the dp3, the erupting p2, the alveoli of the p1, the alveoli of the dc and the alveoli of the incisors. The right ramus holds the anterior alveolus of the dp3, the alveoli of the p2, the alveoli of the p1 (anterior one broken), the alveolus of the dc and the alveoli of the incisors. The symphysis reaches up to the alveoli of the dp3 and is well fused. A mental foramen is present under the posterior root of the p1 and the dp3. Diastemata are between the p2 and the dp3, although the diastem is shorter on the right ramus. It has to be kept in mind that the specimen is juvenile.

The p1 possesses two distinct alveoli. The anterior one is weaker.

The p2 is asymmetrical and distally elongated. Its main cusp is pointing distally. A lingual cingulid is present. There is no apparent cuspid present on the talonid from what can be seen in the x-ray, but it shall be noted, that the tooth is not fully erupted. The anterior root is weaker than the posterior one, similar to the state in the p1.

The dp4 shows wear facets: Dot-like facets on the tips and a slicing facet on its cutting blade. Microwear was observed here too. A lingual cingulid is present. The anterior accessory cusp is low and equal in height with the talonid. On the talonid there is a crest build by two cuspids that are bordered by the cingulid. This gives the talonid a wavy occlusal outline when viewed buccally.

The measurements fall into the size range of *Hyaenodon exiguus* except for the p2, that approaches the size of *Hyaenodon leptorhynchus* (Lange-Badré, 1979). However, overall morphology arguments for the former, smaller species. The alveoli of the p1 are not equally strong and no distinct diastemata can be observed.

	dp4 sin.	dp3 sin. (estimated)	p2 dex. (estimated)	p1 sin. (estimated)
length	8.8 mm	8.8 mm	10.7 mm	7.3 mm
width	3.2 mm			
jaw depth	14.6 mm			

The specimen M2353 (Fig. 6/2 C) was formerly designated to *Hyaenodon leptorhynchus* and can now be referred to *Hyaenodon exiguus*. The mandible comes from Caylux (France; Oligocene).

The specimen is a juvenile, left mandible fragment. The ramus holds the alveolus of the dc, the tips of two germs of incisors are visible, the p1, the alveoli of the dp2, the dp3, the dp4, the m1 and the alveoli of the m2. The mandible is slim and rather small. The symphysis reaches up to the dp3. A mental foramen is present under the p1. The dp3 is broken away. In lingual view the germ of the c inf. can be seen. The tip of the p2 can be observed when viewed from an occlusal perspective. Holes were drilled under the dp3 and the dp4 (the purpose for that and when this happened is not known). No diastemata are present except for a very short one between the dp2 and the dp3.

The p1 is double-rooted with two distinct alveoli. The anterior one is much smaller, because the anterior root is reduced (see the x-ray in the following Chapter 7; Fig. 7/2 D). The tooth is asymmetrical and distally as well as lingually elongated and thus widened. The lingual cingulid is strongly developed.

The dp3 possesses an anterior accessory cusp in equal height to the cusp on the talonid. The lingual cingulid builds a bulge anterior to the anterior accessory cusp. The posterior accessory cusp is globular. The main cusp shows a dot-like flattening.

The dp4 shows an anterior accessory cusp that is higher than the talonid, but still low compared to the main cusp. On the talonid two cuspids build a crest. The distal one is weaker and they are both buccally situated. The cingulid is weak. The talonid is elongated. The anterior accessory cusp and the main cusp are both flattened. A slicing facet is present.

The m1 shows no cingulids. The talonid is distinct, but short. A slicing facet is present.

The size falls into the range of *Hyaenodon exiguus* (Lange-Badré, 1979).

	p1	dp3	dp4	m1	dp2 (estimated)
length	7.1 mm	9.2 mm	8.5 mm	7.8 mm	8.6 mm
width	3.7 mm	3.4 mm	3.5 mm	4.3 mm	

	under dp4	under m1
depth of mandible	13.4 mm	13.6 mm

The specimen **M 2353a** (Fig. 6/2 D) is determined as *Hyaenodon exiguus* and comes from Caylux (France; Oligocene).

The specimen is a juvenile, left mandible fragment. It holds the alveolus of the dc, the posterior alveolus of the p1, the alveoli of the dp2, the dp3, the dp4 and the alveoli of the m1. Diastemata are present between the p1 and the dp2, between the dp2 and the dp3 and between the dp3 and the dp4. The mandible is slim. Mental foramina are placed under the p1 and the dp3. The preservation is not sufficient to give a full description of wear facets. Enamel is partly broken away.

If there was an anterior alveolus present for the p1 — as can be assumed — it must have been small. Due to breakage this cannot be confirmed.

The dp3 is slim and elongated. The anterior accessory cusp is short and formed like a blade. No cingulids are present. The talonid shows two cuspids with the distal one being smaller. The main cusp is broken.

The dp4 shows no cingulids. The anterior accessory cusp is higher than the talonid. The talonid is not well preserved — it might have shown two cuspids. The main cusp is broken.

The milk teeth are fragmented, but the specimen shows more affinities to *Hyaenodon exiguus*: the talonid on the dp4 is elongated. The size falls in the range *Hyaenodon exiguus* as well as in the only other species in question for determination of this specimen, the smaller *Hyaenodon filholi* (Lange-Badré, 1979).

	dp3	dp4	m1 (estimated)	dp2 (estimated)
length	9.1 mm	8.1 mm	6.4 mm	7.4 mm
width	2.9 mm	3.1 mm		

	under dp4	under m1
jaw depth	11.8 mm	11.2 mm

6.1.2 *Hyaenodon filholi*

The specimen **PD 510** (Fig.6/3 A) was formerly designated to *Hyaenodon exiguus* and this determination cannot be affirmed here. It is now assigned to *Hyaenodon filholi*. The mandible comes from Peche Desse (Quercy, MP28, Oligocene).

The lower jaw fragment is an exceptional specimen. The right ramus shows part of the processus coronoideus, the alveoli of the m2, the m1, the fragment of the talonid of the dp4 with its posterior root and tip of the p4 visible, the alveoli of the dp3 and p3 visible (bone broken buccally), the alveoli of the p2, the p1 (double-rooted), the alveolus of the milk canine and an incisor in crypt. The left ramus is preserved with an erupting m3, the alveoli of the m2, the m1, the dp4 (tip of the p4 visible, because the bone is broken on the buccal side), the dp3, the alveoli of the p2, the p1 (double-rooted) and an incisor in crypt. Mental foramina are placed

under the posterior root of the p1 and the posterior root of dp3. The symphysis reaches up to the dp3. The mandible is slim, longirhynch and rather small.

The incisors in crypt are both compressed to the alveolus of the dc inf. on their respective sides. Therefore, these teeth are regarded as the i3. Their crowns are biscuspid.

The p1 is a double-rooted tooth situated in two alveoli. The anterior alveolus is significantly smaller and strongly bent distad. The p1 is asymmetrical with the main cusp situated above the anterior root. This tooth is elongated posteriorly into a talonid and broadened linguad. A crest from the main cusp is running parallel on the talonid. No cingulids are present.

The p2 is missing on both sides. The anterior alveolus is much smaller than the posterior one, similar to the state seen in the p1. There is a small diastem between the p2 and the dp3.

The anterior root of the dp3 is weaker than the posterior one (as in the preceding tooth positions p1 and p2). This tooth broadens posteriorly. The anterior accessory cusp is low compared to the main cusp, but higher than the talonid und thus pronounced. It is compressed to the main cusp. A posterior accessory cusp is present on the talonid. It is connected through a crest with the main cusp and another, smaller posterior accessory cuspid. This crest runs along the talonid linguad. The main cusp is flattened. No cingulids are present.

The dp4 is damaged and the enamel is broken on the buccal side. The roots of this tooth are developed in equal strength. The anterior accessory cusp reaches about half of the height of the main cusp and is thus not exceeding the talonid much. On the talonid there is a cutting crest. The main cusp of the dp4 is flattened. No cingulids are present.

The m1 possesses a distinct talonid. There is a slight wear facet on the cutting blade. No cingulids are present. The m3 is erupting with the protoconid already visible. There is a posterior bulge as vestige of the talonid.

The hitherto only known *Hyaenodon* species from Peche Desse is *H. exiguus. Hyaenodon filholi* occurs together with *Hyaenodon exiguus* in Rickenbach (Switzerland) in the same time (MP 29, Oligocene). For more information about Quercy see Chapter 4. Furthermore, the determination of these two morphological very similar species is complicated (see Chapter 5). Now, the morphology of the milk dentition facilitates the identification and separation (see below). The dp4 shows the typical cutting crest for *Hyaenodon filholi.* The size falls into the range of *Hyaenodon filholi* (Lange-Badré, 1979).

	p1 sin.	p1 dex.	dp3 sin.	dp4 sin.	m1 sin.	m1 dex.
length	5.2 mm	5.5 mm	7.1 mm	7.0 mm	6.5 mm	6.6 mm
width	2.7 mm	3.0 mm	2.4 mm	2.7 mm	3.5 mm	3.6 mm

	under dp4 sin.	under m1 dex.
mandible depth	10.5 mm	10.8 mm

The specimen **Qu 8664** (Fig. 6/3 C1 and C2) was formerly designated to *Hyaenodon vulpinus* (invalid species, see Chapter 5) and can now be referred to *Hyaenodon filholi.* The specimen comes from the "Quercy" (late Eocene/Oligocene).

This juvenile specimen is a skull fragment with the DC sup., the germ of C sup., the DP3, the P4 visible and the M1 on the right side and the DC sup., the germ of the C sup., the P1, the erupting P2, the DP3, the DP4 (P4 visible on the buccal side), the M1 and the anterior alveolus of the M2 on the left side. Diastemata are present between the DC sup. and the P1, between the P1 and the P2 and between the P2 and the DP3.

The permanent incisors are already erupted, the P2 is erupting and the P4 is the next one to erupt.

The nasals are arrow-shaped. The DC sup. are simple and rather weak. Both have a broken tip. The germs of the permanent canines are visible in their cavities, which lie above the milk canines. The permanent canines might give the impression that they are soon erupting, but this impression arises from the good sight on them due to the broken bone.

The P1 is double-rooted and situated in two distinct alveoli. The anterior root is a bit weaker than the posterior one. The tooth is slightly elongated distally. No cingula are present.

In the specimen just the tip of the P2 is visible. Judging from the x-ray (Fig. 7/1 B) the P2 is a simple, conical tooth as the P1.

The DP3 is special in this specimen: The lingual root is not situated distally as usual. It is situated just below the main cusp at half the length of the tooth and strongly projecting linguad. The DP3 possesses a small anterior cuspid, which is the lowest of all tips, but well developed. The main cusp is clearly the highest cusp. Two posterior accessory cusps are present and build a blade. The distal one is smaller. The anterior one of these two posterior accessory cusps is clearly detached from the main cusp. A buccal cingulum is present. All tips are flattened.

The DP4 shows a small anterior cuspid. The main cusp is composed of two unfused cusps (para- and metacone in the molars). This characteristic gives it its two-tipped shape. The anterior one of these two tips is clearly lower. The tips show dot-shaped wear facets. The cutting blade is too bad preserved to observe an eventual slicing facet. The blade overlaps the M1 buccally. The distal blade is relatively long and low compared to the anterior cusps.

Only a part of the P4 is visible when viewed from above. This tooth possesses a low posterior accessory cusp and a protocone with a lingual cingulum.

The M1 is modern. Para- and metacone are fused. A buccal cingulum is present. On the lingual anterior root there is a crest running vertically. The slicing facet is distinct.

The size falls into the size range of the species *Hyaenodon filholi* (Lange-Badré, 1979).

	P1 sin.	P2 sin. (erupting)	DP3 sin.	DP3 dex.
length	6.6 mm	7.5 mm	8.0 mm	8.3 mm
width	2.9 mm	3.4 mm	4.6 mm	4.2 mm

	DP4 sin.	M1 sin.	M1 dex.
length	8.5 mm	7.8 mm	8.2 mm
width	4.5 mm	5.0 mm	5.4 mm

The specimen **MNHN 1875-931** (Fig. 6/3 B) can be referred to *Hyaenodon filholi*. The specimen comes from the "Quercy" (late Eocene/Oligocene).

The specimen is a juvenile, left mandible. The alveolus with the broken dc, the p1, the dp2, the alveoli of the dp3, the dp4, the m1 and the erupting m2 are preserved. Distal to the m2 there is a small opening of the bone that would have widened for the later erupting m3. The symphysis reaches up to the dp3. The mandible is slim. Mental foramina are present under the posterior root of the p1 and under the anterior root of the p3. The processes are broken. A shallow fossa masseterica can be seen. Diastemata are present between the p1 and the dp2 and between the dp2 and the alveoli of the dp3.

The p1 is double-rooted with the anterior root being weaker. There are two distinct alveoli. The tooth is asymmetrical with the main cusp situated above the anterior root. It is elongated distally to a talonid. The anterior crest runs linguad and the posterior one runs parallel to the length of the tooth. The p1 has not fully erupted. No cingulids are present.

The posterior root of the p2 is stronger — similar to what can be seen in the p1. The same is true for its morphology: it is asymmetrical with the main cusp situated above the anterior root, posteriorly elongated to a talonid and possesses an anterior crest running linguad and a posterior one running parallel to the length of the tooth. No cingulids are present.

The alveoli of the dp3 are equally developed.

The anterior accessory cusp of the dp4 is high. The talonid shows a cutting blade, that is going upwards distally.

The main cusp is broken. Due to this breakage a judgement concerning wear facets is not possible. No cingulids are present.

The m1 shows a distinct talonid as does the m2. No cingulids are present. There is a slicing facet present on the m1.

The size falls into the range of *Hyaenodon filholi* except for the m1 and the m2, which are inbetween *Hyaenodon filholi* and *exiguus* (Lange-Badré, 1979).

	p1	dp2	dp4	m1	dp3 (estimated from the alveoli)	m2 (estimated from the alveoli)
length	5.4 mm	5.7 mm	6.7 mm	6.6 mm	7.6 mm	7.8 mm
width	2.8 mm	2.2 mm	2.6 mm	3.3 mm		

	under m1	under dp4
depth of the mandible	10.2 mm	10.0 mm

The specimen **M 2352** (Fig. 6/4 A) is determined as *Hyaenodon filholi* and comes from Caylux (France; Oligocene).

The specimen is a left, fragmented mandible. The ramus holds the cavity with the germ of the c inf., the erupting p2, the alveoli of the dp3 and the cavity of the germ of the p3, the dp4 (distally broken) and the cavity for the germ of the p4. The symphysis reaches up to the dp3.

The p2 is strongly widened lingually. The tooth is asymmetrical and shows a lingual cingulid.

The dp4 possesses an anterior accessory cusp that is lower than the main cusp. The tips of the anterior accessory cusp and the main cusp are dot-like flattened. A slicing facet is present as well. A lingual cingulid is present. On the mesial basis a short buccal cingulid is present. As the distal part of the dp4 broke away, nothing can be said concerning the talonid.

The estimated length of the erupting p2 (judging from the alveoli) is 6.6 mm.

The jaw depth under the dp4 is 11.9 mm.

The size falls into the range of *Hyaenodon filholi* (Lange-Badré, 1979).

The specimen **M 84866** (Fig. 6/4 B) is determined as *Hyaenodon filholi* and comes from Caylux (France; Oligocene).

The specimen is a juvenile, right mandible fragment. It holds the alveoli of the p1, the erupting p2, the dp3 and the dp4. The symphysis reaches up to the dp3. Mental foramina are present under the posterior alveolus of the p1 and the anterior root of the dp3. Just the tip of the erupting p2 is visible.

The specimen is broken in the mesial area at the anterior alveolus of the p1, but there were probably two alveoli for this tooth.

The dp3 is broken. The main cusp is completely broken away. No anterior accessory cusp is present in the anterior fragment. The talonid shows a cuspid, that merges into a cingulid. A lingual cingulid is present.

The dp4 shows a weaker cingulid compared to that on the dp3, but it is well-developed on the talonid. The anterior accessory cusp is lower than the main cusp, but higher than the talonid. On the talonid there is a crest build by a cuspid. This cuspid is distally broken. Therefore, more details about the morphology remain unknown.

The size falls into the range of *Hyaenodon filholi* (Lange-Badré, 1979).

	dp3	dp4
length	6.3 mm	6.5 mm
width	2.4 mm (estimated)	2.7 mm
jaw depth		11.7 mm

The specimen **M 84867** (re-registered from M 2352; Fig. 6/4 C) is determined as *Hyaenodon filholi* and comes from Caylux (France; Oligocene).

The specimen is a juvenile, right mandible fragment. It holds the dp4, the m1 and the m2 in crypt. It is broken lingually and thus gives sight on the germ of the m2. The mandible is very slim, delicate and small (and very young too). There is no sign of the symphysis or a mental foramen.

The anterior accessory cusp on the dp4 is lower than the main cusp, but higher than the talonid. On the talonid a cuspid builds a blade that turns into the cingulid. This cingulid runs around the talonid lingually, but ends abruptly. The tips are not dot-like flattened. A slicing facet is present, although weak.

The m1 shows no cingulids. The talonid is distinct. This makes dp4 and m1 very similar to each other. Just the outline of the cutting blade differs. The blade is rounded in the dp4 and very angular in the m1. The m1 shows a slight slicing facet.

The size falls into the range of *Hyaenodon filholi* (Lange-Badré, 1979).

	dp4	m1
length	6.6 mm	6.3 mm
width	2.7 mm	3.5 mm
jaw depth	8.4 mm	8.2 mm

The specimen **NMHW 2009z0084/0003** (Fig. 6/4 D) is determined as *Hyaenodon filholi* and comes from Mouillac (France, Oligocene?).

The specimen is a fragment of a juvenile, right mandible. It holds the dp4, the alveoli of the m1 and the erupting m2. There is no sign of the symphysis or a mental foramen. The processi are broken, but the shallow fossa masseterica can be seen. The mandible itself is very slim and delicate.

The dp4 possesses a high anterior accessory cusp, nearly as high as the main cusp and much higher than the talonid. The anterior accessory cusp is detached from the main cusp, building a rounded (not angular) blade with the main cusp. The main cusp is broken. The talonid is detached from the main cusp. There is a crest present on the talonid that changes into a cingulid running lingually around the talonid. By bordering the talonid this cingulid becomes crenulated and reaches up to the main cusp on the lingual side. Thus, a shallow basin-like structure can be observed on the talonid between the crest and the cingulid. There is no buccal cingulid present.

The m1 was a very short tooth, judging from the alveoli.

As the m2 is just about starting the eruption, nothing can be stated about it. The x-ray (Fig. 7/3 D) shows that it possesses a short, but distinct talonid.

The size falls into the range of the species *Hyaenodon filholi* (Lange-Badré, 1979).

	dp4	m1 (estimated)
length	7.4 mm	6.3 mm
width	2.8 mm	

6.1.3 *Hyaenodon rossignoli*

The specimen **Qu 8356** (Fig. 6/5 A) is determined as *Hyaenodon rossignoli*. The specimen comes from the "Quercy" (late Eocene/Oligocene).

The specimen is an adult left mandible with the alveoli of the p2, the p3, the p4 and the m1-m3. The processi are broken. The jaw is rather robust and brachyrhynch. The symphysis reaches up to the p3. A mental foramen is present under the posterior root of the p3. There are no diastemata present and a slight overlap of the teeth is observed. The p2 was rotated (the alveoli are rotated). The p4 seems to have not completed eruption.

The p3 shows a buccal cingulid and a strong lingual cingulid. There is no anterior accessory cusp. The posterior accessory cusp is rounded, globular and compressed to the main cusp.

The p4 lacks as well an anterior accessory cusp. Instead there is a mesial, buccal swelling of the crest. The posterior accessory cusp is very short and cutting. A buccal cingulid is present.

The m1 is very small. The tip of the protoconid is broken. A buccal cingulid is present. The blade is rising steeply upwards distad.

The m2 shows a distinct talonid. The tip of the protoconid is broken. It shows as well a steep blade and a buccal cingulid.

The m3 possesses no clear relict of the talonid as does Mo 22 (described below), but instead a crenulation of a small tubercle is present. A buccal cingulid is observed.

The specimen belongs to a small sized species. It falls into the size range of *Hyaenodon rossignoli*, which is inbetween *Hyaenodon filholi* and *exiguus* (Lange-Badré, 1979). However, it is easily distinguished from the other two species. The latter two are longirhynch. *Hyaenodon rossignoli* is robust, brachyrhynch, shows strong cingulids, a low globular talonid on the p3 and a short cutting crest on the p4. All these features are observed in this specimen.

	p3	p4	m1	m2	m3
length	9.0 mm	9.0 mm	6.4 mm	8.4 mm	12.5 mm
width	4.0 mm	4.4 mm	3.8 mm	4.2 mm	4.2 mm
jaw depth			14.0 mm		

The specimen **Mo 22** (Fig. 6/5 B) is determined as *Hyaenodon rossignoli*. The specimen comes from the "Quercy" (late Eocene/Oligocene).

The specimen is a juvenile, left mandible with the broken dc, the alveolus of the p1, the alveoli of the p2, the dp3, the dp4, the m1, the m2 and the erupting m3 (protoconid visible). The mandible is small, but still robust. The symphysis reaches up to the dp3. Mental foramina are present under the p1 and the dp3. There are no diastemata present.

There is just one alveolus for the p1 present. Judging from the alveoli the p2 was rotated.

The dp3 is small and short. It is remarkable, that it is much shorter than the dp4. Its main cusp is broken. It shows a posterior accessory cusp with a crest running linguad. There is no anterior accessory cusp. A buccal cingulid is present.

The dp4 possesses a high anterior accessory cusp. The posterior accessory cusp builds a cutting blade that goes upwards distally. A buccal cingulid is present.

The m1 shows a distinct talonid and a buccal cingulid.

The m2 shows the same: a distinct talonid and a buccal cingulid. There is also a mesial, lingual parastylid present.

The m3 is erupting. The protoconid and the distal part of this tooth can be already examined. The presence of a vestige of the talonid is observed.

Due to preparation and taphonomy, nothing can be stated concerning wear facets.

The size falls into the range of the species *Hyaenodon rossignoli*, although it falls also in the range of the smaller *Hyaenodon filholi* (Lange-Badré, 1979).

Arguments in favour of *Hyaenodon rossignoli* are: only one alveolus for p1 (tendence to fusion), m1 and m2 often show a rudimentary parastylid at the basis of the paracone, m3 shows a rudimentary talonid and the mandible is brachyrhynch.

	p1 (estimated from the alveoli)	p2 (estimated from the alveoli)	dp3	dp4	m1	m2
length	4.4 mm	7.7 mm	4.8 mm	6.0 mm	5.7 mm	8.6 mm
width			2.4 mm	2.8 mm	3.6 mm	4.0 mm

	under dp4	under m1
jaw depth	10.3 mm	10.0 mm

6.1.4 *Hyaenodon brachyrhynchus*

The specimen **Qu 8632** (Fig. 6/5 C) was formerly designated to *H. brachyrhynchus* and this determination is confirmed here. The specimen comes from the "Quercy" (late Eocene/Oligocene).

The specimen is an adult compressed skull with mandibles. It is distorted and fragmented. Due to its preservation teeth can only be observed from their buccal aspect. Most of the teeth overlap with their counter parts in the opposed jaw. The specimen is brachyrhynch and no diastemata are present. On its left side the upper and lower incisors, the upper and lower canines, the P1-P4, the roots of the M1, the p1-m3 and part of the fossa masseterica can be seen. The right side shows the upper and lower incisors, the upper and lower canines, the P1-P3, the M1-M2 (the posterior half of the M2 is broken) and p3-m1.

The P1 and p1 are double-rooted. Both possess two distinct alveoli (for p1 this can be seen in the x-ray, see Fig. 7/1 E).

The P2 and p2 are hook-shaped and high. The p2 is slightly elongated distally.

The P3 and the p3 possess a posterior accessory cusp.

The P4 and the p4 show an anterior and a posterior accessory cusp with the posterior one higher.

The M1 shows a buccal parastyle.

The m3 possesses a column beneath the paraconid on the buccal side. It reaches one third of the crown height.

The buccal cingula are weak on all teeth.

The size falls into the range of the species *Hyaenodon brachyrhynchus* (Lange-Badré, 1979) and other features confirming the designation are: no diastemata, premolars high and short, the P2 is the highest tooth after the canine, P3 with posterior accessory cusp, vestiges of parastylid on the m2 and the m3 with slim column beneath the paraconid reaching two thirds of the crown.

Depth of the mandible under m1 is 17.5 mm.

	P1 sin.	P2 sin.	P3 sin.	P4 sin.	p2 sin.
length	7.2 mm	8.8 mm	11.1 mm	12.1 mm	8.5 mm

	P1 dex.	P2 dex.	P3 dex.	M1 dex.	p3 sin.	m3 sin.
length	7.9 mm	9.3 mm	12.0 mm	12.1 mm	10.5 mm	13.1 mm

6.1.5 *Hyaenodon minor*

The specimen **M 2348** (Fig. 6/6 C) is determined as *Hyaenodon minor* and comes from Caylux (France; Oligocene).

The specimen is a fragment of a symphysis. The symphysis is well fused. The left ramus is preserved with the alveoli of the dp2 and the germ of the p2 visible, the alveolus of the p1, the alveolus of the dc and the alveoli of all incisors. The right ramus is preserved with a fragment of the posterior alveolus and the anterior root of the dp4, the cavity of the germ of the p4, the dp3 with sight on the germ of p3 (bone is broken buccad), the alveoli of the dp2, the alveolus of the p1, the alveolus of the dc, all three alveoli of the incisors and sight on the germ of an incisor. There are mental foramina beneath the left alveolus of the p1 and under the right dp3. The mandible is slim, but rather robust. Diastemata are present between the p1 and the alveoli of the dp2 and between the alveoli of the dp2 and the dp3. The symphysis reaches up to the dp3.

The main cusp of the dp3 is situated in the center of the tooth. This tooth is elongated anteriorly and posteriorly. The dp3 looks buccally very pointed, because the main cusp slopes steeply mesiad and distad. A lingual cingulid is present. A buccal cingulid is not developed. The anterior crest runs linguad. On its basis there is a small cuspid. The lingual cingulum runs around the talonid. A posterior accessory cuspid is present. Its tip is flattened. Distal to this cuspid, another again smaller cuspid is situated on the cingulid.

Determination of fragmented material can be tricky. The only preserved tooth is the dp3. It resembles the dp3 seen in *Hyaenodon exiguus*, but differs in showing three cuspids distal to the main cusp. Diastemata are present, but small — so both an enlarging of the distamata during growth as well as their disappearance with larger erupting permanent teeth could be present in the adult. The size falls into the range of a large individual of *Hyaenodon exiguus* or an individual within the average distribution of *Hyaenodon minor* (Lange-Badré, 1979). Affiliation to *Hyaenodon minor* is favoured, because of the following features: this species shows a single-rooted p1 with a strongly distad flexed alveolus, a small diastem between the p2 and the p3, lingual cingulids well-developed until the talonid and a similar jaw depth. In this case it is considered best to previously assign the specimen to *Hyaenodon minor* with the reservation, that the milk dentition of this species — as is the case with other European species — is not known up to now.

Jaw depth under dp4 is 17.1 mm.

	dp3	dp2 (estimated from the alveoli)
length	10.3 mm	9.5 mm
width	3.5 mm	

The specimen **NMHW 2010/0196/0001** (Fig. 6/6 A) is a left upper jaw fragment holding an erupting C and P1 to M1. It belongs to the same individual as the specimen **NMHW 2010/0196/0002** (Fig. 6/6 B), which is a right upper jaw fragment holding P3 to M2.

They are middle-sized and come from Bach (at Lalbenque, Lot, France, Oligocene?). There is too much bone broken away to combine the two fragments. They were found in one box at the museum. Both are from the same locality, show the same preservation, size, morphology and wear stage. Thus, they are most probable from the same individual and are assigned to the species *Hyaenodon minor.*

The left canine is erupting.

The P1 is double-rooted and possesses two distinct alveoli. The tooth is very low and elongated.

The P2 is hook-shaped and high. The posterior accessory cusp is very small. A lingual and a buccal cingulum are present with the buccal one being weakly developed.

The P3 shows a strong buccal and lingual cingulum. Mesial there is a lingual bulge present. The posterior accessory cusp is compressed to the main cusp. The tooth is disto-lingually widened. The P3 includes with the P4 an angle of 148°.

The P4 shows strong buccal and lingual cingula. The protocone is rounded and is pointing mesially. The cingulum bordering the protocone is crenulated.

The M1 shows a buccal bulge. The buccal and lingual cingula are weaker than the ones on the premolars. The blade shows a slicing facet. A mesial lingual conical cuspid is present, but small.

The M2 possesses a very high paraconid. The tooth has not completed eruption and is not yet in position. There is no lingual or buccal cingulum present. Mesial there is a tiny bulge on the lingual side present. A weak slicing facet is present.

The size falls into the range of *Hyaenodon minor* (Lange-Badré, 1979) and other distinctive features of this species are: short and double-rooted P1, posterior cuspid on the P2, P3 and P4 angulation of about 150°, very strong lingual cingulum with small tubercles on the P3 and the P4, unreduced protocone on the P4 and conical cuspid on the basis of the M1 below the paracone.

	P1 sin.	P2 sin.	P3 sin.	P3 dex.	P4 sin.	P4 dex.	M1 sin.	M1 dex.	M2 dex.
length	8.7 mm	9.7 mm	10.7 mm	11.5 mm	10.1 mm	10.3 mm	9.1 mm	9.9 mm	11.9 mm
width	3.5 mm	4.5 mm	5.7 mm	5.7 mm	8.1 mm	8.2 mm	6.6 mm	6.8 mm	7.1 mm

6.1.6 *Hyaenodon horridus*

The specimen **M 5722** (Fig. 6/7 A-B) was determined as *Hyaenodon horridus* and originates from the White River Formation in Nebraska (USA).

The specimen is a partly fragmented skull with a partly fragmented mandible. The individual was still a juvenile. The upper and lower permanent canines are about to erupt. The right side of the skull holds the I1, the broken I2 and I3, the DC, the broken P1, the P2, the P3, the P4 and the M1. The left side holds the broken I1-3, the DC, the broken P1, the broken P4, the M1 and the M2. The nasals are arrow-shaped. Both germs of the permanent canines are erupting on the left and right side.

The P2 is high and hook-shaped. It is conical.

The P3 possesses a strongly crenulated cingulum. It is just weakly rotated. The P3 and the P4 include an angle of 157°. A buccual cingulum is just present under the posterior accessory cusp. This cusp is compressed to the main cusp. There is no anterior accessory cusp.

The P4 shows a reduced protocone. The protocone is rounded and bound by a strong lingual cingulum with tubercles. There is no anterior accessory cusp. A posterior accessory cusp is present.

The M1 is still primitive. Despite of wear, the separation of the para- and metacone is clear. The tooth shows a large slicing facet.

The M2 has a fully fused para- and metacone. A weak slicing facet is present.

The left ramus of the mandible holds the broken i, the dc, the broken p1 (posterior root and another smaller fragment), the p2, the anterior part of the p3, the m1, the m2 and the m3. The right ramus holds the fragments of the i, the dc, the p4, the m1 and the m2. The symphysis is fused. A mental foramen is present under the anterior root of the p3. The permanent canines are erupting.

The p2 is high. The tooth is hook-shaped and shows a lingual cingulid. The talonid possesses a cuspid.

The p4 shows no anterior accessory cusp and no cingulids. The posterior accessory cusp is a horizontally orientated blade (from a buccal view).

The m1 shows a distinct talonid. The slicing facet is clear.

The m2 shows also a distinct talonid. A slicing facet is present.

The m3 possesses no vestige of a talonid. A slight slicing facet is present. The mesial buccal parastylid is very high.

Jaw depth under m1: 34.1 mm.

	p2 sin.	m1 sin.	m2 sin.	m3 sin.
length	17.1 mm	13.4 mm	20.0 mm	25.8 mm
width	8.1 mm	8.5 mm	10.3 mm	10.4 mm

	p4 dex.	m1 dex.	m2 dex.
length	19.8 mm	14.9 mm	22.3 mm
width	10.0 mm	7.8 mm	7.8 mm

	P2 dex.	P3 dex.	P4 dex.	M1 dex.
length	25.7 mm	19.2 mm	17.9 mm	19.5 mm
width	10.0 mm	10.3 mm	15.5 mm	11.2 mm

	M1 sin.	M2 sin.
length	19.2 mm	30.2 mm
width	11.5 mm	13.7 mm

6.2 New results concerning the milk dentition

The focus on the milk dentition revealed new insights during the study of the above described juvenile specimens.

There is no rotation in the juvenile dentition of the upper jaw. The DP3 is observed to be not rotated (e.g. in Qu 17662, PD 187). The tooth row was in line in material belonging to species that are known to show a rotated P3. Thus, this rotation can only be recognised in adults. This fact unravels questions: What function does a rotated P3 fulfill? Or is the bone growth not sufficient and thus gives the tooth in adults its angled position? An ontogenetic effect is the assumed cause: the DP3 shows a slicing blade that is not present in the successor tooth, the P3; furthermore, the adult individual possesses the molars with their longer slicing blades at its disposal.

The reasons are not clear. A possible cause is that an unrotated DP3 elongates the row of cutting crests and blades in a smaller juvenile. Although the growth from juvenile to adult can be considered as rather low — below 30% (see Chapter 7) — the additional blade of the M2 contributes largely to the row of blades in the adult individual. This lack could be compensated by the blade of the DP3 in the juvenile.

The three smallest species of European *Hyaenodon* are from smallest to largest: *Hyaenodon filholi, rossignoli* and *exiguus*. Although *Hyaenodon rossignoli* is inbetween the range of the other two species, it is clearly set apart. Firstly, its occurrence is known from the late Eocene, in contrast to the other two Oligocene species. Secondly, it is a brachyrhynch form with a robust mandible, no diastemata, that result in overlapping teeth and a rotated p2, with in general more robust teeth and an m3 showing a primitive feature (a vestige of the talonid). Both *Hyaenodon filholi* and *exiguus* possess slim mandibles with the smaller one having really delicate rami. Besides, they are longirhynch, showing distemata and possess slender teeth. For more details concerning the species see Chapter 5.

However, the size range of *Hyaenodon filholi* and *Hyaenodon exiguus* overlaps. The stereotyped dentition makes it hard to separate them from each other, if size doesn´t give a clue. Thus, it was tested, if *Hyaenodon filholi* and *exiguus* are just female and male individuals of the same species. A sexual dimorphism of 30% is known in the American taxa (*Hyaenodon horridus*; Mellett, 1977). Therefore, the measurements of the smallest *Hyaenodon filholi* was compared to the measurements of the largest *Hyaenodon exiguus* (data taken from Lange-Badré, 1979).

The results are listed in the Table 6/1.

Tooth position	Length in smallest *H. filholi*	Length in largest *H. exiguus*	Procent of divergence
p2	7.0 mm	10.0 mm	30.0%
p3	7.7 mm	10.2 mm	24.5%
p4	6.6 mm	11.3 mm	41.6%
m1	5.2 mm	7.3 mm	28.7%
m2	5.9 mm	9.1 mm	35.2%
m3	8.1 mm	13.4 mm	39.5%
P2	7.5 mm	10.2 mm	26.4%
P3	7.4 mm	11.7 mm	36.7%
P4	7.0 mm	10.2 mm	31.4%
M1	6.4 mm	9.0 mm	28.8%
M2	7.9 mm	14.3 mm	44.7%

Table 6/1: Dental measurements of *Hyaenodon filholi* and *H. exiguus* reveal, that they are in fact two separate species and not male and female individuals of the same species. A value above 30% is commonly assumed to exceed what would be expected from sexual dimorphism. Data was taken from Lange-Badré (1979).

It is obvious that *Hyaenodon filholi* and *Hyaenodon exiguus* can not be summarized in one species. The size differences are too great. On the other hand, it is explicable why species determination is difficult: Some of the scores do not greatly exceed the marking border of 30%.

With the maintenance of two similar species, something else was recognised: By determining the juvenile specimens on the basis of size, divergence was found. Surprisingly, differences in the morphology of the milk dentition (dp3, dp4; DP3, DP4) can be observed in the small sized European taxa. This includes also *Hyaenodon rossignoli*. These differences shall be discussed in detail in the following. Select specimens are figured as drawings in Fig. 6/9 and Fig. 6/10. General description of all specimens is given above.

Thus, previously undetermined specimens can be referred now to their respective species. Due to the frequently fragmentary state of ontogentical young specimens and due to a lack of knowledge of the morphology of the deciduous dentition and its variation, such specimens could only be referred to *Hyaenodon* sp. without doubt. The juvenile material described in Bastl et al. (2011) is now determined on species level and listed in the respective paragraph.

Hyaenodon rossignoli

Material: Qu 8356 (adult), NMHW 2009z0084/0002 (juvenile), Mo 22 (juvenile);

The most striking feature is the extremely short dp3 (dp3 in Mo 22, short alveoli in NMHW 2009z0084/0002). This tooth is very different from other observed dp3. It is shorter than the dp4 and there is no anterior accessory cusp present. On its distal end, a short talonid is showing a cuspid building a crest that runs linguad.

The dp4 is not unusual: the anterior accessory cusp is inbetween the height of the main cusp and the talonid. The talonid shows a short blade. In general, the dp4 is similar to the m1 and to the dp4 in *Hyaenodon filholi*. The buccal cingulid is well-developed and like that in the permanent dentition (Qu 8356).

NMHW 2009z0084/0002 (described in Bastl et al., 2011) can now be assigned to *Hyaenodon rossignoli*. There is just one alveolus for the p1, the teeth are overlapping and the mandible is more robust (compared to other small sized species). Unfortunately no juvenile, cranial material for this species was available so far.

The species *Hyaenodon exiguus* and *filholi*
Upper jaw
>   Material for *filholi*: Qu 8664;
>   Material for *exiguus*: Qu 17662, PD 187;

In the DP3 the following differences are observed: in *Hyaenodon filholi* a distinct anterior accessory cusp is present. This cusp is small in *H. exiguus* (very small in PD 187; not present in Qu 17662). In the former species the DP3 possesses a distal cutting blade preceeded by one accessory cusp. This accessory cusp is clearly detached from the main cusp. A blade-like structure is present in the distal part of the tooth. A buccal cingulum is present. The lingual root is situated in the middle of the tooth and somehow reminds of the protocone in the P4 due its strong lingual projection. The DP3 in *Hyaenodon exiguus* is narrower. The distal part shows two clear cuspids. The most distal part is less blade-like. No buccal cingulum is present. The lingual root is situated more distally and is less pronounced in the sense of projecting linguad.

The DP4 in *Hyaenodon filholi* shows the two distinct mesial cusps. The anterior one is clearly lower. The distal blade is low in relation to these cusps. The blade itself is long. A buccal cingulum is present. In *Hyaenodon exiguus* the two cusps are subequal in height, the blade is higher positioned and relatively shorter. The buccal cingulum is weak or not developed.

The M1 shows on its mesial, lingual root a clear crest in *Hyaenodon exiguus*.

Lower jaw
>   Material for *filholi*: M 84867, M 84866, M 2352, MNHN 1875-931, PD 510,
NMHW 2009z0082/0001, NMHW 2009z0082/0002, NMHW 2009z0083/0001,
NMHW 2009z0084/0003, BSPG 1879 XV 18a;
>   Material for *exiguus*: M 2353, M 4498, NMHW 2009z0084/0001;

In *H. filholi* the dp3 can possess an anterior accessory cusp (PD 510, BSPG 1879 XV 18a), but it can also be not developed (M 84866). A posterior accessory cusp that leads into a crenulated cingulid is present. The tooth is lingually broadened in its distal part. A lingual cingulid is ususally present. The dp3 in *Hyaenodon exiguus* shows a globular anterior accessory cusp and a globular posterior accessory cusp. Additionally, there is a smaller, second posterior accessory cuspid. The tooth is distally more elongated. The length of the dp3 is approximately the same as in the dp4 for both species (with the dp3 being subequal or longer).

The dp4 shows an anterior accessory cusp that is inbetween the height of the main cusp and the talonid in *Hyaenodon filholi* (with the only exception in PD 510 with a low anterior accessory cusp). On the talonid a blade is present, either shaped like a true cutting blade or more crest-like and build by a cuspid. This blade is merging into a lingual cingulid. The cingulid is present over the whole lingual side, but is best developed around the talonid. There it forms a lingual facing shallow basin-like structure, that is not too apparent and can be developed in varying degrees. The talonid is shortened. In *Hyaenodon exiguus* the anterior accessory cusp is low, subequal with the talonid in height. The talonid shows two cuspids. This is a significant feature. The talonid tends to be more elongated. There is no lingual cingulid present or if — it is weak. The tooth in general is broader.

The specimens NMHW 2009z0081/0001, NMHW 2009z0082/0002 and NMHW 2009z0083/0001 (described in Bastl et al., 2011) are assigned to *Hyaenodon filholi* due to their cutting crest on the talonid of the dp4.

NMHW 2009z0084/0001 shows the wavy outline of the talonid on the dp4 and two clear cuspids on the talonid and is identified now as *Hyaenodon exiguus*.

These new results give insight into the variation in the milk dentition for the first time: development of cingulids and cingulums are in general variable within *Hyaenodon* (Lange-Badré, 1979). This is also seen in the milk dentition in the small sized species discussed herein. My observations herein lead to the following: in the DP3 in *Hyaenodon exiguus* the anterior accessory cuspid shows some variation — from not present to weakly developed. There is variation in the development of the anterior accessory cups on the dp3 in *H. filholi*: BSPG 1879 XV 18a (described in Bastl et al., 2011) and PD 510 show a distinct anterior accessory cups on the dp3, whereas there is none in M 84866. In *Hyaenodon filholi* the talonid on the dp4 always shows a cutting crest or blade, but the associated cingulid and its development concerning a shallow basin is variable.

Table 6/2 shows a summary of the main separative features. Figures 6/11 and 6/12 (both follow in the text below) are comprehended as visual summary, showing a scheme of the morphology in the small sized species discussed herein.

tooth position	H. rossignoli	H. filholi	H. exiguus
dp3	· extreme short (much shorter than the dp4) · no anterior accessory cusp(id) · two posterior accessory cuspids	· subequal or longer than the dp4 · variable anterior accessory cuspid · one posterior accessory cuspid leading into a crenulated cingulid	· subequal or longer than the dp4 · globular anterior accessory cusp · two globular posterior accessory cuspids
dp4	· buccal cingulid · talonid with short cutting crest	· lingual cingulid · anterior cusp usually higher than talonid · talonid with cutting crest build by cuspid and variable "basin"	· weak lingual cingulid · anterior cusp subequal in height with talonid · two posterior accessory cuspids
DP3	?	· well-developed anterior cuspid · posterior one cusp followed by blade-like structure · well-develeped buccal cingulum · lingual root projecting strongly linguad	· variable anterior cuspid · posterior two cusps · no or weak buccal cingulum · lingual root weak, more distad placed and not far projecting
DP4	?	· blade much lower than the main cusps · blade relatively longer · buccal cingulum strongly developed · cusps of different height	· blade high, approaching cusps · blade relatively shorter · no or weak buccal cingulum · cusps subequal in height

Tab. 6/2: Summary of the main separative features in the milk dentition of small sized European species of *Hyaenodon*.

Fig. 6/11: Mapped summary of the differences within the milk dentition (DP3 and DP4 in lingual (above) and occlusal (below) view) of the small sized European species *Hyaenodon filholi* (left) and *Hyaenodon exiguus* (right). Note the anterior cusp and the lingually placed root in the DP3 and the low placed blade in the DP4 in the former species.
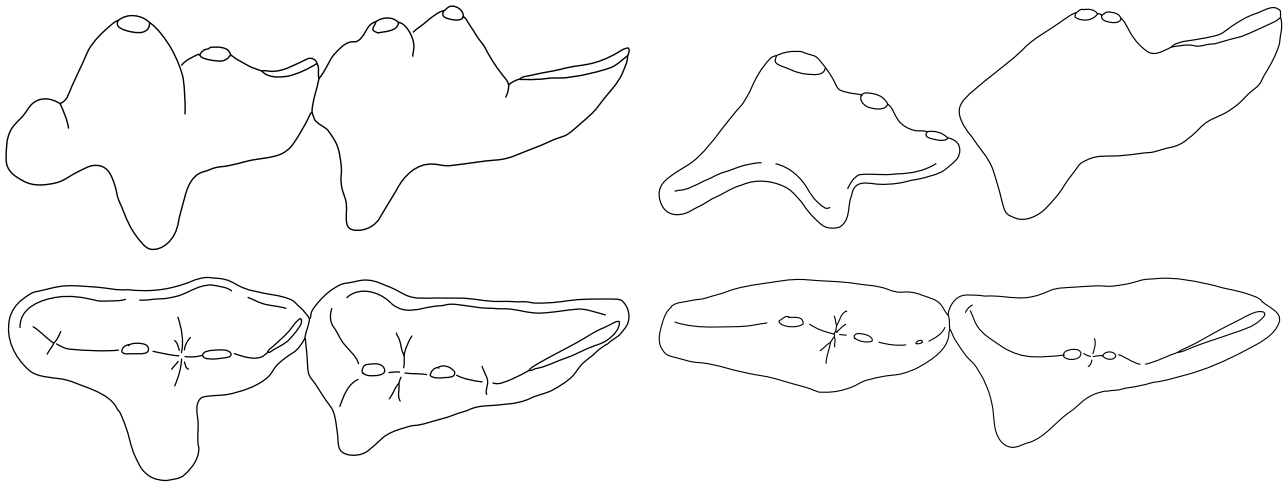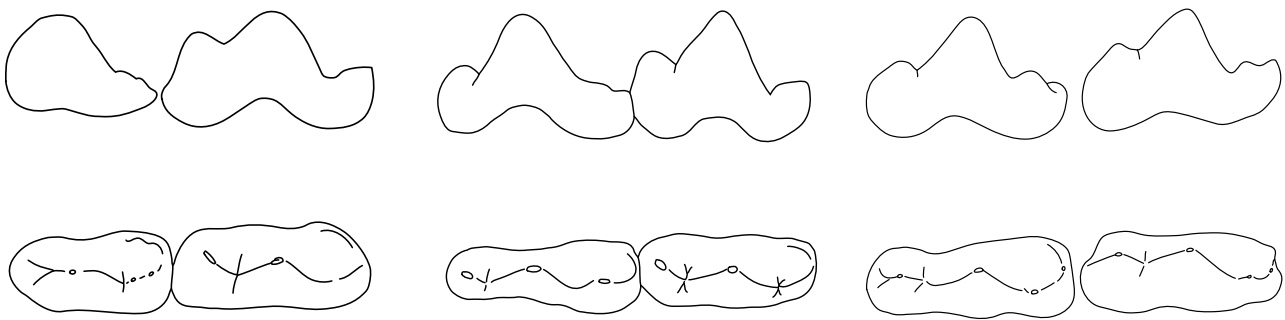

Fig. 6/12: Mapped summary of the differences within the milk dentition (dp3 and dp4 in buccal (above) and occlusal (below) view) of the small sized European species *Hyaenodon rossignoli* (left), *Hyaenodon filholi* (middle) and *Hyaenodon exiguus* (right). Note the differences in the anterior portion of the dp3 and the talonid on the dp4.

6.3 Comparison to the North American and Asian taxa

Not much was known about the milk dentition in *Hyaenodon*. Especially the Asian taxa are poorly known. Concerning the dp4 the following can now be stated: The anterior accessory cusp is in between the height of the main cusp and the talonid. The talonid shows a blade. This is true for large North American taxa (*Hyaenodon horridus*: e.g. AMNH 1009, AMNH 39439, FAM 75725), small North American taxa (*Hyaenodon mustelinus*; e.g. YPM PU 13675) and small Asian taxa (*Hyaenodon* sp.). Juvenile Asian material is about to be worked on (pers. comm., Tsubamoto Takehisa). Figure 6/8 A-B (North American material) and 7/5 A-D (Asian material) show the morphology of the milk dentition in select non-European specimens. Thus, the blade-like talonid on the dp4 is a shared, general feature. The talonid with the cuspids can be seen as European development, that is observed in *Hyaenodon exiguus* and another European species *Hyaenodon minor* (M 2348). It should be noted that the dp4 in GMM A5.103 (*Hyaenodon* cf. *brachyrhynchus*, large sized species; figured and described in Bastl et al., 2011) shows a talonid with one globular cuspid. Concerning the DP3 the strongly linguad projecting root is observed too in *Hyaenodon horridus* (AMNH 39439; Fig. 6/8 A). The tooth is strongly worn, but the presence of two posterior accessory cusps seems probable. There is no anterior accessory cusp. This conforms with the morphology of *Hyaenodon filholi*. The dp3 in the same specimen shows no anterior accessory cusp, only a crest running down from the main cusp and then linguad, and no well-developed posterior cusp (maybe a small cuspid instead) and is in general subequal in length to the dp4. Both, dp3 and dp4 possess a lingual cingulid. The dp4 is — as mentioned above — characterised by its shortened talonid and the cutting crest. The DP4 shows a low cutting blade, an anterior root projecting far linguad (as in the DP3, just more anteriorly situated) and main cusps of different height. This again conforms the morphology of *Hyaenodon filholi*, except the fact, that in *Hyaenodon horridus* the anterior cusp on the DP4 is the clearly higher one.

Concluding from these comparisons the morphology of the milk dentition seen in *Hyaenodon filholi* is the general state and the shared condition with Asian taxa (for dp4) and North American taxa (dp3, dp4, DP3, DP4). Even though the compared *Hyaenodon horridus* is a large sized species and the European material belongs to rather small taxa. Therefore, the assumption of Lange-Badré (1979) that *Hyaenodon filholi* was a new Oligocene immigrant from Asia is emphasized here. Keeping in mind that a similar species — especially in size — *H. exiguus* was prevalent in Europe at that time too, the immigration theory is further pushed. However, according to BiochroM´97 (1997) all Oligocene species in Europe (except for the surviving *Hyaenodon brachyrhynchus* and *gervaisi*) are immigrants from Asia. Milk tooth morphology is a phylogenetic character (Salles, 1992; Guanfang and Schmidt-Kittler, 1983). The strongly differing milk tooth morphology is a strong indication for a different picture: the asiatic forms most probably did not give descent to all the European Oligocene species. Based on these facts it is assumed, that *Hyaenodon exiguus* evolved in Europe and is more distantly related to *Hyaenodon filholi*. Furthermore, the survival of a European lineage is evidenced.
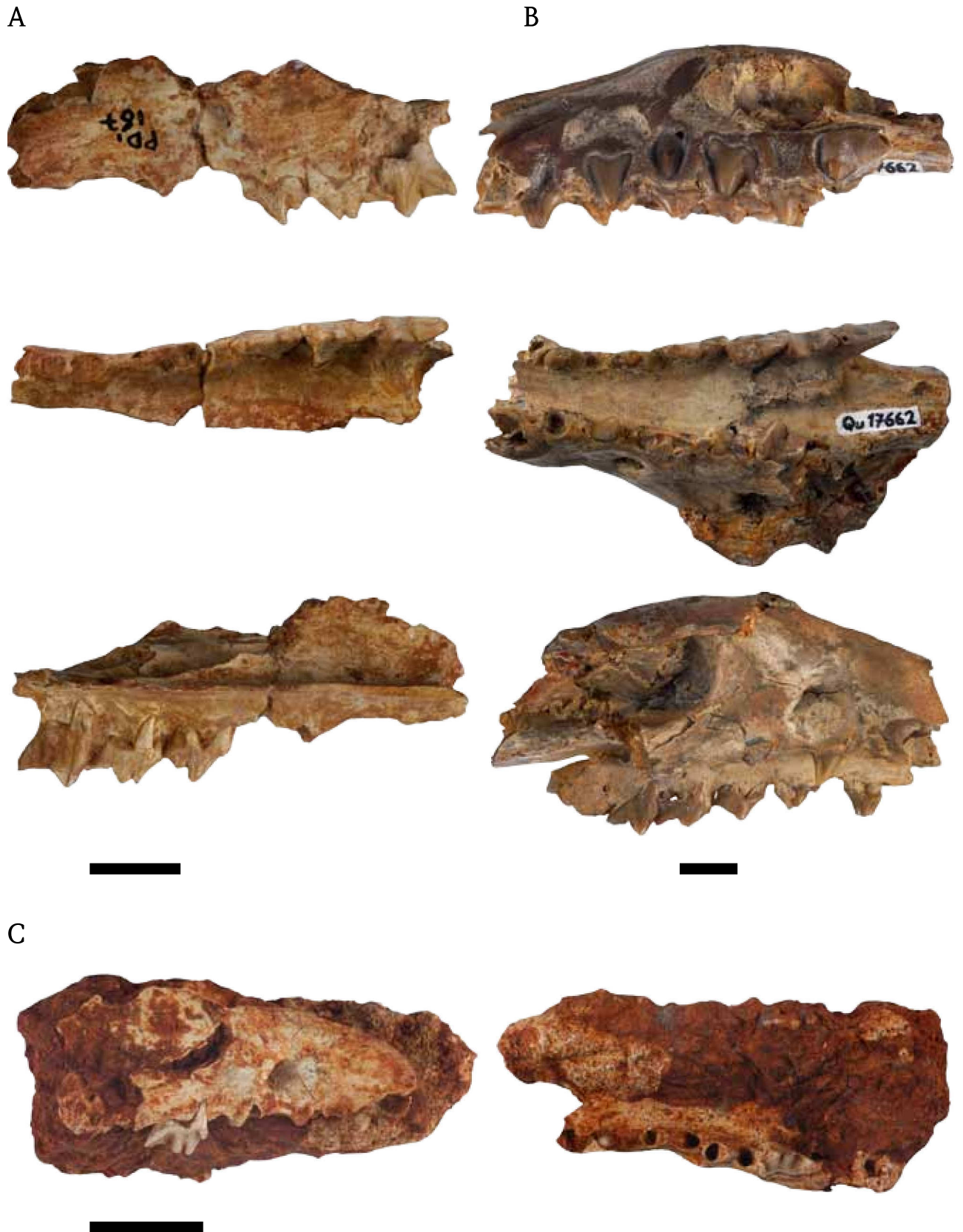
Fig. 6/1: Photos of the described cranial material of *Hyaenodon exiguus*. Bar equals 1 cm. **A**, buccal (upper), occlusal (middle) and lingual (lower) view of PD 187: upper jaw with the DP3, DP4 and the M1; **B**, buccal (upper), lingual (middle) and occlusal (lower) view of Qu 17662: permanent dentition in crypt, presence of the DP3, DP4 and the M1; **C**, buccal (left) and occlusal (right) view of NMHW 2010/0196/0003: the P1 and the DP4 are preserved, note the presence of the alveoli of the M1.

Fig. 6/2: Photos of the described mandibular material of *Hyaenodon exiguus* in buccal (left), occlusal (middle) and lingual (right) view. Bar equals 1cm. **A**, PD 487: germs of the p3 and p4; **B**, M 4498: symphysis with the p2 and the dp4; **C**, M2353: mandible with the p1 and the dp3, dp4 and the m1; **D**, M 2353a: mandible with the dp3 and the dp4; Note the talonid on the dp4.

Fig. 6/3: Photos of the described material of *Hyaenodon filholi* in buccal (upper), occlusal (middle) and lingual (lower) view if not stated differently. Bar equals 1 cm. **A,** PD 510: mandible with juvenile (dp3, dp4 and m1) and permanent dentition in crypt; **B,** MNHN 1875-931: mandible with the p1, p2, dp4, m1 and the erupting m2; B, M 2352; **C1,** Qu 8664 juvenile skull, left side viewed from buccal (upper left), occlusal (lower) and right side viewed from buccal (upper right); **C2,** same specimen as in **C1,** detail of the tooth row from the P1, P2, DP3, DP4 to the M1.
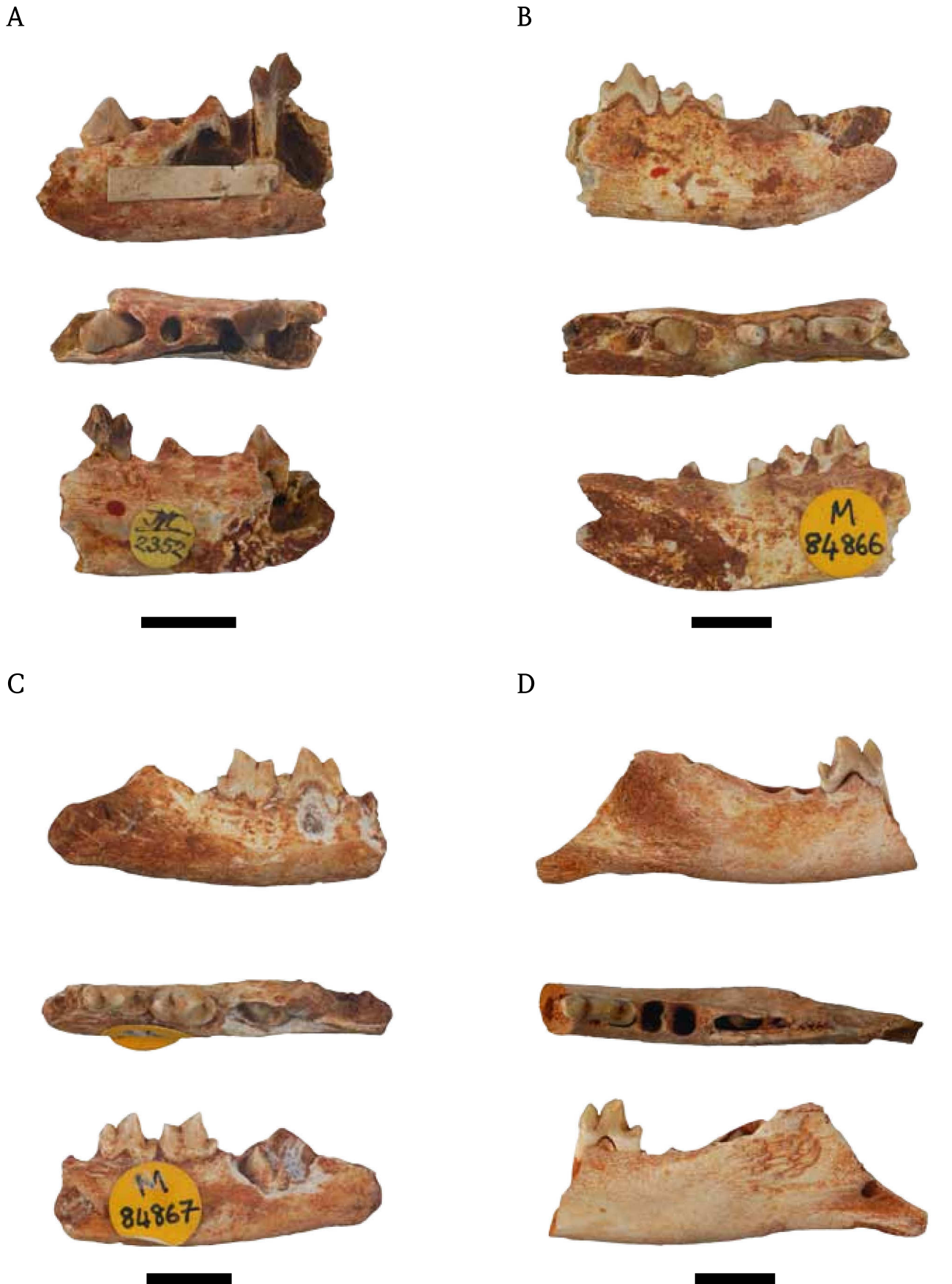
Fig. 6/4: Photos of the described material of *Hyaenodon filholi* in buccal (upper), occlusal (middle) and lingual (lower) view. Bar equals 5 mm. **A**, M 2352: p2 erupting, dp4 fragmented; **B**, M 84866: p2 erupting, dp3 fragmented, dp4 present; **C**, M 84867: mandible with the dp4-m1 and the m2 in crypt; **D**, NMHW 2009z0084/0003: mandible with the dp4 and the m2 in crypt.

Fig. 6/5: Photos of material described above attributed to different species of *Hyaenodon* in buccal (upper), occlusal (middle) and lingual (lower) view if not stated differently. A, *H. rossignoli*, Qu 8356: mandible with p2-m3;
B, *H. rossignoli*, Mo 22: juvenile mandible with the dp3, dp4, m1, m2 and m3 in crypt; C, *H. brachyrhynchus*, Qu 8632, crushed skull with lower jaws viewed from the left (left) and the right (right).
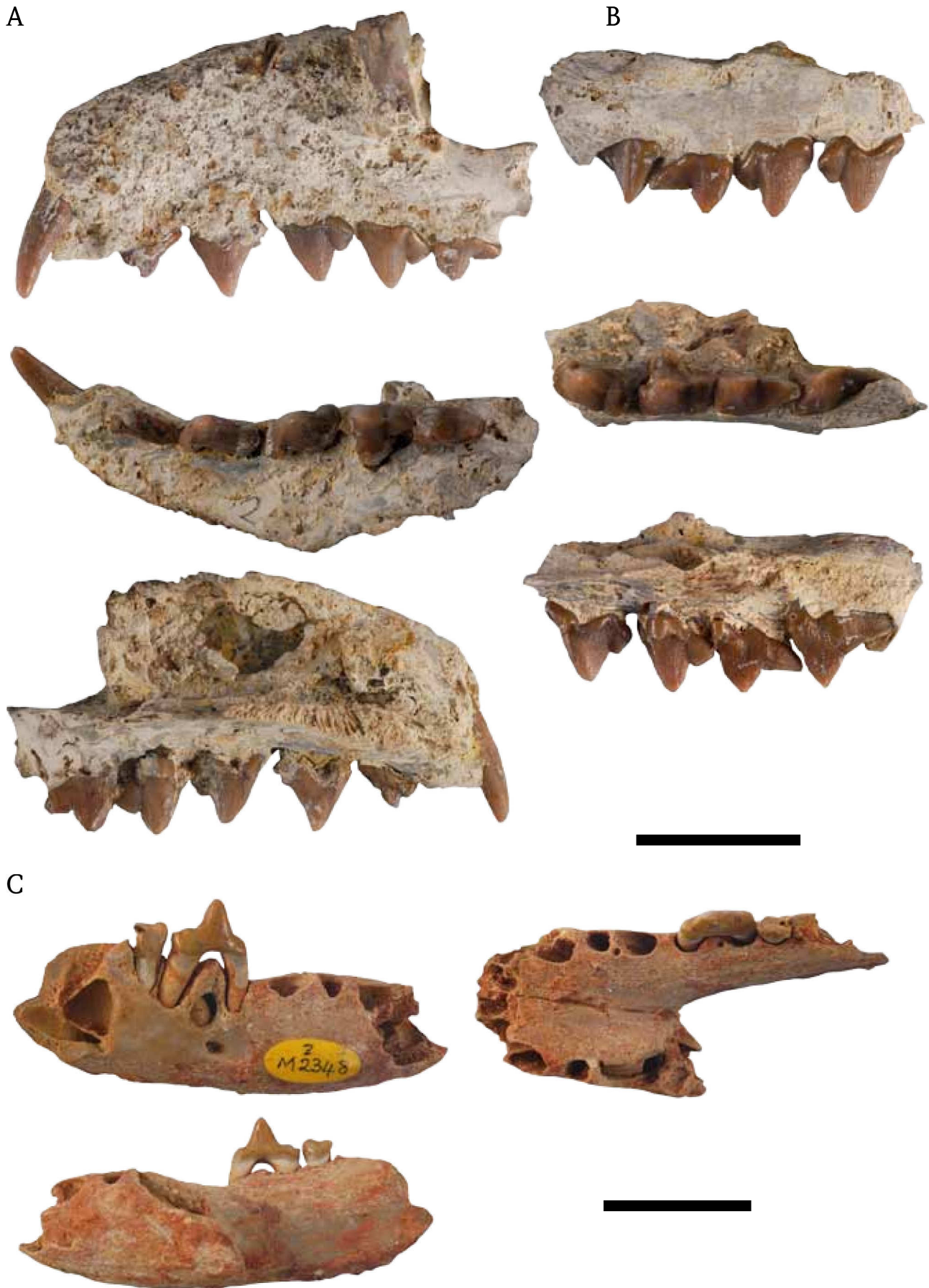
Fig. 6/6: Photos of material described above attributed *Hyaenodon minor* in buccal (above), occlusal (middle) and lingual (lower) view, if not stated differently. Bar equals 1 cm. **A**, NMHW 2010/0196/0001: upper jaw with erupting C and the P1-M1; **B**, NMHW 2010/0196/0002: upper jaw with the P3-M2 (A and B are from the same individual; **C**, M 2348: buccal (upper left, occlusal (upper right) and lingual (lower left) view, symphysis with the dp3.

Fig. 6/7: Fragmented upper and lower jaws (M 5722) of the Amercian taxon *Hyaenodon horridus* from the White River Formation (Nebraska, USA). Right side in buccal view (upper), occlusal view (middle) and left side in buccal view (lower). Bar equals 1 cm. **A**, skull; **B**, mandible.

A

M1
DP4
DP3

B

m2
dp3   dp4

dp3
dp4
m1
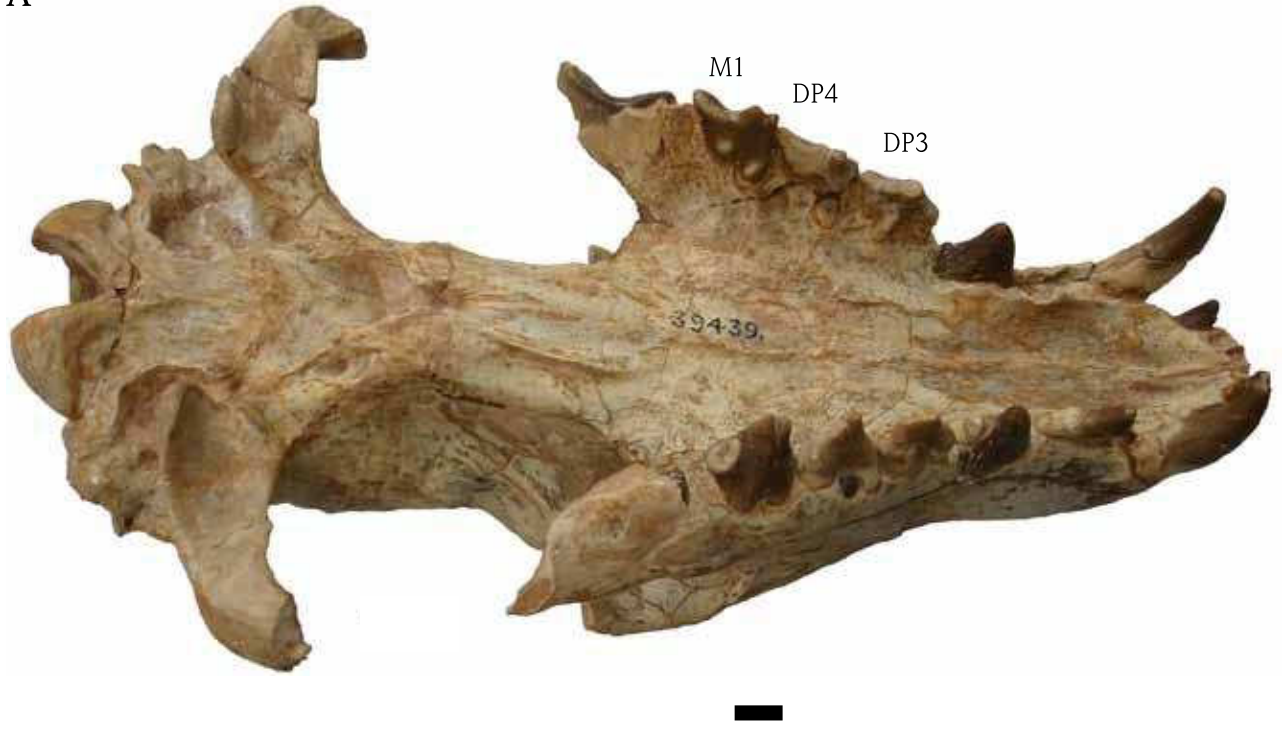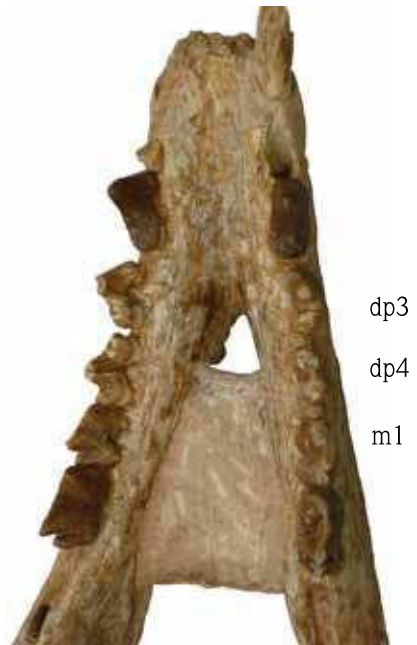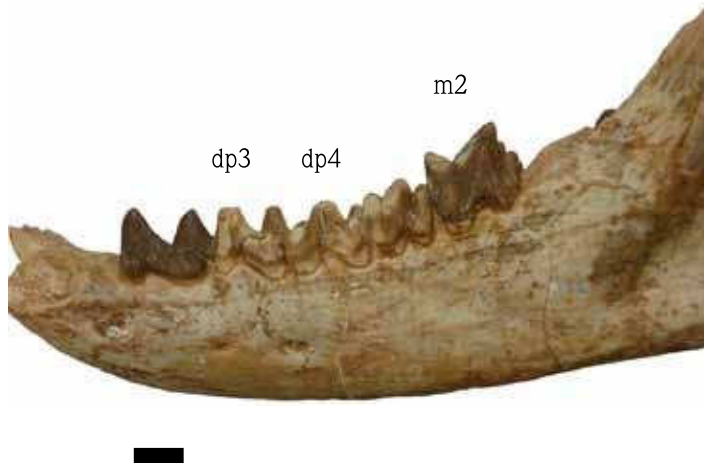
Fig. 6/8: Juvenile material of North American *Hyaenodon*. Bar equals 1 cm. **A-B**, AMNH 39439, *H. horridus* from the White River Fromation (Lower Oreodon Beds; South of Scenic, South Dakota, USA). **A**, skull in occlusal view; **B**, mandible in buccal (left) and occlusal (right) view; Note the projection of the lingual root of the DP3 and the cutting crest on the dp4.
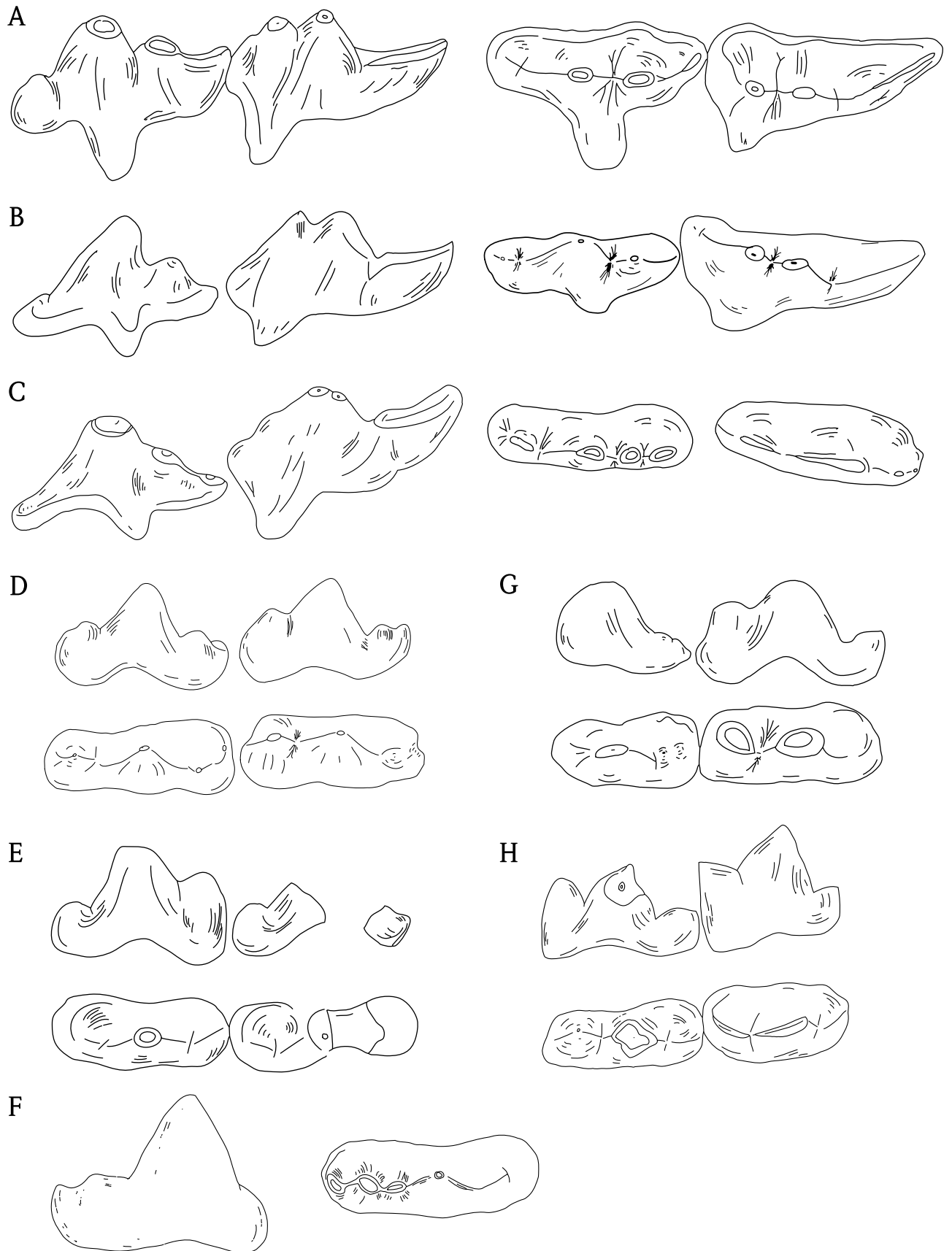
Fig. 6/9: Drawings of select juvenile specimens assigned to different species of *Hyaenodon*. **A-C** show the lingual view (left) and the occlusal view (right) of the upper milk dentition. **D-H** shows the buccal (upper) and occlusal (lower) view of the lower milk dentition, if not stated differently. **A**, *H. filholi*, Qu 8664: DP3-4 sin.; **B**, *H. exiguus*, PD 187: DP3-4 sin.; **C**, *H. exiguus*, Qu 17662: DP3-4 sin.; **D**, *H. exiguus*, M 2353: dp3-4 sin.; **E**, *H. filholi*, M 84866: dp3-4 dex.; **F**, *H. minor.*, M 2348 in buccal (left) and occlusal (right) view: dp3 dex.; **G**, *H. rossignoli*, Mo 22: dp3-4 sin.; **H**, *H. filholi*, MNHN 1875-931: dp4-m1 sin. Note the different morphologies.
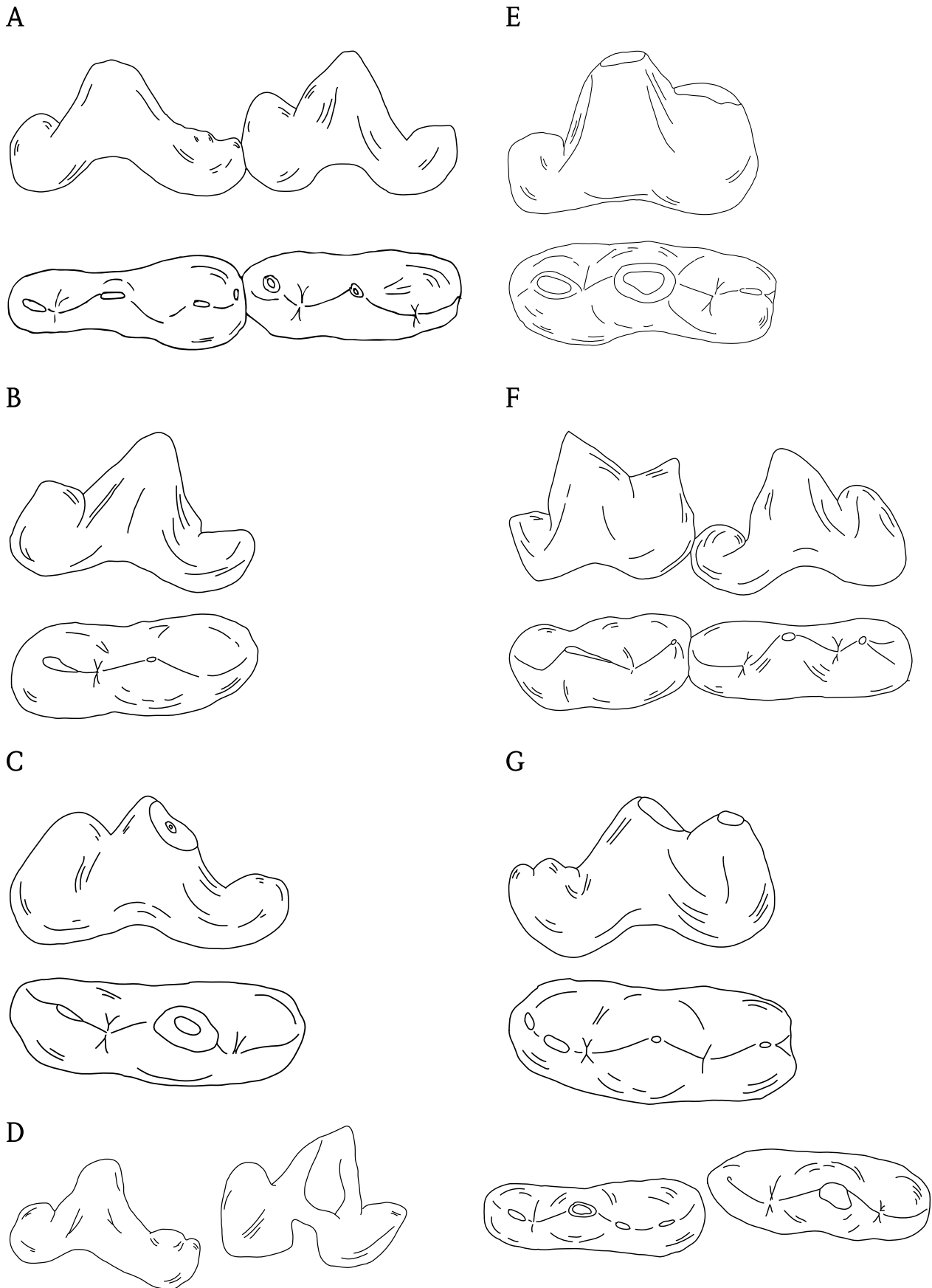
Fig. 6/10: Drawings of the milk dentition in *Hyaenodon* in buccal (upper) and occlusal (lower) view if not stated differently. **A**, *H. filholi*, BSPG 1879 XV 19a: dp3 and dp4; **B**, *H. filholi*, NMHW 2009z0082/0001: dp4; **C**, *H. filholi*, NMHW 2009z0083/0001: dp4; **D**, *H. filholi*, PD 510 in buccal (left) and occlusal (right) view: dp3 and dp4; **E**, *H.* cf. *brachyrhynchus*, GMM A5.103: dp4; **F**, *H. filholi*, NMHW 2009z0082/0002: dp4 and m1; **G**, *H. exiguus*, NMHW 2009z0084/0001: dp4. Note the different morphologies.

Chapter 7

7. On ontogenetic changes and pathologies in the dentition

7.1 Introduction to the tooth eruption sequence

In the last years, various authors became interested in tooth eruption sequences because of their potential to provide useful signals (e.g. Morlo and Habersetzer, 1999; Smith, 2000; Asher and Lehmann, 2008). Tooth replacement was a topic of importance concerning the "creodonts" in the past. In fact, it was a major argument to place "Creodonta" in Placentalia and not in Marsupialia (Filhol, 1876; Schlosser, 1887). Furthermore, it should be noted that Morlo and Habersetzer (1999) found that Proviverrinae differ from Hyaenodontidae in their tooth eruption sequence: the upper canines of *Lesmesodon edingeri* and *Lesmesodon behnkeae* erupt before the P2 (showing the following dentition I1-3, DC, P1, DP2-4, M1-2 and i1-3, dc, p1, dp2-4, m1-2). In contrast to *Hyaenodon*, that shows eruption of the permanent upper canines as the last teeth (Mellett, 1977; see below). Furthermore, it should be added that the x-ray of *Oxyaena woutersi* (Fig. 5, p. 7 in Solé et al., 2011) shows a more developed germ of the p4 compared to the germ of the p2. This implies, that the p4 will erupt earlier and thus the eruption sequence is completely different than in *Hyaenodon*.
The milk teeth resemble in general the permanent tooth distad to them. In the juvenile the DP3/dp4, the DP4/m1 and the M1/m2 are used as carnassials (Mellett, 1977; Lange-Badré, 1979). In the adult (tooth formula: 3142/3143) the M2/m3 are the main carnassials, but the M1/m2 and the P4/m1 have also a shearing function (Mellett, 1977).

Recently, new information about the tooth eruption sequence in European *Hyaenodon* was published (Bastl et al., 2011) based on a master thesis (Bastl, 2008). In the former, the authors provided a new eruption sequence for the lower jaw that differs from the sequence known for the North American *Hyaenodon* (Bastl et al., 2011). The specimens described therein were figured in detail and x-rays were provided as well, so they won´t be figured herein again.
Herein additional juvenile material is provided (described in Chapter 6). The tooth eruption sequence of the upper jaw is reviewed here as well. Juvenile cranial material is rarely preserved and outnumbered by juvenile mandibles.
Mellett (1977) gave the following sequence for North American *Hyaenodon*: M1 – P2 – P4 – M2 – P3 – C; his sequence for the lower jaw was: m2 – p2 – p4 – m3 – p3 – c; Mellett (1977) combined them and gave a complete formula, thus resulting in: M1/m2 – P2/p2 – P4/p4 – M2/m3 – P3/p3 – C/c.
Lange-Badré (1979) described the sequence for the upper jaw in European *Hyaenodon* as the following: both M1 and P1 erupt early, then P2, P4, M2 and P3. There is no indication when the canine erupts. The sequence for the lower jaw was m1 – p1 – m2 – p2 – m3 – p4 – p3 – c (Lange-Badré, 1979). Bastl et al. (2011) corrected the eruption sequence in the mandible of the European *Hyaenodon* and it is now:
m1 – p1 – m2 – i – p2 – m3/p3/c – p4. The evidence comes from juvenile material of different sized taxa. Remarkable is the consistency of the difference between the North American and the European taxa even due to an enriched amount of material herein. Hitherto, no North American specimen showing the European sequence and no European specimen showing the North American sequence is known. Alas, data of Asian forms is still missing.
In *Hyaenodon*, the first premolar has no predecessor or successor, depending on the author´s view.
Mellett (1977) designated the first premolar as p1 and gave except for Bastl et al. (2011) the only detailed study on the tooth eruption sequence. Lange-Badré (1979) regarded the tooth as dp1. It cannot be determined if this tooth is developed by the first of the second tooth lamellae. However, the time of its eruption (after the m1) fits well with the development of the germs of other permanent premolars and I refer to it as p1 (sensu Mellett, 1977; see also Bastl et al., 2011). The same is true for the upper first premolar.

7.1.1 X-rays

For x-raying a digital x-ray (Bucky Diagnost TH, year of manufacture: 2004) in a Vienna hospital (DZU, Donauzentrum Urania) was used. This machine operates with an Optimus 50 generator and an SRO 33100 radiator (serial number 200296). The reader is a PCR Corado and a laser printer (Agfa Drystar 5500) prints on a record foil. The procedure of x-raying was performed together with Andrea Tietze and her team.

Not all x-rays came out equally well. Nevertheless, also the less good ones shall be figured. The quality of the x-rays is variable due to a different preservation of respective specimens and depends on the material it is imbedded in.

These x-rays were scanned, prepared with Photoshop CS5 and inversed for better illustration.

7.1.2 New descriptions

Here the specimens are described respective to the x-rays and concerning to their ontogenetic stage. General descriptions and measurements are found in Chapter 6. Specimens are described in the order of ontogenetic stages, beginning with the youngest stage.

7.1.2.1 Upper jaw

The specimen **NMHW 2010/0196/0003** (*Hyaenodon exiguus*) is a fragment of a very young, right upper jaw. It holds the DP4 and the P1 is erupting. The anterior alveolus of the M1 is observed too. The x-ray (Fig. 7/1 C) shows not much more than that. The P1 is erupting. The alveoli of the DP2, the DP3 and the anterior alveolus of the M1 can be clearly seen. No germs are apparent: either due to the youth of the juvenile specimen or due to preservation; It has to be stated, that this specimen represents an ontogenetic stage unknown for the North American taxa. The earliest known stage in North American *Hyaenodon* shows already erupted P1, p1 and m1. Here, the specimen indicates a very early eruption of the M1 — even before the P1! This is another difference in the eruption sequence (Fig. 7/5). The material that the specimen is connected with is disturbing the x-ray, so the quality of the resulting figure is not too good.

The specimen **PD 187** (*Hyaenodon exiguus*) is a small fragment from a juvenile, left upper jaw. The fragment holds the DP3, DP4 and the M1. The x-ray (Fig. 7/1 A) shows the alveolus of the DC, the cavity for the germ of the C right above the former alveolus, two distinct alveoli for the P1 and the alveoli of the DP2. Furthermore, the germ of the P2 as well as the germs of the P3 and the P4 can be seen. Distally to the M1 the bone is broken, thus nothing can be said of the developmental stage of the M2. The germ of the P2 is clearly the largest. It is situated right below where the DP2 has been. The P2 is the next tooth to erupt. The germs of the P3 and the P4 are in this stage equally developed.

The specimen **Qu 17662** (*Hyaenodon exiguus*) is a famous juvenile specimen, already figured by Filhol (1876). It was formerly cut open to reveal the germs of the permanent dentition. The x-rays (Fig. 7/1 D) are confusing, because both sides are preserved and overlap each other with shadows of the other side. The P1 is present, as well as the DP3, DP4 and the M1. The P2 and the M2 are erupting. The germs of the P3 and the P4 are well developed. The germ of the P4 is larger and closer to its predecessor. So, it assumingly starts eruption before the P3. The germs of the C are preserved as well.

The specimen **Qu 8664** (*Hyaenodon filholi*) is about the same stage as the previous described specimen. It too gives x-rays that are hard to judge, because both sides are preserved. The DC, P1, DP3, DP4 and the M1 are in use. The P2 is erupting, more than in Qu 17662. The specimen is broken distally to the M1, so nothing can be said about the M2. The permanent canines are preserved in a cavity just above to the DC, they can be seen

well in the x-ray (Fig. 7/1 B). They already reach a considerable length. The germs of the P3 and the P4 are well-developed. The P4 is about to start eruption. On one side the dp4 has fallen out. So, the P4 erupts before the P3.

The specimen **NMHW 2010/0196/0001** (*Hyaenodon minor*) shows an erupting C together with the P1, P2, P3, P4 and the M1. A phalanx is attached to the specimen, that is not discussed as it does not belong to *Hyaenodon*. The x-ray (Fig. 7/2 C) reveals the presence of the M2. The anterior alveolus with the root of the M2 can be observed. Thus, this specimen proves that the C erupts as last tooth. The other side of the upper jaw NMHW 2010/0196/0002 is shown too. The permanent dentition from P3-M2 is in place.

The specimen **Qu 8632** (*Hyaenodon brachyrhynchus*) was x-rayed too (Fig. 7/1 E), although it was apparent that the permanent dentition was already in use. It is a broken skull with lower jaws. No germs are visible.

The specimen **M 5722** (*Hyaenodon horridus*) is a rather complete specimen with skull and mandibles. The x-rays (Fig. 7/4 A-B) are not good due to preservation. The material is very compact. Germs are not seen and the erupting upper and lower canines, which appear clearly in the photographs (Fig. 6/7 A-B), are not seen. In the upper jaw there is a dark shadow, that could be correlated with the germ of a C. However, this specimen is representative for the last stage in the eruption sequence for the North American *Hyaenodon*.

7.1.2.2 Lower jaw

The specimen **M 84867** (*Hyaenodon filholi*) is showing the dp4 and the m1. In the x-ray (Fig. 7/3 B) the well-developed germ of the m2 can be seen. No other germs are present.

The specimen **NMHW 2009z0084/0003** (*Hyaenodon filholi*) is a mandible fragment with a dp4. The x-ray (Fig. 7/3 D) shows the alveoli of the m1, the well-developed germ of the m2 in crypt, a forming cavity for the germ of the m3, as well as a small enamel piece (developing germ of the m3) and the small developing germ of the p4. This mandible is showing a young ontogenetic stage and the early beginning of the development of the germs of the m3 and the p4 is interesting.

The specimen **M 2348** (*Hyaenodon minor*) shows the dp3 and a fragment of the dp4. The x-ray (Fig. 7/2 F) shows the alveolus of the p1, the alveoli of the dp2 and the germ of the p2. The germ of the p2 is still small and has to develop further to erupt. The germ of the c is present. It is known from many other specimens that the germ of the p2 and the c develop simultaneously, although the c needs much more time to fully develop and erupt, due to its length. The germ of the p3 is very small, but present. There is no germ of the p4.

The specimen **MNHN 1875-931** (*Hyaenodon filholi*) presents the p1, dp2, dp4, m1 and the erupting m2. The x-ray (Fig. 7/2 A) reveals the germs of the c, the p2, the p3, the p4 and the m3. The germs of the c and the p2 are the largest. The germs of the p3, p4 and the m3 are just about to form and are very small.

The specimen **M 2353a** (*Hyaenodon exiguus*) shows the dp3 and the dp4. The x-ray (Fig. 7/2 E) depicts the alveoli of the p1, the dp2 and the m1. The germs of the p2 and the c are developing. A very small piece of enamel in crypt below the dp3 indicates the beginning development of the germ of the p3.

The specimen **M 2353** (*Hyaenodon exiguus*) presents the p1, dp3, dp4 and the m1. The x-ray (Fig. 7/2 D) confirms the presence of the m2 — the anterior alveolus of the m2 can be seen. The germs of the c and the p2 are developed. They are more developed than in M 2353a. The germ of the p3 and the p4 are small and beginning to form.

The specimen **M 4498** (*Hyaenodon exiguus*) holds the erupting p2 and the dp4. The x-ray (Fig. 7/2 B) shows the alveoli for the p1, the alveoli for the dp3 and the germs of the c, the p3 and the p4. The germ of the p4 seems to be more developed as the germ of the p3.

The specimen **M 84866** (*Hyaenodon filholi*) is preserved with the dp3 and the dp4. The p2 is erupting. The x-ray (Fig. 7/3 A) is showing the alveoli of the p1, the germ of the c and the germs of the p3 and the p4. The germ of the p3 is more developed and larger than that of the p4. This is consistent with the earlier eruption of the p3 in the sequence.

The specimen **PD 510** (*Hyaenodon filholi*) is a beautiful lower jaw with both rami. It shows the p1, alveoli of the p2, dp3, dp4, m1, m2 and the tips of the erupting m3. In the x-ray (Fig. 7/3 C) it can be confirmed that the p2 already erupted. The germs of the c, p3, p4 and the m3 are observed. Interestingly, the germs of the incisors are shown too. Probably they are the second incisors and erupt later than the i1 and i3. The germs of the p3 and the p4 are about equally developed. The m3 is in crypt.

The specimen **Mo 22** (*Hyaenodon rossignoli*) shows the dp3, dp4, m1 and the m2. The x-ray (Fig. 7/3 E) illustrates the beginning eruption of the m3. The germs of the p3 and the p4 are present. Surprisingly, here the germ of the p4 is much larger than the one of the p3. The p3 is smaller than the p4 in the adult, but still it is clear from this x-ray, that at this stage the germ of the p4 is more developed than the germ of the p3. No germ of a canine is detected.

The specimen **Qu 8356** (*Hyaenodon rossignoli*) is showing the permanent dentition from p3-m3. The x-ray (Fig. 7/3 F) reveals that there are no germs. Interesting is that the p4 seems to have not completed eruption. This is remarkable: compared with Mo 22, a specimen of the same species, shows a larger germ of the p4 than the germ of the p3 (described above). Assumingly, the development of the p4 starts earlier, but in consistency to the eruption sequence the p4 erupts later still or needs more time for eruption.

7.2 About undescribed Asian material

Asian material is rare. Juvenile specimens are about to be worked on (pers. comm.; Takehisa Tsubamoto). However, two juvenile specimens are housed in the collections of the AMNH. Both are from Mongolia and are lower jaws. To my knowledge they remained undescribed up to now. Fig. 7/5 A-D shows them.

The specimen **AMNH 26067** (Fig. 7/5 C-D) is from the Shara Murun region (Mongolia, Ulan Gochu Formation). Both rami are preserved, although the specimen is in a bad condition and was prepared by embedding into plaster. The symphysis shows the milk incisors as well as two permanent incisors, the dc, p1, dp2, dp3, dp4, m1 and the m2. Due to breakage of the bone, several germs are revealed: the germ of a permanent canine (in the middle of the symphysis); the germ of the p2 dex. (next to the dp2 dex.); the permanent incisors erupting (it is difficult to determine their position); Compared to the North American and the European material this specimen is in a stage of tooth replacement, that is common in all *Hyaenodon* species: the m2 has erupted, the incisors are about to be replaced and the next tooth to erupt is the p2. This is the third step (Fig. 7/6) in the tooth eruption sequence in North American, European and apparently also in Asian *Hyaenodon*. Interesting is that the germ of the c and the p2 develop simultaneously as seen in European specimens.

The other specimen, **AMNH 26066** (Fig. 7/5 A-B), is from Jhama Obo (Shara Murun region, Mongolia, Ulan Gochu Formation) and a lower symphysis. The specimen shows the incisors (difficult to judge whether permanent or deciduous without x-ray), the dc, p1, dp2, dp3, dp4, m1 and the m2. It is in the same

ontogenetic stage as the previous described specimen. It can give no further information, except for the following point: due to breakage of the bone distally to the m2, the small germ of the m3 is seen. So, the development of the germ of the m3 starts early. This is not different from what is seen in European specimens.

7.3 Tooth replacement in Carnivora

It needs some time for the deciduous dentition to fully erupt. To give an impression on that fact, an overview of this time needed is given in Table 7/1 in the case of felids.

species	completion of eruption of the deciduous dentition in months	completion of eruption of the deciduous dentition in days
Panthera leo	4-5 months	117-152 days
Panthera tigris	2 months	64 days
Panthera pardus	2 months	69 days
Panthera onca	2 months	69 days
Felis concolor	2 months	61 days
Felis catus	1-3 months	37-93 days

Table 7/1: The different periods of time given in months and days for full eruption of the deciduous dentition in various felids. Data was taken from Miles and Grigson (1990) and from Schneider (1959, for *Felis catus*).

After the deciduous dentition was in use, tooth replacement occurs in diphyodont mammals. Then the permanent dentition erupts, including the molars.
Tooth replacement is completed after 6 months in Carnivora (Miles and Grigson, 1990). The permanent canine erupts after 5 ½ months, but normally the deciduous canine is retained until the age of seven months (Habermehl, 1975). Stubbe and Krapp (1993: p. 85, Table 7) describe this in the case of *Canis lupus* as follows: at the age of about four months the tooth replacement starts; from six to seven months the milk and the permanent canines might persist simultaneously, but the tooth replacement concerning the cheek teeth is finished; from nine to eleven months the canines erupt fully (Stubbe and Krapp, 1993). Even longer retention is known in *Canis latrans* (Miles and Grigson, 1990).
There is less information on the tooth eruption sequence in Pinnipedia. Loughlin (1982) stated that p3 erupts before p4 in phocids and otarids. This is also the case in mustelids (Loughlin, 1982). Loughlin (1982) concluded that the eruption sequence of the lower premolars is of no value concerning phyletic origins.
Slaughter, Pine and Pine (1974) and Miles and Grigson (1990) examined tooth eruption sequences. A few shall be mentioned here for comparative purposes:

Slaughter, Pine and Pine (1974) give the following tooth eruption sequences for *Mustela vison*:
M1-M2/P2-P4-P3
m1-m2-p2-p3-p4

The tooth eruption sequence is the same in brown bears (*Ursus arctos*), polar bears (*Ursus maritimus*) and grizzlies (*Ursus horribilis*):
p1-I1/I2/P1/M1/i1/m1-P4/i2-I3/p4/m2-P3/M2/i3/p3-m3/P2-p2-c (Rausch 1961; Pohle 1923)

Rausch (1961) observed, that grizzlies in the wild show eruption of the p1 in May (the third month of their life) und eruption of the canines in October (eighth month of their life). The canines erupt slowly and it can

take until the animals fifth summer until they are fully erupted (Rausch, 1961). Slaughter, Pine and Pine (1974) contributed, that the eruption sequence is the same in *Ursus americanus* (American black bear) except that m1 erupts before the p1.

In contrast to other ursids (above) *Selenarctos thibetanus* shows a different eruption sequence (Miles and Grigson, 1990):

P1-M1-P4-M2-P2/P3
p1/m1-p4-m2-p2/p3-m3

Slaugther, Pine and Pine (1974) give the following sequences for *Canis familiaris:*
P1-M1-M2-P4-P2-P3
p1-m1/m2-p2/m3-p4-p3

Concluding from these facts, it should be noted, that tooth eruption sequences contribute to the knowledge of an animal. However, the phylogenetic impact is not clear. Some genera share a common sequence, some authors think that there is no valuable information about phylogenetic origins (e.g. Loughlin, 1982) and others (e.g. Slaughter, Pine and Pine, 1974) showed wide variations of sequences indicating the need of interpretation.

7.4 New results on the tooth eruption sequence

When the tooth eruption sequences of the upper and the lower jaw in *Hyaenodon* are combined, an interesting picture emerges. Fig. 7/6 compares and illustrates the tooth eruption sequences of the North American and the European *Hyaenodon* from their respective earliest stages to the fully erupted permanent dentition. This is of course a simplified scheme. It tries to catch the beginning of the eruption of a tooth. So, while the next tooth starts eruption another one must not have completed eruption. This is especially true for the m3 and the canines. The crucial stage when m3, p3 and c start eruption at about the same time in European *Hyaenodon* is illustrated as one stage. Of course, some teeth need more time to fully erupt. Successions are known and these are described in the text as well as listed in the Tables (Tab. 7/2 and 7/3). The delayed eruption of the i2 compared to the other lower incisivi is not separately shown, to keep the picture simple. It is not known how long it takes the lower canine to erupt. As it starts eruption earlier than known from North American specimens, it is indicated to be earlier fully erupted too (in Fig. 7/6). However, this is just an assumption. The upper jaw shows less difference in the tooth eruption sequence.

The eruption sequences differ in the following main points:

1) In the European taxa the P1/p1 erupt after the M1/m1. This is different in the North American taxa as the M1 is stated to erupt after the P1 (Mellett, 1977). The situation for the mandible is not known as the youngest specimen shows both, p1 and m1 in place (Mellett, 1977). Remarkably, this is the only observed difference in the tooth eruption sequence for the upper jaw, but evidenced for the first time.

2) The p3 erupts before the p4 in the European specimens, which is contrasted by the vice versa condition in the North American taxa: the p4 erupts well before the p3 (Mellett, 1977).

3) The m3 and the c start eruption earlier in the European taxa — together with the p3! In North American taxa these teeth erupt later and the m3 erupts earlier than the p3 (Mellett, 1977).

approximate stage	material	testifies that
1	NMHW 2010/0196/0003	P1 erupts after M1
4	Qu 17662	P2 erupts before M2
4	PD 187	P2 erupts after P1
5	Qu 17662, Qu 8664	germ of P4 more developed than germ of the P3
8	NMHW 2010/0196/0001, NMHW 2010/0196/0002	C is the last tooth to erupt

Table 7/2: Direct evidence from the material concerning the tooth eruption sequence of the upper jaw in European *Hyaenodon*.

approximate stage	material	testifies that
1	NMHW 2009z0082/0001*, NMHW 2009z0084/0001*	p1 erupts after m1
5	PD 510, Mo 22	m3 starts eruption before p3 and p4
5	M 2353a, M 2348	germ of p3 more developed than germ of p4
5	GMM A5.103*, SMNS 47259*	p3 erupts before p4
5	NMHW 2009z0084/0002*	c starts eruption with p3
8	Qu 8356	p4 last tooth to complete eruption

Table 7/3: Direct evidence from the material concerning the tooth eruption sequence of the lower jaw in the European *Hyaenodon*. The asterisks marks material described and figured in Bastl et al. (2011).

These differences are remarkable as the dataset now increased. Still, there is no European specimen showing a North American pattern and vice versa. These constant differences indicate divergence within the genus, as already stated by Bastl et al. (2011). The hitherto only known Asian forms conform to a stage of tooth eruption sequence, that is showing no differences in North American and European *Hyaenodon*. Thus, no information about the crucial stages and whether the Asian forms follow the one or the other pattern or even show their own one, cannot be determined. More juvenile findings of Asian forms would be very interesting to make further inferences.

7.5 First examination of dental rings

In order to get an impression how fast tooth replacement takes place in *Hyaenodon* and how old individuals could grow compared to modern Carnivora, an attempt of counting dentine growth lines or cementum layers was applied for the first time. These techniques were widely used for age determination in mammals (e.g. Fancy, 1980). In general, one dark line per year was formed in mammals (Spinage, 1976): for example in a lion 20.1 lines were counted on average and 22 were expected based on its age. This method for age determination is especially useful for taxa with no seasonal nutritional changes, like carnivores. Evidence from buffalo teeth show, that the formation of lines is influenced by the environment (Spinage, 1976): An annual unimodal rainfall pattern is reflected by one dark-stained line per year, whereas a bimodal rainfall pattern (in the equatorial zone) is displayed in two lines per year. Despite the use of this method it has to be noted, that it

has to be applied with care. Spinage (1976) further stated, that the accuracy of the method is affected, because the increase of cementum growth could be influenced or triggered by alveolar and mesial shift of the tooth with increasing age. Nevertheless, seasonal change was herein not assumed for a carnivorous mammal like *Hyaenodon* and a counting of dentine growth lines was tried as approach for age determination.

The thin sections were prepared as follows: the respective tooth or root was first stabilized with resin. The whole block was cut with a thin saw and applied on a glass slide. This slide was grinded per hand with grinding powder (grain size 600, then 1000) and observed frequently under the binocular microscope.
For the thin sections specimens that were already broken or isolated were chosen. The following teeth were tested: anterior root of a DP4 (NHMW 2009z0084/0005) and the posterior root of an m3 (NHMW 2009z0084/0004a) of *Hyaenodon* sp. Due to the relative small size of these specimens (see Table 7/4) a fox of similar size was chosen for comparison: roots of the dp4 dex. (IUPW 1409) and the p2 (IUPW 1037b) of *Vulpes vulpes*.

Tooth — *Hyaenodon*	length	width
DP4 (NHMW 2009z0084/0005)	9.0 mm	4.5 mm
m3 (NHMW 2009z0084/0004a)	11.1 mm	4.4 mm

Table 7/4: Size of the selected *Hyaenodon* teeth for thin sections.

The DP4 shows a slicing facet, thus this animal was already in the process of tooth replacement. The m3 is a very worn tooth — belonging to a senile individual. The aim of this study was to draw conclusions on the individual age of a juvenile *Hyaenodon* and an aged *Hyaenodon*. This aim could not be met entirely.
Lines are not seen in milk teeth in both *Hyaenodon* (Fig. 7/7 A) and *Vulpes* (Fig. 7/7 C). This was expected as Carnivora commonly finish tooth replacement well before being one year old. The same can be assumed for *Hyaenodon*. The permanent tooth of *Vulpes* (Fig. 7/7 D) shows a growth pattern, whereas the root of the m3 of *Hyaenodon* is difficult to interpret (Fig. 7/7 B): due to preservation and crystallization no obvious pattern emerges.
Interesting is the section of a DC in the North American *Hyaenodon horridus* (M 5722). A count of four lines along the whole tooth could be made. A section is seen in Fig. 7/7 E. This individual was still in the process of tooth replacement. Although the canines are the last teeth to erupt, this would infer that the individual was quite old at the end of tooth replacement. Modern Carnivora usually finish after half a year, but latest after one year (Miles and Grigson, 1990).

The prepared slides with the sections were used to measure the thickness of enamel. As mentioned above, the *Hyaenodon* specimens were of approximately the same size as *Vulpes*. Thus, the measurements are comparable (Tab. 7/5). The enamel of *Hyaenodon* is thicker than that of the fox. This is already apparent in the milk dentition, but also in the permanent dentition. This is not surprising as the diet of *Hyaenodon* included much tougher foods than that of a fox (see Chapter 8).

tooth position	taxon	max. width of enamel
dp4 dex. (IUPW 1409)	*Vulpes vulpes*	0.3 mm
p2 (IUPW 1037b)	*Vulpes vulpes*	0.75 mm
DP4 (NHMW 2009z0084/0005)	*Hyaenodon* sp.	0.4 mm
m3 (NHMW 2009z0084/0004a)	*Hyaenodon* sp.	1.0 mm

Table 7/5: Measurements of maximum enamel width in *Hyaenodon* and *Vulpes*.

7.6 First estimate on growth rates

In order to get additional information about the ontogeny of *Hyaenodon*, growth rates from juvenile material (e.g. comparing the milk to the permanent teeth) were calculated (Table 7/6).

specimen number	length in mm	length in mm	growth in %
GMM A5.103	dp4: 11.8	p4: 16.4	28.0%
	opening for m3: 18.8	m3: 20.2	6.9%
	dp4-m2: 34.5	p4-m2: 39.2	**11.9%**
BSPG 1879 XV 18a	dp3: 7.4	p3: 7.8	5.1%
	dp4: 6.9	p4: 7.6	9.2%
	dp3-dp4: 14.0	p3-p4: 16.6	**15.6%**
SMNS 47259	opening for m3: 11.6	m3: 20.2	42.5%
SMNS 47276 (m3)	p4-opening m3: 44.3	p4-m3: 52.9	**16.2%**
NMHW 2009z0084/0002	dp3: 6.7	p3: 7.5	10.6%
Mo 22	dp3: 5.5	p3: 6.1	9.8%
	dp4: 6.7	p4: 9.0	25.5%
	dp3-dp4: 12.1	p3-p4: 15.0	19.3%
	dp3-m2: 25.6	p3-m2: 28.5	10.2%
	opening for m3: 7.5	m3: 10.7	29.9%
	dp3-opening m3: 33.1	p3-m3: 39.2	**15.6%**
PD 187	dp3: 7.3	p3: 8.4	13.0%
	opening for m3: 7.4	m3: 11.5	35.7%
PD 487	dp3: 8.8	p3: 10.7	17.8%
	dp4: 7.6	p4: 8.1	6.2%
M 4498	dp3: 8.8	p3: 8.8	0.0%
	dp4: 8.1	p4: 9.0	10.0%
	p2-dp4: 27.1	p2-p4: 28.0	3.2%
M 2353	dp2 (alveoli): 7.7	p2: 8.8	12.5%
M 84866	dp3: 6.7	p3: 7.8	14.1%
Qu 17662	DP2 (alveoli): 6.5	P2: 7.5	13.3%
H. rossignoli: Mo 22	dp3-m2: 25.6		
Qu 8356		p3-m2: 33.1	22.6%

Table 7/6: Measurements of deciduous and permanent teeth and the inferred growth rates.

The length measurements were made with a caliper on the specimens itself or their x-rays respectively. Only well-developed germs were measured.

The growth during tooth replacement in *Hyaenodon* concerns mainly the length of the mandible. The permanent teeth are not greatly larger than their milk predecessors. They range from 0-14% larger size. The dp4-p4 relation can be an exception. In some cases (e.g. Mo 22), the p4 can exceed the dp4 more than 4 mm, giving a growth rate of 28% in the most extreme case (GMM A5.103). The situation is similar for the m3. As the last carnassial it is peculiar for possessing a long blade and the growth rate is thus high, as the mandible has to grow considerably in length to give enough space for this tooth. It should be noted that the successor can

be smaller than the predecessor (Qu 17662: DP4 (10.4 mm) — P4 (9.1 mm) or PD 487: dp2 (7.3 mm) — p2 (6.1 mm)), although this is a single result yet.

To get a better impression of general growth, the growth rates of the tooth rows were calculated. They show that the overall growth was between 12 to 16% (bold rates). These results are reasonable and fit the authors´ observation that the small juvenile specimens cannot grow into large adults. Thus, although the length of the whole mandible/skull grows during tooth replacement, a valuable estimation of adult size can be given for juvenile material.

Mo 22 and Qu 8356 reperesent a juvenile and an adult individual of the same species: *Hyaenodon rossignoli.* The juvenile shows a tooth row made up by milk teeth: dp3, dp4 and m1 and m2. The adult tooth row from p3-m2 was measured in Qu 8356. They were compared and the size growth gives a value of 22,6%. This is even within the range of sexual dimorphism.

Consequently, the juvenile specimen (Qu 8660) assigned to *Hyaenodon brachyrhynchus* by Lange-Badré (1979: Planche XX Fig. 6) has to be previously determined as *Hyaenodon* sp. It is far too small for the species *Hyaenodon brachyrhynchus.* Another juvenile specimen figured on the same plate (Mo 40, Planche XX Fig. 3) shows a true juvenile individual of *Hyaenodon brachyrhynchus*: the mandible is much more robust and the jaw depth more similar to an adult individual of the respective taxa (e.g. Mo 15, Planche XX, Fig. 4).

specimen number	length of the germ of the permanent canine
M 2353a; *Hyaenodon exiguus*	4.3 mm
M 2353; *Hyaenodon exiguus*	7.7 mm
PD 187; *Hyaenodon exiguus*	8.2 mm
M 84866; *Hyaenodon filholi*	9.8 mm
BSPG 1978 XV 19a*; *Hyaenodon filholi*	12.2 mm
NMHW 2010/0196/0001; *Hyaenodon minor*	32.0 mm

Table 7/7: Specimens and the length of the germ of the permanent canine. The asterisk indicates a specimen described and figured in Bastl et al. (2011).

The following specimens are described from the earliest stage to the last stage of tooth replacement concerning the development of the germ of the canine. The length of the germ of the canine increases of course with ontogenetic age. This can be observed in the following paragraph as well as in the Table. The sample consists of material belonging to small sized taxa (except the last one), allowing a good comparison.

M 2353 holds dp3, dp4 and m1. The germs of the p2 and the c are present, but small. Thus, the length of the canine is low. But both less developed than in M 2353.

M 2353 holds p1, dp2, dp3, dp4 and m1. The germs of the p2 and the c are more developed than in M 2353.

PD 187 holds DP3, DP4 and M1. Here, the P2 erupts. The length of the canine is higher.

M 84866 holds the dp3 and the dp4. The p2 erupts. This is about the same ontogenetic age as in PD 187.

BSPG 1879 XV 19a still holds milk teeth: dp3 and dp4. The p2 has nearly completed eruption. The germs of the p3 and the p4 are well developed. The canine length therefore is again exceeding that of the specimen above.

The germ of the canine is longest in NMHW 2010/0196/0001. This specimen is in the last stage of tooth replacement (canines are the last teeth to erupt), thus the tooth is well-developed. Also, the C is erupting and the individual belongs to middle-sized species.

For the small sized specimens and the germs of the canine a well-documented succession of the growing length of the germ can be observed.

7.7 Pathologies

7.7.1 Pathologies in Carnivora

In 1893 Sir Frank Colyer collaborated with Morton Smale on the book "Diseases and Injuries of the Teeth". The third edition changed its title to "Dental Surgery and Pathology" in 1910. This work was the basis for the revised edition by A. Miles and C. Grigson "Colyer´s Variations and diseases of the teeth of animals".
This comprehensive book focuses on various dental pathologies in mammals, although marsupials are treated as well. The topics are variations in number, size and shape of teeth, variations in position, abnormalities of eruption and disorders of teeth and jaws including injuries, enamel hypoplasia, caries, abscesses, periodontal disease and odontomes.

In order to compare known pathologies in *Hyaenodon*, this chapter focuses on pathologies in the order Carnivora. Finally, pathologies in *Hyaenodon* are discussed. The following section follows entirely Miles and Grigson (1990), if not cited explicitly elsewhere.

Supernumary teeth and loss of teeth

Family (Carnivora)	% of affected specimens
Felidae	2.7%
Hyaenidae	0.7%
Viverridae	1.6%
Mustelidae	1.1%
Procyonidae	1.7%
Ursidae	2.4%
Canidae	2.7%

Table 7/8: Percentages of specimens with extra teeth in the families of the order Carnivora (data taken from Table 4.1, p. 63 in Miles and Grigson, 1990).

In general, extra teeth occur in 1.9% of cases in Carnivora (included families are Felidae, Hyaenidae, Viverridae, Mustelidae, Procyonidae, Ursidae, Canidae; Miles and Grigson, 1990). Felidae and Canidae both had the highest score with 2.7% of the observed specimens (Table 1 herein; Table 4.1, p. 63, Miles and Grigson, 1990). The lowest score was found in Hyaenidae with 0.7% although the sample size was smallest here too. More detailed information can be found in Miles and Grigson (1990).

An impressive example of extra teeth in the Felidae is figured in Miles and Grigson (Fig. 4.1, p. 63, 1990) showing two canines in the right maxilla of *Panthera tigris*.
Absence of teeth among Carnivora is in the Felidae least common, because the dentition is already reduced (Hall, 1940). Certain taxa like the cheetah (*Acinonyx jubatus)* or the North American lynx (*Felis caracal*) or the rusty-spotted cat (*Felis rubiginosus*) showed a more frequent loss (Hall, 1940): the P2 was often absent. In some instances the alveolar process was rough and though the tooth could have been lost during life. Surprisingly, Lüps (1980) found a geographical component: A cline from north to south in the absence of the P2 in feral and domestic cats from 3.4% in Great Britain to 28.4% in the Kerguelen islands. Glass and Todd (1977) found the absence of the P2 to be 40% in the North and 11% in the South of the Himalayas in *Felis bengalensis*. They were uncertain if this result was related to latitude or to genetic isolation.

The m2 was lost early in the Felidae, namely in the Miocene (Kurtén, 1963). It is already lost in the lynx-like *Felis issiodorensis* (Kurtén, 1963). However, it is occasionally present — in 10% of the cases — in *Felis lynx lynx* (Miles and Grigson, 1990; Kvam, 1985). Whether due to a reactiviation of the molarization field that was never genotypically lost (= return of a lost structure; Kurtén, 1963) or due to evolutionary pressure (= evolution of a new character; Werdelin, 1987) is not clear.

The P2 in felids is also variable in size and this can be seen even in collaterals (Graf et al., 1976). In the m1 the metaconid has been lost during evolution. *Felis issiodorensis* shows no metaconid and the talonid is reduced to a bulge (Kurtén, 1963). Kurtén (1963) found the presence of a metaconid in *Felis lynx lynx*. The author interpreted this finding as well as the occasional presence of m2 as exception to the rule that lost structures can´t reappear in their original form.

In the Hyaenidae the only known variations are (Miles and Grigson, 1990): an extra tooth between the canine and the p2 in *Crocuta* and the absence of the M1 in *Hyaena* — both occurring rarely.

In the Mustelidae several variations are known. Marshall (1952) observed a tendence to reduction of the first premolars in *Martes americana*. Neuenschwander and Lüps (1975) found in some cases supernumerary premolars or molars, shape variation of p2 and m2 and absence of p2 and m3 in *Mustela*. Hancox (1988) stated that there is regional variation in *Meles*, for example for the second premolars in having one, two or three roots. However, the frequent absence of the first premolars was consistently common.

In the Ursidae additional upper incisors and malformed roots are common (Fig. 4.22-Fig. 4.24, p. 79; Fig. 4.25-Fig. 4.29, p. 80 in Miles and Grigson, 1990).

In the Canidae supernumerary teeth occur in the area of the first premolar or as disto-molar. Whereas absence of teeth as well as extra roots of premolars occur rarely (Miles and Grigson, 1990).

The most common variation in Pinnipedia is the presence of extra cheek teeth (Miles and Grigson, 1990).

Variation in tooth position

Family (Carnivora)	% of affected specimens
Felidae	6.4%
Hyaenidae	15.0%
Viverridae	7.9%
Mustelidae	18.6%
Procyonidae	18.9%
Ursidae	11.4%
Canidae	7.2%

Table 7/9. Percentages of specimens with positional variations in Carnivora (data was taken from Table 11.1, p.239 in Miles and Grigson, 1990).

Concerning variation in tooth position the lion (*Panthera leo*) scores high within the genus *Panthera* and the tiger (*Panthera tigris*) scores low (Table 11.2, p. 239 in Miles and Grigson, 1990). An extreme example of misplacement is the eruption of the upper right canine to the right side of the midline of the palate in a tiger (Fig. 11.3, p. 241 in Miles and Grigson, 1990). The tooth crown lies obliquely across the left palate. The pulp

cavity was exposed and caused an abscess. This state was interpreted as consequence of a maldevelopment of the canine or as displacement after a trauma (Miles and Grigson, 1990).

In felids the P2 is liable to be rotated. However, abnormalities of tooth position are more common in captive than in wild individuals.

The family Hyaenidae shows variation in tooth position only in the premolars: most commonly in the P2 and less common in the P3 and the p2. These variations were observed more often in *Hyaena* than in *Crocuta* (Miles and Grigson, 1990).

In the Viverridae there is a tendency to overlapping of the lower incisors and tilting of the p4, as well as a more common variation of tooth position in captive individuals. The M2 and the m2 are the last cheek teeth to erupt and are thus the most commonly misplaced teeth (Miles and Grigson, 1990).

Within the Mustelidae, the Lutrinae show the highest percentage of irregular arrangements of teeth compared to the Mustelinae and the Melinae (Tab. 11.7, p. 250 in Miles and Grigson, 1990).

The Procyonidae show variation of tooth position in the arrangement of the upper premolars and molars. The mandibular teeth tend to be similar in the various taxa showing straight rows of cheek teeth (Miles and Grigson, 1990).

Within the Ursidae Miles and Grigson (1990) did not find any special features of variation of tooth position. The lower incisors are more often irregular positioned compared to the maxillary teeth. The third and the fourth premolar may rotate. Molars can also be rotated: in polar bears the rotation of M1 is an observed variation.

In the Canidae variation of tooth position is well known and described (Miles and Grigson, 1990). Irregularities range from overlap and protrusion to misplacement.

Within the Pinnipedia the arrangement of cheek teeth varies within the species of seals and among individuals (Miles and Grigson, 1990): the Otariidae usually show spaced teeth, gaps between the upper molars being larger than between other teeth; rotation of premolars can occur; the Phocidae show depending on the species spaced or rotated teeth (Miles and Grigson, 1990). However, the ontogenetic age has to be considered, as Ooë and Esaka (1981) found decrease of overlap of the cheek teeth with advancing age in *Phoca vitulina*.

The effect of captivity is not clear. Whereas Nehring (1884) described captivity as a marked effect in wolves and Klatt (1921) in red foxes, Fabian (1933) showed that these effects must not show up in captivity: he kept silver foxes on a good diet in good conditions for 10-15 generations and found no reduction in jaw size or any irregular tooth position. Thus, poor diet may be the explanation for these abnormalities rather than captivity (Fabian, 1933).

Disorders

Injuries

The true prevalence of fractures of the jaw and other injuries is unknown as evidence is based almost exclusively on specimens in which healing was sufficient to survive (also taking sample bias in count; Miles and Grigson, 1990). Curiously, fractures of the upper jaw heal differently from fractures in the lower jaw: the union of a fracture in the maxilla is frequently a union by fibrous tissue, not a union by bone (for example in a lion, Fig. 18.1 p. 373 in Miles and Grigson, 1990). A fracture of the mandible is usually healed by a callus, which has less density than the orginal bone (e.g. cheetah, Fig. 18.4, p. 376 in Miles and Grigson, 1990). As a consequence of a well-united fracture teeth can be displaced (m1 displaced upwards in a leopard Fig. 18.5 B, p. 377 in Miles and Grigson, 1990) or severely damaged (Fig. 18.6, p. 378 in Miles and Grigson, 1990). Injuries vary from perfectly healed to extreme cases like in a specimen of *Vulpes vulpes*: the anterior part of the mandible bearing incisors and canines had been broken and displaced downwards and backwards. This fragment was united with the rest of the mandible, but a mass of callus has formed over the symphysis (Breuer, 1932; and Fig. 18.12, p. 386 in Miles and Grigson, 1990).

Malformations of canines (Fig. 19.5, p. 197; Fig. 19.8 p. 398; Fig. 19.9, p. 399; Fig. 19.10, p. 400 in Miles and Grigson, 1990) and premolars and molars (Fig. 19.11, Fig. 19.12, p. 401 in Miles and Grigson, 1990) are known in Carnivora.

Enamel hypoplasia

Enamel hypoplasia is influenced by nutritional supply (Miles and Grigson, 1990). Mellanby (1929) showed that diets of progressive degrees of deficiency in vitamin D lead to progressive degrees of enamel hypoplasia (Fig. 20.14, p. 446 in Miles and Grigson, 1990). Individuals that suffered from distemper show hypoplasia lesions too. However, some nutritional experiments with domestic dogs concerning hypoplasia were claimed to be not valid (Bodingbauer, 1949), because of distemper. The ones done by Mellanby (1937) were not criticized (Miles and Grigson, 1990).

Caries

Dental caries seems to be rare in wild state carnivores: "Colyer examined 7635 skulls of carnivores in various museums and found only one instance, in a marbled cat (*Felis marmorata* BMNH 1855.12.24.254); it was a captive animal." (p. 477 in Miles and Grigson, 1990). Additionally, more cases are mentioned in Miles and Grigson (1990) for example concerning *Meles meles* or *Ursus americanus* and *Ursus arctos* (*horribilis*) (the American brown bear; *Ursus horribilis* in Miles and Grigson, 1990). Fruit and honey as part of their diet serves as an explanation.

Dento-alveolar abscess

Abscesses occur after injuries and accidents to teeth apart from fractures or in case of Pinnipedia as a result of excessive tooth wear (Miles and Grigson, 1990).

Periodontal disease

Normally, wild individuals of Felidae remain free of periodontal disease due to their diet (Miles and Grigson, 1990). Interestingly, the physical and not the chemical aspect of consuming fresh meat seems to be important: domestic cats fed on flesh which they rend and cut on their own are free from the disease. Others, fed with chopped meat tend to develop periodontal disease (Miles and Grigson, 1990).

Procyonidae, Ailuropodidae and Canidae seem to be entirely free of periodontal disease in wild state, whereas Viverridae frequently acquire it. It occurs in Ursidae and Mustelidae, although rarely in wild state in the latter. Also, it was assumed by Eklund et al. (1968) that periodontal disease occurs in mustelids at least in part due to an infection with a virus (Aleutian disease).

7.7.2 Pathologies in *Hyaenodon*

Hyaenodon tooth abnormalities
Various diseases, malformations and pathologies in size, shape or function are known in Carnivora as in other mammals (Miles and Grigson, 1990). It shall be noted, that the author never noticed any pathologic alteration in any *Hyaenodon* specimen (examining most of the collections in the Naturhistorisches Museum Wien, Musée d´historie naturelle Paris, Natural History Museum London, American Museum of Natural History (New York), Yale Peabody Museum (New Haven). However, pathologies are known in *Hyaenodon* and were described by Mellett (1977; p. 123, Fig. 69 if not cited differently):

1) Loss of P1 (AM 647, *Hyaenodon crucians*, holotype of "*Hyaenodon paucidens*")

2) Duplication of right p3 (FAM 75693, *Hyaenodon crucians*)

3) Third generation canine on a very aged individual (FAM 75595, *Hyaenodon crucians*)

4) Surplus lingual root in P3 (AM 1488, *Hyaenodon horridus*)

5) Fraction of the mandible resulting in an upward flexure at the symphysis and a condition where the canines would have been driven through the roof of the mouth each time the jaws closed (FAM 75604, *Hyaenodon horridus*)

6) Anomaly of M2 morphology showing a surplus posterior portion (PU 12656, *Hyaenodon horridus*, p. 40 Fig. 21)

7) Although not a tooth anomaly, but for completeness: fractured, healed scapula in a juvenile (FAM 75653, *Hyaenodon horridus*) Mellett (1977; p. 123, Fig. 69)

In the National Geographic documentation "Razor Jaws" (2009) Dr. James Mellett shows a fractured, healed scapula and gives an explanation: *Hyaenodon* had to compete with *Entelodon* in North America. The scapula broke in a fight with *Entelodon*. Other evidence for the competition between the two genera is a *Entelodon* skull with bite marks of *Hyaenodon* ("Razor Jaws", 2009).

7.7.3 Conclusions

All possible pathologies known in Carnivora were summarized here to compare to the fossil genus *Hyaenodon*. Pathologies of the North American taxa were described by Mellett (1977; see above). Hitherto no pathologies of any kind were found in the European species. My personal observation of the numerous specimens especially in the Musée d´Historie Naturelle in Paris gives the impression that pathologies were rare in *Hyaenodon*. It shall be emphasized that the occurring degree of rotation of certain teeth (like the P3 or the p2) are no pathology and known from various taxa on different continents.

Thus, pathologies in *Hyaenodon* occurred rarely, as they do in modern wild state Carnivora. However, all varieties of abnormalities observed in Carnivora like extra teeth, loss of teeth, anomalous tooth morphology, root variations and fractures have been found in *Hyaenodon* too.
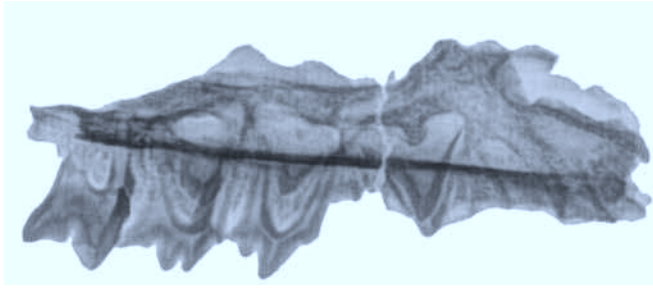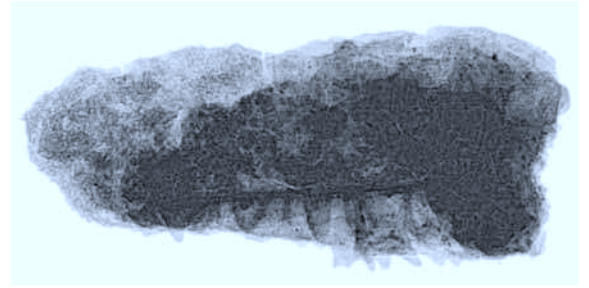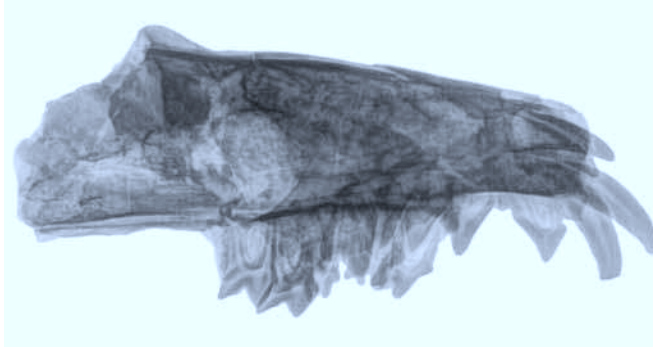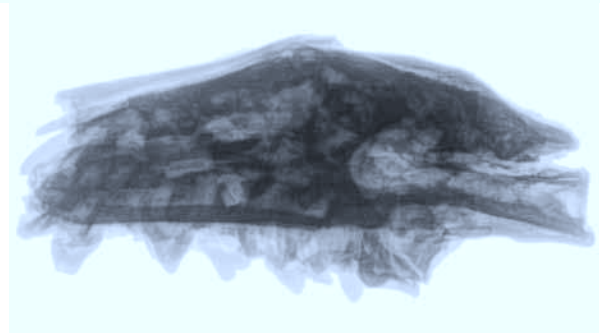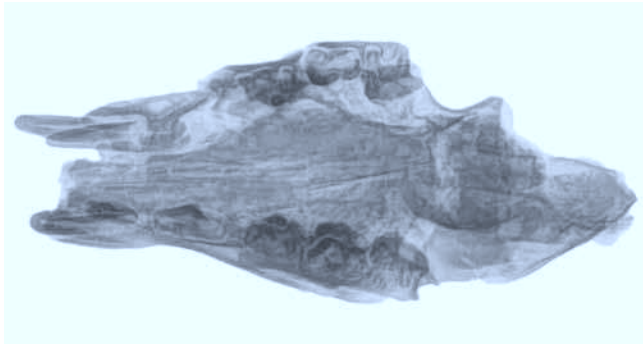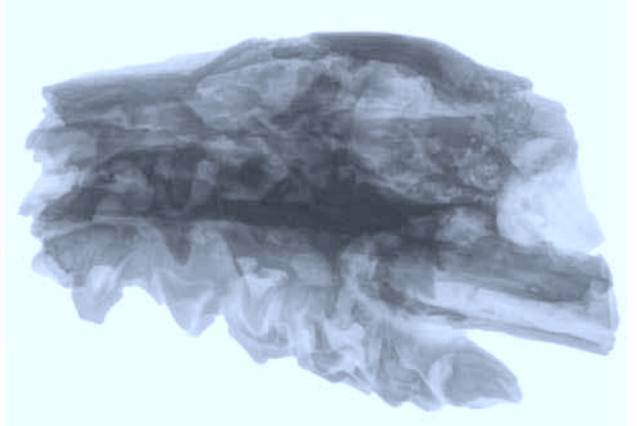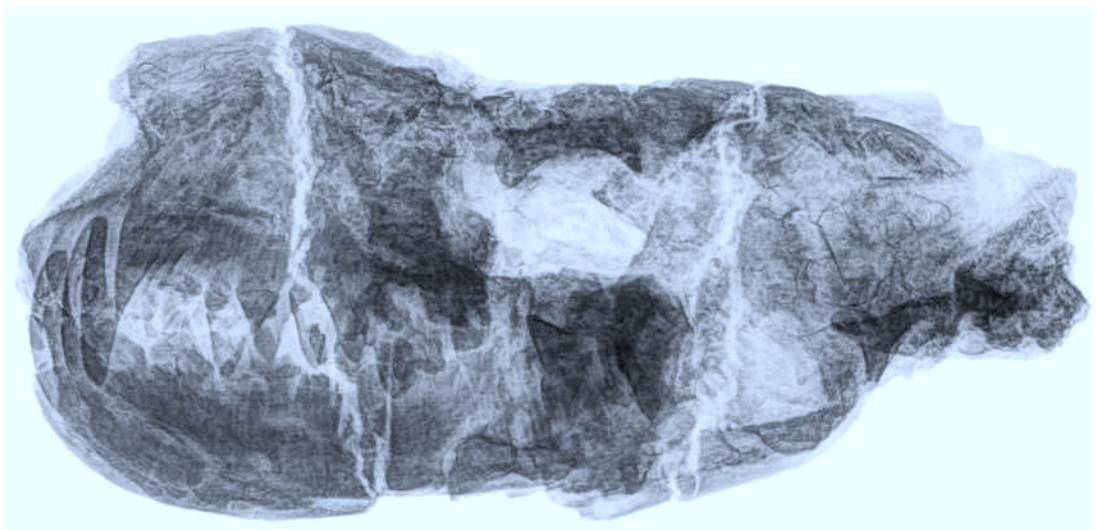
Fig. 7/1 : Inversed x-rays of upper jaws of *Hyaenodon*. **A**, PD 187, *H. exiguus*, note the well develped germ of the P2 and the cavity for the germ of the C; **B**, Qu 8664, *H. filholi*, note the germs of the C; **C**, NMHW 2010/0196/0003, *H. exiguus*, note the erupting P1 and the presence of the anterior alveolus of the M1; **D**, Qu 17662, *H. exiguus*, in lateral (upper) and occlusal (lower) view, note the germs of the C; **E**, Qu 8632, *H. brachyrhynchus*, permanent dentition.
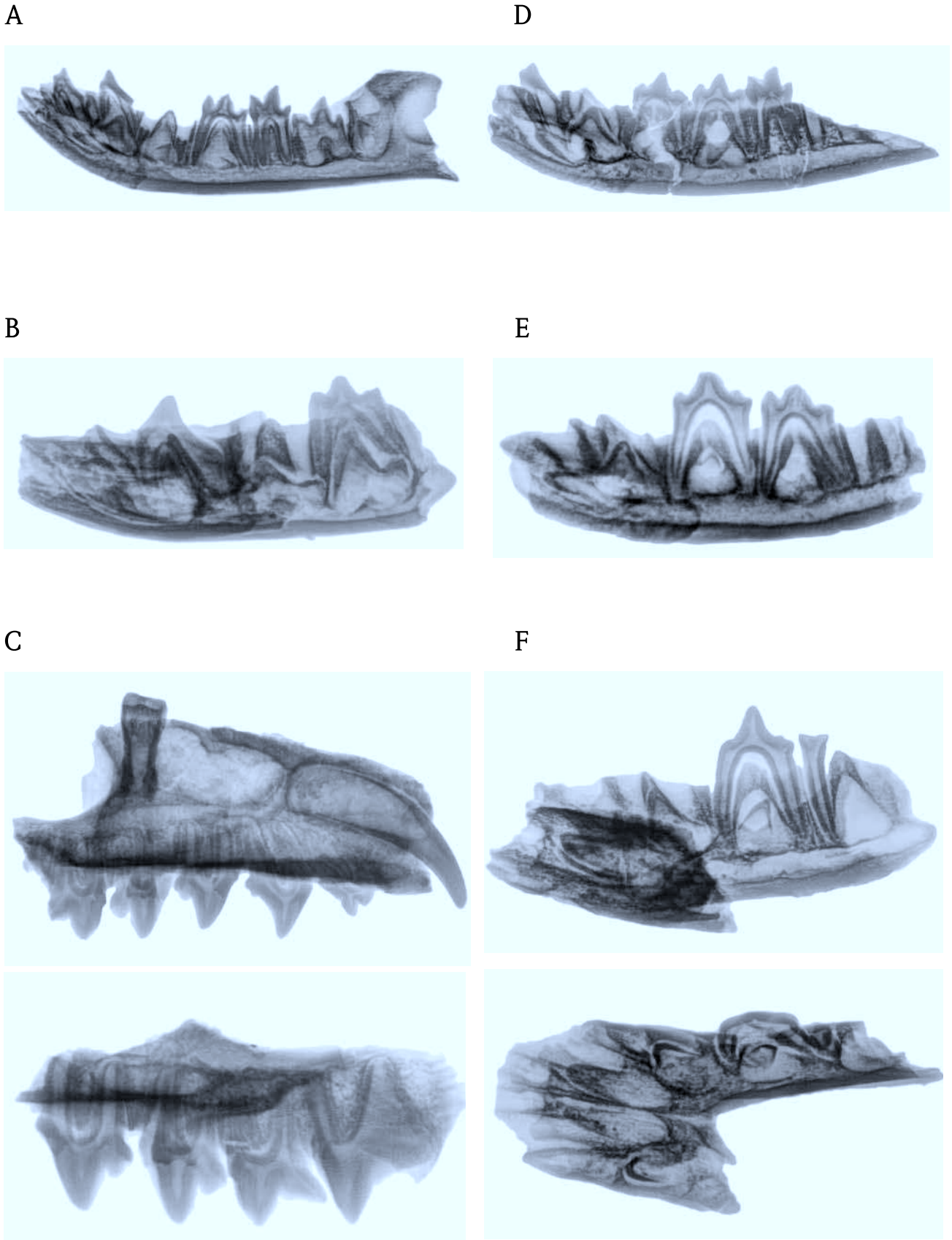
Fig. 7/2 : Inversed x-rays of upper (**C**) and lower jaws (all other) of *Hyaenodon*. **A**, MNHN 1875-931, *H. filholi*, note the erupting m2 and the germs; **B**, M 4498, *H. exiguus*, note the erupting p2 and the germs of the c, p3 and p4;
C, NMHW 2010/0196/0001 (upper) and NMHW 2010/0196/0002 (lower), *H. minor*, note the erupting C and the erupted C; **D**, M 2353, *H. exiguus*, note the germs of the c and the p2; **E**, M 2353a, *H. exiguus*, note the germs of the c and the p2; **F**, M 2348, *H. minor*, in lateral (upper) and occlusal (lower) view, note the p2 and c germs.
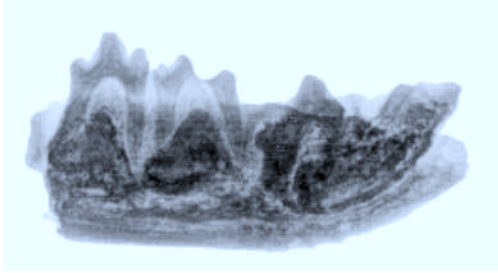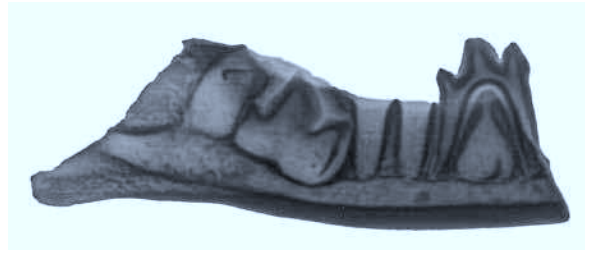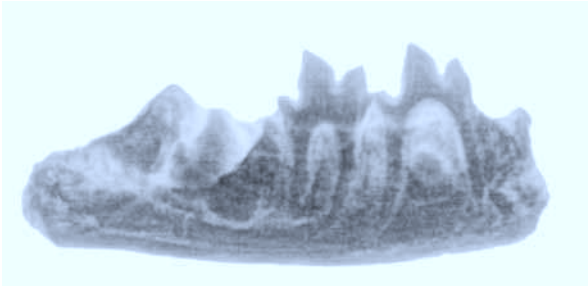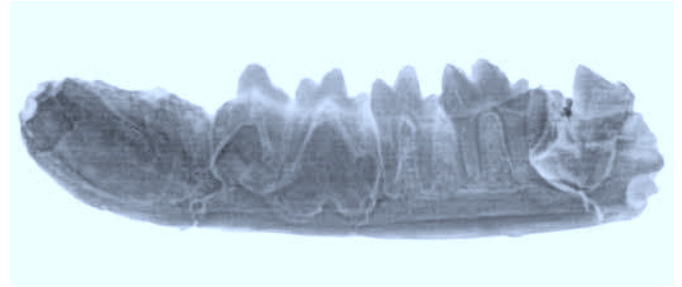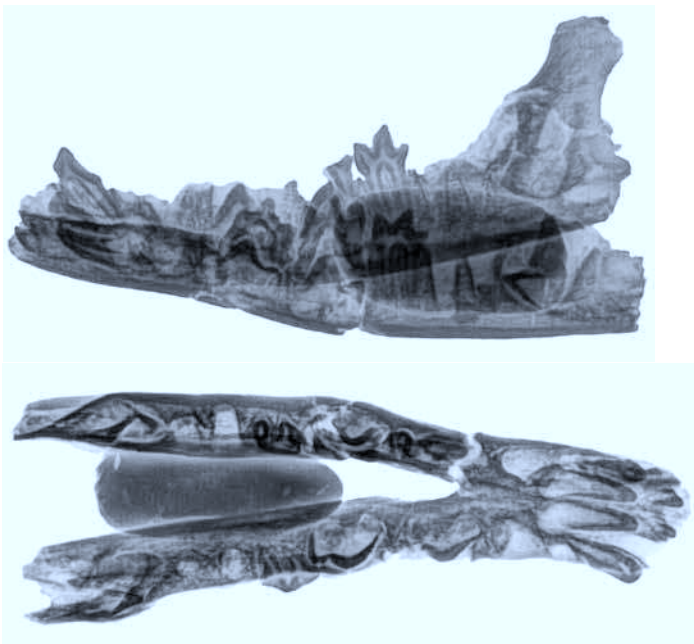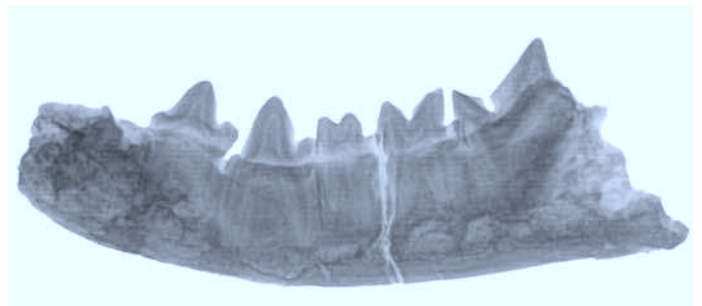
Fig. 7/3 : Inversed x-rays of lower jaws of *Hyaenodon*. **A**, M 84866, *H. filholi*, note the erupting p2; **B**, M 84867, *H. filholi*, note the germ of the m2; **C**, PD 510 in lateral (upper) and occlusal (lower) view, *H. filholi*, note the different developed germs of the c, the p3, the p4 and the m3 and even the i (probable the i2); **D**, NMHW 2009z0084/0003, *H. filholi*, note the germ of the m2; **E**, Mo 22, *H. rossignoli*, note the germs of the p3, the remarkably large germ of the p4 and the erupting germ of the m3; **F**, Qu 8356, *H. rossignoli*, permanent dentition.

A
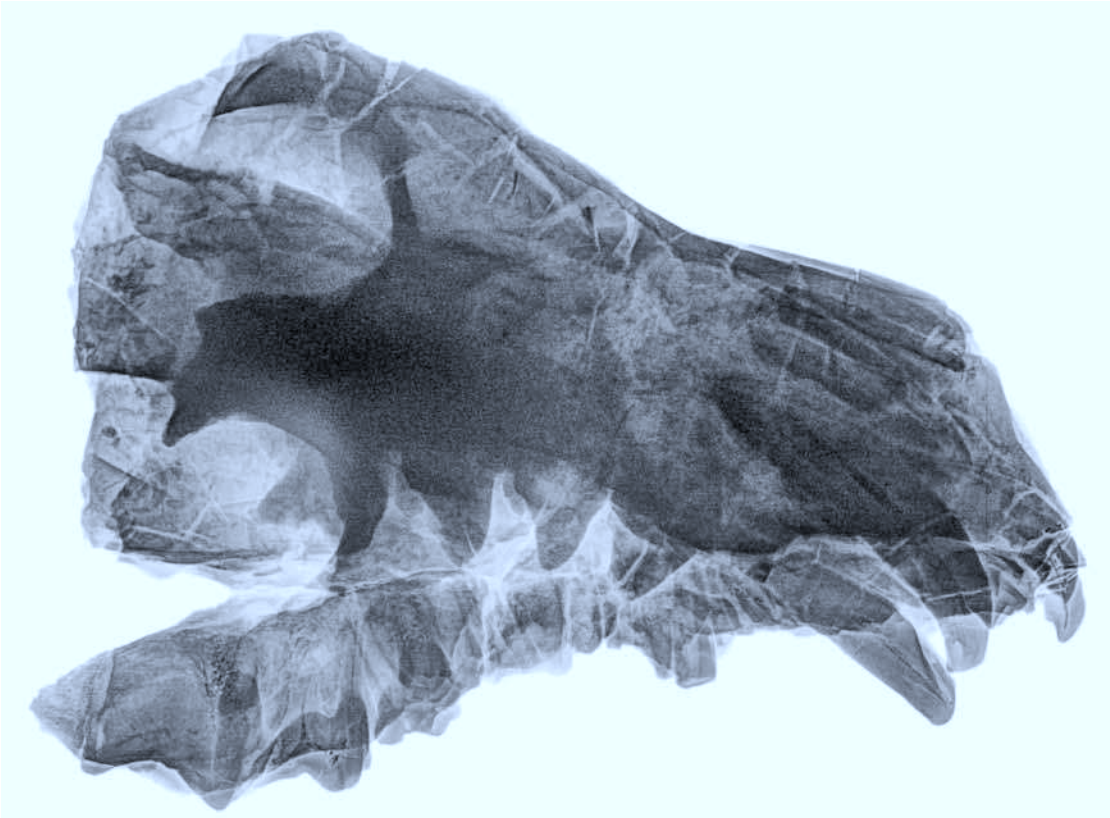
B
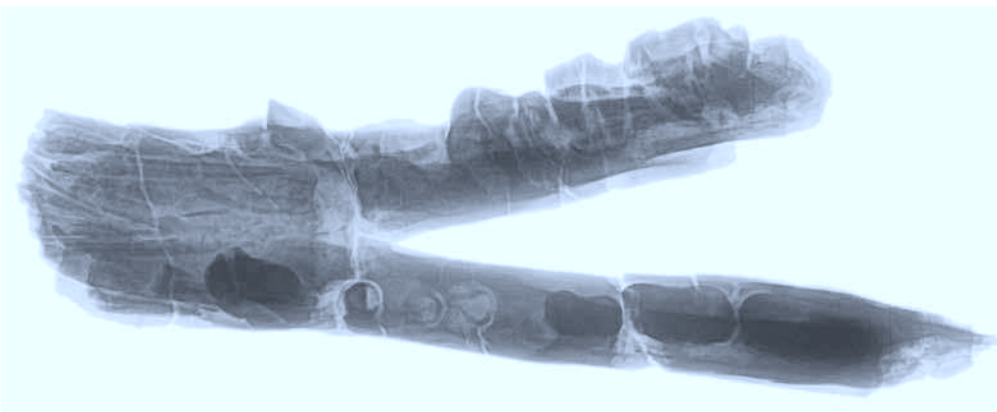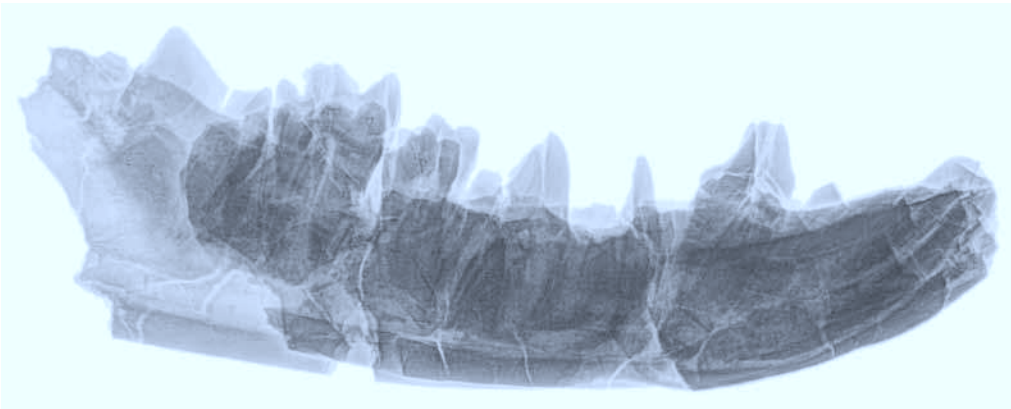
Fig. 7/4 : Inversed x-rays of upper (**A**) and lower jaws (**B**) of *Hyaenodon horridus.* Due to perservation this specimen from the White River Formation is not as suited for x-ray as e.g. specimens from the Quercy (see previous Fig. 7/1-3. **A,** M 5722, note the darker area above the DC; **B,** M 5722, note the darker area below the dc.
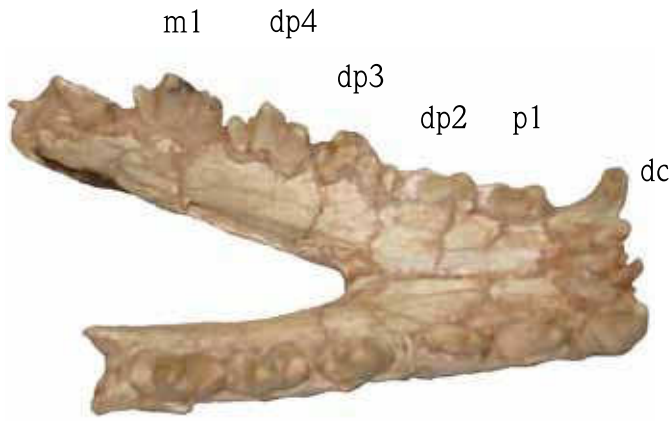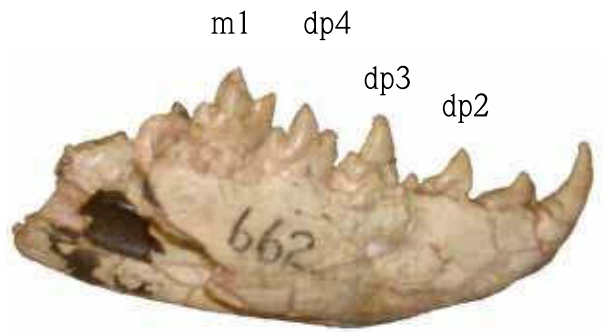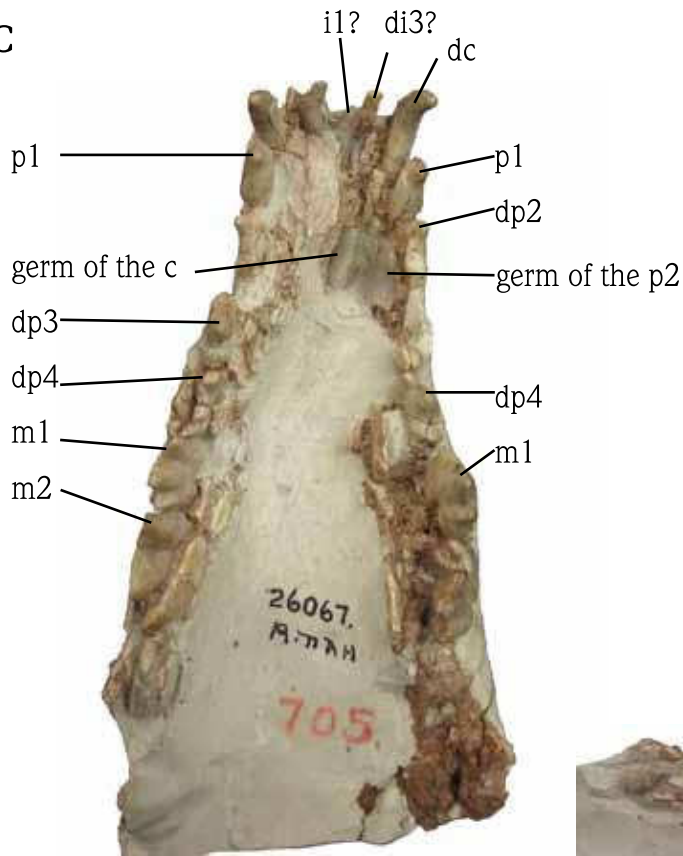
Fig. 7/5 : Juvenile material, lower mandibles, of Asian *Hyaenodon* from the Shara Murun region (Ulan Gochu Formation, Mongolia. Bar equals 1cm. **A**, AMNH 26066, *Hyaenodon* sp., in occlusal view ; **B**, AMNH 26066, *Hyaenodon* sp., in buccal view; **C**, AMNH 26067, *Hyaenodon* sp., in occlusal view; **D**, AMNH 26067, *Hyaenodon* sp., in occlusal view.

North America   Europe

P1
p1

M1
m2

I
i

P2
p2

P4
p4

P4
c, p3, m3

M2
m3

M2

P3
p3

P3
p4

C
c

C
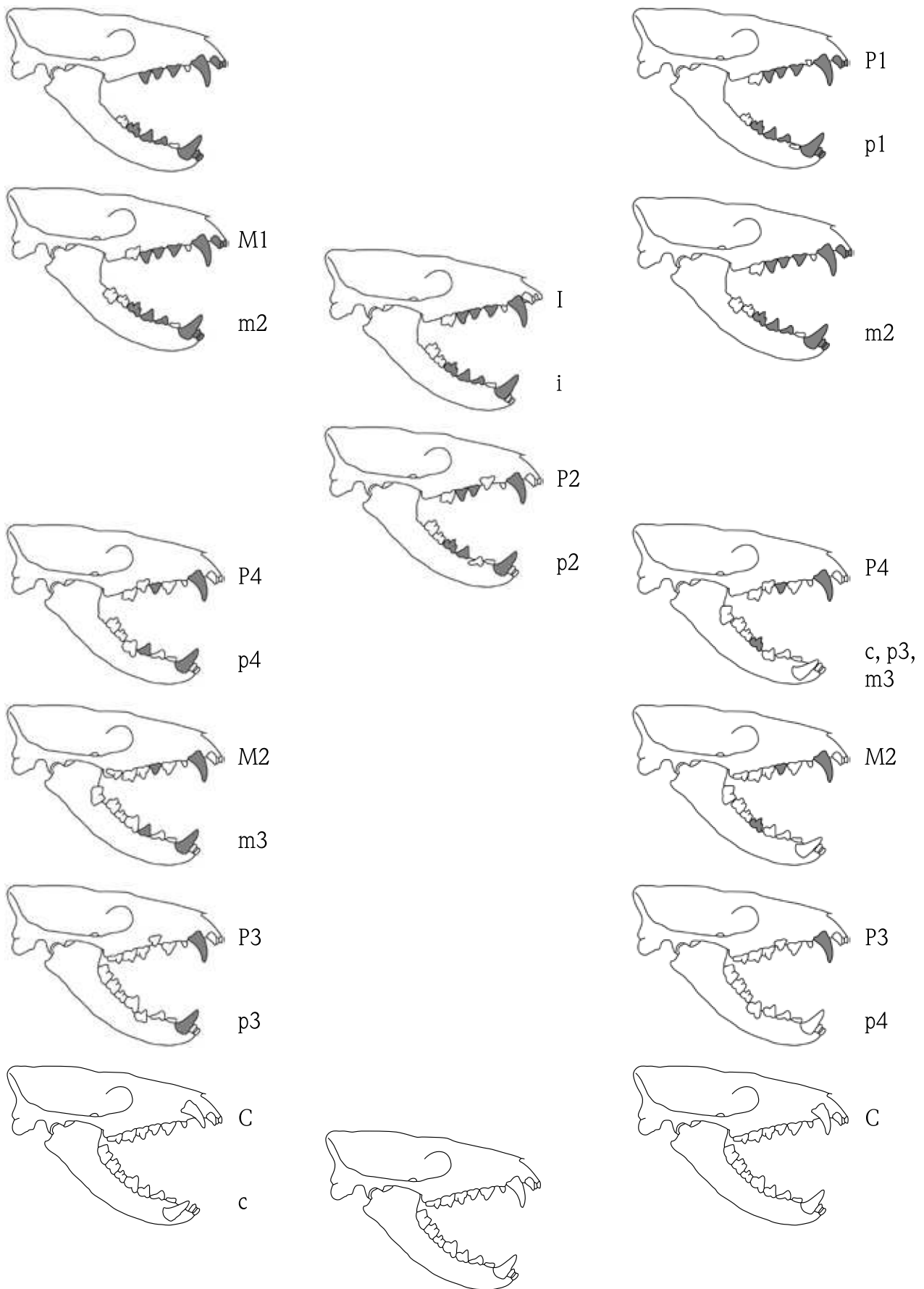
Fig. 7/6: Tooth eruption sequence in the North American (left) and the European (right) *Hyaenodon*. Starting with the earliest known stage above and the adult state below. Milk teeth are grey. The erupting teeth are indicated on the right. Shared stages are depicted in the middle.

Fig. 7/7 : Thin sections of roots of milk and permanent teeth. **A-D** bar equals 1mm. **E** bar equals 0.1mm. **A**, NMHW 2009z0084/0005, root of DP4, *Hyaenodon* sp., note the absence of rings; **B**, NMHW 2009z/0084/0004a, root of m3, *Hyaenodon* sp.; **C**, IUPW 1409, root of dp4, *Vulpes vulpes*, note the absence of rings; **D**, IUPW 1037b, root of p2, *Vulpes vulpes*; **E**, M 5722, upper canine, *Hyaenodon horridus*, note the rings (3-4).

Chapter 8

8. Stereomicrowear and Ultrastructure of the enamel

8.1 Introduction to stereomicrowear

Microwear analysis has not been as exhaustively applied to carnivorous mammals as it has been to other mammals. Only a few studies have dealt with the topic of carnivory by applying microwear techniques. Some of these studies are summarized here.

The first publication that addressed carnivore microwear examined the slicing facet on the m1 (Van Valkenburgh et al., 1990) and used scanning electron microscopy. Van Valkenburgh et al. (1990) inferred the diet of *Smilodon fatalis* compared to canids (*Canis lupus*, *Lycaon pictus*), mustelids (*Gulo gulo*), felids (*Panthera leo*, *Panthera pardus*, *Acinonyx jubatus*) and hyaenids (*Crocuta crocuta*, *Hyaena hyaena*) with special inferences made regarding the amount of bone consumed. In that study, the widest features and highest pit densities were expected to be found in hard object feeders. The authors could not entirely confirm this expectation (e.g. in the case of *Crocuta crocuta*), but they did observe the finest microwear features in *Acinonyx jubatus* (a meat eater avoiding bone), whereas *Smilodon fatalis* exhibited even fewer pits and narrower, longer features compared to the cheetah and thus was inferred to depend strictly on meat, leaving substantial amounts of prey behind (Van Valkenburgh, 1990).

Dewar (2004) applied the low magnification stereomicrowear technique (after Solounias and Semprebon, 2002) using an extant sample of *Lycaon, Canis, Ursus, Otocyon, Urocyon* and *Ailuropoda* to compare results obtained on fossil miacids, condylarths, "creodonts" and fossil carnivores. He used the paracone on the M1. His study found some overlap between the hypocarnivorous forms and certain ungulates and reported that pits discriminate carnivorous mammalian diets better than scratches. This can be confirmed herein as well. Herein the same method was applied on Carnivora with different known diets and on the fossil hyaenodont *Hyaenodon*.

Goillot et al. (2009) used a variation of the Solounias and Semprebon low magnification method (after Merceron et al., 2004) to reconstruct the possible diet of *Amphicyon major* and used as their extant comparative dataset ursids (*Ailuropoda melanoleuca, Melursus ursinus, Tremarctos ornatus, Ursus maritimus*), ailurids (*Ailurus fulgens*), hyaenids (*Crocuta crocuta, Hyaena hyaena*), mustelids (*Enhydra lutris, Lutra lutra, Meles meles*), euplerids (*Eupleres goudotii, Fossa fossana*), herpestids (*Galerella sanguinea, Mungos mungo*), felids (*Leptailurus serval*), procyonids (*Potos flavus*) and canids (*Vulpes vulpes*). That study examined the slicing and grinding facet — if present — on the m1 or the M1 and demonstrated as did Dewar (2004) that optical stereomicroscopy can be successfully applied to carnivorous mammals to distinguish different dietary patterns among them. The inferred diet of *Amphicyon major* in their study (Goillot et al., 2009) was fox-like. Recently Ungar et al. (2010) applied texture analysis to carnivores. Dental microwear texture analysis is a combination of scanning confocal profilometry and scale-sensitive refractal analysis. The shearing facet on the m1 and the m2 was examined and their data set was comprised of canids (*Lycaon pictus, Canis latrans*), hyaenids (*Crocuta crocuta*) and felids (*Acinonyx jubatus, Panthera leo*). The data of the two latter groups was taken from Schubert et al. (2010). The study reported a similar pattern in the African wild dog and the cheetah as well as a different pattern in the m1 than in the m2 which led to a conclusion that texture patterns may be caused partly by processes other than diet. Hence, slicing facets may not be comparable across the order Carnivora (Ungar et al., 2010).

Since its development the low magnification stereomicrowear (Solounias and Semprebon, 2002) has been successfully applied to various groups like lemurs (Godfrey et al., 2004), mastodons (Green et al., 2005), dromomerycids (Semprebon et al., 2004b) or antilocaprids (Semprebon and Rivals, 2007). As time and cost saving method, this technique was chosen also due to its robustness to the selection of the measurement site and the intra- and interobserver reproducibility (Semprebon et al., 2004a).

For examination some of the repeatedly examined taxa in previous studies (Van Valkenburgh et al., 1990; Goillot et al., 2009) were chosen, e.g. *Crocuta crocuta* and *Acinonyx jubatus*. More were added to get

information about different dietary niches, although the aim was not to overload a basic carnivorous data set with too many taxa.

8.2 Introduction to the enamel ultrastructure analysis

The description of enamel microstructure and nomenclature follows Koenigswald & Clemens (1992). The enamel of *Hyaenodon* has already been described by Stefen (1997b). She examined North American forms of this genus besides other hyaenodontids and oxyaenids: *Hyaenodon brevirostris*, *H. horridus*, *H. mustelinus* and *Hyaenodon* sp. Herein it was applied for the first time on European *Hyaenodon*.

Genus separation is normally not seen in enamel ultrastructure, and therefore, it is generally used for higher taxonomy and ecology (Stefen, 1997a). Carnivora and "creodonts" all have prismatic enamel and their Hunter-Schreger-Bands (HSB) usually run horizontally around the tooth crown and show differing degrees of waviness such as: undulating (>140° at wave crests and troughs), acute-angled (140°-70°) and zigzag HSBs (70°-50°; see Fig. 5 in Stefen, 1997a). According to Stefen (1997a), acute-angled and zigzag HSBs are derived and evolved in parallel in different groups of carnivorous mammals. Zigzag HSBs are reported (1997a) to most likely have a higher resistance to internal stress induced by chewing forces than other types of HSB and thus are characteristic for bone cracking carnivores (e.g. hyaenids).

While enamel ultrastructure of carnivorous mammals has been examined before by various authors (Tomes, 1906; Reif, 1974; Skobe et al., 1985; Zhao and Li, 1987; Koenigswald, 1992), Stefen (1997a) presented in her study both a good overview of prior results on the enamel ultrastructure of carnivorous mammals as well as the taxonomic, phylogenetic and biomechanical relevance of these enamel structures. A transition from undulating to acute-angled and/or zigzag HSBs is found in amphicyonids, ursids, canids (e.g. wolf), otariids, felids, hyaenids, hyaenodontids, oxyaenids, mesonychids and condylarthra while in hyaenids, canids (Borophaginae), the hemicyonids, the hyaenodontid *Hyainailouros* and the oxyaenid *Sarkastodon* display exclusively zigzag HSBs.

In an evolutionary sense, the starting point for the "creodonts" and Carnivora is the radial enamel found in *Cimolestes* (Stefen, 1997a). The various types of enamel microstructural patterns are thought to have been developed through parallel evolution. Thus, the occurrence of particular HSB types is thought to reveal dietary preferences as follows: zigzag HSBs are characteristic for ossiphagous habits, seen in *Crocuta*, *Hyaena* and *Parahyaena*; exclusively undulating HSBs are found in the insectivorous hyaenid *Proteles cristatus* as well as the cheetah; and *Canis lupus*, *Gulo gulo* and the genus *Panthera* show a transition from undulating to zigzag HSBs, indicating tendencies towards ossiphagous feeding habits (Stefen, 1997a).

The amount of bone consumed correlates largely with the zigzag type of HSBs (e.g., in *Panthera*; Stefen, 1997a). Exceptions are *Hyaena* which shows the same pattern as *Crocuta*, although it consumes less bone and *Gulo gulo* which has about the same amount of bone consumption as *Hyaena*, but shows a transition from undulating to zigzag (only in the tips) HSBs. Cracking bones puts vertical, horizontal and radial tensile stresses on the teeth. Thus the three dimensional complex structure of the zigzag HSBs are thought to reinforce the enamel to prevent destruction (Stefen, 1997a).

Stefen (1997b) also reports enamel types in certain "creodonts" as follows: *Hyaenodon horridus, Pterodon dasyuorides* and *Hyainailourus* sp. display the zigzag only HSB type like recent hyaenids; *Hyaenodon brevirostris* and *Hyaenodon mustelinus* show a transition from undulating over acute-angled to zigzag HSB. Stefen (1997b) argued that a certain body size is needed to crack bones, but that *Nimravus* as a large animal shows exclusively undulating HSBs and thus size is not the main factor for the development of zigzag HSBs. *Hyaenodon* has long been considered to have occupied an hyena-like niche in its time (Mellett, 1977). This assumption is based on the fact that *Hyaenodon* premolars (especially in old individuals) are often worn down to a plateau similar to what is seen in *Crocuta* and also due to the extreme wear on the m1, which is often completely worn down to its stumps.

8.3 Material and Methods

Specimens used are housed in various museums in the USA, UK, France and Austria (see Abbreviations). Modern Carnivora with known diets (e.g. Van Valkenburgh, 1988; Wilson and Mittermeier, 2009) were tested. Hyaenidae were chosen for a range of bone/meat diet: *Parahyaena brunnea* (n=6), *Hyaena hyaena* (n=7) and *Crocuta crocuta* (n=25, hyena with the most amount of bone in its diet). Felidae represent meat specialists: *Acinonyx jubatus* (n=19, exclusive meat eater) and *Panthera leo* (n=8, meat/bone in different proportions). Representative for a carnivore with a piscivore diet *Lutra lutra* (n=24, fish and invertebrate eater) was picked. Canidae include taxa with a mixed carnivorous diet: European *Vulpes vulpes* (n=32) and Asian *Vulpes vulpes* (n=5). *Genetta genetta* (n=12, mixed/fruit carnivorous) and *Nandinia binotata* (n=6, fruit as major part of the diet) are representative for carnivorous mammals with differing amounts of fruit in their diet.

The *Hyaenodon* sample was comprised of 13 North American specimens, 2 Asian specimens and 15 European specimens for the m2 alone.

A buccal enamel fragment of an already broken permanent premolar of *Hyaenodon brachyrhynchus* was used for the enamel ultrastructure analysis. The specimen (a mandible, NMHW A 4471) and the resulting specimen (tangentionally and transversally sectioned enamel on a REM-desk) is hold by the NMHW.

The supposed hyena-like dietary niche for *Hyaenodon* (Mellett, 1977) was tested using microwear analysis which classifies and quantifies food scars etched into dental enamel. Microscopic enamel microwear features of select extant carnivores and the hyaenodontid *Hyaenodon* were assessed via standard light stereomicroscopy to discern differential refractive properties of enamel scar features at low magnification (after Solounias and Semprebon, 2002). External oblique illumination was used to direct a fiberoptic light source across the surface of toothcasts at a shallow angle to the occlusal surface to visualize microwear scar topography. A standard $0.4 \times 0.4 = 0.16$ mm^2 ocular reticle was employed at 35× magnification to quantify the number of small and large pits (round scars), scratches (elongated scars with parallel sides), and gouges (large scars with irregular borders). In addition, scratches were classified in terms of their textures as being either fine, coarse, or hypercoarse following the criteria developed to recognize these differences via differential light refraction described in Solounias and Semprebon (2002) and Semprebon et al. (2004). Figure 8/1 E shows a photomicrograph of the *Hyaenodon* enamel band at 35 times magnification. What is immediately obvious in Figure 8/1 E is that not all scratches are alike, nor are all pits. The dietary significance of such differences in low magnification microwear scars is discussed at length in Solounias and Semprebon (2002) and Semprebon, et. al. (2004). Note the large numbers of large (dark) and small (white) pits and irregularly shaped gouges throughout the enamel surface of *Hyaenodon* (Fig. 8/1 E, photo taken by Gina Semprebon during my stay at the Bay Path College). A wide hypercoars scratch is defined by a width of more than 0.025 mm (see Appendix for more details). The width of a narrow hypercoarse scratch lies below that value.

Premolars and molars were sampled. In the case of *Hyaenodon* the P4-M2 and the p4-m3. For standardization, only data taken from the carnassial, the P4 or m1 in Carnivora or the m2 in *Hyaenodon* was further analysed and plotted in diagrams (Fig. 8/1 A-D). The m2 in *Hyaenodon* was chosen, because most data came from this tooth position and it is functionally a carnassial. During this study, no significant differences were found between the pattern in the upper and lower carnassial. The standard deviations of the different tooth positions, the P4 and the m1, were calculated for taxa with a sample number of about ten. *Crocuta crocuta* shows an especially good correspondence in this respect (P4: 3.4; m1: 3.9), but conformity can also be seen in *Acinonyx jubatus, Vulpes vulpes* (from Europe) and *Lutra lutra* (see Appendix). The same is seen in the different tooth positions acting like a carnassial in *Hyaenodon* from different continents, where we have enough data (not for the M1 and the M2): the P4, the m1, the m2 and the m3 give all values of approximately 12 standard deviations. The same can be stated for the p4-m3 and the P4-M2 in *Hyaenodon* — as they all function as a carnassial.

To analyse the enamel ultrastructure and the appearance of Hunter-Schreger-Bands, a fragment of the enamel of a tooth was embedded in polyester resin and sectioned (tangentially and transversally). Afterwards the specimen was grinded with grinding powder with a grain size of 500, then 1000 and then with polishing powder. Then the specimen was etched with 2N HCl for four seconds. Afterwards it was cleaned in an ultrasonic bed and dried. To analyse the specimen it was coated with gold and studied under the scanning electron microscope (see Fig. 8/2). The fragment was regularly studied under the binocular microscope during the procedure. This proceeding was supervised by Daniela Kalthoff, who supported me during her lecture at the Department for Paleontology (University Vienna) in December 2008.

The photographs (including REM-photos) were all produced at the Department of Paleontology (University Vienna) and proceeded with Adobe Photoshop (CS 5). The PCA analysis was performed in PAST with standardized values using a correlation matrix (see Appendix).

8.4 Results

8.4.1 Microwear results

Extant Carnivora with different dietary habits can be seen to occupy different parts of a dietary morphospace when simple plots are constructed. Fig. 8/1 A-B represents bivariate plots of total scratches versus total pits. In Fig. 8/1 A the extant comparative carnivore taxa are shown. Note that *Vulpes vulpes* and *Acinonyx jubatus* possess lower numbers of pits relative to the other extant taxa studied. Taxa with total pit numbers around 110 are those with a considerable amount of tough or hard foods (fruits, shells, bone) in their diets (e.g., *Genetta genetta, Nandinia binotata, Lutra lutra, Panthera leo, Parahyaena brunnea, Hyaena hyaena* and *Crocuta crocuta*). Also, Fig. 8/1 A reveals that higher scratch numbers are found in those taxa with more hard items in their dietary regimes. Not surprisingly, the cheetah and the lion are well separated. Fig. 8/2 B represents a total scratch versus total pit plot with only the meat and/or bone consuming taxa (as well as the fox as an outgroup) represented as well as *Hyaenodon* from different continents.

Hyaenodon plots together with the hyenas and the lion. Biogeographic differences are subtle, but the European *Hyaenodon* taxa plot closer to the hyenas (especially near *Crocuta crocuta*) and the North American taxa plot closer to *Panthera leo*. Asian *Hyaenodon* taxa are more similar in total scratch/pit results to those taxa from North America. Biogeographic differences can also be seen in *Vulpes vulpes* (Fig. 8/1 C). The small Asian number of individuals plot once with the lion and once with the hyena *Crocuta*. These results are consistent with *Hyaenodon* as a genus displaying a broad range of dietary habits depending on locality and the concomitant differences in food acquisition.

Figure 8/2 A shows where extant forms plot when three variables (total scratches versus total pits versus gouges) that reflect in a simple manner the relative degree of abrasiveness of food items are plotted. It is obvious in Fig. 8/2 A that the hyena bone crunchers have the coarsest microwear features of the extant taxa studied (i.e., they have more pitting, scratching, and gouging) followed by the lion. It is also clear that *Hyaenodon* plots closer to the hyenas than to the other extant taxa studied, but does not exhibit the same extreme level of pitting and gouging as in extant hyenas. The African palm civet (*Nandinia binotata*) which is known to consume a large amount of fruit in its diet is intermediate in terms of its diet between the coarse-wear hyenas and lion and those forms with relatively fine microwear patterns (e.g., foxes, genet, otter and cheetah).

Interestingly, pits rather than scratches are the discriminating feature among carnivores of different diets. Fig. 8/1 C-D shows bivariate plots of small versus large pit numbers. These two variables separate the various trophic groups better than the total scratch versus total pits plots (Fig. 8/1 A-B). In Figure 8/1 C, the cheetah and the fox are now more distinctly separated. *Nandinia binotata* is rather extreme with high values for small

pits. The cheetah and the lion are still well separated and the lion once again plots within a wide range, most likely demonstrating that the amount of bone taken in is quite variable from one individual to another. *Lutra lutra*, *Genetta genetta* and *Panthera leo* display some overlap together with the hyenas (except *Crocuta*). A hierarchical cluster analysis (Fig. 8/2 B; this analysis as well as the 3D-plot were performed together with Gina Semprebon) was also performed including extant carnivorous comparative taxa and *Hyaenodon*. This analysis grouped *Hyaenodon* with those modern animals possessing similar microwear in terms of the 8 microwear variables measured (see Appendix). The results of the cluster analysis (Fig. 8/2 B) shows four subclusters: *Vulpes vulpes* and *Acinonyx jubatus* are clustered because of relatively lower abrasion microwear patterns than the other extant taxa studied (e.g. less gouging, pitting and scratching of enamel). *Nandinia binotata* is clearly distinct from the other extant forms and from *Hyaenodon* mainly because of the relatively large numbers of puncture-like seed pits found in its enamel which are characteristic of taxa that consume a fair amount of fruit. The other two subclusters are comprised of extant taxa with fairly coarse microwear patterns either due to bone crushing (e.g., in the hyenas and the lion or shell crushing in the otter) or grit encroachment due to consumption of a large amount of arthropods (e.g. in the genet). *Hyaenodon* from Asia clusters more closely to the extant *Crocuta crocuta* which consumes a large amount of bone, whereas the North American and European *Hyaenodon* cluster more closely to *Panthera leo* which consumes less bone.

The previous described diagrams get additional evidence from the calculated standard deviations. First, in general the values for the small pits and the total pit number are the most interesting ones (see Appendix). In the following the standard dviations for the total pit number is discussed. The standard deviation of the North American *Hyaenodon* and the lion *Panthera leo* are the highest ones (around 12). This correlates with the wider spreads of these taxa in the plots. The European *Hyaenodon* scores high too (9.9). The hyena *Crocuta crocuta* is showing low variability (3.6).

The range of the total pit number in all recent Carnivora and the North American and European *Hyaenodon* is shown in Fig. 8/2 C (reconstructed with Prism 5.0). It shows the 95% confidence interval (box), the mean value (black line) and the total range of all data points. *Hyaenodon* overlaps mainly with *Crocuta crocuta* and *Panthera leo*. In this plot no difference between the European and the North American *Hyaenodon* is apparent. A principal components analysis was done too (Fig. 8/2 D). The first component explains 63.54% of variance and the second one 36.45%. The values are given in the Appendix. The plot of the PCA indicates: 1) the clustering of *Hyaenodon* with carnivores that include bone in their diet: *Panthera leo* and *Crocuta crocuta*; 2) the stronger correspondence of the North American *Hyaenodon* with *Panthera leo* opposed to the stronger correspondence of the European *Hyaenodon* with *Crocuta crocuta*; 3) the extreme frugivory in *Nandinia binotata*, that clearly sets it apart from all other taxa; 4) the "soft" diet of *Acinonyx jubatus* and *Vulpes vulpes*, that clusters them on the opposite end of the x-axis compared to those with more tough foods (mentioned above under 1).

In this plot as in almost all others, *Hyaenodon* exhibits microwear that is more similar to those of the extant hyenas than to the other carnivore taxa studied although its microwear is not as extreme as those of the extant bone consumers making it somewhat unique. Of the hyenas studied, *Hyaenodon's* microwear pattern is closer to that of *Crocuta crocuta* than to *Hyaena hyaena* or *Parahyaena brunnea*.

8.4.2 Results of the enamel ultrastructure analysis

Results of the analysis of the enamel ultrastructure of European *Hyaenodon* are similar to what has already been described for the North American forms (Stefen, 1997b) and features seen in both European and North American *Hyaenodon* are summarized below:
The prism shape varies from (hexagonal)-polygonal to polymorph. A rounded shape is rarely found (Fig. 8/2 A). Open prism-sheaths dominate, but most polygonal and hexagonal prisms possess closed sheaths (Fig. 8/2 A). Crystallites within the prisms are oriented parallel to the axis of the prism (Fig. 8/2 D and B). The

interprismatic matrix surrounds the prisms with equal thickness (Fig. 8/2 E). The HSB consist of six prisms on average (6.3 in Stefen 1997b; Fig. 8/2 C and F).

The zigzag HSB can be clearly seen in the light microscope (Fig. 8/2 G). They change from undulating at the base of the tooth, via the acute-angled type to the zigzag configuration in the tips.

Certain ultrastructural features that were diagnosed by Stefen (1997b) (e.g., angle between prisms varying from 40-70° of adjacent bands and undulating zig-zag patterning of the Hunter-Schreger Bands — especially toward the tip of the tooth) could not be tested here, because only a small enamel piece from the middle of the height of the premolar was available for study.

Finally all the features of the enamel of the European *Hyaenodon* studied here conform with the hitherto known enamel from North American *Hyaenodon* (Stefen, 1997b).

8.5 Conclusions on the diet of *Hyaenodon*

Overall, pits are more effective than scratches in separating the various extant taxa into their known dietary groups. In carnivores, comparing small pit versus large pit numbers gives better dietary separation than comparing scratches versus pits as in most other mammalian groups analyzed with microwear. The microwear pattern in *Panthera leo* is intermediate between the cheetah (*Acinonyx* — relatively strict meat diet) and the hyenas (e.g. *Crocuta* — more bone in their diets). This conforms to its known diet (meat and some bone) and previous patterns seen in other studies (Van Valkenburgh, 1990). *Panthera leo* is known to occupy a rather broad niche, as the amount of bone taken in varies.

Fruit eating taxa vary in their microwear pattern depending on the amount of fruit taken in. The genet (*Genetta*) is an animal that depends on a broad diet consisting of worms, larvae, insects, fruit and other plant matter, whereas the African palm civet (*Nandinia binotata*) depends on a diet composed of 80% fruit (Wilson and Mittermeier, 2009). Fruit contains abrasive phytoliths in pericarps and seed coats that are thought to cause very characteristic types of puncture-like large pitting of dental enamel (see Solounias and Semprebon, 2002; Semprebon, 2004). Such pitting is high in *Nandina*.

The European otter (*Lutra lutra*) plots close to *Genetta genetta* most likely because abrasive shell cracking is part of the diet of the former and grit along with arthropods as well as fruits are consumed by the latter — both of which have been shown to cause abrasive microwear patterns. The fox *(Vulpes vulpes)* is known to have a more omnivorous diet and this is reflected in its lower numbers of scratches, small pits and large pits compared to more meat consuming species as the cheetah and the lion. The hyenas are very distinctive in terms of their microwear and show very high pit numbers, presumably to their consumption of bone. Hard food like bone seem to result in high pit numbers. *Nandinia binotata* shows also high pit numbers, probably due to hard seeds and fruits as part of its frugivorous diet. This taxon is — as all fruit consumers — easily separated by showing large puncture pits. Puncture pits seem to be produced by seeds and fruits (e.g. Godfrey et al., 2004) and do not occur in carnivores that do not consume these fruit items.

Crocuta crocuta separates very well from the other taxa, because it is the extremest bone crusher of the hyenas. In addition, *Hyaenodon* displays a relatively wide pit distribution compared to *Crocuta crocuta* (also evident from the higher standard deviation values), possibly indicating a more generalized diet than modern hyenas. In fact, most North American taxa of *Hyaenodon* fall into the plotting space of *Panthera leo*, which is a meat eater with varying degree of bone intake. *Hyaenodon* obviously consumed relatively coarse foods in its diet, indicated by

1) high pit numbers

2) overlap with the bone crusher *Crocuta crocuta* and

3) overlap with the meat/bone eater *Panthera leo*.

There are even some individuals that plot near the cheetah. Thus, microwear results indicate a broader dietary niche than that seen in most modern carnivores.

The European species differ from the pattern seen in North American forms. However, for the Asian taxa further material is needed. Up to now, no solid inferences can be made, because data for these taxa is sparse.

The same pattern in the enamel ultrastructure features was found for European *Hyaenodon* as what was described for North American species by Stefen (1997b). Furthermore, the occurrence of zigzag HSB is known from the configuration of tooth enamel under the binocular microscope for European *Hyaenodon*, even in the smallest European species *Hyaenodon filholi*. This configuration is showing the transition from undulating to zigzag HSB in different European species, as it is known in North American taxa (except for *Hyaenodon horridus*, Stefen, 1997b). Such pattern is found in recent Carnivora with tendencies to ossiphagy (Stefen, 1997a): e.g. the wolf and large felids. Hyenas show exclusively zigzag HSB (Stefen, 1997a). However, zigzag HSB are highly important for resistance to cracks in the enamel, when high biting forces are produced (Stefen, 1997a).

The functional morphology of the mandible in *Hyaenodon* was discussed by Valentin and Lange-Badré (1991): the symphysis is frequently fused, lateral movements were nearly impossible, but anteroposterior movements rare in carnivorous mammals could be performed; furthermore, the carnassials are in an extreme posterior position (Valentin and Lange-Badré, 1991). Concluding, *Hyaenodon* was unique in this constellation of characters and this further evidences that the head with its rows of carnassials was the most powerful weapon (Mellett, 1977; "Razorjaws", 2009).

The extreme wear facets in the dentition, the hyenid-like microwear pattern prevalent in European *Hyaenodon* studied here and the fact that zigzag HSB occurred in the enamel, suggests that bone cracking was indeed part of the European *Hyaenodon* diet.
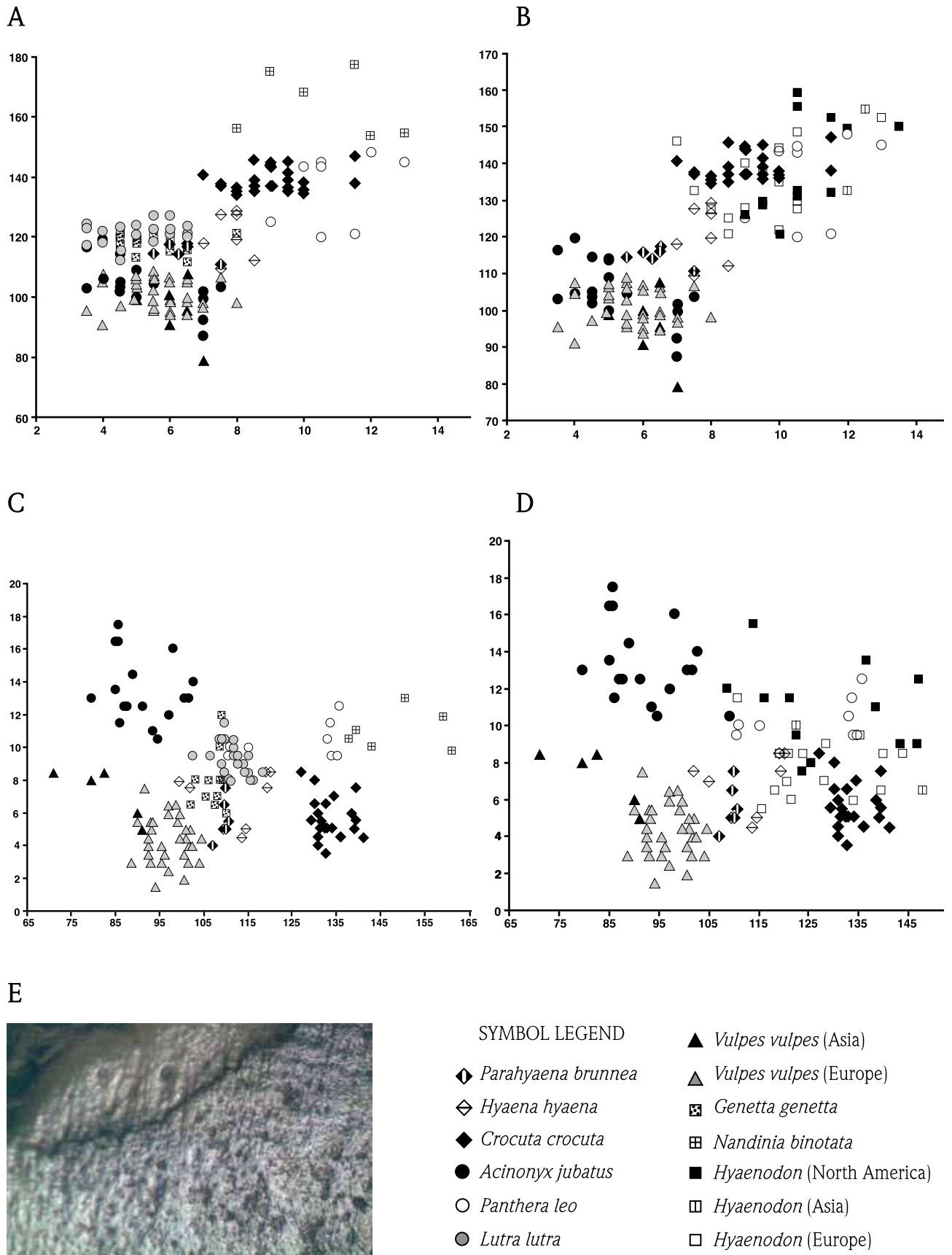
Fig. 8/1: Diagrams plotting the raw data of the stereomicrowear results. **A**, total count of scratches (x-axis) versus total count of pits (y-axis) in recent Carnivora; **B**, total count of sratches (x-axis) versus total count of pits (y-axis) in select Carnivora and *Hyaenodon*; **C**, total count of small pits (x-axis) versus total count of large pits (y-axis) in recent Carnivora; **D**, total count of small pits (x-axis) versus total count of large pits (y-axis) in select Carnivora and *Hyaenodon*. Note the better separation in diagrams using exclusively pit numbers; **E**, photo of microwear in an Asian *Hyaenodon*, note the gouging.
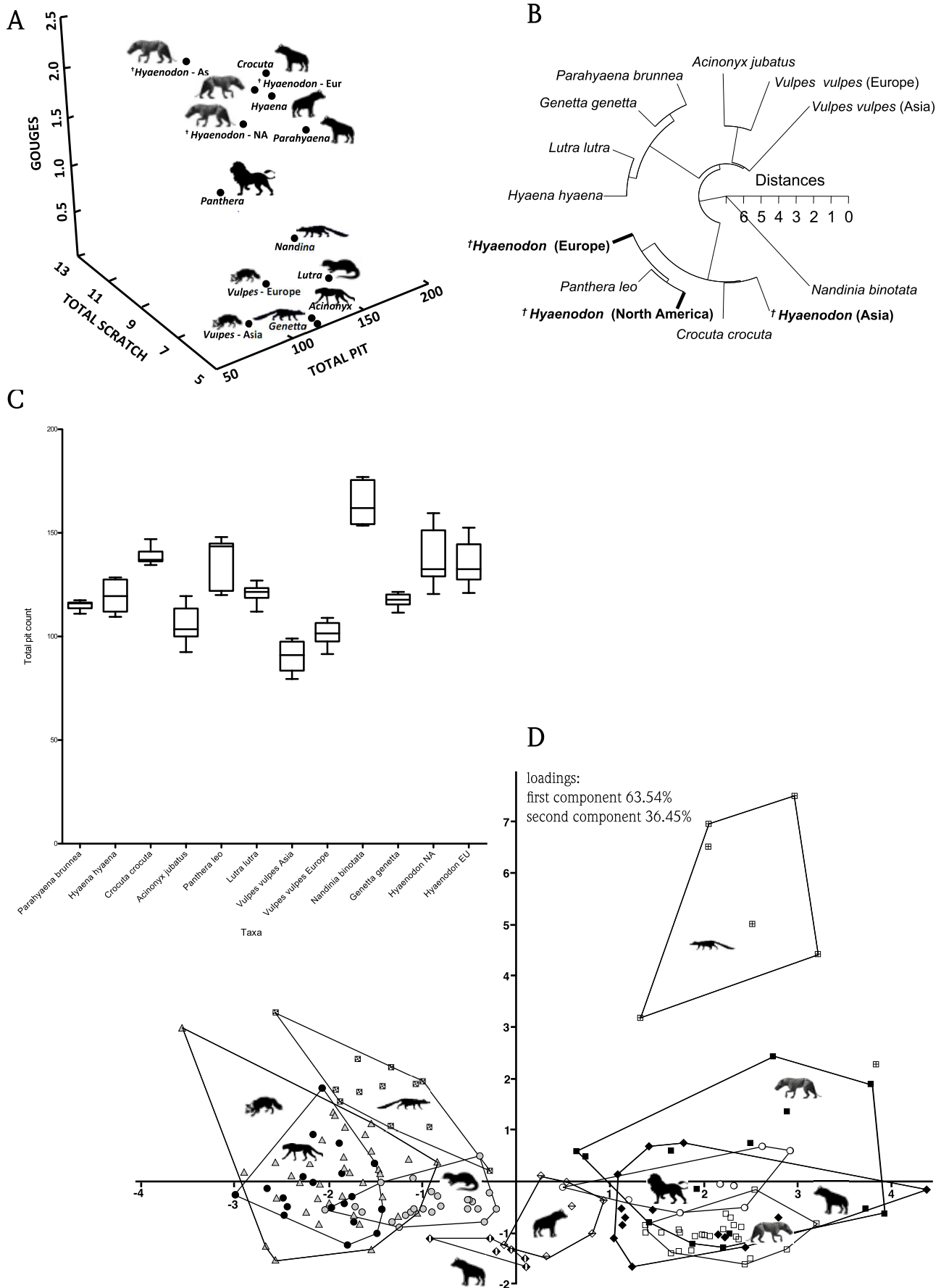
Fig. 8/2: Additional diagrams using the data of the stereomicrowear results of recent Carnivora and *Hyaenodon*.
A, 3D-plot using the scratch count, the pit count and the gouging; B, hierarchical cluster plot, note the position of the North American *Hyaenodon*; C, bar diagram showing the range of the total pit count within a 95% confidence interval and the mean value (black line); D, PCA-diagram with silhouettes.

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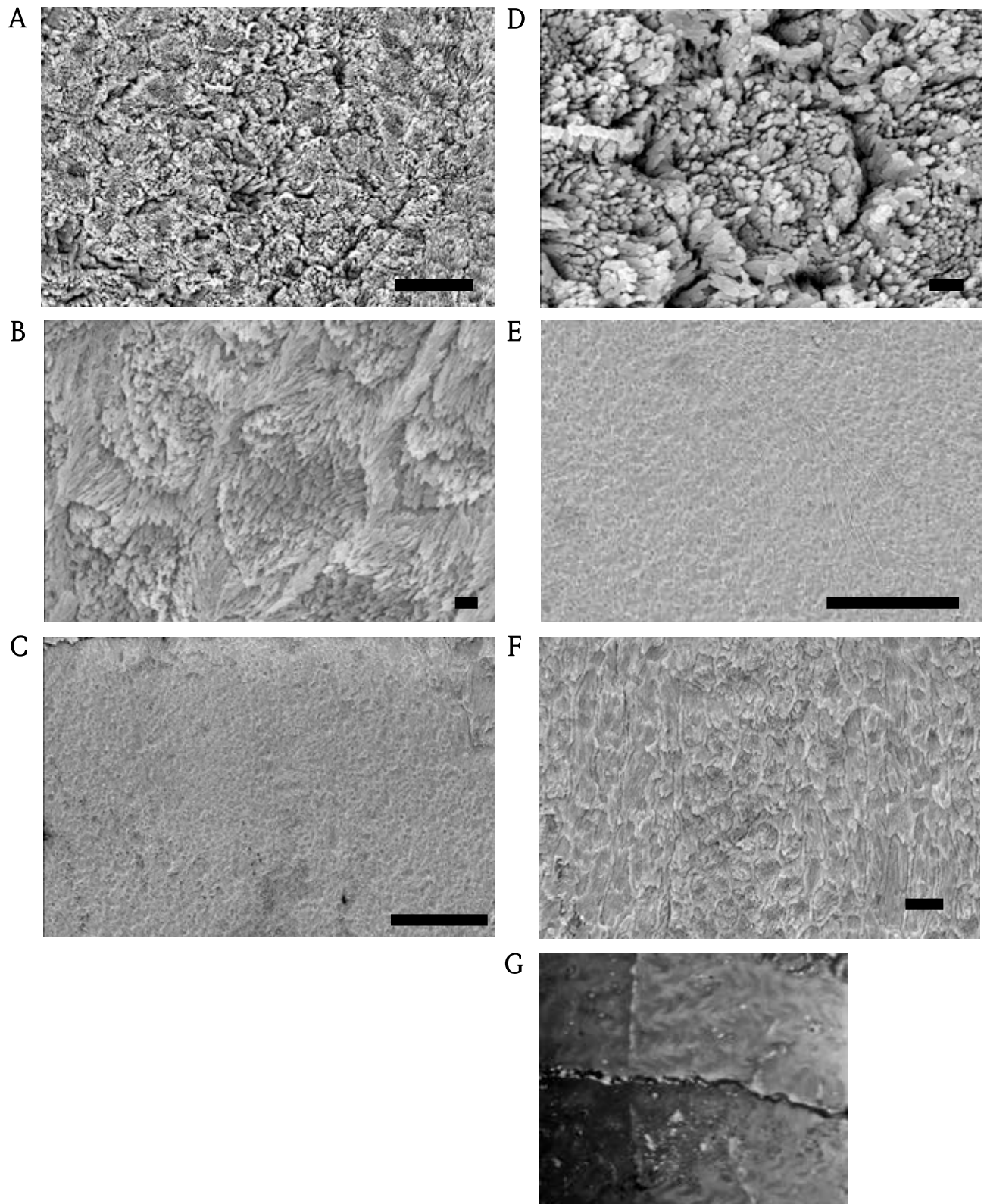
Fig. 8/3: REM-photos of the ultrastructure of the enamel of European *Hyaenodon brachyrhynchus* (NMHW A4471, premolar fragment) from Quercy (France, late Eocene/Oligocene). **A**, tangentional section; note that the shape of prisms varies from hexagonal/polygonal to polymorph and open prism sheaths dominate at 3000x magnification. Bar equals 10μm.; **B**, transversal section; prism with crystalites oriented along the long axis of the prism at 5500x magnification. Bar equals 1μm; **C**, tangentional section; the interprismatic matrix surrounds the prism in equal thickness at 350x magnification. Bar equals 100μm; **D**, tangentional section; prism with crystalites oriented along the long axis of the prism at 8500x magnification. Bar equals 1μm. ; **E**, tangentional section; Hunter-Schreger-Bands consist of six prism on average and show the undulating type at 250x magnification. Bar equals 100μm; **F**, tangentional section; Hunter-Schreger-Bands and prism in closer view at 950x magnification. Bar equals 10μm; **G**, Lightmicroscopic photo of the zigzag Hunter-Schreger-bands in the M1 of *Hyaenodon filholi* (Qu 17662), on the right is the tip of the the protoconid.

Chapter 9

9. Skeleton of *Hyaenodon*

9.1 Hitherto knowledge about the postcranial skeleton

Review of the hitherto knowledge about the North American *Hyaenodon* postcranial skeleton

The skeleton of *Hyaenodon* concerning the North American taxa (Fig. 9/14 D-E) was described early. Osborn and Wortman (1894) and Scott and Jepsen (1936) contributed with detailed publications. However, the most recent study by Mellett (1977) is a revision and includes his new results about the skeleton.

The following section follows Scott and Jepsen (1936) and Mellett (1977) and thus is based on North American taxa. Mellett (1977) compared to *Hyaena hyaena*, *Felis concolor* and *Canis lupus*. So these are the modern Carnivora to which Mellett (1977) is referring to and which are mentioned in the text.

In general the head is oversized, the limbs are short and the feet are weak. All muscles seem to be less developed except for the masticatory muscles (Scott and Jepsen, 1936). Mellett (1977) contradicts this statement and it is also emphasized herein that the musculature must have been strong. Fore- and hindlimbs are approximately of the same length. The femur shows nearly the same length as the humerus (Scott and Jepsen, 1936).

The cranial cavity is larger than in other "creodonts", but considerably smaller than in fissipeds. The olfactory lobes are large. The neck is quite short, the body and the tail are long. The tail of *H. mustelinus*, a small species, is longer due to relatively longer vertebrae (Scott and Jepsen, 1936).

The vertebral formula is C 7, T 14, L 6, Cd 26-27 (based on PU 10995, PU 13603, AMNH 1375, AMNH 39130, FAM 75565, FAM 75566, FAM 75652, FAM 75668; Mellett, 1977). The cervical vertebrae are relatively short and compared to Carnivora more "felid" than "canid" (Mellett, 1977). The cervicals of *Hyaena* are different in being massive. The neural spines are prominent and posteriorly projecting in *Hyaenodon* and not comparable to those in Carnivora (slim, cranially projecting spines). The atlas shows no canal or foramen for the vertebral artery. A long, bladelike and posteriorly projecting neural spine is present. This is in contrast to the small and cranially projecting spine in Carnivora. In general, the atlas was considered more "felid" (Mellett, 1977). A large neural spine is present on the epistropheus, showing an axe shape (Scott and Jepsen, 1936). The seventh and last cervical vertebra showed no vertebroarterial canal — common in most Carnivora and Hyaenodontidae. The transverse processes and neural spines of the thoracic vertebrae are larger and more robust than in Carnivora. The spines in the thoracic vertebrae are in large taxa similar to the wolf and in smaller ones similar to larger mustelids. The twelfth vertebra is the anticlinal vertebra (Scott and Jepsen, 1936).

The more developed spines support the supraspinous ligament, which supports the large head with the hypothetical nuchal ligament. The lumbar vertebrae possess a special feature: interlocking zygapophyses. The articular surface of the lumbar postzygapohysis encloses the prezygapophysis of the succeeding vertebra. This is common in primitive hyaenodontids and prevents dislocation. The anterior two of the three fused sacral vertebrae articulate with the sacrum. The sacrum itself is strongly developed unlike the state in *Hyaena hyaena*. The caudal vertebrae were not described, except for the statement, that the tail length is proportionally greater in the smaller species (Mellett, 1977). Scott and Jepsen (1936) gave more details: the tail length is moderately long in *Hyaenodon horridus* and comparable to the tail in the wolf. In *Hyaenodon mustelinus* the tail length is proportionally as long as in large cats. The first four caudal vertebrae possess complete, well-developed processi (Scott and Jepsen, 1936).

Seven segments build the sternum. The manubrium is the longest, keeled ventrally and of triangular cross section in the cranial portion. The fourteen ribs are not unusual with the first five ones being more heavy and flattened. The succeeding ones become more rounded in cross section (Mellett, 1977).

The scapula is differing between the species (Mellett, 1977), e.g. the scapula of *Hyaenodon mustelinus* is more different as would be expected within a genus and more than in any other part of the skeleton (Scott and Jepsen, 1936). *Hyaenodon horridus* shows a straight scapular spine, a strong metacromion extending below

the glenoid, a teardrop shaped glenoid fossa, a coracoid process shaped as a conspicuous raised nubbin on the antero-medial border of the scapular head and a mediad curve in anterior view (Mellett, 1977). It resembles the scapula of the wolf (Fig. 9/13 A and B). The smaller *Hyaenodon crucians* shows a cat-like scapula with an anteriorly extended supraspinous region and a T-shaped acromion.

The humerus is short and massive, with a large and rounded head. Unlike to the compared Carnivora the greater tuberosity has a more irregular shape and faces anteromedially. This tuberosity is the insertion site for the supraspinatous muscle. A separate process on the lateral side of the head served as insertion site for the infraspinatous muscle. This process is not known in modern Carnivora, because the infraspinatous muscle inserts on the lateral side of the greater tuberosity. The lesser tuberosity — insertion point for the subscapularis muscle — is positioned on the medial side of the head like in modern Carnivora. The deltoid tuberosity extends distally over the half of the shaft. Medial to the trochlea the entepicondylar foramen is present. The capitellum is more prominent than in Carnivora. Mellett (1977) found little functional difference between the humerus of *Hyaenodon* and that of Carnivora.

Radius and ulna are short, especially compared to the respective bones of the wolf (Fig. 44, p. 84 in Mellett, 1977). The head of the radius shows a kidney shaped outline (Mellett, 1977). The articulation between the humerus, the radius and the ulna is tight. The radius looses any possible rotatory capability (Scott and Jepsen, 1936). A ridge is developed, that is confluent with the ridge on the semilunar notch of the ulna. This limits movements and thus supination. In Carnivora this ridge is reduced, because the medial side of the radial head retreats away from the middle of the semilunar notch. In *Hyaenodon* the humerus locks the head of the radius into position. A bicipital tubercle is present and large and located near the head. The shaft of the radius is not flattened as in Carnivora, but is quadratic in cross section. The distal part is heavy. The ulna is described as having a relatively longer olecranon, with a heavy shaft and a radial notch facing almost completely to the front. An extremely deep channel runs from the radial notch to the styloid process and provides space for the extensor pollicis brevis muscle (extends the dew claw; Mellett, 1977). Radius and ulna have distally relatively large articulation surfaces for contact (Fig. 9/5 F).

The metacarpals are shorter than those seen in Carnivora. The carpals in *Hyaenodon* are relatively wider. Most important is that the scaphoid, lunar and centrale remained separate. In Carnivora they are always fused. The fused scapholunar (YPM 10076, Fig. 46, p. 86 in Mellett, 1977) reported as *Hyaenodon crucians* by Wortman (1902) was determined as fissiped (probably *Daphoneus*) by Mellett (1977). He also assumed, that the reference of a fused scapholunar in European taxa (Scott, 1895) will turn out as a misidentification. The manus is primitive and more "insectivore" than "carnivore". The scaphoid is broad and proximo-distally short. The lunatum is associated, but there is no sign of fusion (Scott and Jepsen, 1936). They suggested therefore a plantigrade stance. However, Mellett (1977) was one of the authors who classified *Hyaenodon* as digitigrade. Scott and Jepsen (1936) stated further, that the lunatum is proximo-distally longer than the scaphoid, the pyramidal is the largest carpal of the proximal row and articulates with the unciforme distally and the ulna proximally through a simple concavity. Its palmar side shows a large facet for the pisiforme. The pisiforme is large and massive. Its proximal facet articulates with the ulna and the pyramidal. The trapezium is the largest carpal — after the unciforme — of the distal row. It exhibits a large, lateral area for the metacarpal II and a much smaller one for the trapezoid. Distally the trapezium articulates with the first metacarpal. The trapezoid is much smaller than the trapezium and possesses a dorsal, rectangular surface. This carpal articulates distally only with the second metacarpal. The central is small, wedge-shaped and articulates with four other carpals: proximally with the scaphoid and the lunatum and distally with the trapezoid and the magnum. The magnum is the smallest bone in the carpus except for the centrale and articulates also with four carpals, the scaphoid, the lunatum, the central and the unciforme. The magnum articulates with the head of the third metacarpal and has only limited contact to the second metacarpal. The unciforme is the largest carpal, especially in transverse width. Its proximal surface is convex and fits into the distal concavity of the pyramidal. Distally it shows large facets for the fourth and fifth metacarpal, although a very small, but clear facet for the third metacarpal is present too (Scott and Jepsen, 1936).

The manus and pes are pentadactyl with long and slim metapodials. They describe the metapodials as diverging. The metacarpals are short and shorter than the metatarsals. *Hyaenodon's* foot is short and mesaxonic confirmed Mellett (1977). The third metacarpal is the longest. The third and fourth are about the same length and the longest metacarpals (Scott and Jepsen, 1936). The second, fifth and first ones decrease in length with the latter being the shortest and slimmest metacarpal. Carnivora show long, paraxonic feet with subequal long Mc II and III (Mellett, 1977). Besides, *Hyaendon* retained all five metacarpals with the first one being nearly as long and the fifth one. The metacarpals are tightly interlocked proximally and closely appressed distally. The second metacarpal overlaps the proximal part of Mc III — which is also not unusual in Carnivora. The dorsal articular surface of the distal ends of the metacarpals is rounded, the ventral surface is strongly keeled. A saddle shaped facet on the Mc I suggests freedom of movement for the pollex (Scott and Jepsen, 1936). The distal trochlea on the Mc I is hemispherical. The Mc II is much longer than the Mc I and is not symmetrical with the Mc IV, because its head is projecting farther in the carpus. The Mc III is the longest metacarpal and the slimmest after the Mc I. It is articulating proximally with the magnum. The articulation with the unciforme is more laterad than proximad. The shaft is slim and broadens distad. The Mc IV is slightly shorter and heavier than the Mc III. The Mc V is shorter than Mc II, III and IV, but longer and more compressed than the Mc I. At the metacarpal-phalangeal joints sesamoid bones are present (Mellett, 1977). They are large and crescent-shaped.

The deeply cleft terminal phalanges are the most characteristic phalanges (Mellett, 1977). Compared to Carnivora they are relatively large. The distoventral portion of the tips is flattened. The terminal phalanges are thick, blunt, curved palmad and canid like, though split at the tip (as in nearly all "creodonts", pinnipeds and insectivores; Scott and Jepsen, 1936).

The pelvis shows a long, narrow ilium with a deeply excavated gluteal surface (Mellett, 1977). In general more "felid", but completely unlike the short, expanded ilium in *Hyaena*. The obturrator foramen is surrounded by heavy bone — a feature not seen in modern Carnivora. The ischial tuberosity is prominent like in the wolf. The pelvic outlet is "canid" too, showing the same diameter as in canids of similar size. This suggests that the newborns were about the same size at birth. The pelvis is also different in small and large sized taxa (Scott and Jepsen, 1936): in large species the ilium is relatively broader and the acetabulum borders are more rounded. The femur is only slightly shorter than in a wolf (Mellett, 1977). In contrast to the latter taxon, *Hyaenodon* shows larger greater and lesser trochanters as well as a third trochanter. The conspicuous third trochanter is more prominent in *Protohyaenodon* species. The third trochanter is distinct in small species and reduced in large species (Scott and Jepsen, 1936). The shaft is compressed, cylindrical and straight. The surface is smooth and shows no lineae asperae (that are distinct in *Canis*). The trochlea is proximo-distally longer and deeper than in *Canis*. There is no supra-patellar fossa. The condyles are large, prominent and separated through a considerably wide intercondylar notch. The patellar surface is shallower and thus rather "felid" than canid-like (Mellett, 1977).

The patella is not unusual, but relatively large (Mellett, 1977): it is relatively broader and thicker than in *Canis*, but otherwise similar (rough anterior side, broad proximal and conspicuous distal end; Scott and Jepsen, 1936). The tibia and the fibula are short and heavy (Mellett, 1977). A wide interosseus space separates them. The tibia is of about the same length as the radius (Scott and Jepsen, 1936). The shaft is straight and shows proximally the triangular outline in cross-section. It merges into a more cylindrical outline in cross-section distally. Mellett (1977) confirms, that the proximal half of the tibia is triangular in cross section. The tibia is compressed in large species as in *Hyaenodon horridus* and slimmer and weaker in *Hyaenodon crucians* and *mustelinus* (Scott and Jepsen, 1936). The tibia shows a deeply grooved distal articulation surface (Mellett, 1977). The contact between the tibia and the fibula is extensive, both proximally and distally. A special feature is the large facet on the distal end of the fibula. It articulates with the calcaneus, which is quite unique.

The fibula is not reduced and separated from the tibia through a wider interosseus space (Scott and Jepsen, 1936). In contrast to *Canis*, the fibula is not closely attached to the tibia over more than the half of its length.

The proximal end is heavy and thick antero-posteriorly. A deep tendinal sulcus is present. The shaft is straight and cylindrical in cross section. The distal end is again thickened and broad. The calcaneo-fibular joint is a characteristic of "creodonts".

The tarsals are tightly packed together (Mellett, 1977). The calcaneus has a relatively long neck. It articulates with the cuboid along a caudally and laterally sloping surface. This is special, because in canids and felids the surface is horizontal and flat, reducing lateral motion in the tarsus. However, hyenas show a similar articulation. The calcaneus is compressed and shows an elevated facet for articulation with the fibula (Scott and Jepsen, 1936). Its distal end is broad and concave and covers the slight convex proximal end of the cuboid. The tuber is heavy and has a thickened proximal end without a tendinal sulcus.

The naviculare is wide, proximo-distally elongated and does not articulate with the cuboid. Distally there are three facets for all the cuneiforms. The entocuneiforme is long and dorso-plantad wide. It supports the first metacarpal and contacts the second metatarsal laterally. The mesocuneiforme is proximo-distally much shorter, shows a quadratic, dorsal surface and articulates exclusively with the Mt II. The ectocuneiforme is proximo-distally much longer and articulates with the Mt III and laterad with the Mt II. The cuboid is the largest of the distal tarsals.

The astragalus is more grooved than in all other "creodonts". Mellett (1977) also describes the astragalus as deeply grooved, although the trochlea is shallower in smaller species. The trochlea encompasses more than 180°. Its neck is described as long in Scott and Jepsen (1936), but characterized as short in Mellett (1977). No astragalar foramen is present (Mellett, 1977). The distal facet for the astragalus is more developed than in other "creodonts" (Scott and Jepsen, 1936). The three distal tarsal elements were not described by Mellett (1977) except being not unusual.

In the foot there were also five metatarsals present. The pes is pentadactyl and digitigrade (Scott and Jepsen, 1936). The metatarsals are slimmer and elongated compared to the metacarpals. They are mesaxonic with Mt III being the longest, Mt II and IV being a symmetrical pair and Mt V being much longer than the Mt I. The Mt I articulates exclusively with the entocuneiforme. The Mt II is articulating with the ecto- and entocuneiforme laterad and proximally with the mesocuneiforme. The Mt III articulates exclusively with the ectocuneiforme and the Mt IV and V with the cuboid. The external side of the head of the Mt V shows a prominent buttress structure, that is reminding of *Canis*. The metatarsals are slightly longer than the metacarpals and resemble in this aspect hyenid metatarsals (felids and canids show much longer metatarsals compared to metacarpals; Mellett, 1977). Mellett (1977) agrees that the foot is mesaxonic. The Mt III is the longest. The Mt I is prominent and projects mediad. The phalanges were noted to be of the same morphology as the respective ones in the forefoot (Mellett, 1977; Scott and Jepsen, 1936).

Forelimb function

Hopwood (1947) stated that the serratus magnus and levator anguli scapuli muscles tie the forelimb to the trunk and thus their development influences the mobility of the shoulder. The deeper the scars, the more mobile is the scapula and the more cursorial is the individual (Mellett, 1977). These muscle scars are well developed in larger *Hyaenodon* species and like the ones seen in the wolf. Mellett (1977) found the length/breadth ratio of the scapula to lie on the canid regression line in Müller´s study (1967). Müller (1967) found the length/breadth relationship to be independent of body size and to form functionally clusters. The smaller *Hyaenodon crucians* has a "felid" scapula (Mellett, 1977): The enlargement of the anterior border indicates a larger supraspinatous muscle, important for digging and climbing as the muscle fixes the shoulder joint. The T-shaped acromion-meatacromion is also developed in *Felis* and *Lynx*. It is the insertion site for the levator calviculae muscle and part of the deltoid muscle. The levator claviculae muscle draws the scapula craniad and is important in climbing. Together with the shallower astragalus trochlea in smaller taxa, Mellett (1977) proposed a semiarboreal living for these forms. Modern Carnivora have a much more elongated distal segment including the radius, the ulna and the metacarpals. This is an adaptation to fast running (Gray, 1968). Longer limb segments distal to the humerus move faster and farther for a given amount of muscle contraction within

a given period of time (Gray, 1968; Mellett, 1977). Mellett (1977) concluded that *Hyaenodon* was concerning locomotion equally or more derived compared to contemporary Carnivora. Yalden (1970) discussed the role of the carpus during locomotion in detail. According to him the distal ends of the limbs have to be brought close to the midline of the body in order to make the feet touch the ground almost one behind the other during a stride. This prevents toppling of the whole body and twisting of the trunk during rapid motion. A saddle-shaped facet for the radius forces the carpus to swing ulnad when the carpus is flexed and the distocaudal portion of the radius hits the facet. This way the feet can pass without hitting each other in the midline of the body (Yalden, 1970). Mellett (1977) described the lateral deviation in *Hyaenodon*. A saddle-shaped stop is present on the scaphoid that initiates ulnad deviation when the radius hits it. The lateral motion can be continued because a large, distal facet of the ulna can slide over a deep, laterally inclined facet of the cuneiforme. The pisiforme articulates caudad with the cuneiforme and probably played a role during motion with stopping and lifting action. Carnivora show a reduced contact of the ulna with the carpus. An advantage in carpal deviation is a fused scapholunatum as in Carnivora. Very different to modern Carnivora is also that pronation-supination (= axial rotation) can take place in the carpus in *Hyaenodon*. The radius is interlocked and the large cuneiforme and unciforme with their saddle-shaped articulation suggest that axial rotation is possible in the carpus (Mellett, 1977).

Hindlimb function

No trace of fusion at the proximal or the distal contact between the tibia and the fibula can be found (Mellett, 1977). Fibular rotatory mobility is possible in *Hyaenodon*. Such a rotatory mobility is known amoung Carnivora in cats and bears (besides other orders e.g. Primates) and indicates either well adapted progression over rocky and uneven surfaces often at high speeds or partially to full arboreality (Barnett and Napier, 1953). The features indicating a mobile fibula (Barnett and Napier, 1953) were noticed in *Hyaenodon* by Mellett (1977): large fibula, extensive fibula-calcaneus contact, extensive proximal tibia-fibula contact and appressed distal fibula (10% or more of its length). In canids and hyaenids the fibula is distally tightly bound to the tibia. Intratarsal mobility also suggests progression over irregular ground surfaces (Mellett, 1977).

Review of the hitherto knowledge about the European *Hyaenodon* postcranial skeleton

The skeleton of the European taxa of *Hyaenodon* is not as known and analysed as it is for the North American taxa. Even less is known about the Asian species (see below). However, the major problems are the isolated European findings and that an affiliation to *Hyaenodon* can be doubted sometimes. Moreover, Lange-Badré (1979) did not examine postcranial material in her study, which is the most recent review of the European *Hyaenodon*.

European researchers often excluded the postcranial material. In Filhol (1882) just cranial and dental material was described, as in Helbing (1928), Filhol (1876) and Martin (1906). Forster Cooper (1926) attributed only mandibular material to his new erected species *Hyaenodon aimi*, which is no longer valid (Lange-Badré, 1979; see also Chapter 5). Gaudry (1878) figured and described an epistropheus he assigned to *Hyaenodon*. It was available at the MNHN. For discussion see below.

Skeletal remains belonging to *Hyaenodon* were described in few publications and the most important facts shall be summarized here:

Blainville (1841-1842) described postcranial remains. Helbing (1925) reported a tibia fragment he assigned to *Hyaenodon* from Belfort (France). This determination has to be doubted as the figures are not too clear.

Bonis (1964) described remains of *Hyaenodon* found in la Débruge (Upper Ludien, latest Eocene) and the following section follows him. Besides *Hyaenodon requieni* the only other carnivorous mammals known from La Débruge are the hyaenodontid *Pterodon dasyuroides* and the carnivore *Cynodictis lacustris*. Bonis (1964) mentions a maxilla and a mandible fragment, an anterior skull fragment, two humeri, a complete radius and two radius fragments, a forepaw and some feet elements. However, he gave a description of the following

elements: a right humerus, a radius, a left carpus including the scapholunatum, the unciforme, the magnum and the trapezium, metacarpals, an astragalus and metatarsals. The humerus is described as extremely robust with a length of about 155 mm and a distal width of 27 mm. Compared to the wolf it appeared to Bonis (1964) wider and shorter. The deltoid surface is canid-like and stops at about the half of the length of the shaft. The epicondylus is weak and shows muscle marks that are comparable to those in fissipeds. The epitrochlea is well developed and possesses strong muscle impressions by the internal cubital muscle and the flexor of the digits. The radius is not much longer than the respective bone in a fox (length of 127 mm). It is robust like in a wolf, but of greater width concerning the distal end. The facet for the ulna is running in a straight band around the posterior portion of the radial head. This type of articulation prevents supination movements. The bicipital tuberosity is faible and changes into a crest distally. Distally the radius increases in robustness. The distal facet for the ulna is small and oval shaped. The articulation surface for the carpus is large and concave. The described specimen of Bonis (1964) misses the pyramidal and the trapezoid. Like in fissipeds he found a scapholunatum (discussed in a following section). There is a large, convex articulation surface for the radius and an external, elongated facet for the pyramidal. On its distal surface there are three marked and distinct facets present and another, small one. In the drawing (Fig. 5 p. 11 in Bonis, 1964) he indicates the facets from internal to external as articulation area for the unciforme, followed by the facet for the magnum, followed by the largest facet, which is for the trapezoid and the last, small facet for the trapezium. The unciforme itself is massive. The facet for the pyramidal is convex and elliptical. Distally a facet for the mc IV and V is present. The magnum is laterally flattened and articulates with the scapholunatum via a straight band. Two other facets are present, one for the unciforme and one for the trapezoid. It articulates with the mc III too. The trapezium is well developed and shows a triangular, convex facet for the scapholunatum, a concave facet for the trapezoid and an elongated facet for the mc II. The metacarpals are distally elongated and possess a posterior keel. The mc III and IV are significantly longer than the other metacarpals. The mc I is short, slim and curved. The mc V is not as short as the mc I, but robust and curved. The mc II is missing in the respective specimen. The astragalus shows a trochlea narrower and shallower than in a canid. The collum is long and the head is globular with a slight dorso-plantad elongation. The sustentacular facet is convex and elliptical. The posterior calcaneal facet is concave, elongated and canid like. A feature reminding of a felid is the occurrence of the foramen tali. The metatarsals are longer than the metacarpals. The mt III and IV dominate, as seen in the manus. In the respective specimen the mt I is missing. Bonis (1964) concluded from these findings that the North American taxa are plesiomorph. A fused scapholunatum in the European *Hyaenodon* is the most striking difference. He also found, that the astragalus is different in showing a flattened head. The limbs are mesaxonic with a dominating third digit. Bonis (1964) inferred that the ancestors of the North American taxa cannot be found within the forms of the late European Eocene. He further mentioned the following features as plantigrade characters: robustness of the long bones, development of an epicondyle and an epitrochlea, probable presence of the coraco-brachial muscle, articulation of humerus and ulna in two different planes, development of a first digit; Features indicating digitigrady are: a deltoid impression that is weakly marked and does not run further distally than the half of the length of the shaft, a canid like scapholunatum-cuneiforeme articulation, long metapodials, dominance of the third and fourth digit, elongated collum of the astragalus, globular astragalar head, clearly concave surface of the posterior calcaneal surface on the astragalus; He concluded that *Hyaenodon* was digitigrade. Bonis (1964) mentioned the assumption of previous workers that the genus could have been aquatic (due to the extremely elongated palatinum) and rejects it with the statement that the skeleton is in favour of a cursorial animal.

Lydekker (1885) listed in his catalogue the Bravard and the Pomel collection besides other collections (e.g. Hastings collection) and acquisitions, hold by the BMNH. Herein, only the postcranial material shall be mentioned. This material was assigned by Bravard to the family Hyaenodontidae with many of the specimens labeled as *Pterodon* or *Hyaenodon* (see Table 9/1).

specimen number	element	remarks
M 28165	scapula fragm. dex. with glenoid (Vaucluse)	was not available
M 27576	humerus dex.fragm. (Vaucluse)	described herein
M 28187	humerus sin. fragm. (Vaucluse)	was not available
M 26758	humerus dex. fragm. (Vaucluse)	was not available
M 28166	humerus dex. fragm. (Vaucluse)	was not available
M 28167	humerus sin. fragm. (Vaucluse)	was not available
M 27709	humerus dex. fragm. (Sauvetat, Puy-de-Dôme)	was not available
M 28188	ulna dex. fragm. (Vaucluse)	was not available
M 26760	humerus sin. fragm. (Vaucluse)	described herein
M 28168	ulna dex. fragm. (Vaucluse)	was not available
M 11909	cast of ulna dex. fragm. (Vaucluse)	"*Taxotherium parisiense*" Blainville
M 29869	radius dex. (Hordwell, Hampshire)	was not available
M 28155	radius sin. (Vaucluse)	examined, in bad condition
M 28169	radius sin. (Vaucluse)	described herein
M 26759	radius dex. (Vaucluse)	was not available
M 28239	radius sin. (Vaucluse)	examined, not *Hyaenodon*
M 28289	radius dex. (Vaucluse)	examined, not *Hyaenodon*
M 28210	radius dex. (Vaucluse)	was not available
M 28196	radius fragm. (Vaucluse)	was not available
M 27583	fore foot dex. (Vaucluse)	was not available
M 26751	metacarpals dex. (Vaucluse)	was not available
M 26752	scapholunatum sin. (Vaucluse)	was not available
M 28193	femur fragm. (Vaucluse)	was not available
M 29726	femur sin. (Vaucluse)	described herein
M 28195	tibia sin. (Vaucluse)	described herein
M 30132	tibia sin. fragm. (Hordwell)	described herein
M 27582	tibia dex. fragm. (Vaucluse)	was not available
M 26750	calcaneus dex. (Vaucluse)	was not available
M 27581, 28197	2x astragalus sin. (Vaucluse)	was not available
M 28162, 28170	2x four metatarsals (Vaucluse)	M 28162 described herein
M 30342	3x terminal phalanges (Hordwell)	was not available

Tab. 9/1: Data taken from Lydekker (1885). List of hyaenodontid postcranial material housed in the BMNH. For more information (e.g. collection affiliation) see Lydekker (1885).

Schlosser (1887) had the impression that the skeleton of *Hyaenodon* is greatly different from Carnivora. He measured and figured postcranial material and provided some descriptions and comparisons. This section follows him: the humerus is a bone with a straight, circular (in cross section) shaft. The olecranon fossa is perforated. The trochlea is massive, with a spheroidal swelling. The radius is distally broadened and possesses a circular, deepened surface. The olecranon is remarkable in showing a short olecranon. The distal part of the ulna is well-developed. The third trochanter on the femur is present, but small. The femur condyles are relatively high. The tibia is laterally compressed. Its cross section is oval. Schlosser (1887) designated vertebrae to *Hyaenodon*. Significant is the broadening of the neural arches and the dorsal and ventral articulation surfaces on *Hyaenodon* vertebrae. He found them to be similar to *Viverra*. The unciforme is compact. The mc III articulates via a short surface with this carpal. The pisiforme is very short and massive. He emphasized the tight packing of the carpals. The mc I is relatively longer in slim forms. The mc II shows a triangular, deeply grooved articulation surface for the trapezoid. It overlaps the mc III. It is very similar to felids. The mc III overlaps the mc IV and thus articulates with the unciforme. He concluded that overall *Hyaenodon* is more similar to Carnivora than to Marsupialia (e.g. *Thylacinus*) and within Carnivora more felid like. The mc IV shows only a shallow notch for the mc V (seen in *Canis*). The mc V resembles that of felids. The tarsus shows a peculiar character, that is seen within carnivorous mammals only in "Creodonta": the cuboid articulates with the astragalus. Part of the cuboid is pushed between the astragalus and the calcaneus. The astragalus is loosely attached to the calcaneus, except for the articulation with the sustentaculum tali. The facet for the tibia is not broad, but deeply grooved. The naviculare is remarkably high and the facet for the cuneiforme I must have been small. The cuneiforme III touches the cuboid in a small extent. In marsupials (*Didelphis, Thylacinus*) the cuneiforme III usually articulates with the naviculare and the cuboid. In general the tarsus is judged as being more similar to Carnivora than to Marsupialia. The mt I is short, but relatively longer in slimmer taxa. The mt II is proximally higher placed than the mt III. It articulates with the cuneiforme III via two facets. This tarsal is described to hardly touch the mt I and not too be appressed to the mt III. There is also a facet for the cuneiforme II, which is of triangular shape. The proximal facet of the mt III is canid-like due to a missing lateral aperture for the mt II. The facet for the mt IV is not deep. The mt IV is placed in the same level as the mt III and similar to *Amphicyon*. The mt V is weak, short and curved. Schlosser (1887) concluded that the limbs were of digitigrade stance. It is common among Carnivora that the metatarsals are longer than the metacarpals (except for *Hyaena* which actually shows shorter metatarsals). Still, Schlosser (1887) considered the differing length as remarkable.

Review of the hitherto knowledge about the Asian *Hyaenodon* postcranial skeleton

Concerning the Asian species Matthew and Granger (1924) stated, that *Hyaenodon pervagus* (No. 19002, Hsanda Gol Formation, Loh, Mongolia, Oligocene) showed hind limbs and feet like *Hyaenodon horridus*, both in size and morphology (Fig. 9/14 B and C). However, the material was not further described.

Morlo and Nagel (2006) described material from the lower Oligocene of Mongolia and gave the hitherto most detailed study on that topic: a proximal fragment of the ulna (Planche 2, Fig. 20, p. 314) and a radius dex. (Planche 2, Fig. 21 a-c, p. 314) both assigned to *Hyaenodon incertus*, a right ungual (Planche 2, Fig. 23, p. 314) determined as *Hyaenodon* cf. *mongoliensis* and a right scapula fragment with glenoid fossa (Planche 1, Fig. 4, p. 312; all in Morlo and Nagel, 2006) assigned to *Hyaenodon eminus*. Their remarks are given in the following.

The glenoid fossa of the scapula is described as shallow, with a very oval outline and an acromion ending far distally from the glenoid (a cursorial feature). Due to its size it was confidently assigned to *Hyaenodon eminus*. The fragment of the ulna shows only the preserved facets for the humerus and the radius. The olecranon is broken too and described as angled laterally. The humeral facet is bordered by a strong ridge. The radial facet is narrow and broad. The radius is preserved only as a proximal fragment. The head is highly oval in outline and narrow. It also is highly uneven and shows a strong capitular eminence. Designation to *Hyaenodon incertus* is not fully verified and thus was referred to *Hyaenodon* cf. *incertus*. However, ulna and radius fragment are both

very similar to the North American *Hyaenodon horridus* in size and morphology. A terminal phalanx assigned to *Hyaenodon* cf. *mongoliensis* due to its large size, twice as large as *Hyaenodon horridus*, but showing the same morphology (Morlo and Nagel, 2006).

9.2 New description of the second cervical vertebra

The second cervical vertebra — named the epistropheus or axis — is described in the following section. Mellett (1977) assumed the presence of a nuchal ligament as observed in canids also for *Hyaenodon*. That would be a valuable adaptation for an animal with a large head, but it was hitherto not discussed in detail.

9.2.1 Epistropheus of the North American *Hyaenodon*

Scott (1895) gave a detailed description of the whole skeleton, including the epistropheus (= axis). He described that vertebra in the following paragraph:

"The axis is a rather remarkable bone. Its centrum is of only moderate length, but broad and very much depressed, with distinct ventral keel ending in a hypapophysical tubercle behind. The dorsal surface of the centrum, forming the floor of the neural canal, also bears a strong median ridge. The atlanteal facets are low and wide, of oval shape, and with convex surfaces. Like the corresponding facets of the atlas, the outlines of the two together describe nearly a semicircle, very much as in the badger (*Meles*) to the axis of which, indeed, that of *Hyaenodon* bears a close general resemblance. The odontoid process is very long and prominent, and of irregularly conical shape, tapering to a blunt point. The transverse processes are short, compressed and slender; they are directed backward and but little outward, and are perforated by the relatively large vertebrarterial canals. The neural canal is higher and narrower in front, broader and lower behind. The pedicles of the arch are thick and heavy, but narrow antero-posteriorly, leaving considerable open space between themselves and the atlas. The neural spine forms a large, thin, hatched-shaped plate, which, though not very high, is of great fore-and-aft extent, and much exceeds the length of the centrum, beyond which it projects at both ends. The hinder border of the spine is thickened, especially in *H. horridus*. The postzygapophyses of the axis are of moderate size." (Scott, 1895, p. 508)

Scott (1895) concluded that the neck as a whole is surprisingly short and light: the skull even exceeds the neck considerably in length; the epistropheus is the only strongly developed cervical vertebra; He stated that the processes of the cervical vertebrae are small and thus concluded that this indicates a neck that is not as heavy and muscular as in recent Carnivora (Scott, 1895).

Mellett (1977) gave a shorter description of the epistropheus in North American *Hyaenodon* and characterized it as follows: completely unlike the vertebra in modern Carnivora due to the possession of a long, bladelike, posterior projecting neural spine.

The following specimens could be personally observed and shall be mentioned and figured (Fig. 9/2 C-E) for a more complete picture.

An epistropheus assigned to *Hyaenodon cruentus* (AMNH 8775, from Cedar Creek, Logan County, Colorado, White River Formation, Oligocene) was found associated with other fragments of the skeleton. It is fused with the atlas and the rest of the cervical vertebrae and some thoracic vertebrae too, but figured only with the atlas and the third cervical vertebra (Fig. 9/2 C). It confirms the old description of Scott (1895) and Mellett (1977). The strongly posterior elongated spine is the most apparent feature. Particularly interesting is the very narrow development of the spine — best seen in dorsal view (Fig. 9/2 C left).

A nearly complete skeleton of *Hyaenodon horridus* (AMNH 39130, Fig. 9/2 D) was found in situ (alas, no precise information was available). Again, the peculiar development of the neural spine is apparent.

A mounted skeleton of *Hyaenodon* sp. (YPM-PU 13603, Fig. 9/2 E) also shows an epistropheus. The neural spin is dorsally slim.

Scott (1895) already gave a good description (see above) of the epistropheus. Therefore, only some points concerning the morphology should be emphasized in summary: the neural spine is conspicuous, low, extremely elongated cranio-caudally and forms a thin-bladed, axe-shaped spine; due to this development the neural spine reaches over the third cervical vertebra; the transverse processes are short and slender; the body itself is short; the facets for the atlas are of semicircular shape; All these features are known for the North American *Hyaenodon* and are figured (Fig. 9/2 C-E).

9.2.2 New description of the epistropheus of the European *Hyaenodon*

The skeleton of the European *Hyaenodon* is due to sparser material not as well known as the skeleton of the North American *Hyaenodon* (see the following).

An epistropheus was assigned to *Hyaenodon* by Gaudry (1878, Fig. 9, p. 18). He argued that *Hyaenodon* is found frequently in the site of La Salle (near Caylux, France) and that the size approaches the known remains of that genus. Gaudry (1878) generally considered *Hyaenodon* being marsupial-like. Thus, he emphasized the similarity of the epistropheus he determined as *Hyaenodon* and an epistropheus assigned to a marsupial, *Didelphis cancrivora* (Fig. 10, p. 18 in Gaudry, 1878). This specimen (Qu 8322) was available at the MNHN and is figured herein too (Fig. 9/2 B).

Scott (1888) already noticed, that this epistropheus, described and figured by Gaudry (1878), cannot be assigned to *Hyaenodon*. Lange-Badré (1979) stated the same opinion. This finding is ascertained here. It is obvious when comparing an epistropheus of a North American *Hyaenodon* with the epistropheus described by Gaudry (1878), that they are not belonging to the same genus. I consider Gaudry´s determination as misidentification and confirm Scott (1888) and Lange-Badré (1979).

The morphology is completely different: the facets for the atlas are circular in shape; the transverse processes are short; the neural spine is extremely robust; the neural spine shows a completely different shape and lacks the characteristical caudal elongation; the neural spine is more robust and thick. However, there is similarity to the epistropheus of *Didelphis cancrivora* (Fig. 10, p. 18 in Gaudry, 1878). Thus, the specimen should previously be referred to as Marsupialia indet.

There is another epistropheus hold in the collections of the MNHN (Fig. 9/2 A): alas it has no number, but there is a note saying it belongs to *Hyaenodon vulpinus* (invalid species, see Chapter 5). This specimen is smaller than Gaudry´s specimen (Qu 8322), but shows the overall same morphology: the facets for the atlas are circular; the neural spine is massive, rounded and not caudally elongated; It most probable belongs to the same taxon or a taxon related to Qu 8322. As the figured specimen of *Didelphis* in Gaudry (1878) matches the morphology very well, it is proposed here to assign it to a marsupial, maybe *Didelphis* itself.

Hitherto no other second cervical vertebra of European material was described. Two specimens in the Quercy collection of the NMHW could now be determined as *Hyaenodon* sp. (NMHW 2010/0196/0004, Fig. 9/1 C; NMHW 2010/0196/0005, Fig. 9/1 D).

Alas, both are fragmented and especially the neural spine is broken distally. They are of the same morphology as the North American specimens and shall be described in the following: the facets for the atlas are semicircular; in general the vertebra is slim and more delicate; the neural spine is thin, low and axe-shaped; the neural spine is elongated and conspicuous; the ventral keel is strongly developed; The odontoid process is long, prominent and of irregularly conical shape as described in Scott (1895). It shows a blunt tip. In these characteristics it matches with the morphology of the epistropheus of the North American *Hyaenodon*. Nevertheless, there is a difference: the body of the epistropheus is not as short as seen in the North American taxa. Whether the transverse processi are long or short, cannot be judged as they are broken in the European material, but they have been slender as well.

9.2.3 On the ligamentum nuchae

The focus on the second cervical vertebra was important for the question if a ligamentum nuchae was present in *Hyaenodon* as Mellett (1977) assumed. First, the function of the neck in predators shall be discussed. Wang et al. (2008) gave a great synopsis of fossil canids and the topic of the ligamentum nuchae:
Canids have relatively long, straight necks. Their necks are also well muscled, but relatively weaker than felid necks. Necks of felids are short and follow a strong S-curve. Naturally, a shorter muscle contracts more efficiently than a longer muscle. Therefore, a very short neck is developed in saber-toothed cats. Saber-toothed cats need to avoid unexpected stress during the bite to protect their saber-teeth. Interestingly, the processi for muscle insertion on each cervical vertebra are smaller in dogs than in cats. Thus, dogs need a compensation for their long necks. This compensation is the possession of a nuchal ligament comparable to the one found in ungulates. The nuchal ligament stretches along the back of the neck from the tips of the anterior thoracic vertebrae. It helps to support the weight of the head without the need for active muscle contraction. In ungulates the situation is different: the ligament attaches on the back of the skull. In canids the ligament attaches on the back of the axis. No other extant carnivore has a nuchal ligament. Fossils show that earlier dogs had shorter necks and more prominent processi. Thus, Wang et al. (2008) found that the nuchal ligament is not present in all fossil dogs. The ligament was developed in Caninae and its presence implies that dogs depend since then more on their nose and needed longer necks to follow scent trails. In contrast, cats emphasized eyesight and hearing. An example for a canid without a nuchal ligament is the fossil hypercarnivorous dog *Aelurodon*. This genus shows a short, S-shaped neck and developed processi for muscle insertion. This state is advantageous for hunting large prey and combined with shorter, more flexible, more muscular forelimbs that are capable of dealing with large prey (Wang et al., 2008).

If a nuchal ligament is present, the site of its attachment can be traced on the bone (e.g. Wang et al., 2008). In ungulates a nuchal crest — a thick, transverse crest — is present on the occipital bone, because the nuchal ligament attaches in ungulates to the skull. In canids the nuchal ligament attaches to the epistropheus (Wang et al., 2008). More precisely, the ligamentum nuchae attaches cranially to the caudal part of the neural spine of the epistropheus and caudally to the neural spine of the first thoracic vertebra (Shires, 2003). A simple comparison of two recent Carnivora was made: a canid epistropheus, (IUPW 1248, Fig. 9/1 B) assigned to *Canis anthos* and a felid specimen (IUPW 1772, Fig. 9/1 A) assigned to *Felis sylvestris* were chosen. A canid epistropheus compared to a felid epistropheus shows a caudal broadening of the neural spine. This can be very well seen from a dorsal view (Fig. 9/1 A-B right). That is the site of attachment for the ligamentum nuchae.

Scott (1888) stated that the neural spine on the epistropheus in *Hyaenodon* forms a stout rod projecting distally up to the fourth cervical vertebra. The extreme elongation of the neural spine is clearly seen (e.g. AMNH 8775, AMNH 39130; Fig. 9/2 C, E). Mellett (1977) mentioned the presence of a nuchal ligament. Either he had seen evidence for this in more material or he has made an assumption. Of course, the presence of a nuchal ligament would have been advantageous or nearly essential for an animal with such a large head. However, no broadening of the spine as seen in the canid epistropheus can be observed in the European or the North American material of *Hyaenodon*. Thus, a clear attachment site for a nuchal ligament on the epistropheus cannot be proved for *Hyaenodon*. There is another possibility: a nuchal ligament could have attached directly to the skull (as in ungulates). This hypothesis could not be tested due to the fragmented European material and the lack of complete skulls or fragments with an occipital.
Concluding, it shall be stated, that a nuchal ligament is a special adaption in canine dogs to support the muscles. *Hyaenodon* had a rather short neck, but a large and heavy skull. Therefore the muscles did contract more efficiently than in a long neck. The question if this was sufficient enough to support the head remains unsolved. A nuchal ligament could have been present, but it seems unlikely that it inserted as in canines on the epistropheus.

9.3 New description of the European skeletal material

In this section I describe the hitherto known postcranial material attributed to the genus *Hyaenodon*. An overview is given below. However, the material comes from two collections — the BMNH (used abbreviation for material is M herein) and the MNHN (used abbreviations for material herein are LDB and Au depending on the site). A loan of the material of the BMNH was possible, so this material is described first in the following section. Additional information on the material of the MNHN is following, but not extensive, because the stay in Paris did not allow a detailed study of the postcranial material alone.

The material was compared to respective bones of Carnivora of the collection of the IUPW and to the catalogue of Pales and Lambert (1971).

Hyaenodon sp. large sized species
   Humerus: M 27576, LDB 19-21
   Ulna: M 26760
   Radius: M 28169, LDB 22-23
   Femur: M 29726
   Tibia: M 28195
   Metatarsals: M 28162
   Astragalus: LDB 43, 44 and 46

Hyaenodon sp. small sized species
   Radius: Au 1028
   Phalanx: Au 18?, Au Ru 56
   Scapholunatum?: Au 6754, 2319
   Femur: Au 2361
   Tibia: M 30132, Au 776
   Fibula: Au 2359
   Calcaneus: Au 731
   Metatarsal: Au 2078

Carnivora indet.
   Forepaw: M 26761 (not mentioned in Lydekker, 1885)

Hyaenodon sp. large sized species
   Humerus: M 27576 from Vaucluse (France, Upper Eocene; Fig. 9/3 A)
The specimen is a fragmented right humerus. The proximal part with the caput humeri is missing. The bone is heavy and of robust built. The morphology of this element is easily identified as *Hyaenodon*: the fossa anconeus and the foramen entepicondylium are present. The crista deltoideus and the brachial flange are well-developed. The shape of the trochlea is particular in *Hyaenodon*. The trochlea shows two constrictions and a deep midtrochlear furrow. A dent is protruding distally on the internal side of the trochlea. A proximal swelling is present on the external side of the trochlea.

The humerus of the wolf and the hyena are similar to the *Hyaenodon* humerus. More similar is the hyaenid humerus, which shows an anconeal fossa, a well-developed brachial flange and a similar elongated trochlea shape (but not with the protrusion distad). No entepicondylar foramen is present. This foramen is present in felids like the lion and the panther. However, those show a different trochlea. Interestingly, *Nandina binotata* (IUPW 1305) shows also both foramina: a fossa anconeus and a foramen entepicondylium. The trochlea is completely different: It is not broadened and not as sculptured. Moreover, a well-developed epicondylus

is present. Concerning especially the trochlea, *Vulpes vulpes* is similar to *Hyaenodon*: the shape of the *Hyaenodon* trochlea is closer to that of the trochlea in the fox than of a hyaenid trochlea.

This element is alike the respective bone of the North American taxa (pers. obs.; e.g. AMNH 39130, AMNH 1381).

HuL	HuWl	HuWm	HuWd	HuTrH	HuTrW	HuTrD
~ 135 mm	20.9 mm	19.4 mm	44.5 mm	31.4 mm	31.9 mm	12.8 mm

Ulna: M 26760 from Vaucluse (France, Upper Eocene, Fig. 9/4 A and B)

The specimen is a proximal fragment of a left ulna. On its lateral aspect a deep groove is present — as seen in the radius too (described below). The olecranon is prominent and posteriorly oriented. The radio-ulnar joint is more ungulate as it limits rotation. It is concave and from a lateral view the articulation surface is strongly bulged. The semilunar notch viewed from dorsal is bulged too (upwards curved shape). Two proximal tubercles border a deep sulcus on the olecranon and are high. A very deep tendinal groove is present on the shaft of the ulna.

Comparing to modern Carnivora, the ulna of *Hyaenodon* is short and wide. In the hyena the olecranon is also posteriorly oriented. The radial facet on the other hand, is more similar to the lion.

The North American material shows the same features: posteriorly oriented olecranon, deep tendinal groove on the shaft and an upwards curved semilunar notch (pers. obs.; FAM 75692, FAM 75699).

UlL	UlWl	UlWm	UlWp	UlOlL	UlApL	UlInraW	UlprOlDia
~ 89.2 mm	11.0 mm	17.4 mm	21.6 mm	33.2 mm	26.1 mm	19.5 mm	11.6 mm

Radius: M 28169 from Vaucluse (France, Upper Eocene, Fig. 9/5 A and C)

The specimen is a left radius. It is robust, short and shows strong muscle scars. Especially distad the bone grows very broad and heavy. The proximal articulation surface is elongated laterad and somewhat rectangular in outline. The surface declines internad. The distal arcticulation surface is heart-shaped (in another European specimen it is triangular; Fig. 9/5 E) and slopes steeply. On its lateral side there is a large, oval articulation surface for the ulna. On its palmar aspect the radius shows an extremely deep and broad groove (for a massive tendon).

Concerning the distal articulation surface the specimen is most similar to the hyena. The tiger is totally different: in *Felis tigris* (IUPW 1254) the proximal facet is round, the distal facet is rectangular, but it shows a distinct facet for the ulna. The fox *Vulpes vulpes* (IUPW 2621) is proximal more similar with an elongated facet, but the distal facet is again completely different. The *Hyaenodon* radius has a more ungulate appearance.

Comparing to North American material the following shall be mentioned: the outline of the proximal articulation surface is differing, because the North American species show a deeper constriction (Fig. 9/6 A). The distal articulation facet is similar (AMNH 8775, Fig. 9/5 F right). In another specimen (FAM 75601; Fig. 9/5 left) it is significantly different. The facet is of triangular outline, but is bordered by a second, much smaller facet. The remaining radial features are of the same morphology in European and North American taxa.

RaprDiamin	RaprDia	RaL	RadisDia	RaWl
14.9 mm	23.2 mm	134.2 mm	20.4 mm	10.0 mm

RaWm	RaApL	RaApW	RaAdL	RaAdW
13.5 mm	22.6 mm	12.4 mm	16.9 mm	14.2 mm

Femur: M 29726 from Hordwell (Hants, Great Britain, Eocene, Fig. 9/7 A)

The specimen is a left femur and complete. It is a robust element. The trochanter major is as high as the caput femoris and broad. The trochanter minor is well-developed and a small trochanter tertius is also present. Their development indicates the presence of strong tendons. The fossa trochanterica is steep and comparable to *Sus*. The fossa plantaris is weak as in *Canis lupus*. The condyles protrude strongly laterad. A strong lateral crest is present. The fovea capitis has a low position like in *Panthera leo* or *Ursus*. The axis´ of the condyles are diagonal like in *Crocuta crocuta*.

The trochanter major of subequal height is most similar to *Panthera leo* or *Canis lupus*. In general the femur is showing more shared features with *Canis lupus*. Although *Canis* is much more slender and does not show a trochanter tertius. Interestingly, *Nandinia binotata* is similar in the proximal part of the femur: showing a protruding trochanter minor and a trochanter major of the same height as the caput. Compared to *Felis catus* the *Hyaenodon* femur is much more robust, but not too different.

Interestingly, the smaller sized European *Hyaenodon* had a much lower trochanter major (i.e. lower than the caput, see the Aubrelong material below and Fig. 9/7 B). This morphology was observed in the North American material too (pers. obs.; AMNH 9809).

FeL	FeWm	FeWl	FeWd	FemCH	FemCL	FemCW
125.6 mm	13.1 mm	10.4 mm	27.7 mm	13.3 mm	11.5 mm	27.1 mm

FelCH	FelCL	FelCW	FeCW	FeCF	FeCH	FeNeW
14.6 mm	11.5 mm	27.8 mm	15.6 mm	13.0 mm	14.1 mm	11.9 mm

FeNeW2	FePagH	FePagHl	FePagW	FeWpr	FeWinf	FedisH
9.6 mm	24.3 mm	17.9 mm	11.6 mm	30.9 mm	18.5 mm	32.5 mm

Tibia: M 28195 from Vaucluse (France, Upper Eocene, Fig. 9/8 A and C)

The specimen is broken and distorted. It is quite complete and a left tibia. The bone as a whole is very robust and compressed. A strong crista tibiae is present. This crest runs distad to the malleolus medialis. Viewed from above the proximal joint shows rounded condyles. There is a notch between the condyles. The proximal half of the tibia has a triangular cross section as in most Carnivora. On the plantar side strong ridges, marks for the muscles, are present. The distal joint for the astragalus is relatively deep. The articular surface declines laterad. The outline of this articular surface is rectangular (Fig. 9/8 C).

Compared to Carnivora the tibia of *Hyaenodon* differs in robustness and strong markings for insertion of strong muscles. The outline of the distal joint is rectangular in Carnivora. The proximal condyles are more rounded. The tibia of *Panthera leo* fits best with the morphology of the *Hyaenodon* tibia and shows a similar process styloideus.

The tibia in the North American taxa is comparable (pers. obs.; AMNH 1381).

TiL	TiWm	TiWl	TidisL	TidisW	TiPrDia	TiPrW
170.3 mm	16.4 mm	17.1 mm	24.8 mm	26.6 mm	~ 33.3 mm	37.7 mm

Metatarsals: M 28162 from La Débruge (Vaucluse, France, Eocene, Fig. 9/9 A)

The specimens are four right metatarsals II-IV. They are elongated, rather slim and were closely appressed to each other. The latter feature is apparent when putting them together. Expecially, Mt III and IV fit perfectly and leave no doubt that the animal was digitigrade. The proximal articulation surfaces are smooth. The distal joints are plantad bowed and show a medial ridge, which is more apparent on the plantar side. Most unusual for carnivorans are strong muscle scars on the plantar and dorsal side. These are not known in other European material (e.g. Fig. 9/9 B). It seems unlikely due to their distinctness that they are a product of preservation of taphonomy. Rather, they are interpreted as feature occurring in Eocene taxa, no more present in Oligocene forms (as seen for the trochanter major of the femur above too).

The metatarsals are most similar to the wolf and the hyena. In *Canis lupus* the metatarsals are more elongated and in *Crocuta crocuta* they are distally more broadened.

The North American material is of the same morphology as the Oligocene European material (personal observation; AMNH 9809).

Mt II	MtL	MtWm	MtWl	MtWmd
	53.7 mm	7.1 mm	6.6 mm	8.8 mm

Mt III	MtL	MtWm	MtWl	MtWmd
	66.2 mm	7.9 mm	7.2 mm	10.6 mm

Mt IV	MtL	MtWm	MtWl	MtWmd
	66.4 mm	7.8 mm	7.6 mm	12.1 mm

Mt V	MtL	MtWm	MtWl	MtWmd
	54.5 mm	7.9 mm	6.2 mm	10.2 mm

Hyaenodon sp. small sized species

Tibia: M 30132 from Hordwell (Hants, Great Britain, Eocene, Fig. 9/8 B)

The tibia is considerably smaller than the one described above, but comparable to material of Aubrelong (see below or Fig. 9/8 D). The proximal part is broken away, but it is otherwise well preserved and not distorted. It is a left tibia. In general it appears from a dorsal view rather straight and still robust. The crista tibialis is well-developed and runs down distad to the malleolus medialis. A strong ridge, a muscle scar, is present over the whole length of the plantar aspect of the bone. The distal articular surface is broad and not as rectangular as in the tibia described above, but otherwise not significantly different. The articular surface declines laterad and is deeply grooved.

Shared features with the above described tibia (M 28195) are: strong crista tibialis, strong muscle scars, malleolus medialis and similar depressions of the distal articular surface. However, they differ in proportion e.g. the smaller one being less robust. Also the shape of the distal articular surface is not as rectangular elongated as in the larger one. The North American material shows the same features, as well as the Asian material (pers. obs.; AMNH 19002 A; AMNH 1381).

TiL (broken)	TiWm	TiWl	TidisL	TidisW
min. 115.5 mm	8.5 mm	11.1 mm	15.6 mm	13.5 mm

Carnivora indet. (*Cynodictis*?)

Forepaw: M 26761 from Vaucluse (France, Upper Eocene, Fig. 9/10 A)

The specimen is a cast of a partial left and a partial right forepaw with carpals, metacarpals and phalanges. It was made from an original housed at the MNHN (Paris). The original specimen for the left forepaw (without number) was examined in their collections (Fig. 9/10 B). The original of the right forepaw was unavailable. The cast (M 26761) was previously determined as Hyaenodont? and the specimen in Paris as *Hyaenodon requieni*. Herein, it is stated, that this material should be referred to Carnivora indet.

The third and last phalanx is deeply split in *Hyaenodon*. This cannot be observed in the specimen. The phalanx is broken, but most of it is preserved. The beginning of the split should be present, as the split is running far proximally in *Hyaenodon*. Furthermore, a proximal constriction present in *Hyaenodon* (Fig. 9/11 A) is not seen here. The phalanges in general are broad and heavy. The metacarpals are within the range of *Hyaenodon* and their affiliation to it cannot be outruled, if a mixture of the material is assumed. They show strong muscle marks. However, they are diverging and not closely appressed as in *Hyaenodon*. The unciforme is the largest carpal in the distal row in *Hyaenodon* (Mellett, 1977; see Fig. 9/10 C and D). In this specimen the respective carpal is small. The most striking element is the fused scapholunatum. The fusion of scaphoid and lunatum is a derived feature seen in the order Carnivora. North American taxa of *Hyaenodon* show a scaphoid and a lunatum with no tendence to fusion (see Fig. 9/10 C and D for reconstructions of the manus in *Hyaenodon*). It is known in other hyaenodontids (*Hyainailouros*), but this state is restricted to a few forms. It was stated to be present in the European taxa of *Hyaenodon* (Scott, 1895b; Bonis, 1964). Bonis (1964) determined the Paris specimen as *Hyaenodon*, relying on other findings of the same site. However, also *Pterodon* and the *Cynodictis* (Carnivora) are known from the same site. When comparing the scapholunatum it is noticed that it is very bear-like. So, there is no evidence for a fused scapholunatum in *Hyaenodon* and the specimen is belonging to an individual of the modern order Carnivora rather than to a hyaenodontid. The affiliation to the carnivore *Cynodictis* is possible and previously proposed here based on the ursid appearance of the carpal.

Additional material from the MNHN

Two sites yielded postcranial material assigned to *Hyaenodon*: the Eocene site La Débruge and the Oligocene site Aubrelong (see Chapter 4).

The following material from Aubrelong 1 was collected and determined by Brigitte Lange-Badré, but remained undescribed up to now: femur, tibia, radius, humerus fragment, calcaneus, metapodials and phalanges.

Au 1057 is a fragment of a left distal humerus (Fig. 9/3 C). The bone shows the typical features of a *Hyaenodon* humerus: the entepicondylar foramen, the anconeal fossa and the strongly shaped trochlea.

HuWd (broken)	HuWm	HuWl	HuTrH	HuTrW	HuTrD
26.9 mm	9.2 mm	9.1 mm	14.6 mm	19.5 mm	10.6 mm

Au 1028 is a complete radius (Fig. 9/5 D and E). It is not as robust and heavy as in large sized species. The proximal articulation surface is elongated laterally and thus rectangular. The distal articulation surface is of approximately triangular shape and concave. The shaft is straight. Au 869 is a proximal fragment of a radius and was suitable only for some measurements.

RaL	RaWl	RaWm	RaprDiamin	RaprDia
110.9 mm	6.9 mm	8.6 mm	6.2 mm	9.6 mm
RadisDia	RaApL	RaApW	RaAdL	RaAdW
11.0 mm	16.0 mm	9.6 mm	12.8 mm	13.0 mm

Au 1028

RaprDiamin	RaprDia	RaApL	RaApW
6.6 mm	10.1 mm	16.4 mm	10.1 mm

Au 869

Au 6754 and Au 2319 (Fig. 9/11 B) are both a scapholunatum and were attributed to *Hyaenodon*. These two bones are very small (see measurements below). There are no clear facets present. However, to my opinion these bones show no large, smooth area for articulation with the radius. Such an area is typical for a scapholunatum. Other facets are missing as well. Therefore, I do not agree with the former identification. I acknowledge that these elements could be a sesamoid of *Hyaenodon*.

Au 2319		Au 675	
length	12.6 mm	length	13.8 mm
width	9.9 mm	width	10.1 mm
depth (dorso-ventrally)	7.1 mm	depth (dorso-ventrally)	7.3 mm

Au Ru 56 is determined as first phalanx of *Hyaenodon*. It is symmetrical and similar to the respective element in the North American specimen FAM 75692 (metacarpals with a proximal phalanx).

A terminal phalanx (Au 18?) is preserved as well (Fig. 9/11 A; attributed to *Hyaenodon dubius* by Lange-Badré). One of the tips is broken. The split is deep and the body is proximally waisted. It is curved in lateral view and its dorsal articulation surface is strongly concave. Split unguals are characteristic and their function is still not clear, as well as the question of how the horny sheath of the claw could have looked like (split too?) is unresolved. Its shape (Fig. 9/12 A) was compared to the mean shapes of different locomotory guilds in mammals analyzed by MacLeod and Rose (1993) via Eigenshape Analysis (Fig. 9/12 B). Interestingly, the lateral shape is similar to the generalistic terrestrial type: a strong ventral curvature and a smaller curvature are present, as well as the concave proximal articulation area. The dorsal shape is not resembling this type — it is more similar to the cursorial type, because of its greater width and the proximal constriction.

Au 2361 (Fig. 9/7 B) is a complete femur. Comparing to large sized forms of the genus, it appears not as robust and more elongated. The shaft is straight. The greater tuberosity is subequal in height to the caput. The trochanter minor is distinct. The third trochanter was present, although small — the femur is broken in this region. The neck is short. The caput is rounded and the fovea is not preserved. The condyles show a large extension ventrally. The patellar groove is deep and bordered by high ridges.

FeL	FeWm	FeWl	FeWd	FemCH	FemCL	FemCW
140.9 mm	9.5 mm	12.4 mm	27.7 mm	16.0 mm	32.5 mm	10.6 mm

FelCH	FelCL	FelCW	FeCW	FeCH	FeNeW	FeNeW2
17.3 mm	29.9 mm	12.7 mm	15.0 mm	12.2 mm	10.9 mm	8.3 mm

FePagH	FePagHl	FePagW	FeWpr	FeWinf	FedisH
24.2 mm	32.6 mm	12.0 mm	32.7 mm	6.0 mm	33.7 mm

Au 776 is a juvenile tibia (Fig. 9/8 D). The proximal epiphysis is missing. The tibial crest is developed and is reaching approximately the half of the shaft. The distal articulation area is concave and shows deep grooves. The cross-section of the shaft would be triangular.

TiWm	TiWl	TiCrH	TiDiH	TidisL	TidisW
10.2 mm	9.1 mm	19.3 mm	15.3 mm	19.1 mm	14.6 mm

Au 2359 is a complete fibula (Fig. 9/14 A). It is long and not reduced. The proximal end is heavy and antero-posteriorly thickened. A tendinal sulcus is present. The shaft is straight and cylindrical in cross section. The distal end is again thickened and broad, showing a smooth facet of approximately triangular shape. This facet was the articulation with the calcaneus. The length of the fibula is 120.9 mm.

Au 2078 is a metatarsal V (Fig. 9/9 B). It is of the same morphology as the respective bone in M 28162. The dorsal articulation surface is of triangular outline. Its shaft is curved. It was determined as *Hyaenodon dubius* by Lange-Badré.

MtL	MtWm	MtWl
40.8 mm	3.6 mm	4.5 mm

Au 731 is a calcaneus (Fig. 9/11 D). The laterally sloping facet for the navicular is clearly present. This feature is a characteristic of the genus and seen in the North American taxa, as well as in the Asian forms. The tuber is slim. The body is narrow. The sustentacular facet is rounded. The external facet for the astragalus is elongated and kidney-shaped. A deep sulcus between the two facets is present.

CalL	CalW	CalCol	CaluFaL	CaluFaW
41.2 mm	18.1 mm	21.6 mm	12.7 mm	7.4 mm

CallFaL	CallFaW	CalTuW	CalTuWlat
12.7 mm	6.8 mm	12.8 mm	5.8 mm

It is apparent from the material from Aubrelong, that the long bones have a more modern appearance compared to the long bones of the older site La Débruge. They are more elongated and less robust. The species designation (*Hyaenodon dubius*, by Lange-Badré) cannot be confirmed or rejected for now. This species has a time range that falls into the time of the site and dental material attributed to *Hyaenodon dubius* is known from the same site. However, *Hyaenodon exiguus* — though smaller — is known too from Aubrelong. As long as associated findings of *Hyaenodon* are not known from Europe, determinations on species level should be carefully considered.

The following paragraph deals with the additional material from La Débruge:
LDB 19 is a complete humerus dex. (Fig. 9/3 B and D), although damaged in its dorso-proximal part. The humerus is of the same morphology as the North American forms. It is robust, shows the characteristic trochlea with the capitellum and the anconeal fossa as well as the entepicondylar foramen are present. The trochlea is deep. The caput is not rounded. The shaft is medially broad. Due to fragmentation it is hard to judge upon the extension of the deltoid crest, but it seems that it was not very prominent. The tuberculum major exceeds the caput and the tuberculum minor in height. LDB 20 is another complete humerus dex. and LDB 21 is a distal fragment of humerus dex. Both show the same features.

measurements	LDB 19	LDB 20	LDB 21
HuL	155.0 mm	155.0 mm	/
HuWl	19.6 mm	22.3 mm	/
HuWm	14.4 mm	/	/
HuWd	16.6 mm	16.7 mm	16.3 mm
HuTrH	22.4 mm	20.0 mm	20.2 mm
HuTrW	28.9 mm	25.6 mm	25.5 mm
HuTrD	13.7 mm	12.6 mm	13.5 mm
HuEpcW	12.9 mm	16.3 mm	13.2 mm
HuCaW	29.4 mm	/	/
HuCaH	20.2 mm	21.8 mm	/

LDB 22 (Fig. 9/5 B) is a complete radius and LDB 23 a proximal fragment of a radius. Both show features that are typical for *Hyaenodon*: robust in general, heavy, distally widened, elongated proximal articulation surface and concave distal articulation surface.

measurements	LDB 22	LDB 23
RaL	126.6 mm	/
RaWl	27.0 mm	/
RaWm	11.8 mm	/
RaprDiamin	9.6 mm	9.6 mm
RaprDia	14.7 mm	14.6 mm
RadisDia	22.3 mm	/
RaApl	/	25.6 mm
RaApW	/	14.6 mm
RaApdl	17.9 mm	/
RaAdW	17.4 mm	/

LDB 43, 44 and 46 (Fig. 9/11 C) are astragali, the first two are right ones and the latter (LDB 46) is a left one. In general the astragalus in the European *Hyaenodon* is similar to the astragalus of the North American taxa. The neck length is lower in the European specimens. The neck is slightly longer in North American specimens (e.g. in a similar sized astragalus 18.8 mm — compared to 13.3 mm in LDB 43 and 46, see below). The sustentacular facet is broader in North American forms (11.6 mm vs. 10.4 mm). The most apparent difference is the shape of the head of the astragalus: it is much more rounded and not as wide as in the North American astragalus. Neither an astragalar foramen is present, nor a tubercle that is higher than the ridge of the trochlea. Thus, the tibia could be rotated on the whole trochlea.

measurements	LDB 43	LDB 44	LDB 46	cast of a North American astragalus
AstL	30.2 mm	33.3 mm	32.8 mm	33.5 mm
AstW	22.3 mm	23.7 mm	21.2 mm	23.9 mm
AstTrW	25.9 mm	25.9 mm	24.5 mm	26.1 mm
AstTrH	21.5 mm	20.5 mm	21.5 mm	21.8 mm
AStTrL	23.9 mm	23.1 mm	21.5 mm	24.4 mm
AstNeL	13.3 mm	12.1 mm	13.3 mm	14.8 mm

The original specimen of the cast (M 26761 in the BMNH) — a manus dex. with carpals, metacarpals and phalanges, emphasizing the scapholunatum — was found in the collections of the MNHN. The specimen is without number and attributed to *H. requieni* and comes from La Débruge. The affiliation was discussed above.

For completeness the specimen SNB 424 shall be mentioned. It is mentioned together with an m3 from Sainte Néboule and determined as *Hyaenodon brachyrhynchus*. This astragalus looks completely unlike the other respective elements in the genus and thus the affiliation is doubted here.

As postcranial remains of *Pterodon dasyuroides* remained undescribed up to now — the presence of two element in the collections of the MNHN shall be mentioned: an astragalus (Qu 9974) and a calcaneus (Qu 9972). Both come from the Quercy, but without precise location and both were determined as *Pterodon dasyuroides*. The astragalus was unavailable, but a note indicates that it should have been together with the calcaneus. The calcaneus is not completely unlike that of *Hyaenodon*. It shows the laterally sloping facet for the naviculare, although it is here even more extreme. Furthermore, it is in general wider and more robust.

In the collections of the AMNH the calcaneus and the astragalus of the Asia *Hyaenodon pervagus* (AMNH 19002 A, Öbör, Hangay province, Loh, Mongolia, Hsanda Gol Formation) could be compared to the North American *Hyaenodon horridus* (AMNH 1381, Cheyenne River, South Dakota, White River Formation, Oligocene; both Fig. 9/14 B and C). The astragalus is not much different, but on the calcaneus a few diverging features should be mentioned: the Asian calcaneus is smaller, slimmer, its sustentacular feacet is not circular and its body is not as broad. It is more similar to the European calcaneus (see above).

Additional measurements can be provided from North American taxa (YPM-PU 10995, *Hyaenodon horridus*, Fig. 9/14 E and YPM-PU 13603, *Hyaenodon* small sp.; see Tab. below). These show that the hindlimb was not shorter than the forelimb as in recent hyenas. Also, the Metatarsal III – Femur ratio (MtIII/Fe Ratio) can now be calculated. It is 0.36 (in YPM-PU 10995); The same is true for a smaller North American specimen (YPM-PU 13603) — the MtIII/Fe ratio is 0.36 as well;

CaputL	HuL	RaL	FeL	FeWm	FeWl	TiL	FiL	MtIIIL
253.3 mm	149.7 mm	109.8 mm	177 mm	12.8 mm	13.2 mm	148.6 mm	138.5 mm	64.8 mm

YPM-PU 10995, *Hyaenodon horridus* from the Corral Draw (South Dakota, Brule Formation), note the longer length of the long bones of the hind limbs (humerus vs. femur and radius vs. tibia).

HuL	UlL	RaL	McIIIL	ScL	ScW	PhIIIfL	PhIIIfWm
96.3 mm	109.1 mm	79.1 mm	34.5 mm	82.9 mm	41.8 mm	10.8 mm	3.4 mm
FeL	FeWm	FeWl	TiL	FiL	MtIIIL	PhIIIhL	PhIIIhWm
108 mm	9.0 mm	10.4 mm	107.2 mm	100.1 mm	39.7 mm	12.2 mm	4.0 mm

YPM-PU 13603, *Hyaenodon* small sp., juvenile with canines (sup. and inf.) erupting.

9.4 Divergence within the genus concerning the postcranial material

The differences in postcranial remains of *Hyaenodon* from Europe and North America was discussed early (Scott, 1895). In this section his remarks are mentioned and listed concerning the respective element.

Humerus
The supratrochlear fossa is connected via a foramen with the anconeal fossa in the North American species, whereas there is no connection between the supratrochlear fossa and the anconeal fossa in the European species (Scott, 1895). I was not able to confirm any obvious difference in that region.
The humeral trochlea is lower, more 'felid' with an indistinct intercondylar ridge in European forms and more 'ungulate' with a broad median facet and a strongly convex intercondylar ridge in North American forms (Scott, 1895). The observed material is to me of the same morphology (see the new descriptions herein).

Carpus
In European *Hyaenodon* scaphoid and lunatum are fused to the scapholunatum (Scott, 1895; Martin, 1906), whereas there is no trend to fusion in North American *Hyaenodon* (Scott, 1895; Mellett, 1977). Later Wortman (1902) reported a finding of a fused scapholunatum of North American *Hyaenodon* (YPM 10076). Mellett (1977) stated that this was misidentification and it belongs to *Daphoenus*, an Oligocene 'Fissiped'. However, there is no evidence for a fused scapholunatum in European *Hyaenodon* as the reported findings were misidentifications (see above).

Calcaneus
The calcanear processus is more prominent in European species than it is in the North American species.
I observed that the tuber calcanei is larger in proportion the body in European and Asian species, compared to North American ones.
This results in a more extensive fibular facet in the North American forms (Scott, 1895) than in the European forms (Fig. 9/11 D). In European *Hyaenodon* the sulcus between the astragalar facet and the sustentaculum is deeper (Scott, 1895). I can confirm that and observed that this sulcus is also deeper and alike those in the European forms in an Asian calcaneus (AMNH 19002 A).

Astragalus
The collum length of the astragalus is greater in the North American forms (Scott, 1895). This can be confirmed (see measurements in the following). Scott (1895) states a more extensive sustentacular facet in North American taxa, which I could not confirm on the available material. The incline of the external calcaneal facet is greater in North American *Hyaenodon*. I could not observe a difference in inclination in the limited material that was available, but size cannot be outruled as a cause of such differences.

9.5 Locomotion

9.5.1 Skeletal indicators for inferring locomotion

A lot of work has been done on skeletal indicators and inferences on locomotion in fossil mammals. The following section is not dealing with the entity of hitherto knowledge. It rather summarizes some features on the most important elements in the skeleton. An excellent study on morphofunctional analysis of the postcranium of a carnivore (*Amphicyon major*) was performed by Argot (2010). This publication was a guide to me.

Characteristics of plantigrade animals are shorter and heavier long bones and freer articulation of the joints, which allow more movement between the elements (e.g. between tibia and tarsus; Ginsburg, 1961).
The outline of the scapula, the glenoid, the neck and the acromion provide information for inferring locomotion (see Tab. 9/2).

The humerus provides many features that give clues on the locomotion type (Tab 9/3). It takes part in two important joints: the shoulder and the elbow joint. However, it is also important to the topic of body weight: mechanical loads weigh more on the humerus than on the femur with increasing weight (Heinrich and Biknevicius, 1998). The presence of the entepicondylar foramen of the humerus is the plesiomorph condition in Caninae (Tedford et al., 1995). This foramen is also seen in *Nandinia binotata*, so it might be a plesiomorph condition in Carnivora in general (pers. obs.).
The shaft of the radius and its articulation areas are the regions of interest (Tab. 9/4).
This is valid for the ulna too (Tab. 9/5). It is also important to mention, that the longer the olecranon is, the more power can be exerted in the claws (Taylor, 1989). Some authors also provide information about the anatomy of the soft tissues, for example concerning muscles and tendons: plantigrade carnivores possess a shallow groove at the top of the olecranon and the tubercles at its borders are asymmetrical, whereas in digitigrade carnivores the groove is deep and bordered by two equal high tubercles (Ginsburg, 1961; Wang 1993). In the latter group these osseous features prevent the tendon for the triceps brachii to slide out (Ginsburg, 1961; Wang, 1993). Concerning the orientation of the olecranon the following fact shall be added: the angle of the olecranon increases much with size, especially in terrestrial and scansorial forms (Van Valkenburgh, 1987). In same sized forms the angle is larger in terrestrial than in arboreal and scansorial forms (Van Valkenburgh, 1987). Semi-fossorial taxa show an angle that is inbetween scansorial and terrestrial forms, but in contrast to these, semi-fossorial animals have relatively longer olecrana (Van Valkenburgh, 1987). Tab 9/6 summarizes features of the carpus, the metapodials and the phalanges. The outline of the latter is for example an important feature (MacLeod and Rose, 1993). In a plantigrade carpus movements between the scapholunatum and the cuneiforme are possible (Ginsburg, 1961): the articulation area between the scapholunatum and the unciforme in most plantigrade taxa forms a single curve and allows wider movement. The contact between the ulna and the carpus is reduced in modern Carnivora, as well as the role of the pisiforme (Mellett, 1977). The fusion of the scaphoid and the lunatum in Fissipedia leads to a smooth, undisturbed area between radius and carpus — this leads to a simple sliding area and is one of the characteristics of Carnivora (Mellett, 1977). Yalden (1970) emphasized that with the statement, that the scapholunatum is typical for modern carnivores. Furthermore, he explains the fusion of scaphoid and lunatum due to statics and because the resulting scapholunatum shows a proximal area that provides a devinational hinge and a smooth curve. Another important feature is located on the middle phalanx. In cats the trochlea is transversely elongated to the lateral sides and thus is asymmetrical (dorsal and in cross-section; Wang, 1993). That asymmetry indicates retractility and is correlated with relatively short, deep, laterally compressed and sharp distal phalanx (Wang, 1993). The shape of the claw, the distal phalanx, was examined by MacLeod and Rose (1993) with morphometric analysis. Interestingly the fore ungula are two times longer than the hind ungual phalanges (Van Valkenburgh, 1987).

The acetabulum is informative due to articulation with the femur, but there are other regions of interest on the pelvis (Tab. 9/7) too. More power in propulsion comes from the hindlimb (Gray, 1968), so the femur shows many features (Tab. 9/8). The important features on the tibia (Tab. 9/9) are the articulation facets and the tibial facet.

The development of the fibula (Tab. 9/10) also gives clues on locomotor behaviour. Cursors tend to reduction of this bone, e.g. the middle part of the fibula in the cheetah is synostosed with the tibia (Taylor, 1989).

The calcaneus (Tab. 9/11) is giving information about the stance and the locomotion pattern (e.g. Ginsburg, 1961; Laborde 1987; Wang 1993). The shape of the calcaneus indicates its locomotory function (Polly and MacLeod, 2008): animals with four digits have narrower calcanea and broader sustentacular facets than animals with five digits. A long tuber of the calcaneus acts as lever for the plantarflexion of the foot (insertion for gastrocnemius and soleus muscle; Polly and MacLeod, 2008).

The astragalus (Tab. 9/12) is the other highly important tarsal. There is a tendency in terrestrial forms to deeper grooved astragali (Van Valkenburgh, 1987). Due to more foreaft-movements in cursors and not medial-lateral-flexion a tighter interlocking with the tibia is necessary and thus a deeper groove. However, there are exceptions and Van Valkenburgh (1987) found that depth tells more about phylogeny. The naviculare in plantigrade forms is elongated and in digitigrades it is rectangular (Ginsburg, 1961).

SCAPULA

feature	development	adaptation	cited from
outline of the corpus	rectangular and flat short and wide	cursorial arboreal and/or primitive	Gunnell (1998), Taylor (1989); Wang (1993);
acromion	long, exceeds the glenoid does not exceed the glenoid	arboreal and/or primitive terrestrial	Gebo and Rose (1993), Laborde (1987), Wang (1993); Laborde (1987);
glenoid notch	shallow deep	arboreal terrestrial	Taylor (1974), Heinrich and Rose (1997)
neck	width greater width narrower	arboreal terrestrial	Heinrich and Rose (1997)

Tab. 9/2: Skeletal indicators for certain locomotor adaptations on the scapula.

feature	development	adaptation	cited from
deltoid/supinator crest	large and low	plantigrade	Ginsburg (1961);
	broad and robust	fossorial	Gebo and Rose (1993);
			Heinrich and Rose (1997);
	narrow and laterally flared	arboreal	Gunnell (1998), Taylor (1989), Wang (1993)
	small and reduced	cursorial	
tuberculum major (= greater tuberosity)	lower than caput	arboreal	Laborde (1987);
	large and protrudes proximally	cursorial	Taylor (1989);
medial entepicondylus (= epicondyle)	large	plantigrade	Ginsburg (1961);
	wide, large	arboreal	Laborde (1987), Heinrich and Rose (1997);
			Laborde (1987);
	not wide	terrestrial	Gebo and Rose (1993);
	well-developed	scansorial/ambulatory	
bicipital groove	narrow and clearly defined	arboreal	Gebo and Rose (1993), Laborde (1987), Taylor (1974);
			Wang (1993);
	deep	cursorial	
brachioradialis crest	well-developed	scansorial/ambulatory	Gebo and Rose (1993); Wang (1993);
	thin-bladed	cursorial	
olecranon fossa	shallow	arboreal	Heinrich and Rose (1997), Wang (1993);
			Laborde (1987);
	perforated	terrestrial	
trochlea	small, shallow and not projecting	arboreal	Laborde (1987);
	large, deep and projecting	terrestrial	Laborde (1987);
	narrow, box-like and with deep midtrochlear furrow	cursorial	Andersson (2003);

Tab. 9/3: Skeletal indicators for certain locomotor adaptations on the humerus.

RADIUS

feature	development	adaptation	cited from
shaft	curved	arboreal	Laborde (1987);
	straight	terrestrial	Laborde (1987);
length compared to humerus	shorter	arboreal	Laborde (1987);
position to ulna	placed more anterior	cursorial	Taylor (1989);
radial head	round	aboreal	Heinrich and Rose (1997);
	ovoid	scansorial/ambulatory	Gebo and Rose (1993);
tubercles	strong and prominent	arboreal	Laborde (1987), Heinrich and Rose (1997);
	not prominent	terrestrial	Laborde (1987);
distal articulation area	shallow and large	arboreal	Heinrich and Rose (1997), Laborde (1987); Laborde (1987);
	concave	terrestrial	

Tab. 9/4: Skeletal indicators for certain locomotor adaptations on the radius.

ULNA

feature	development	adaptation	cited from
olecranon	anterior inclined	arboreal	Laborde (1987), Taylor (1974), Wang (1993);
	inclined following the axis of the shaft	terrestrial	Taylor (1974);
	posteriorly inclined	cursorial	Van Valkenburgh (1987)
proximal groove between the tubercles	shallow and asymmetrically bordered	plantigrade	Ginsburg (1961), Wang (1993);
	deep and bordered by two equally high tubercles	digitigrade	Ginsburg (1961), Wang (1993);
styloid process	small but present	arboreal	Gebo and Rose (1993);
diaphysis	wide	arboreal	Laborde (1987);
	slender	terrestrial	Laborde (1987);
radial notch	shallow	arboreal/fossorial	Taylor (1974);

Tab. 9/5: Skeletal indicators for certain locomotor adaptations on the ulna.

feature	development	adaptation	cited from
carpus	broad	cursorial	Gunnell (1998);
pisiforme	laterally inclined	arboreal	Taylor (1974);
	large and ventrally positioned	cursorial/digitigrade	Taylor (1974);
magnum	hook-shaped with stop facet	arboreal	Yalden (1970);
metapodials	short, straddled and with well-developed I and V	plantigrade	Ginsburg (1961);
	closely adjoined, with III and IV of subequal length	digitigrade cursorial	Ginsburg (1961); Wang (1993);
distal phalanx	deep, hook-shaped and long	arboreal	Taylor (1974), Wang (1993);
	laterally compressed	scansorial	Gebo and Rose (1993);
	not much curved and flattenend	fossorial	Van Valkenburgh (1987);
	curved and not flattened	terrestrial	Van Valkenburgh (1987);

Tab. 9/6: Skeletal indicators for certain locomotor adaptations in the carpus, on the metapodials and the phalanges.

PELVIS

feature	development	adaptation	cited from
ilium	wide	cursorial	Gunnell (1998), Taylor (1976, 1989);
pelvic floor	sharply angled	cursorial	Wang (1993);
acetabulum	wide	arboreal	Laborde (1987);
	narrow	terrestrial	Laborde (1987);
tuberculum (ventro-caudal on the ilium for the rectus femoris)	prominent	arboreal	Laborde (1987), Gebo and Rose (1993);
	not prominent	terrestrial	
ischial spine	large	arboreal	Heinrich and Rose (1997);

Tab. 9/7: Skeletal indicators for certain locomotor adaptations on the pelvis.

FEMUR

feature	development	adaptation	cited from
patellar groove	shallow and wide deep with high marginal ridges	arboreal cursorial	Heinrich and Rose (1977); Taylor (1976, 1989);
third trochanter	strongly developed weak	plantigrade digitigrade	Ginsburg (1961); Ginsburg (1961);
neck	long short	arboreal terrestrial	Laborde (1987); Laborde (1987);
trochlea	wide, relatively shallow and not prominent narrow and deep	arboreal terrestrial	Laborde (1987); Laborde (1987);
condyles	posterior placed not posterior placed well separated behind the long axis of the shaft	arboreal scansorial terrestrial	Laborde (1987); Laborde (1987); Laborde (1987);
caput	rounded	not cursorial	Heinrich and Rose (1997), Egi at al. (2005);
fovea capitis	laterally oriented	cursorial	Wang (1993);

Tab. 9/8: Skeletal indicators for certain locomotor adaptations on the femur.

TIBIA

feature	development	adaptation	cited from
tibial crest	small well-developed	arboreal cursorial	Taylor (1976); Taylor (1976, 1989);
tibio-tarsal joint surface	not deep, flat prominent and deep	arboreal terrestrial	Heinrich and Rose (1997), Laborde (1987); Laborde (1987);
proximal tubercles	regularly distributed concentrated in anterior region	arboreal terrestrial-cursorial	Taylor (1976); Taylor (1976);
articulation facets with fibula	significant and large, especially distally	arboreal or plantigrade or locomotion over uneven terrain	Taylor (1976);

Tab. 9/9: Skeletal indicators for certain locomotor adaptations on the tibia.

FIBULA

feature	development	adaptation	cited from
fibula itself	reduction immobile	cursorial jumping, burrowing, swimming	Taylor (1989); Barnett and Napier (1953);
distal articulation area	semilunar shape	progression (at high speeds) over uneven terrain	Barnett and Napier (1953);
	no tibio-fibular contact	primitive	Barnett and Napier (1953);

Tab. 9/10: Skeletal indicators for certain locomotor adaptations on the fibula.

CALCANEUS

feature	development	adaptation	cited from
calcaneus itself	short and robust narrow	plantigrade digitigrade	Ginsburg (1961); Wang (1993);
manubrium	long	plantigrade	Ginsburg (1961);
sustentaculum tali	prominent and wide	plantigrade	Ginsburg (1961), Polly and MacLeod (2008);
	high position low position	arboreal terrestrial	Laborde (1987); Laborde (1987);

Tab. 9/11: Skeletal indicators for certain locomotor adaptations on the calcaneus.

ASTRAGALUS

feature	development	adaptation	cited from
caput	transversally flattened	arboreal or plantigrade	Ginsburg (1961), Laborde (1987);
	spherical	terrestrial or digitigrade	Ginsburg (1961), Laborde (1987);
trochlea	wide narrow	arboreal terrestrial	Laborde (1987); Laborde (1987);
posterior joint area	shallow deep	arboreal terrestrial	Laborde (1987); Laborde (1987);
neck	heavy and short elongated	plantigrade digitigrade	Ginsburg (1961); Ginsburg (1961);

Tab. 9/12: Skeletal indicators for certain locomotor adaptations on the astragalus.

9.5.2 Hitherto studies on the locomotor behaviour of *Hyaenodon*

The locomotion type is defined according to Egi (2001):
arboreal = rarely moving on the ground, forages and shelters in trees;
scansorial = capable of/good at climbing, forages mainly on the ground;
terrestrial = climbs rarely/never, scarcely running;
semi-aquatic = some swimming adaptation;
aquatic = swimming specialization, forages mainly in water;
semi-fossorial = digs frequently for food and protection;
generalistic = none of these specialisations;
cursorial = does not climb, adapted to running;

The following review of locomotion behaviour and ecological niche of *Hyaenodon* is based on North American specimens. O´Harra (1920) considered *Hyaenodon* as semi-plantigrade. On the contrary, *Hyaenodon* was often described as digitigrade (e.g. Gunnell, 1998; Mellett, 1977; Scott & Jepsen, 1936). In most publications the genus was seen as cursorial (e.g. Gunnell, 1998; Mellett, 1977; Morlo, 1999) or at least as the most cursorial predator of its time (Egi, 2001; Egi et al., 2005;). In Werdelin (1996) *Hyaenodon* is mentioned as true terrestrial form within fossil carnivorous mammals (possible semicursorial large prey specialist). Still, there is no agreement, because in Janis & Wilhelm (1993) *Hyaenodon* is stated to be not cursorial and seen as terrestrial in Van Valkenburgh (1987). Terrestrial features are (Van Valkenburgh, 1987): relatively straight ungual phalanges, short phalanges, intermediate long metatarsals, caudally orientated olecranon process, but long olecranon (that could indicate frequent digging like in the grizzly today). The astragalar sulcus is deeper compared to that of contemporous fissipeds and that fact is interpreted as cursorial feature (Mellett, 1977). In earlier publications even the assumption was stated, that the genus could have been semi-aquatic, because of the elongated nasals (O´Harra, 1920). For smaller species (semi-)arboreal adaptations are considered (Mellett, 1977). The question if *Hyaenodon* frequently digs is still open. Digging was an idea mentioned by some authors (Gunnell, 1998; Mellett, 1977, Van Valkenburgh, 1987). This was based on observations on the forelimb (see above), but the same features could indicate that *Hyaenodon* strongly relied on its forelimbs to bring down pray as did sabertoothed cats (Van Valkenburgh, 1987). Another subject of interest is the difference in morphology within the genus: Smaller forms like *Hyaenodon mustelinus* have longer tails in proportion to their body compared to larger forms like *Hyaenodon horridus* (Scott & Jepsen, 1936). Scott & Jepsen (1936) stated that there is more difference in the scapula than ususally found within a genus and that the phalanges of the pes are totally different in *Hyaenodon horridus* than in other species (which triggered taxonomic suggestions like the proposal of a new genus for *Hyaenodon horridus*).
Hyaenodontidae tended to hunt on short distance (Van Valkenburgh, 1999). It was early supposed that *Hyaenodon* was a carrion-feeder (O´Harra, 1920). However, there was doubt that the genus provided active predators (discussed in e.g. Gunnell 1998; Mellett, 1977; Egi et al., 2005).
The skeleton itself was considered as more canid-like (Van Valkenburgh, 1999), having a wolf-like appearance (O´Harra, 1920) or both sharing felid and canid features (Mellett, 1977). Regarding the paleoecology, *Hyaenodon* was seen as big cat (Gunnell, 1998), especially the largest species *Hyaenodon horridus* (hyena- or lion-like; Mellett, 1977) and as fulfilling the same ecological role as the nimravid *Hoplophoneus* and later the felid *Lynx* (Wesley-Hunt, 2005). Differences between the species suggest different habitats to avoid competition (Scott & Jepsen, 1936). There is sexual dimorphism in *Hyaenodon* (Gunnell, 1998; Mellett, 1977), whereas Egi (2001) specifies the dimorphism as not as significant as expected in *Hyaenodon horridus* and possible as well in *Hyaenodon crucians*. Generally, sexual dimorphism is less developed in carnivores that hunt small pray (Dayan & Simberloff, 1996).
It is not known if "creodonts" were replaced actively trough competition or passively due to the increase of carnivores (Wesley-Hunt, 2005): Taxonomic decrease of "creodonts" in the late Eocene coincides with the beginning radiation of carnivores. Taxonomic diversity of carnivores was suppressed by "creodonts", but it

seems like there was no morphological release in carnivores. The occupied morphospace has not changed, just the inhabitors. Probably because carnivorous forms rely on a relatively stable ressource, that is not changing much (Wesley-Hunt, 2005).

Egi (2001) described evolutionary trends within North American species of *Hyaenodon*: The species of earliest Oligocene age are different to Wasatchian and Bridgerian hyaenodonts. They differ in increasing body size and cursorial adaptation. Chadronian species like *Hyaenodon mustelinus* with an estimated body weight of 5 kg and *Hyaenodon microdon* were smaller that Orellan species like *Hyaenodon crucians* and *Hyaenodon montanus*. In the Chadronian there was the greatest diversity in body size. Smaller hyaenodonts diminished at the end of the Bridgerian. Uintan forms were larger than forms in the Wasatchian and Bridgerian. Smaller forms occur again in the Duchesnean. Egi (2001) proposed that these changes might be due to environmental changes, changes of prey composition or occurrence or disappearance of predators. The Eocene of North America was connected with a cooling and a more arid climate. Thus, the tropical forest changed into less dense vegetation, probable a subtropical forest with open grasslands. Many carnivore families originated in the Eocene (Duchesnean, Chadronian): amphicyonids, nimravids, canids, ursids, mustelids. Species diversity of *Hyaenodon* was greatest in the Chadronian. The decrease of smaller species of *Hyaenodon* is associated with the diversity of canids (that evolved from scansorial to cursorial). The decrease of big species like *Hyaenodon horridus* could have been influenced by competition with nimravids (Egi, 2001). Her focus was on *Hyaenodon*, but to judge on the ecomorphological position of this genus a detailed comparison with contemporaneous competitors is necessary (as it was done by Morlo et al., 2011).

Janis and Wilhelm (1993) refuted the hypothesis that the relative limb length increased in coevolution between ungulates and carnivorous mammals. They worked with the Mt/F-ratio and found no correlation with maximum speed. Furthermore, the ratio cannot be used to distinguish between ambush and pursuit predators. Pursuit predators were stated to be a Plio-Pleistocene phenomenon. Their set of Carnivora, including felids, hyaenids, canids, mustelids and ursids, scores concerning the Mt/F-ratio between 0.20 and 0.50 (Table 2, p. 110 in Janis and Wilhelm, 1993). The score of *Hyaenodon* (0.36, see above) is comparable to *Panthera leo* (0.35), *Panthera tigris* (0.35), *Crocuta crocuta* (0.36) and *Nyctereutes procyonoides* (0.37; data taken from Table 2, p. 110 in Janis and Wilhelm, 1993). However, they did not consider *Hyaenodon crucians* as cursorial (Janis and Wilhelm, 1993).

9.5.3 Predator behaviour

In order to infer possible behavior and predation style in a fossil mammal, a review of known habits in modern Carnivora is helpful. A predator risks to get hurt during a fight/chase and to loose energy when failing to catch the prey. In 90% of all cases a larger sized predator kills a smaller sized prey (Cohen et al., 1993). To overwhelm a smaller sized prey is easier, but does not provide as much energy as larger sized prey.

Van Valkenburgh et al. (2004) stated that the selection for increasing size (Cope´s rule) leads to dietary specialisations — hypercarnivory — and a greater threat for extinction. In general, one family or subfamily diversifies and dominates for 10 Ma (Van Valkenburgh et al., 2004). All recent carnivores with a body weight higher than 21 kg hunt prey of equal or larger size. Due to the large size of hypercarnivores they have larger home ranges and lower population densities. The risk of extinction augments with the trend to deeper jaws, reduced grinding area and enlarged cutting blades as seen in the case of Permian therapsids, "creodonts", amphicyonids and hyaenids (Van Valkenburgh et al., 2004).

Modern Carnivora show different hunting styles: felids kill with a penetrating killing bite, wheras canids and hyaenids inflict more and shallow bites on their prey (Biknevicius and Van Valkenburgh, 1996). Different groups evolved different solutions to handle large prey: felids and mustelids possess retractile claws and interlocking jaws and canids developed cooperation. Hard food can be processed with postcarnassial teeth

(canids) or with buttressed precarnassial teeth (hyaenids). The round shape of the canini in felids and mustelids indicate their use to stab prey (Biknevicius and Van Valkenburgh, 1996). Canines of felids are more rounded due to a different killing strategy (suffocating, deep bites) and to stress in medio-lateral direction (in case of contact with bone; Jones, 2003). The canines of canids are powerful in anterior-posterior direction, because they are medio-laterally compressed (Jones, 2003). Those medio-laterally compressed canini are used for slashing (Biknevicius and Van Valkenburgh, 1996). The same type of canini are observed in *Hyaenodon* (personal observation). Short snouts are advantageous for more biting power, because the temporalis muscle is more massive (Biknevicius and Van Valkenburgh, 1996). A fused symphsysis does not correlate with body size, tooth morphology or diet (Biknevicius and Van Valkenburgh, 1996). In *Hyaenodon* species with fused as well as species with unfused jaws are known, although most of them had fused jaws.

In order to catch a prey, different methods are applied. The grappling of the cat is only possible due to extensive forearm supination (Andersson, 2003). Felids use their forelimb to bring down prey, whereas canids are adapted to running and exhausting their prey. The humeral trochlea is a compromise between manipulation and locomotion, separating ambushers (grapplers) from pursuiers (locomotors). Andersson (2003) considered *Hyaenodon* as the most cursorial adapted carnivorous mammal of the Oligocene.
There are three types of cursorial cursors (Taylor, 1989): extended trotting (not at high speeds) in the case of hyaenids and many canids; fast runners that depend on speed and endurance in the case of the wolf or *Lycaon pictus*; and sprinters with rapid acceleration (cheetah). Felids are not perfectly digitigrade, because they possess retractile claws to clamp on their prey (except for *Acinonyx jubatus*; Taylor, 1989).

Hyaenodon was most probable a solitary predator (Gunnell, 1998; Mellett, 1977). Defecating on food is an indicator for solitary hunting (Gunnell, 1998). Coprolithes affiliated to *Hyaenodon* are known from North America and Europe. The more bone a mammal takes in, the larger is the fossilization potential of the faeces. In "Razorjaws" (2009) a coprolith is shown with its content: the incisor of a horse. *Hyaenodon* is one of the candidates (focus on Mustelidae, Canidae, Felidae and Hyaenodontidae) for producing a coprolite containing snake vertebrae and a fragmentary centrum of a medium sized mammal (Brule Formation, Oligocene; Parris and Holman, 1978). Coprolithes are known from Europe too, from the Quercy. However, a certain identification of those coprolithes as being produced by *Hyaenodon* is not possible. Interestingly, *Hyaenodon* was already assumed to defecate on its prey (to keep it) by Mellett (1977). He concluded that it was a solitary hunter. Mellett (1977) also assumed tooth gnashing as part of the behaviour.

9.5.4 On body weigth inferences

Size still remains as the most significant difference to separate species. It was the most obvious criterium for establishing the new species *Hyaenodon montanus* (Douglass, 1901). Body size is difficult to estimate, because cranial indicators like skull length tend to overestimate and sceletal indicators like body length tend to underestimate the true size (e.g. Egi et al., 2005).
Small and large sized mammals scale unequally, the critical point is 30 kg (Diaz, 2002). From then on the body weigth correlates more with maximum relative speed than with maximum absolute speed. In most cases the prey is smaller than the predator (Diaz, 2002).
Four main measurements were repeatedly used in literature to infer body weigth (Van Valkenburgh, 1990): head-body length, caput length, occiput-orbita length and the length of the m1. Three classes of body weight were used: <10 kg, 10-100 kg, >100 kg. Larger sized carnivores are 40% lighter than the head-body length calculates. Felids are heavier than canids in comparable body lengths. There is a high correlation between the caput length and the body weight, but larger species have smaller heads. The occiput-orbita length produces similar results as the head length. The m1 length was found to be the weakest predictor, but its error is not higher than in calculations with the other parameters. In fact, it works better for felids. The results for

Hyaenodon were differing about a factor of 4.5, depending on which measurement was used (caput length resulted in heavier weights than the head-body length. Van Valkenburgh (1990) proposed to use a mean value of those, because the head length overestimates and the head-body length underestimates weight in *Hyaenodon*. Body weights hitherto calculated are 93 kg for *Hyaenodon horridus* and 19 kg for *Hyaenodon crucians* (Van Valkenburgh, 1987).

Egi (2001) examined proportions of cross sections of the shaft and bone lengths with bivariate linear regression analysis. She found that the proportions of the humerus and the femur work best for the calculation of body weigths. The shaft correlates more with weight than the joints (except for the femoral shaft in *Hyaenodon* — it overestimates). The body weight of *Hyaenodon* ranged between 9.1 and 43 kg. The error is smaller and the range is narrower when using those measurements rather than head or tooth measurements (Egi, 2001).

Egi et al. (2005) found an average of 20-40 kg in European-North American faunas.

Mechanical loads rest with increasing size more on the humerus than on the femur (Heinrich and Biknevicius, 1998): most mammals bear 55-65% of their weight on the forelimbs.

Morlo (1999) placed the European species *Hyaenodon brachyrhynchus* and *minor* in the 10-30 kg and *Hyaenodon gervaisi* and *requieni* in the 30-100 kg body mass class.

Andersson (2004) found that the size of the humeral trochlea is more influenced by its weigth bearing function than by locomotory adaptations. He calculated an average weight of 38 kg (range: 28-52 kg) for *Hyaenodon horridus*. Andersson (2004) mentioned that *Hyaenodon horridus* scales totally different from carnivores.

9.5.5 Conclusions on the locomotory behavior in *Hyaenodon*

The skeleton of *Hyaenodon* as above described exhibits many features that indicate certain locomotion patterns. This genus and its family are fossil. Due to missing comparison to a similar recent animal, *Hyaenodon* partly appears like a mixture of features seen in modern Carnivora, e.g. being canid- or felid-like (Mellett, 1977) in certain aspects. In the following I summarize the indications for respective locomotory behavior (the citations refer where the feature described has been interpreted as cursorial/terrestrial etc.). Figures showing the discussed feature herein are given too.

Cursorial features in *Hyaenodon* are: a rectangular and flat scapula corpus (Gunnell, 1998; Taylor, 1989; Fig. 9/13 A), a large tuberculum major (exceeding the caput humeri in height and protruding proximally; Taylor, 1989), a perforated olecranon fossa = that is the presence of the fossa anconeus (Laborde, 1987; Fig. 9/3 A-D), the shape of the humeral trochlea (deep midtrochlear furrow, projecting; Andersson 2003; Laborde 1987; Fig. 9/3 A-D), a posterior inclined olecranon (Van Valkenburgh, 1987; Fig. 9/4 A and B), a large pisiforme (cursorial and digitigrade feature; Taylor, 1974; Fig. 9/10 C-D), a deep patellar groove on the femur with high marginal ridges (Taylor, 1976, 1989; Fig. 9/7 A-B), a laterally oriented fovea capitis on the femoral caput (Wang, 1993; Fig. 9/7 B) and a well-developed tibial crest (Taylor, 1976, 1989; Fig. 9/8 A-B and D).

The reduction of digits was interpreted as indication for digitigrady and cursoriality (Wang, 1993). However, adjoined metapodials do not correlate with digitigrady, but with cursoriality (Wang, 1993)!

The shape of the radial head is of the cursorial type (MacLeod and Rose, 1993; Fig. 9/6 A-B). The shape of the distal phalanges is in dorsal view also of the cursorial type (MacLeod and Rose, 1993) — the outline in lateral aspect is more similar to the generalistic terrestrial type (Fig. 9/12 A and B), because the claw of *Hyaenodon* is very curved. Jones (2003) states that the shape of the distal phalanx is phylogenetically influenced. So, the shape is interpreted here with reservation.

Terrestrial features in *Hyaenodon* are: a narrow neck of the scapula (Heinrich and Rose, 1997; Fig. 9/13 A), a deep glenoid notch (Heinrich and Rose, 1997), the concave distal articulation area on the radius (Laborde, 1987; Fig. 9/5 B and E), the curved and not flattened distal phalanges (Van Valkenburgh, 1987; Fig. 9/11 B and C), a short femoral neck (Laborde, 1987; Fig. 9/7 A and B), a narrow and deep femoral trochlea (Laborde, 1987; Fig. 9/7 A and B), the well separated femoral condyles behind the long axis of the shaft (Laborde, 1987; Fig. 9/7 A and B), a deep tibio-tarsal joint surface (Laborde, 1987; Fig. 9/8 C), the proximal tubercles on the tibia that are concentrated in the anterior region (terrestrial-cursorial feature; Taylor, 1976), a spherical astragalar caput (Ginsburg, 1961; Laborde, 1987; Fig. 9/11 C) and a deep posterior joint area on the astragalus (Laborde, 1987; Fig. 9/11 C).

A radius shorter than the humerus (Laborde, 1987) and the wide ulnar diaphysis (Laborde, 1987) are in indication for arboreality. An arboreal and/or primitive feature is the long acromion (exceeding the glenoid; Gebo and Rose, 1993; Laborde, 1987; Wang, 1993) on the scapula. These features are interpreted herein rather as plesiomorph than as evidence for arboreality. The general impression of a ground dwelling animal cannot be refuted. However, these features have to be mentioned.

The well-developed deltoid/supinator crest on the humerus indicates plantigrady (Ginsburg, 1961) or a fossorial adaptation (Gebo and Rose, 1993). This character is not easy to interpret, especially in context with the terrestrial and cursorial indicators. Still, there is a possible explanation: all the long bones are robust and show muscle marks of strongly developed muscles or tendons (e.g. the extreme furrow on the ulna). A powerful musculature is assumed in *Hyaenodon* (e.g. "Razorjaws", 2009). Furthermore, the some features indicate fossoriality or reliance on the forelimb in the hunting style. Here it is proposed that *Hyaenodon* used its forelimbs for fixation of the prey.

Meanwhile, it is widely accepted that *Hyaenodon* was digitigrade. The following features are the most important indicators: a deep proximal groove bordered by two high tubercles on the olecranon (Ginsburg, 1961; Wang 1993), the closely adjoined metapodials (Ginsburg, 1961) and a narrow calcaneus (Wang, 1993; Fig. 9/11 D). Digitigrady in *Hyaenodon* is confirmed herein.

The large articulation facets (Fig. 9/14 A) between tibia and fibula (arboreal, plantigrade or locomotion over uneven terrain; Taylor, 1976) and the semilunar shape of the distal articulation facet on the fibula (progression over uneven terrain at high speeds, Barnett and Napier, 1953) both indicate locomotion over uneven terrain. The radial notch on the ulna is deep and there is no doubt, that the pronation-supination capabilities were limited. Those bones were interlocking and the only possible area for manipulation movements was located within the carpus (Mellett, 1977).

There is no evidence for a fused scapholunatum in European *Hyaenodon*. Based on an old description of a misidentified carpal by Bonis (1964), this information was cited again and again (e.g. Schlosser, 1887; Scott, 1895b). However, no new findings could confirm the existence of a scapholunatum. In contrast, there is essential doubt about the correct determination about the hitherto known scapholunati in *Hyaenodon*. One (from La Débruge) is determined as belonging to an ursoid carnivore (*Cynodictis*?) and the other two from Aubrelong1 are stated not to be scapholunati of *Hyaenodon* herein: the former is a scapholunatum, but possesses the ursoid facets for the distal carpals. The latter are too small — even for the smallest species of *Hyaenodon* — and possess no articulation areas (they are considered as sesamoids). The distal articulation surface of the radius is not differing between some forms of the European and some forms of the North American *Hyaenodon*. Thus, there is no indication that the carpus differed in general build between the species of different continents.
However, the advanced state of fusion of the scaphoid and the lunatum is known in a hyaendontid, namely in *Hyainailouros* (Ginsburg, 1999). Thus, the scapholunatum is not an exclusive feature of Carnivora.

In "Razorjaws" (2009) the following situation was described: It was assumed that *Hyaenodon* could not rundown *Mesohippus*, due to its short-legged body. James Mellett disagreed and showed an experiment: He chose a pitbull of similar build like *Hyaenodon* (short-legged, but powerful musculature). The speed of the pitbull was measured with a radar gun. The result was 36 mph (about 58 km/h), which is 6 mph (about 9.6 km/h) faster than a horse. James Mellett assumed a similar speed for *Hyaenodon*.

However, *Hyaenodon* applied other hunting strategies as well ("Razorjaws", 2009): e.g. lunging into the prey in the case of a camel, that was probably faster or running up to a rhino and inflicting it with bites. A strong competitor was *Entelodon* (270 kg, shoulder height of 1.2 m). *Hyaenodon* (70 kg, shoulder height of 0.9 m) hunted juvenile pigs, but was likely to loose prey to adult *Entelodon* individuals. A broken shoulder blade of *Hyaenodon* is an evidence for a fight between the two competitors. The scapula of *Hyaenodon* was in the height of the jaw of *Entelodon*. In "Razorjaws" (2009) evidence for an attack of *Hyaenodon* on *Dinictis* was shown as well: the puncture holes in the skull of *Dinictis* line up with the teeth of *Hyaenodon*. Such fossils are precious as they allow inference of behavior. They evidence that *Hyaenodon* was a top-predator of its time.

Concluding, the skeleton indicates that *Hyaenodon* was a digitigrade, terrestrial mammal with cursorial adaptation. The genus clearly was terrestrial in the sense that it dwelt on the ground. It depends on the definition of "cursorial", if it should be applied to *Hyaenodon*. Of course, *Hyaenodon* is not alike modern cursors and thus exhibits a mixture of features known from canids, felids and hyaenids or even unique characters. The genus was seen as cursorial by Gunnell (1998), Mellett (1977) and Morlo (1999) and judged as the most cursorial animal of its time by Egi (2001) and Andersson (2003). I follow Egi (2001) concerning the definition of cursorial (= adapted to running). In this sense I conform with the authors above and identify *Hyaenodon* as Oligocene cursorial predator. Maybe the preferred progression was the extended trotting (most canids, hyaenids; Taylor, 1989). It should be noted, that *Hyaenodon* was adapted for progression over uneven surface (I completely agree with Mellett, 1977 conerning the fibio-tarsal complex; see above) — useful to a runner in a forested landscape (Eocene) or a more open landscape (Oligocene).

James Mellett´s experiment in "Razorjaws" (2009) definitely shows that *Hyaenodon* was not succumbed in a chase. The robust bones and muscle marks indicate powerful musculature. Strong muscles were essentiell for *Hyaenodon* to speed up.
The strong forelimbs were likely used to hold the prey down. Comparable to canids (and indicated by the diameter of its canines), *Hyaenodon* inflicted shallow bites and not a killing bite like modern felids.

The long nasals of *Hyaenodon* do not indicate aquatic adaptations — they allowed the predator to swallow and breathe at the same time ("Razorjaws", 2009). In this respect, the row of carnassials should be considered: *Hyaenodon* possessed more than one pair of carnassials. Thus, the area of slicing is larger and food could be ingested more quickly. The option to feed and breathe at the same time even accelerates this process. This is a useful adaptation, especially when keeping in mind that competitors like *Entelodon* were around. The long row of premolars and the results of the microwear and enamel ultrastructure analyses (Chapter 8) indicate ossiphagous tendencies. A coprolithe containing a horse incisor ("Razorjaws", 2009) provides further evidence. The ability to process all of the prey is another advantage.

The evidence draws a picture of *Hyaenodon* being an active, agile predator. The long survival of the genus (late Eocene-early Miocene) proved its success.

9.6 New insights into the postcranial elements of the European *Hyaenodon*

More apparent than differences in the skeleton between species of different continents, are differences in the skeleton of European species of different times: the distal articulations facet on the radius (Fig. 9/6 B and E) is heart-shaped in an Eocene taxon and triangular in an Oligocene taxon; the trochanter major is higher than the caput femoris (Fig. 9/7 A) in an Eocene form and lower in an Oligocene form (Fig. 9/7 B); the metatarsals show strong ridges (Fig. 9/9 A) in an Eocene species and a smooth surface in an Oligocene species (Fig. 9/9 B); the fossa anoconeus on the humerus is round in an Eocene *Hyaenodon* (Fig. 9/3 A) and of semilunar shape in an Oligocene *Hyaenodon* (Fig. 9/3 C);
The North American taxa show: triangular outline of the distal radial facet, a trochanter major lower than the caput femoris, no ridges on the metatarsals and a round anconeal fossa on the humerus (in small and large sized taxa; pers. obs.).
As determination of isolated elements on species-level remains problematic and immigration of Oligocene species is not well understood, the question if these changes were a product of European evolution or an Asian import cannot be answered for now.

Fig. 9/1: Epistropheus in lateral (left) and dorsal (right) view (A, B) or lateral (left), dorsal (middle) and ventral (right) view (C, D). Bar equals 1 cm. A, IUPW 1772, *Felis sylvestris*, note the slim spine ; B, IUPW 1248, *Canis anthos*, note the distal broadening of the spine; C, NMHW 2010/0196/0004, *Hyaenodon* sp., from Bach (Quercy), note the spine; D, NMHW 2010/0196/0005, *Hyaenodon* sp., from Bach (Quercy), note the spine.
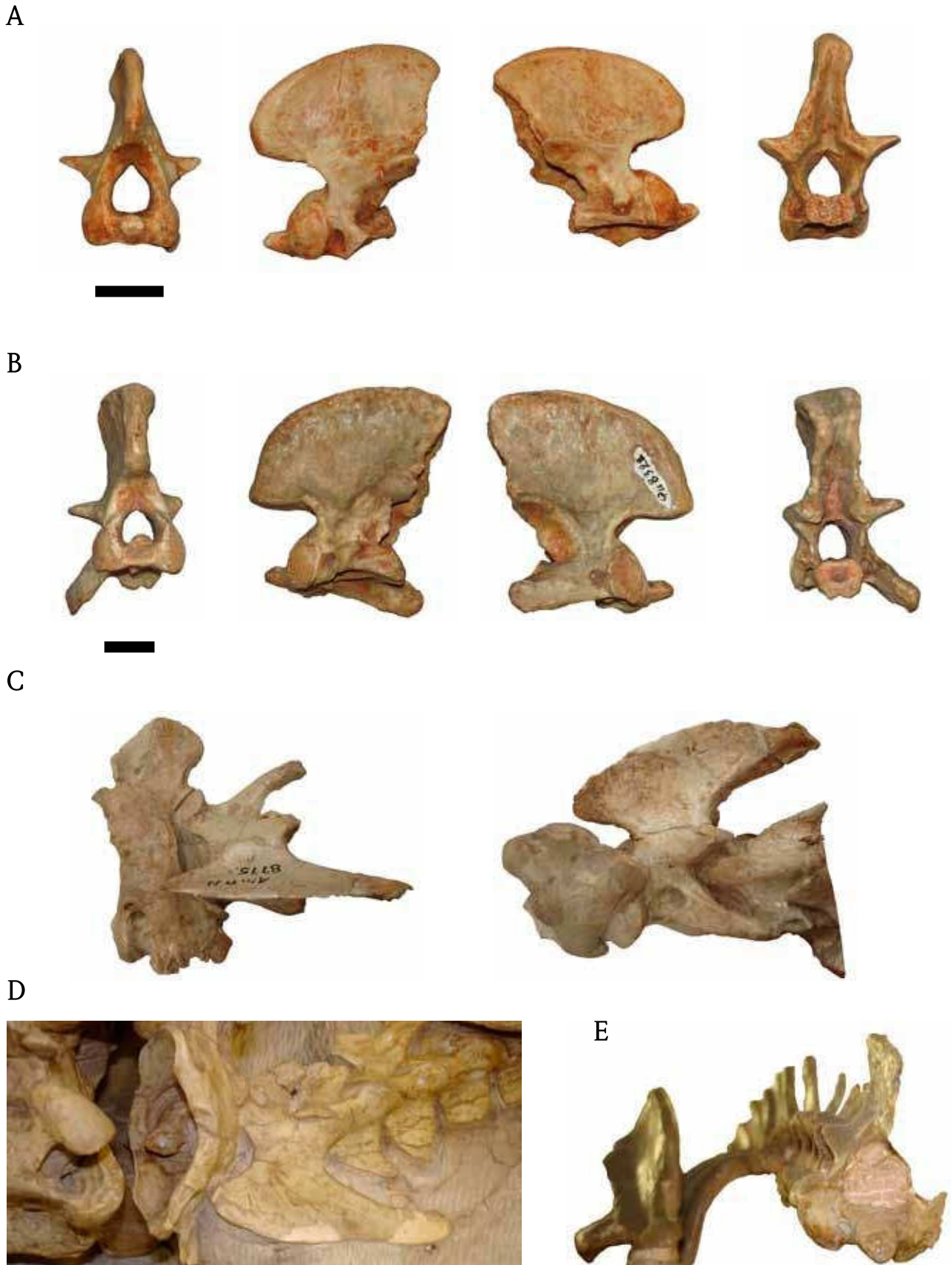
Fig. 9/2: Epistropheus of specimens incorrectly previously determined as *Hyaenodon* (**A**, **B**) and of North American *Hyaenodon* (**C-E**). Bar equals 1 cm. **A**, MNHN without number, from the Quercy, Marsupialia indet., in proximal (left), lateral (middle ones) and distal (right) view, note the completely different morphology; **B**, Qu 8238, Maruspialia indet., in proximal (left), lateral (middle ones) and distal (right) view, note the completely different morphology; **C**, AMNH 8775, *Hyaenodon horridus*, from Cedar Creek (Logan County, Colorado; Oligocene) in dorsal view (left) and lateral view (right); **D**, AMNH 39130, *Hyaenodon horridus*, in lateral view; **E**, YPM-PU 13603, *Hyaenodon* sp., in proximal view.

Fig. 9/3: Photos of the humerus in *Hyaenodon*. Bar equals 1cm. **A**, M 27567, from Vaucluse (France, Upper Eocene) in dorsal (left) and ventral (right) view; **B**, LDB 19, from La Débruge (France, Upper Eocene) in dorsal (left) and ventral (right) view; **C**, Au 1057, from Aubrelong 1 (France, Oligocene), *H. dubius* (?), in the same scale as all the other humeri (left) and enlarged (right), note the presence of the anocenal fossa and the foramen entepicondylium; **D**, the same as in **B**, but in internal (left) and external (right view).
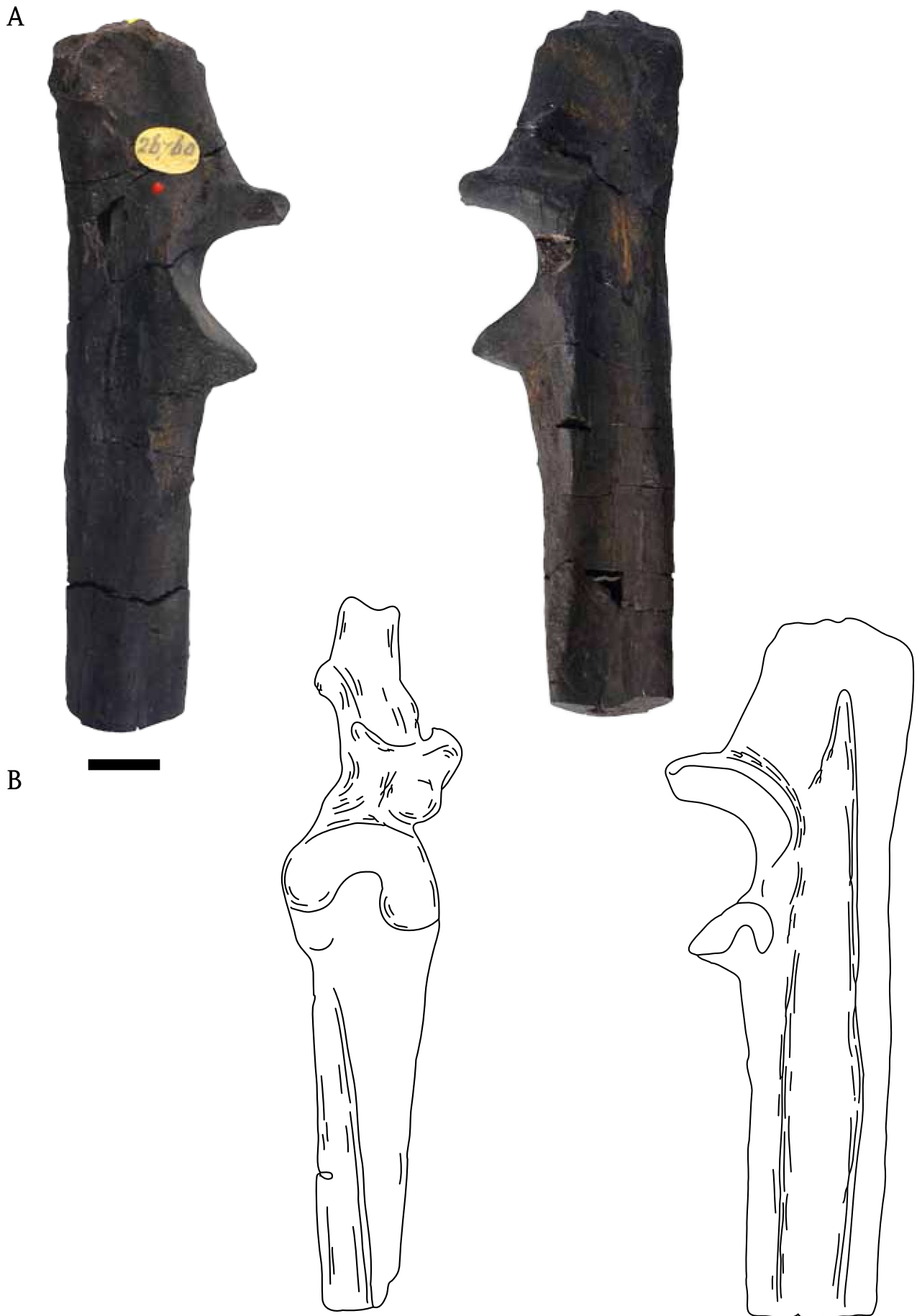
Fig. 9/4: Photos and drawings of the ulna (M 26760, from Vaucluse, France, Upper Eocene) in *Hyaenodon*. Bar equals 1cm. A, in external (left) and internal (right) view; B, in dorsal (left) and internal (right) view. Note the posterior inclined olecranon, the deep ridge for tendons on the shaft and the semilunar notch.
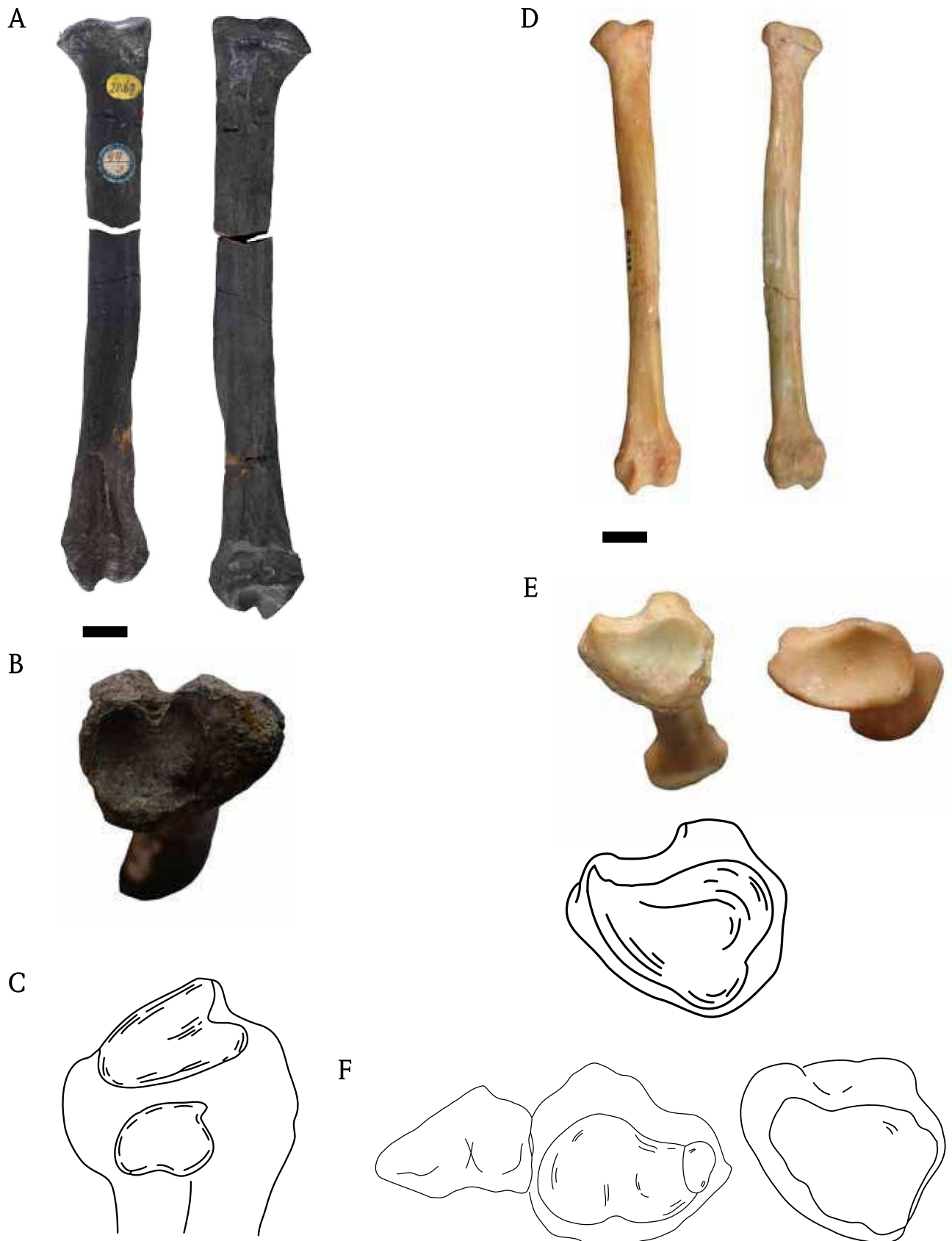
Fig. 9/5: Photos and drawings of the radius in *Hyaenodon*. Bar equals 1cm. **A**, M 28169, from Vaucluse (France, Upper Eocene) in dorsal (left) and ventral (right) view; **B**, LDB 22, from La Débruge (France, Upper Eocene, *H. requieni*), distal articulation area, note its outline; **C**, M 28169, drawing of the distal joint area with the lateral facet for the ulna in the same specimen as in **A**, note the similar outline as in **B**; **D-E**, Au 1028, from Aubrelong 1 (France, Oligocene, *H. dubius*?); **D**, radius in dorsal (left) and ventral (right) view; **E**, distal (left) and proximal (right) articulation surface, below is a drawing of the distal articulation surface, note the different outline; **F**, distal articulation surface in North American *Hyaenodon*, both *H. horridus*, together with distal ulna FAM 75601 (left) and radius alone AMNH 8775 (right).

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A

small sized *Hyaenodon*   large sized *Hyaenodon*

European *Hyaenodon*

Hyaenodon, Au 1028   *Hyaenodon*, M 28169

North American *Hyaenodon*

AMNH without number *Hyaenodon*   *Hyaenodon* horridus , AMNH 8775

B

cursorial   generalistic terrestrial   fossorial

scansorial   arboreal   aquatic
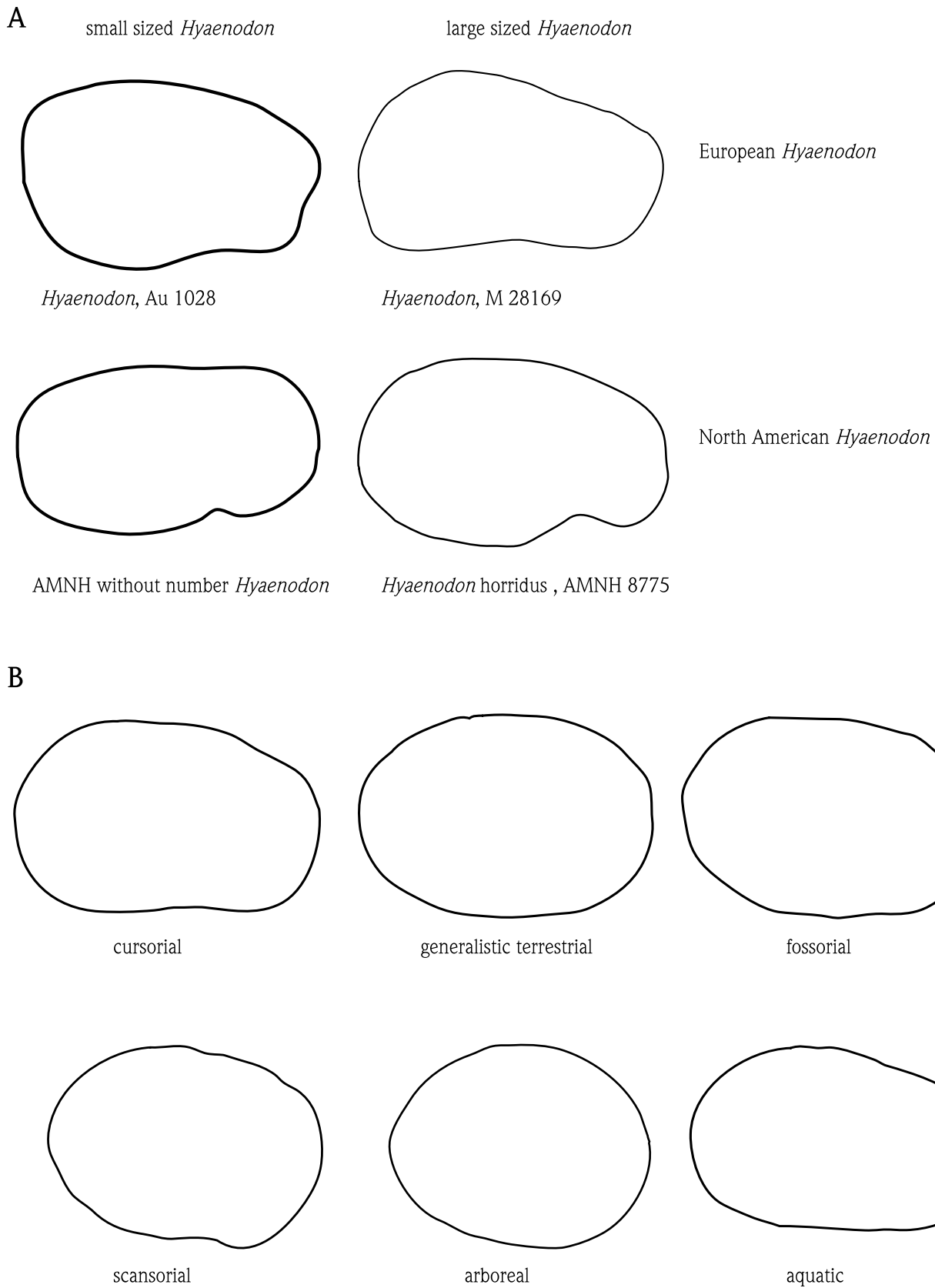
Fig. 9/6: Outline of the proximal articulation surface of the radius (all dex., thus dorsal is up, ventral downwards, internal is left and external on the right). A, outline in *Hyaenodon*: European taxa (upper row) and North American taxa (lower row) with small sized taxa (left) and large sized taxa (right), note the elongated shape in all of them; B, redrawn after MacLeod and Rose (1993), mean proximal radial head shapes of a typical cursorial, generalistic terrestrial, fossorial (upper row) and scansorial, arboreal, aquatic (lower row) mammal.

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A

B

C
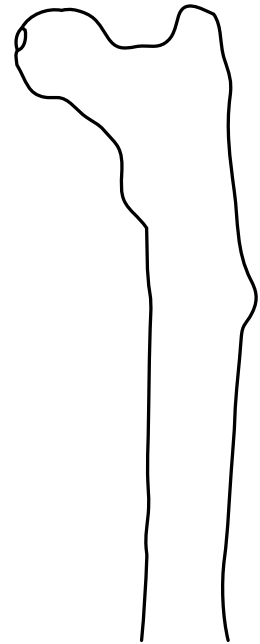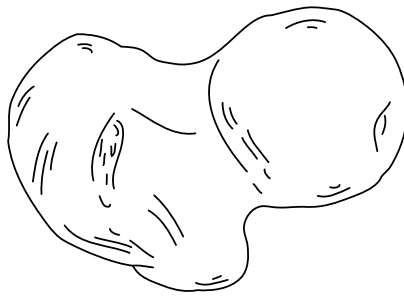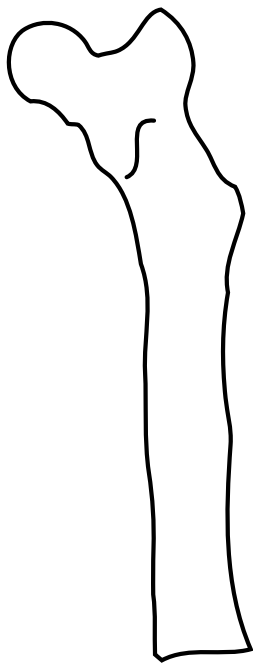
H. crucians (FAM 75596)   H. horridus (AM 9809)

Fig. 9/7: The femur in *Hyaenodon*. Bar equals 1 cm. **A**, M 29726, from Hordwell (Hants, Great Britain, Eocene), femur sin. in anterior (left) and posterior (right) view; **B**, Au 2361, from Aubrelong 1 (France, Oligocene), femur sin. in anterior (left), lateral (middle) and posterior (right) view; **C**, redrawn after Mellett (1977, Fig. 49, p. 91): posterior view of the proximal part of the femur, note the development of the third trochanter. Note the expansion of the femoral condyles and the patellar groove, in the middle is a drawing of AMNH 8775 (*Hyaenodon horridus*) in occlusal view, note the lateral position of the fovea capitis.
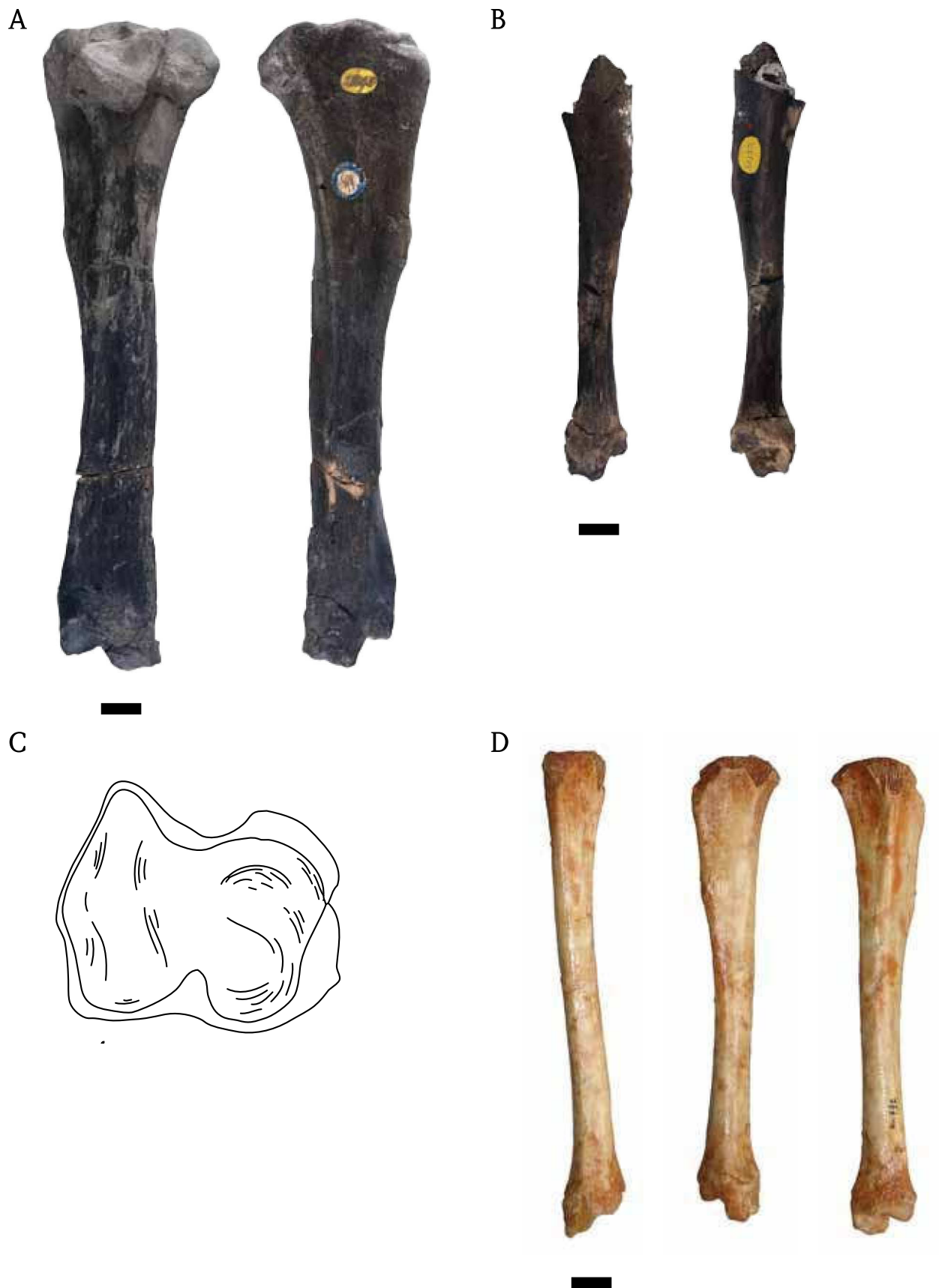
Fig. 9/8: The tibia in *Hyaenodon*. Bar equals 1 cm. **A**, M 28195, from Vaucluse (France, Upper Eocene), tibia sin. in posterior (left) and lateral (right) view; **B**, M 30132, from Hordwell (Hants, Great Britain, Eocene), tibia sin. in anterior (left) and posterior (right) view; **C**, the same as in **A**, drawing of the distal articulation surface, note deep grooving; **D**, Au 776, from Aubrelong 1 (France, Oligocene), tibia sin. in anterior (left), lateral (middle) and tilted posterior (right) view.
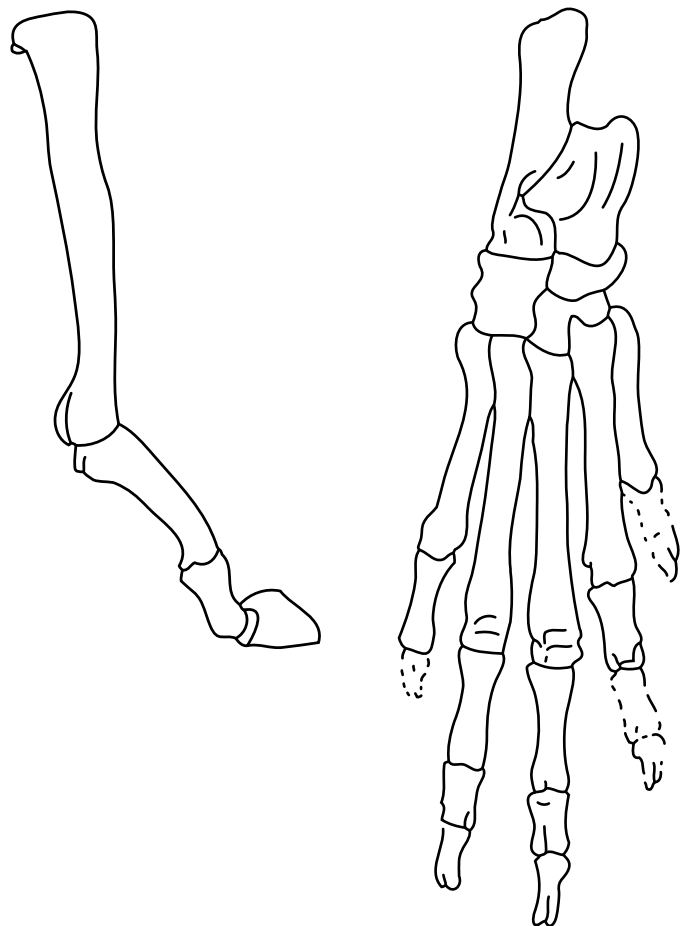
Fig. 9/9: The metatarsals in *Hyaenodon*. Bar equals 1 cm. **A**, M 28162: from La Débruge (Vaucluse, France, Upper Eocene), metatarsals II-IV dex. in posterior (left) and lateral (right) view; **B**, Au 2078, Aubrelong 1 (France, Oligocene, *H. dubius?*) in lateral (left) and ventral (right) view; **C**, foot reconstruction in the North American *Hyaenodon*, redrawn from Mellett (1977; left) and from Scott and Jepsen (1936; right), note the digitigrade foot posture and the closely appressed metapodials.
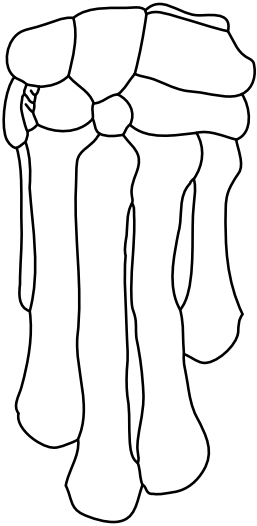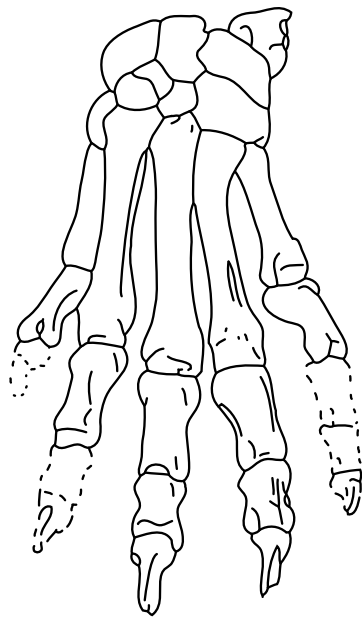
Fig. 9/10: The manus in *Hyaenodon* and specimens wrongly determined as *Hyaenodon*. Bar equals 1 cm. **A**, M 26761, cast from a specimen at the MNHN (**B**) from Vaucluse (France, Upper Eocene), partial left and right forepaw with carpals, metacarpals and phalanges in dorsal view, wrongly determined as *Hyaenodon*, in fact it has to be attricuted to Carnivora (ursoid, *Cynodictis*?); **B**, MNHN without number, the original of the right forepaw in **A** in dorsal view; **C**, redrawn after Mellett (1977), reconstruction of the manus in the North American *Hyaenodon*; **D**, redrawn from Scott and Jepsen, reconstruction of the manus in North American *Hyaenodon*; **E**, drawing of AMNH 39130 (*H. horridus*), distal radius and ulna with (from right to left) carpals, note the small scaphoid (right) and lunatum (left to the latter) and the large pisiforme and unciforme (lowest carpal). Note the more appressed metacarpals in Mellett's reconstruction. Note the presence of a scapholunatum in the carnivore (**A, B**) and the unfused scaphid and lunatum in the reconstructions. The unciforme is the largest carpal of the distal row in *Hyaenodon* — compare to the different state in the carnivore.
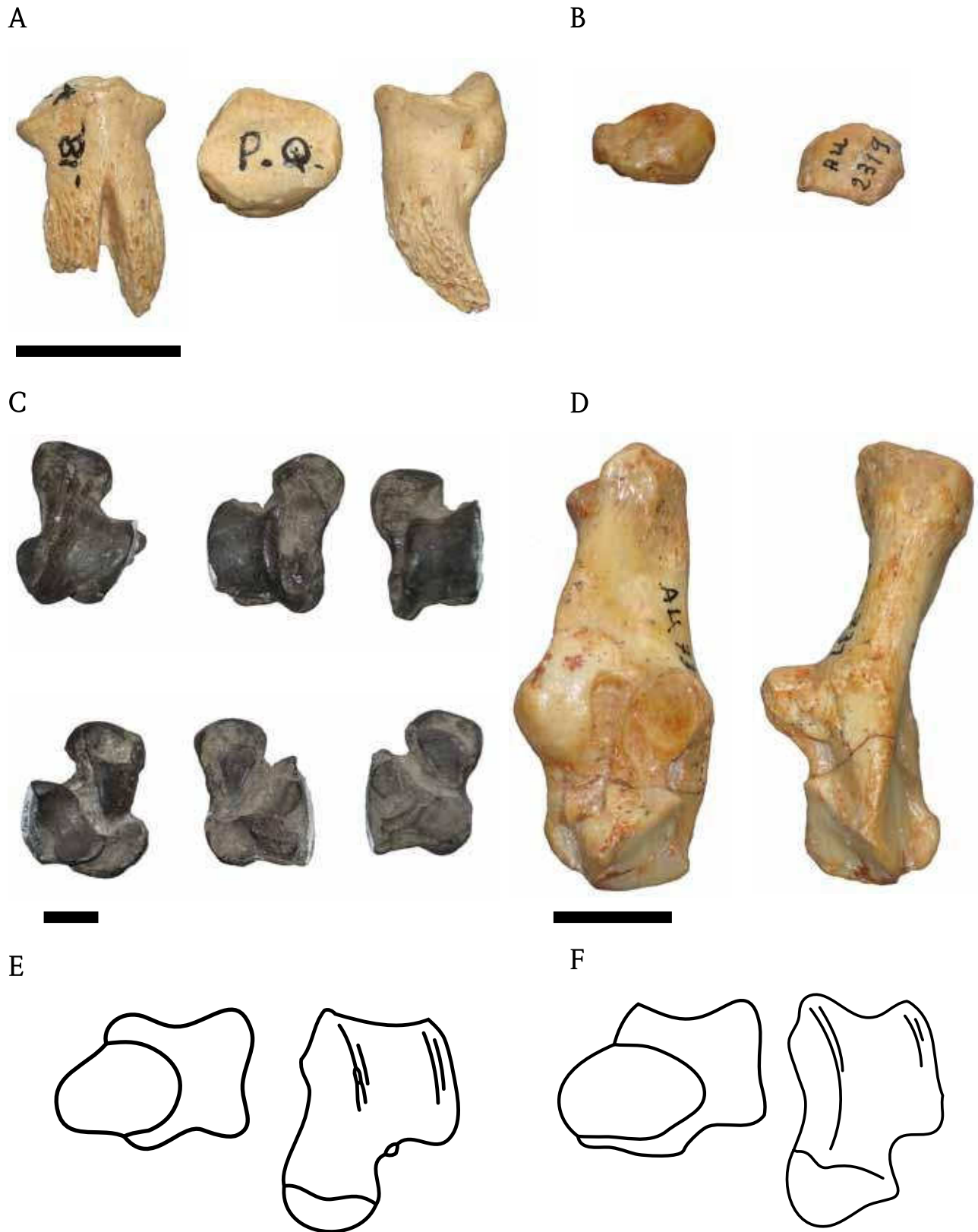
Fig. 9/11: Elements of the zygopodium in *Hyaenodon*. Bar equals 1 cm. **A**, Au 18?, from Aubrelong 1 (France, Oligocene, *H. dubius?*), terminal phalanx in dorsal (left) and lateral (right view), the proximal articulation area is shown too (middle), note the deep split and the curved shape; **B**, Au 6754 (left) and Au 2319 (right), from Aubrelong 1 (France, Oligocene) in dorsal (left) and ventral (right) view, natural size; **C**, LDB 43 (left), 44 (middle) and 46 (right) in dorsal (upper row) and ventral (lower row) view, from La Débruge (France, Upper Eocene, *H. requieni?*), note the grooved trochlea and shape of the caput; **D**, Au 731, from Aubrelong 1 (France, Oligocene, *H. dubius?*), note the laterally sloping facet for the navicular; **E**, redrawn from Mellett (1977): astragalus in distal (left) and dorsal (right) view of *H. crucians*; **F**, redrawn from Mellett (1977): astragalus in distal (left) and dorsal (right) view of *H. horridus*, note the different shape of the trochlea and the caput in comparison to the specimen in **E**.

A

Hyaenodon (Au 18?)

B

cursorial

generalistic terrestrial

fossorial

scansorial

arboreal

aquatic
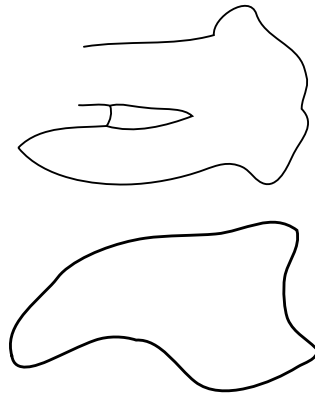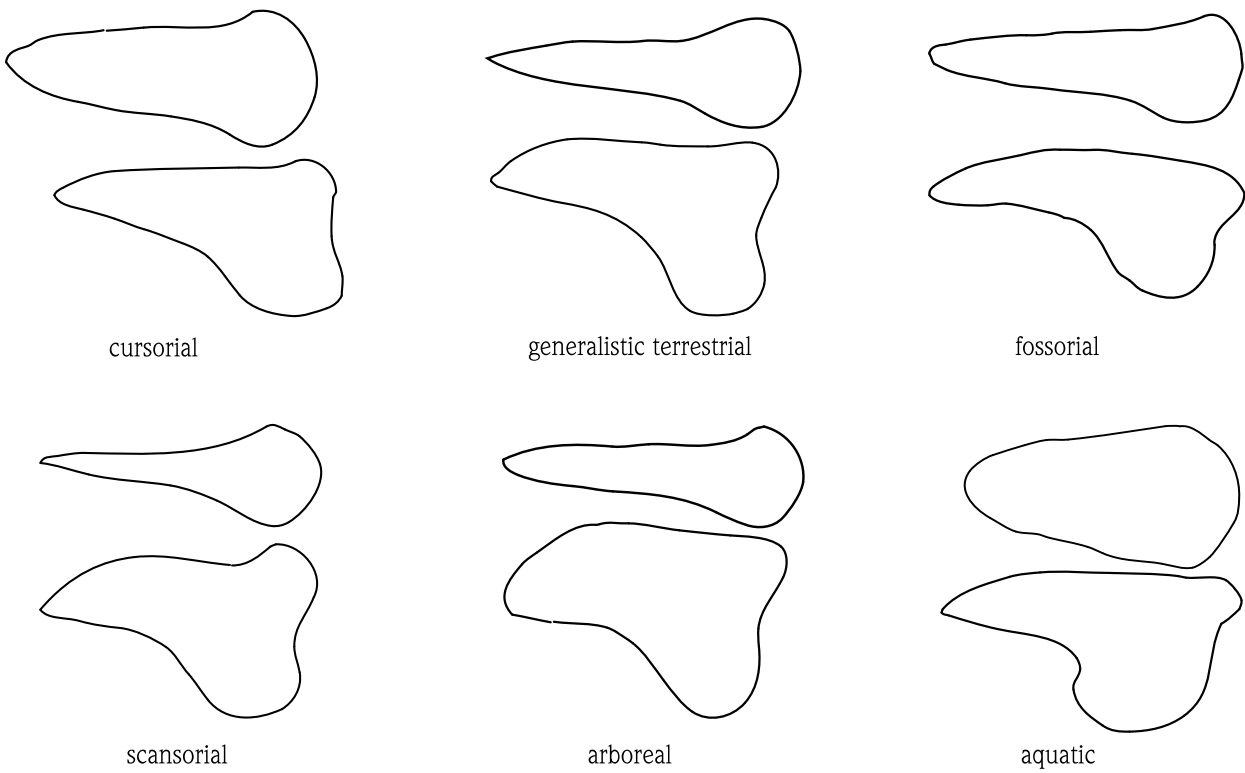
Fig. 9/12: A comparison of the shape of the distal phalanx in *Hyaenodon* to different locomotory types in mammals.
A, Au 18?, from Aubrelong 1 (France, Oligocene, *H. dubius*?), drawn shape — dorsal (upper) and lateral (lower) — of
the distal phalanx in ; **B**, redrawn from MacLeod and Rose (1993): mean dorsal (upper) and lateral (lower) phalanx shapes
of locomotory types in mammals. Note that the lateral outline of the *Hyaenodon* phalanx is similar to the generalistic
terrestrial type and that the dorsal aspect resembles more the cursorial type.

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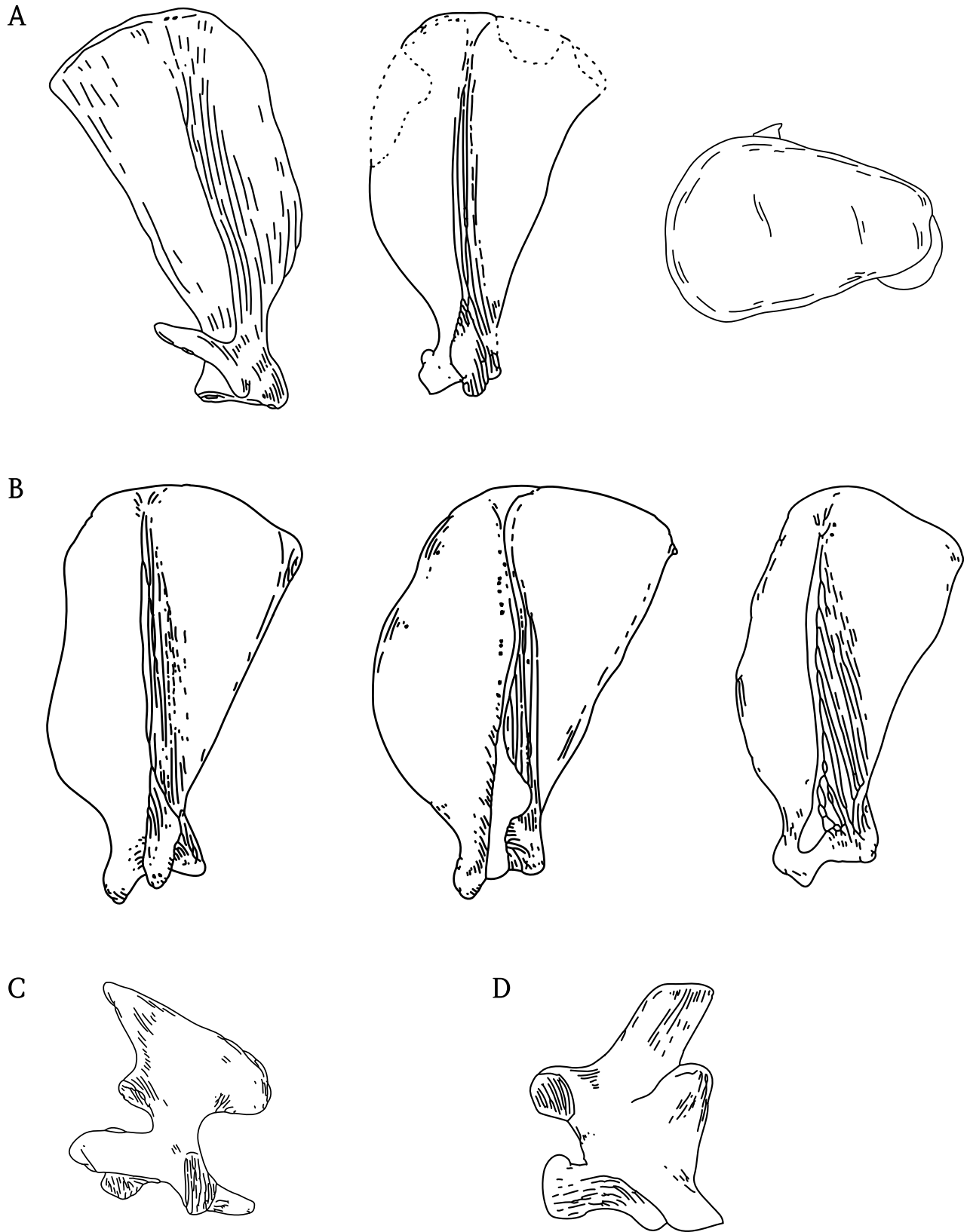
Fig. 9/13: Drawings of the scapula and some vertebra in *Hyaenodon* and Carnivora. **A**, redrawn from Scott and Jepsen (1936; left) and from Mellett (1977; middle): scapula of *H. horridus*, note the narrow outline of the corpus and the different development of the acromion, drawing of FAM 75692 (*H. horridus*), glenoid; **B**, redrawn from Mellett (1977): scapulae of Carnivora for comparison: *Canis lupus* (left), *Felis concolor* (middle) and *Hyaena hyaena* (right); **C**, redrawn from Scott and Jepsen (1936): epistropheus in lateral view, note the neural spine; **D**, redrawn from Scott and Jepsen (1936): lumbar vertebra in lateral view.
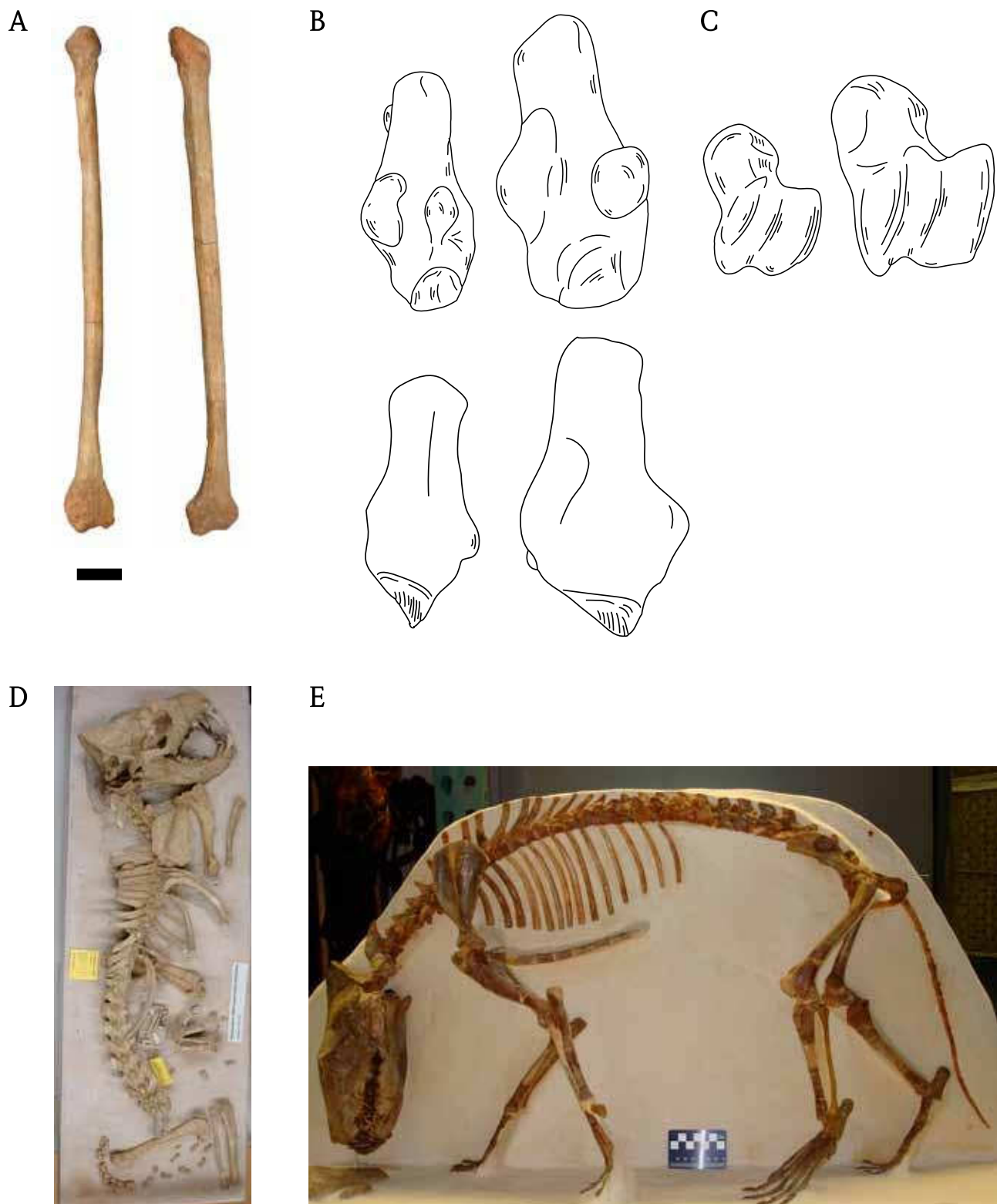
Fig. 9/14: Fibula of *Hyaenodon* and drawings of tarsals. Bar equals 1 cm. **A**, Au 2359, from Aubrelong 1 (France, Oligocene, *H. dubius*?), in external (left) and internal (right) view, note the distinct articulation facets; **B-C**, drawing of a calcaneus or astragalus belonging to Asian *Hyaenodon* (AMNH 19002A, left) and of a North American *Hyaenodon* (right). **B**, calcaneus in anterior (upper) and posterior (lower view); **C**, astragalus in anterior view; Note the similarities and the differences, e.g. the Asian calcaneus is narrower and its sustentacular facet is not as rounded; **D**, AMNH 39130, skeleton of *Hyaenodon horridus*; **E**, YPM 10995, reconstructed skeleton of *Hyaenodon horridus*. Note the large head and the equal length of the forelimb and hindlimb.

Chapter 10

10. Skull and Senses

10.1 Divergence within the genus concerning the cranium

Divergence within the genus was topic of discussion. Interestingly the focus was laid on the North American taxa:

Thorpe (1922) separated *H. horridus* from the other North American species and placed it in a new genus called *Neohyaenodon*. He based this on the following seperative features: larger than the species of *Hyaenodon*, dolichocephalic, glenoids placed far below the basicranial level, shortened basicranial region, dentition similar to *Hyaenodon* except for a buttress-shaped crest on the paraconid on the m3; All species of *Hyaenodon* show glenoids at the level of the basisphenoids and are thus not as depressed and more anterior placed than in *Neohyaenodon* (more mammal- and carnivore-like). Glenoids placed below the basicranial level and short and weak zygomatic arches are seen in *Smilodon* too. Thorpe (1922) concluded that this character state allows a larger gape of the lower jaws. The small lever power of the temporalis due to its long way from the occipital and sagittal crest to the low coronoid process of the lower jaw is compensated with the posterior position of the teeth. The pterygoid muscles were more anteriorly positioned than in *Smilodon*. All three muscles (masseter, temporalis, pterygoideus) were weak, but strong together. The mastoid muscle is very small and in line with the anterior part of the occipital condyles, in contrast to *Smilodon*. This is an indication for a weak development of the mastoid and sternomastoid muscles. Their main function is pulling the head downwards. Thorpe (1922) mentions a small external buttress also in the m3 of *Hyaenodon cruentus*. He still thought the structure is not the same as in *H. horridus* or more specifically in his *Neohyaenodon horridus* (Thorpe, 1922). However, *H. cruentus* was later assigned to *H. horridus* (Mellett, 1977).

Stock (1933) erected the subgenus *Protohyaenodon* with the following diagnostic features: distinct internal cusp on the P4, tiny protocone on the M1, slight bicuspid anterior cusp on the M2. He states that a biscuspid cusp is known in the American species on the M1 (Stock, 1933). In fact, this feature on the M2 shows, that the described taxon is just plesiomorph (see Chapter 5).

Scott and Jepsen (1936) state that *H. horridus* is so different from the other species, that it might be a separate genus — *Neohyaenodon*. Different species occupied different niches to avoid concurrence. Scott and Jepsen (1936) already proposed that *Hyaenodon cruentus* should be recognised as female *Hyaenodon horridus*, which was later realized by Mellett (1977).

Mellett (1977) comprehended *Protohyaendon* and *Neohyaenodon* not as two different subgenera, but rather as two diverging lineages. *Protohyaenodon* includes the species *Protohyaenodon venturae, mustelinus, microdon, crucians* and *brevirostrus*. *Neohyaenodon* includes the species *Neohyaenodon horridus, vetus, montanus* and *megaloides* (see also Chapter 5).

This discussion did not consider European and Asian forms. However, Scott (1895) described differences between European and North American *Hyaenodon* and this summary shall mainly follow him. The features concerned are located at the skull (and also at the humerus, the carpals and tarsals; described in Chapter 9).

In no North American species of *Hyaenodon* an alisphenoid canal is present (Scott, 1895), whereas there is a distinct alisphenoid canal in the European species (Martin, 1906). But according to Mellett (1977) the North American *Hyaenodon* does possess a distinct alisphenoid canal, except for *Hyaenodon brevirostrus*. I can confirm that. Thus, this described divergence is invalid.

The foramen lacerum posterius is fused with the carotid canal in North American species and distinct from the carotid canal in European species (Scott, 1895). Mellett (Fig. 38, p. 70, 1977) showed that these are not fused. Thus, there is no difference between North American and European taxa in this aspect.

Two types of mandibles are present within *Hyaenodon* (Schlosser, 1887; Scott, 1895). The European forms possessed a massive mandible with a more straight than curved inferior border and a steeply inclined symphysis. The teeth are overlapping and the p2 is in an oblique position to the long axis of the jaw. The North American forms possessed an elongated mandible, the inferior border is curved throughout the length and the symphyseal region rises gently. The p1 and p2 are elongated and isolated. Probably Scott (1895) had only limited access to material. The described difference is the difference between longirhynch and brachyryhnch forms — but both are present on the different continents.

The m1 is relative smaller in European species of *Hyaenodon* (Mellett, 1977). I can neither confirm or reject that statement — a large dataset of dental measurements would be needed for that.

The p1 is single-rooted in North American species (Mellett, 1977) and single- or double-rooted in European species (Lange-Badré, 1979).

The M1 in North American *Hyaenodon* is plesiomorph (two-tipped with para- and metacone) and in most European taxa para- and metacone fused (pers. obs.; in Oligocene species respectively, see Chapter 5).

The most striking difference concerns the tooth eruption sequence. It is of significant difference in the lower jaw (Bastl et al., 2011). However, there is also a differene in the eruption sequence of the upper jaw (see Chapter 7).

For a review concerning the postcranial material see Chapter 9.

Summarising, most diverging features could not be confirmed after revision. However, new characters can be added. All in all there are not much consistent differences between the taxa of different continents. *Hyaenodon* was conservative and had a stereotyped dentition (Mellett, 1977). The genus followed a slow evolution (Mellett, 1977). The evolutionary trends in North American *Hyaenodon* are: fusion of the symphysis, reduction of the protocone size on the P4 and loss of the p2 (in *H. brevirostrus*; Mellett, 1977). The evolutionary trends in European *Hyaenodon* are: fusion of para- and metacone on the M1 (Lange-Badré, 1979 and pers. obs.), reduction of cingula and cingulids, lower P2, reduction of the lingual expansion of the P3, reduction of the protocone on the P4 (as in the North American taxa) and loss of the vestige of the metaconid on the m3 (Lange-Badré, 1979).

1) The most striking difference between European and North American *Hyaenodon* is the tooth eruption sequence (see Chapter 8). There is consistent evidence for different patterns.

2) The dp1 is single-rooted in most North American species (Mellett, 1977). The Eocene European species mostly show a single-rooted p1 too. However, the Oligocene European species all show a double-rooted p1. The situation does not get clearer when considering the Asian species: the oldest Asian species *Hyaenodon yuanchensis* has a single-rooted p1 as most of the Asian species. *Hyaenodon pervagus* (Asia) does have a double-rooted p1.

3) The M1 in North American *Hyaenodon* is plesiomorph, even in the Oligocene *Hyaenodon horridus*. In European material only the oldest species show a M1 with two anterior unfused tips. Alas, no suitable Asian material was available to observe this feature.

Thus, I agree with Mellett (1977) that *Hyaenodon* followed an endemic evolution in North America after immigration. The oldest findings of the genus are from Asia. Thus, Asia is the assumed origin of *Hyaenodon*. However, migrations are not well understood, although immigrations from Asia to Europe in the Oligocene are known (different milk dentitions, see Chapter 6 and Lange-Badré 1979). Especially, the Asian material is sparse. The relationships outside North America are not revealed. As stated above I acknowledge the evolution of North American *Hyaenodon* as an own lineage. The strongest argument is the different tooth eruption sequence. This fact suggests separation into a North American subgenus or genus. However, no further evidence could be found in the skeleton. It is now known that there is divergence itself in the European

material (see above) and the variability of the genus cannot be evaluated confidently up to now. Without further knowledge from Asian material, in my opinion a new genus or subgenus cannot be proposed for the North American *Hyaenodon* with the hitherto knowledge.

10.2 New insights into the sense of touch

Besides the other senses (e.g. for hearing see Chapter 11) touch is an important source for information. Due to the nature of preservation, soft tissues are in most cases completely lost. There are exceptions in which inferences are possible, e.g. tracks of cats (Turner and Anton, 1997) that show the morphology of foot pads. A structure important for touch are the vibrissae and these are discussed in this section.
The following paragraph follows Turner and Antón (1997), who gave a great synopsis of big cats. In cats vibrissae are present above the eyes and on the sides of the head. The whiskers of the upper lip named also the mystacials are the most obvious vibrissae. Whiskers are sensitive to touch in a great extent. Individual hairs are enlarged and stiff and their bases, the vibrissal pads, are richly supplied with sensory nerves. Cats depend on their whiskers, because once whiskers made contact with prey a precise killing bite can be performed. The sensory nerves that serve the whiskers pass through the infraorbital foramen. Therefore Turner and Anton (1997) stated, that they can confidently infer that any cat with a well-developed infraorbital canal most probably had a well-developed cluster of nerves passing through it to the base of the whiskers and thus possessed excellent vibrissae like recent cats. Fossil examples are *Smilodon* and *Megantereon*: they show a large infraorbital foramen and thus similar whiskers as in recent felids are assumed (Turner and Anton, 1997).

This infraorbital foramen was examined for the first time in *Hyaenodon*: the specimen Qu 8664 (*Hyaenodon filholi*; described in Chapter 6) is a fragmented skull. It is still juvenile, but not much growth is expected. Similar sized skulls of a felid and a canid were chosen for comparison: *Canis anthos* (IUPW 1248) and *Felis catus* (IUPW 2900/1). In the recent Carnivora the size difference of the infraorbital foramen is apparent: the felid infraorbital foramen is much larger (Fig. 10/1 B), especially wider, because more nerves are needed to supply the more sensitive whiskers. Additionally, the foramen is more circular in shape. It is viewed best mesially. The canid shows a smaller infraorbital foramen (Fig. 10/1 A). Observing the infraorbital foramen in *Hyaenodon* (Fig. 10/1 C), it is clear, that it did not possess as specialized whiskers as felids do possess, because it is small and comparable to the canid. Also, other species of *Hyaenodon*, large and small sized, from North America and Europe, show a relatively smaller sized infraorbital foramen (personal observation).

10.3 Brain and Smell

Brain evolution in Carnivora

The evolution of the brain and the inferring of behaviour is a difficult topic. Concerning the fossil taxa only indirect evidence based on endocasts is available. Brain evolution in mesonychids, "creodonts" (Radinsky´s sample was mainly comprised of hyaendontids) and the miacids was discussed in Radinsky (1977). Groups without descendants as e.g. hyaenodontids do not provide as much data as e.g. Carnivora. The knowledge of certain aspects as ecology, breeding and behavior and the combination of structures in the brain with certain adaptations help to make inferences for fossil Carnivora.
The plesiomorphic status of a brain of a carnivore is a simple neocortex with few foldings (Wang et al., 2008). Insectivorous taxa largely show a neocortex with no folds (www.brainmuseum.org; Fig. 10/6). So the legitimate assumption is that an early mammal brain was rather small, with an unfolded neocortex. Carnivora show a trend to sulcal arching due their evolution (Radinsky, 1977). However, it is not clear if the arching is the result of the expansion of the auditory complex or if it is the answer to less space ("packaging") due to general cortical expansion (Radinsky, 1977).

Gittleman (1986) examined relative brain sizes within Carnivora: canids have relatively larger brains except for the ursids. Furthermore, Gittleman (1986) outruled that social taxa have larger brains than solitary taxa. There is an impact of the diet on the brain size: carnivorous and omnivorous Carnivora possess relatively larger brains compared to insectivorous Carnivora. Gittleman (1986) concluded, that groups with increasing carnivory show larger brains due to more complex foraging strategy, selection for rapid prey detection, pursuit, capture and consumption.

Wang et al. (2008) gave information on the evolution of the canid brain. *Hesperocyon* — a genus occurring from the late Eocene to the early Oligocene — shows relatively simple foldings and an underdeveloped frontal region of the brain. This state was possibly the primitive condition for all carnivorans. In the early Miocene, most canids possessed an expanded prefrontal cortex of the orbital gyrus immediately behind the olfactory bulb. This trend continued (Wang et al., 2008). Radinsky (1969, 1973) speculated that a relatively large prorean gyrus in the prefrontal cortex may be related to pack hunting behavior (in *Canis lupus, Cuon alpinus* and *Lycaon pictus*). This aspect as inferring behavior in general, especially from structures of the brain, has to be treated with caution. The evolution of the canid brain has recently been discussed in Lyras (2009).

The nimravid *Hoplophoneus* and the early felid *Proailurus* show a simpler pattern of sulci (furrows) and gyri (convolutions) compared to modern felids, implying less brain complexity (Turner and Antón, 1997): *Smilodon* displays a modern sulcal pattern, just like *Panthera* and all other felids of post Miocene age. Compared with the primitive condition, the brain of modern felids has increased sulcal complexity in the regions that control hearing, eyesight, and limb coordination (Turner and Antón, 1997).

Hitherto studies on the brain of *Hyaenodon*

Early descriptions of endocasts attributed to *Hyaenodon* were made by Gervais (1870), Scott (1888), Klinghardt (1934) and Piveteau (1961). The studies of Gervais (1870) and Klinghardt (1934) have to be read critically, because the material they used cannot be attributed to *Hyaenodon* (Lange-Badré, 1979; Radinsky, 1977; Scott, 1888).

Scott (1888) described endocasts of *Hyaenodon*. Species included were North American forms. He stated, that an endocast described by Gervais (1870, p. 127) as the European species *Hyaenodon leptorhynchus* (1870, p. 127) does not belong to *Hyaenodon* (see above). Radinsky (1977, p. 337) agrees with that and arguments that the sulcal pattern and the relative size of the cerebellum do not fit with that of *Hyaenodon*. He added that a specimen described as *Hyaenodon* by Klinghardt (1934) belongs to a carnivore (probably *Pachycynodon*).

It was commonly assumed that *Hyaenodon* was extinct due to concurrence with the modern carnivores (e.g. Klinghardt, 1934; Mellett 1977). Surprisingly, Radinsky (1977) stated that the brains of modern carnivores are not superior to the brains of "creodonts" or mesonychids. He observed differences, but didn´t interpret them, because the biological consequences resulting from these differences are unknown. In his sample of "creodonts", including also *Hyaenodon*, he could find the same evolutionary trends as in Carnivora: an increase of the relative brain size and an expansion of the neocortex. Furthermore, Radinsky (1977, p. 337) described the brain of *Hyaenodon* as follows: the neocortex is relatively high convoluted and shows two major sulci and secondary sulci, which subdivide into one or two gyri. In more detail: the first sulcus (the most dorsal one in lateral view, that borders the narrow gyrus at the dorsal midline) is short and straight; the second sulcus is long and borders a broad gyrus above the rhinal fissure. There are differences within species of *Hyaenodon*. To mention one of them: smaller forms like *Hyaenodon crucians* possess a narrow middle gyrus, whereas larger forms like *Hyaenodon horridus* show a broader and subdivided (by one or two sulci) middle gyrus (Fig. 4 A and B, p. 338 in Radinsky, 1977). Such a difference in folding within congeneric taxa is rare among carnivores. So, in the larger *Hyaenodon horridus* the lowest sulcus is curved mediad at its rostral end and delimits the small frontal lobe. The frontal pole did not reach the olfactory bulbs. The posterior pole covered the midbrain. Radinsky (1977) found evidence for a developed ansiform lobule (larger than in other hyaenodontids, smaller than in modern Carnivora), which borders the frontal lobe. In *Hyaenodon* the ventral sulcus extended far rostrally. The sulcal pattern of *Hyaenodon* reminded Radinsky (1977) of early

ungulates (the tapiroid *Hyrachyus*). He inferred — based on this similarity — that the lowermost major sulcus is probably the suprasylvian sulcus (ventral to it the auditory cortex) and the short, straight dorsal sulcus is probably the lateral sulcus (bounding the primary visual cortex). The inferred location of somatosensory and motor cortices is on the frontal pole of the cerebrum, rostral to the medially curving portion of the suprasylvian sulcus. Radinsky (1977) stated that the olfactory bulbs appear large, but mentions, that this impression can be misleading: the expansion of the neocortex can make the olfactory bulbs look smaller, even if they are not reduced compared to the body size. Furthermore, according to Radinsky´s (1977) opinion one needs to know the scaling relationships of olfactory bulbs to infer on olfactory capabilities.

Lange-Badré (1979) dealt in her thesis with the topic of the *Hyaenodon* brain. Three endocranial casts from the Quercy were available to her: a natural one of *Hyaenodon exiguus* (Qu 8997; Fig. 10/2 A) and two artificial and incomplete ones of *Hyaenodon brachyrhynchus* (one of the original braincases, she most probably used is seen in Fig. 10/2 B herein). She also provided drawings (redrawn in Fig. 10/2 C). In general, the endocast of the brain is long and low. In dorsal view, the maximal width of the whole brain is situated in the posterior part of the cerebral hemispheres. The cerebellum is approaching in width. The volume of the cerebellum is approximately half the volume of the cerebrum (= telencephale). An osseous tentorium separated the cerebellum from the cerebrum cavity. The paramedian groove is large and separates the vermis cerebelli clearly from the two hemispheres. The flocculus is distinct, but in the background of the internal auditory meatus. The tractus of the olfactory bulbs is large. The rhinencephalon is very apparent. She described the most ventral sulcus as suprasylvian sulcus. The neocortex appears like an elevation posterior to the rhinencephalon. Three grooves are present on the lateral side of the neocortex. To Lange-Badré (1979) the folding of the neocortex appeared in some aspects similar to ungulates and in other aspects similar to fissipeds. She did not answer the question if these similarities are plesiomorphic characters or if they evolved in convergence. However, the folding is more complex than in Proviverrinae. Lange-Badré (1979) concluded, that *Hyaenodon* was capable of a conscient control of vegetative functions and had good sensory and motory reflexes.
Lange-Badré (1979) furthermore found, that the folding of the necortex is comparable to the folding seen in North American taxa, although she stated that there are minor differences. She mentioned that there is less difference in the folding between the small European *Hyaenodon filholi* and the large European *Hyaenodon brachyrhynchus* than between the North American species *Hyaenodon horridus* and *crucians* or between the European *Hyaenodon brachyrhynchus* and the similar sized North American *Hyaenodon crucians*. However, the stratigraphic distribution has to be taken into account. The neocortex is in proportion even smaller in the North American species than in the European taxa (Lange-Badré, 1979).
In comparison to *Pterodon*, *Hyaenodon* was of approximately the same evolutionary state (Lange-Badré, 1979): three principal furrows — sulci — on the neocortex, weak flexion of the telencephalon and the importance of the rhinencaphalon. Lange-Badré (1979) mentions also differences between the two genera of hyaenodontids, for example the neocortex and the rhinencephalon are considerably less developed in *Pterodon*.

The most recent results were presented in the documentation "Razor jaws" (National Geographic Channel, 2009) by Lawrence Witmer (Ohio University). He found that most of the skull was filled with muscles. The brain is composed of three small lobes that are devoted to intelligence, smell and coordination. The most anterior part — the olfactory bulbs — that is responsible for smell, is enormous. Thus, it was inferred that smell is the primary method for finding prey and that *Hyaenodon* could follow a scent from 1.6 km away. The neocortex is small sized. The conclusions were that *Hyaenodon* was driven by instinct and probably didn´t hunt in packs. The hypothesis that *Hyaenodon* had not the mental capacity to adapt to a changing environment was developed with the background that the prey evolved larger brains and that *Hyaenodon* fell behind the intelligence curve ("Razor jaws", 2009).

New notes on the brain

The general morphology of the brain in the European *Hyaenodon* described by Lange-Badré (1979) can be ascertained here. There is not much contact between the cerebrum and the cerebellum. The cerebellum is quite small and it shall be emphasized that the folding consists of three grooves on each lateral side. The most dorsal one is a straight and short sulcus. The other two are long. The pyriform lobe (also called olfactory cortex, olfactory lobe or paleopallium) is the ventral bulge in lateral view and part of the rhinencephalon. It is large. The endocast in Fig. 10/2 B shows this and it is even apparent from the braincase (Fig. 10/2 B). The last feature can be better seen in Fig. 10/3 E-F. Contradicting Lange-Badrè (1979) and confirming Radinsky (1977), the most ventral sulcus is acknowledged as the rhinal fissure (and not as the suprasylvian sulcus). In comparison to the evolution of the canid brain (Lyras, 2009) the upper two sulci could be regarded as the endolateral and the coronolateral sulcus. However, as Radinsky (1977) stated the identification of homologous sulci and the interpretation of cortical structures are difficult for fossil groups. Thus, those two sulci should remain unnamed.

Concerning the North American *Hyaenodon* the following shall be added: Lawrence M. Witmer (Department of Biomedical Sciences, Ohio University) kindly supplied images of a CT-scan of brain and inner ear of *Hyaenodon horridus* (SDSMT 3017). These are depicted in Fig. 10/3 A-F. Judging from these the findings on the brain of the North American taxa (see above) can be affirmed: as in the European forms the brain consists of three parts, the olfactory bulbs, the neocortex and the cerebrum. The olfactory bulbs appear large in relation to the other parts. The vermis of the cerebellar hemispheres is a strong ridge. The neocortex shows three foldings: a dorsal, short and straight one and two more ventral, longer sulci. The pyriform lobe is large. In relation to the skull the brain as a whole appears small.

The following hyaendontids shall be mentioned to allow a comparison within the family: *Tritemnodon, Pterodon* and *Apterodon* (from Radinsky, 1977). The brain of *Tritemnodon* is characterized by a high rhinal fissure, voluminous pyriform lobe, exposed midbrain and one major neocortical sulcus. *Pterodon* shows two longitudinally extended cerebellar sulci and possibly a short, third one. The most expanded hyaenodontid neocortex so far is seen in *Apterodon*. Furthermore, the rhinal fissure is relatively low and three major sulci are present. The most ventral one is gently arched and reminded Radinsky (1977) of the suprasylvian sulcus of modern carnivores (unlike to other "creodont" brains). Thus, *Hyaenodon* shows an evolved brain compared to other hyaenodontids, except for the brain of *Apterodon*.

For comparison to modern Carnivora the database of the Michigan State University (http://www.brains.rad.msu.edu or http://www.brainmuseum.org) was used and discussed specimens were reproduced with permission of Prof. John Irwin Johnson.

The most apparent feature of modern Carnivora is a large, densely folded neocortex. In this respect the hyaenid *Crocuta crocuta* (spotted hyena, Fig. 10/4), the canid *Canis lupus* (wolf, Fig. 10/4), the canid *Vulpes vulpes* (red fox, Fig. 10/6), the felid *Felis catus* (domestic cat, Fig. 10/4), the felid *Panthera leo* (lion, Fig. 10/4), the mustelid *Mustela putorius* (European polecat, Fig. 10/5) and the ursid *Ursus americanus* (American black bear, Fig. 10/5) are completely different from the hyaenodontid *Hyaenodon*. It is interesting that the canid *Vulpes zerda* (fennec fox, Fig. 10/4) shows a less folded neocortex in comparison to the red fox *Vulpes vulpes*. The herpestid *Cynictis penicillata* (yellow mongoose, Fig. 10/5) also shows a less folded neocortex. Marsupials commonly exhibit a simpler, less folded neocortex (even less folded than in *Hyaenodon*) as seen in *Dasypus novemcinctus* (nine-banded armadillo, Fig. 10/5), *Didelphis albiventris* (white-eared opossum, Fig. 10/5), *Didelphis virginiana* (Virginia opossum, Fig. 10/5) and *Sarcophilus harrisii* (Tasmanian devil, Fig. 10/6). Surprisingly, the neocortex in the short-beaked echidna *Tachyglossus aculeatus* (Fig. 10/6) is more folded. The monotreme Platypus *Ornithorhynchus anatinus* (Fig. 10/6) shows a completely unfolded neocortex. Insectivores also show an unfolded neocortex, like the hedgehog *Erinaceus europaeus* (Fig. 10/6), the mouse *Mus musculus* (Fig. 10/6) and the brown rat *Rattus norvegicus* (Fig. 10/6). Rats are commonly known to be intelligent. Furthermore, an animal like a bat needs a lot of brain capacity for its specialized orientation and

still the neocortex is unfolded in *Rhinolophus hipposideros* (Fig. 10/7). The same is valid for the Indian flying fox *Pteropus giganteus* (Fig. 10/7). An extreme grade of folding is present in the bottlenose dolphin *Tursiops truncatus* (Fig. 10/7). The giant anteater *Myrmecophaga tridactyla* (Fig. 10/7) shows an elongated, low brain with large olfactory bulbs and a moderately folded neocortex.

Concluding, the degree of folding does not automatically infer intelligence. The brain of *Hyaenodon* is not comparable to the brains of modern Carnivora. It is more similar to the marsupial *Sarcophilus harrisii* (Tasmanian devil) and the giant anteater *Myrmecophaga tridactyla*. All three share the following features: large olfactory bulbs, large pyriform lobe, low neocortex and a moderately folded neocortex. The two recent taxa are commonly known for their good sense of smell.

Smell

CT-scans of skulls of the North American species *Hyaenodon crucians*, *Hyaenodon brevirostris* and *horridus* were performed by Joeckel et al. (1997) in order to reveal the internal anatomy of the snout. They found that *Hyaenodon* shows: large maxillary sinuses (proportionally larger than in extant Carnivora of similar size) due to a smaller olfactory compartment; well-developed, paired sphenoid sinuses; small sinuses (at least four) that make up the frontal sinus (as in extant ursids); simple maxilloturbinate (spiral in cross section); a caudally divided nasopharyngeal meatus (divided by the vomer); circular to oval nasopharyngeal meatuses (in cross section); a nasopharyngeal meatus floor with troughs excavated.

Carnivora show different patterns: large olfactory compartment; complex scrolled (Feliformia) or complex branching (Caniformia) maxilloturbinate; caudally undivided nasopharyngeal meatus; rectangular cross section of the nasopharyngeal meatus; flat and nearly horizontal floor of the nasopharyngeal meatus. Joeckel et al. (1997) concluded that the internal anatomy of the snout does not support a Creodonta + Carnivora clade. Further, they mentioned that the simple scrolled maxilloturbinate in *Hyaenodon* is of primitive eutherian grade (and within Carnivora only present in viverrids and herpestids). Joeckel et al. (1997) speculated if this character led to the extinction of the large-sized hyaenodontids, when similar sized amphicyonids and ursids with complicated maxilloturbinates became competitors. The elaborate maxilloturbinates are a good solution for thermoregulation as well.

Joeckel et al. (1997) found it convincing that *Hyaenodon* had less acute olfactory capabilities as Carnivora due to the simplicity of the ethmoturbinates and the smaller size of the olfactory compartment. This would have been a disadvantage in many respects, especially concerning prey detection (Joeckel et al., 1997).

Conclusions

When it comes to brain size there are two problems with comparisons:

Many authors compared the brain size to the body size. As Radinsky (1977) pointed out — the negative allometry (the brain size lags behind the body size in increase) poses a problem: Brains are relatively smaller in larger animals (Fig. 6, p. 343 in Radinsky, 1977).

Secondly, carnivores have different relative head sizes (Radinsky, 1977). Thus, brains of taxa with large heads appear much smaller. This is especially true for *Hyaenodon*. Another obstacle is the interpretation of brain structures as in the case of early Carnivora (Radinsky, 1977): *Vulpavus* shows two sulci, that can be correlated with the lateral sulcus and the suprasylvian sulcus in modern Carnivora. These sulci delimit important sensory fields: The lateral sulcus is the ventral boundary for the visual cortex and the suprasylvian sulcus is the dorsal boundary of the auditory complex. Is it legitimate to infer expansion of visual and auditory cortices in *Vulpavus*? Radinsky (1977) further adds that these sulci can be also seen as evidence for general cortical expansion. Therefore, inferences should be made with caution especially on a fossil taxon as *Hyaenodon*.

Radinsky (1977) found the same two major trends in miacids, mesonychids and "creodonts", that occur in other mammals too (e.g. undulates and primates): the expansion of the neocortex and the increase of the relative brain size. It has to be taken into account that members of different phylogenetic lineages show different rates of brain evolution (Radinsky, 1977).

The brain of "creodonts" was not inferior to that of contemporary miacids (Radinsky, 1977). It was believed for a long time, that "creodonts" had much smaller brains, because this feature was once used for definition of this group (Matthew, 1909) and it was believed that the cerebral hemispheres did not extend under the frontal bones (Denison, 1938). However, the frontoparietal suture is present caudally of the frontal pole of the cerebrum in *Hyaenodon* (Radinsky, 1977).

Concerning the olfactory capabilities some facts should be considered: the internal of the snout reveals simple ethmoturbinates and relatively smaller olfactory compartements (Joeckel et al., 1997); the soft-tissue component of the turbinate structure is unknown in fossils and so the possibility that *Hyaenodon* had more extensive mucosal conchae cannot be excluded (Lawrence Witmer, pers. comm.); the neural territory devoted to olfaction is relatively large; extant carnivorans generally have an excellent sense of smell and therefore may distort a comparison; These facts were discussed in personal communication with Lawrence Witmer. However, based on the relative size of the olfactory bulbs and the pyriform lobe, the sense of smell was relatively important in *Hyaenodon* (following Lawrence Witmer).

Fig. 10/1: Infraorbital foramen in Carnivora (a canid and a felid) and in *Hyaenodon*. It is best viewed from mesial (right column). Bar equals 1 cm. **A**, IUPW 1248, *Canis anthos*, note the small infraorbital foramen; **B**, IUPW 2900/1, *Felis catus*, note the enlarged infraorbital foramen as specialisation in felids for supply of the sensitive whiskers; **C**, Qu 8664, *Hyaenodon filholi*, compare the infraorbital canal to the Carnivora, it is unlike the felid and similar to the canid.

A

B

C

neocortex   cerebellum

pyriform lobe
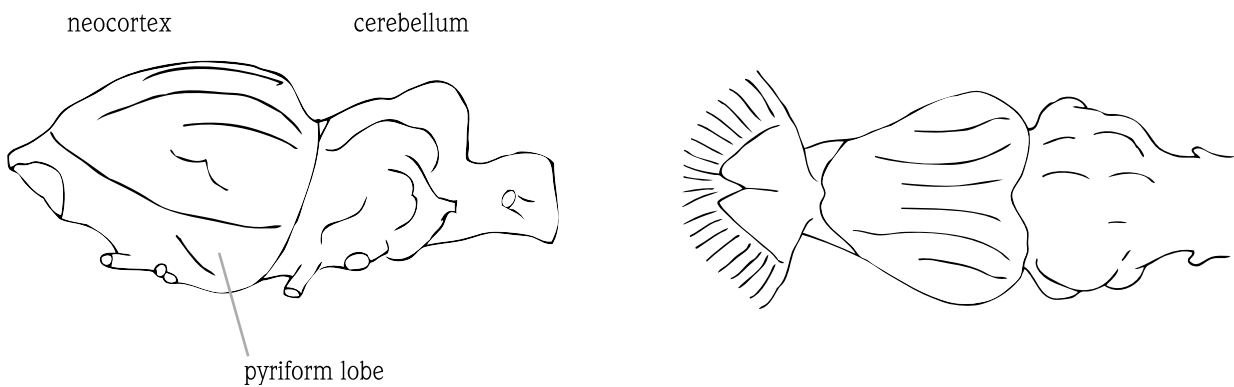
Fig. 10/2: Brain of the European *Hyaenodon*. Bar equals 1 cm. **A**, Qu 8997, *Hyaenodon exiguus*, natural endocast and partial skull from the Quercy, in lateral view (left) and in dorsal view (right); **B**, MNHN without number, *Hyaenodon brachyrhynchus*, fragmented skull, revealing the braincase; **C**, *Hyaenodon brachyrhynchus*, endocast, in lateral view (left) redrawn from Lange-Badré (1979, Fig. 26, p. 112) and in dorsal view redrawn from Lange-Badré (1979, Fig. 25, p. 111).
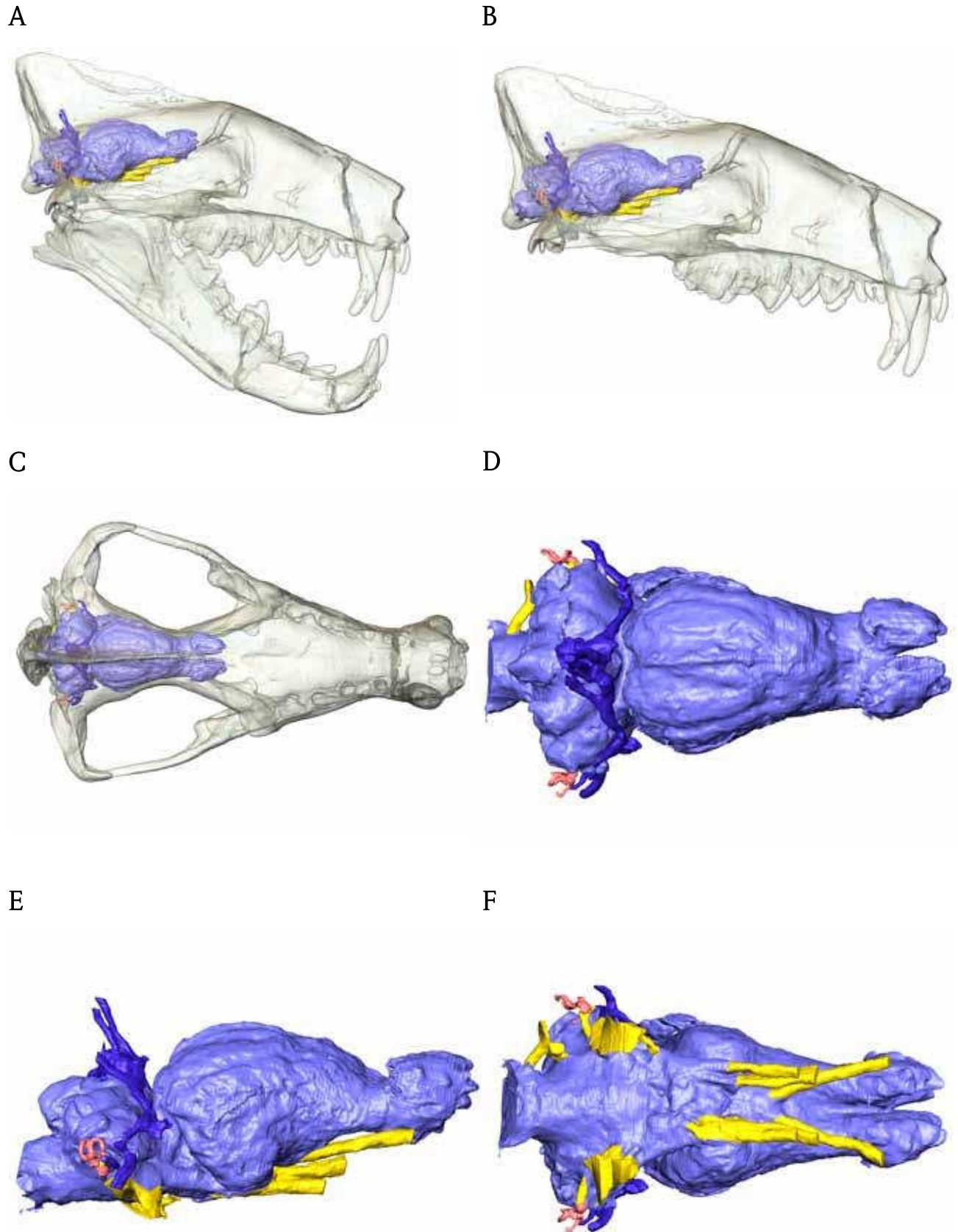
Fig. 10/3: Reconstruction of the brain of the North American species *Hyaenodon horridus* (SDSMT 3017) in different views. Courtesy of WitmerLab at Ohio University — kindly supplied by Lawrence M. Witmer. The brain itself (light blue), blood vessels (dark blue), the inner ear (rose) and the cranial nerves (yellow) are depicted. **A**, in lateral view with skull and mandibles; **B**, in lateral view within the skull; **C**, in dorsal view within the skull; **D**, in dorsal view; **E**, in lateral view; **F**, in ventral view. Note the relationship of the brain to the skull, the three areas of the brain — olfactory bulbs, the neocortex and the cerebellum — and the sulci on the neocortex.
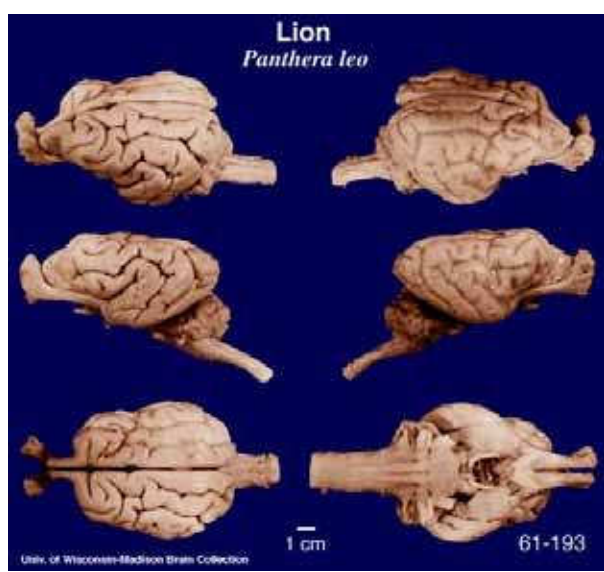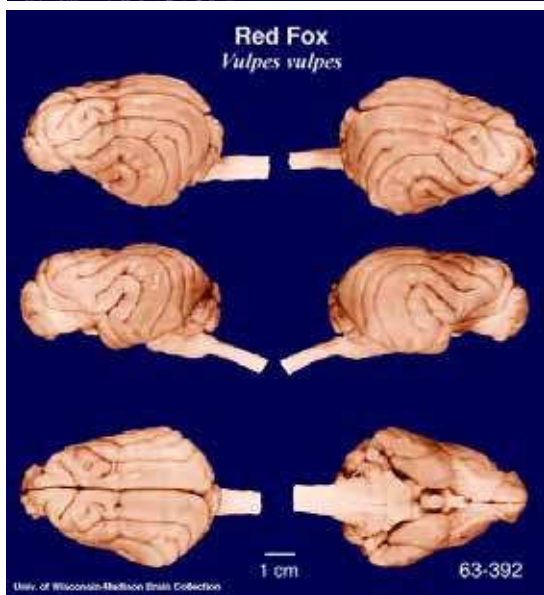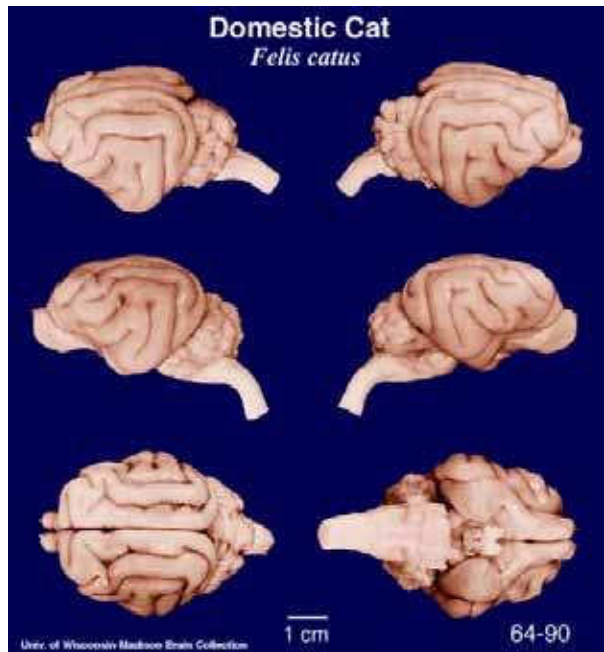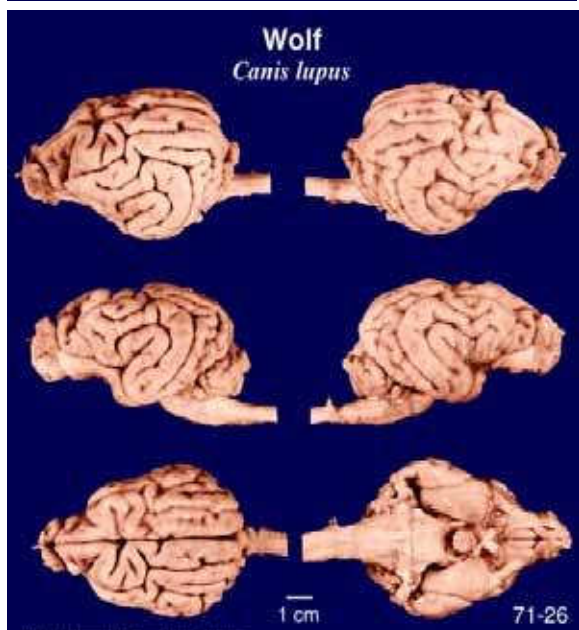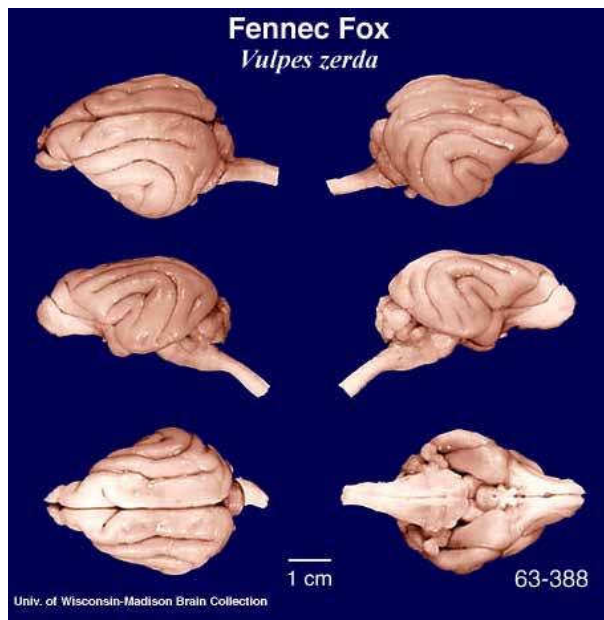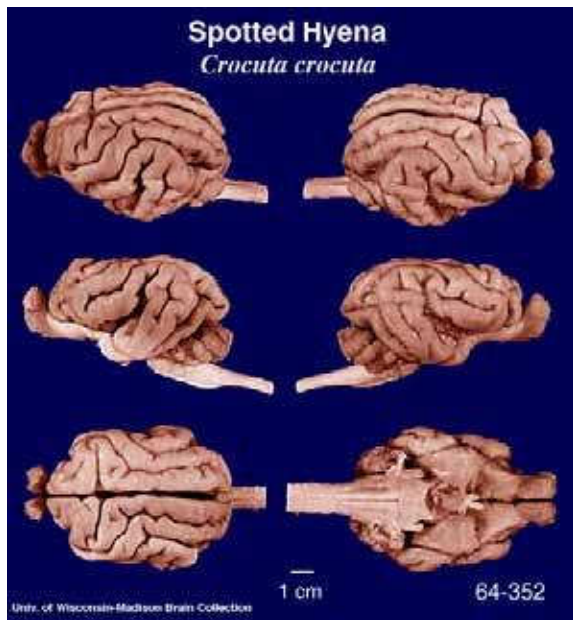
Fig. 10/4: Brain of different modern Carnivora. Reproduced with permission from http://www.brains.rad.msu.edu, and http://brainmuseum.org, supported by the US National Science Foundation.
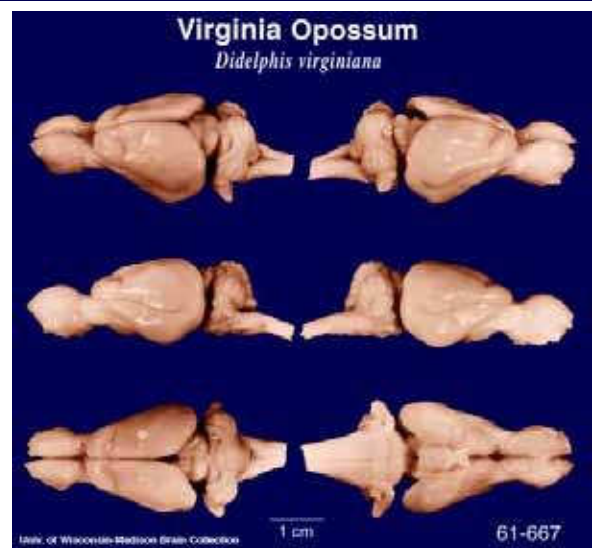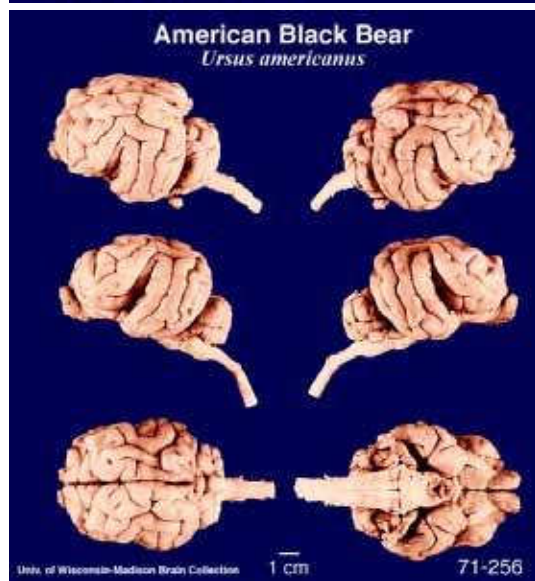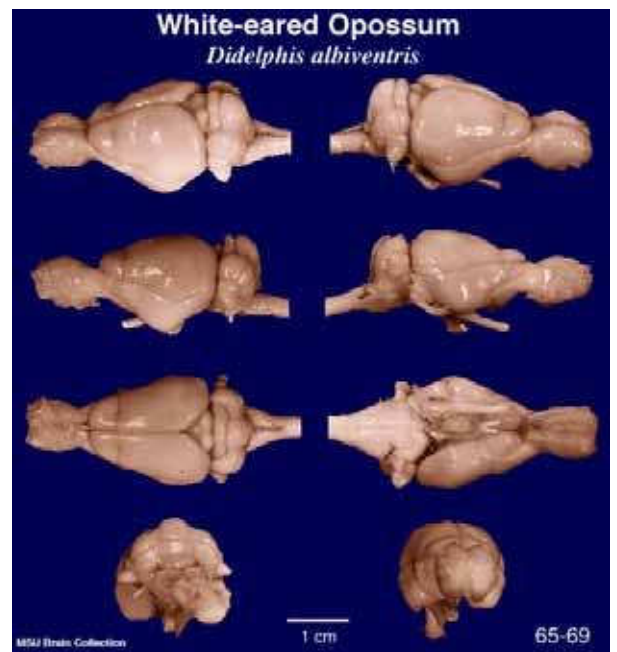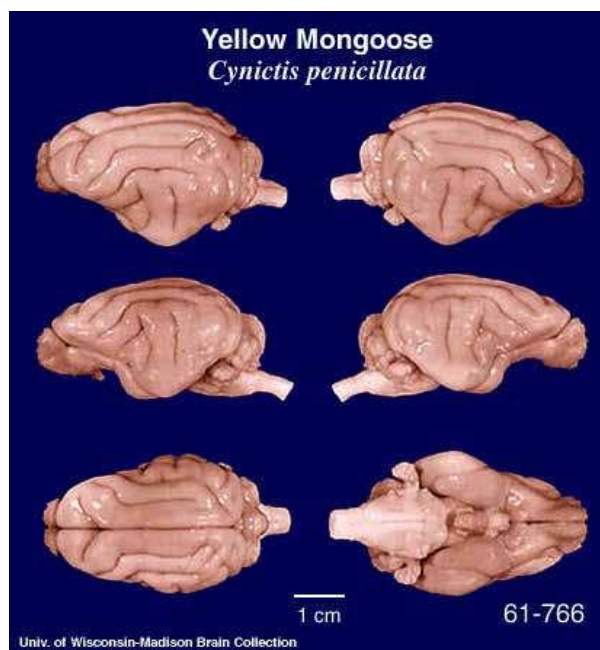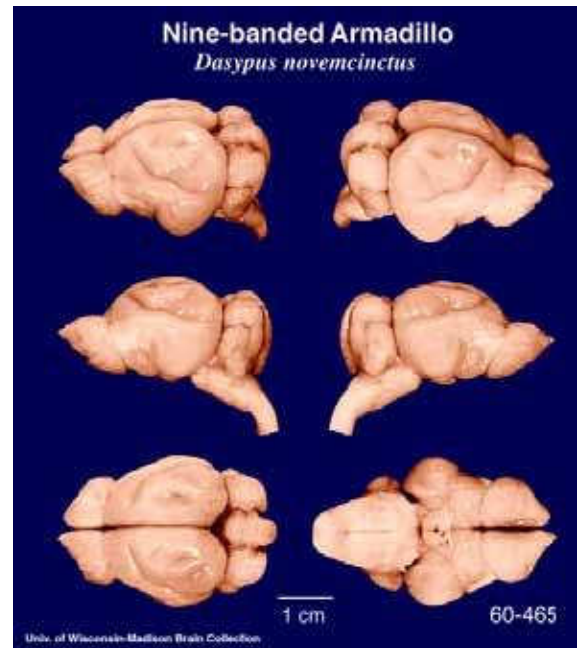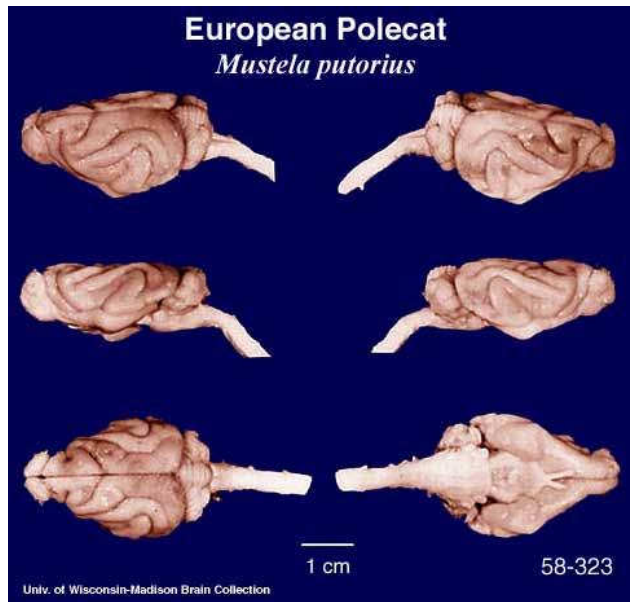
Fig. 10/5: Brain of different modern Carnivora. Reproduced with permission from http://www.brains.rad.msu.edu, and http://brainmuseum.org, supported by the US National Science Foundation.
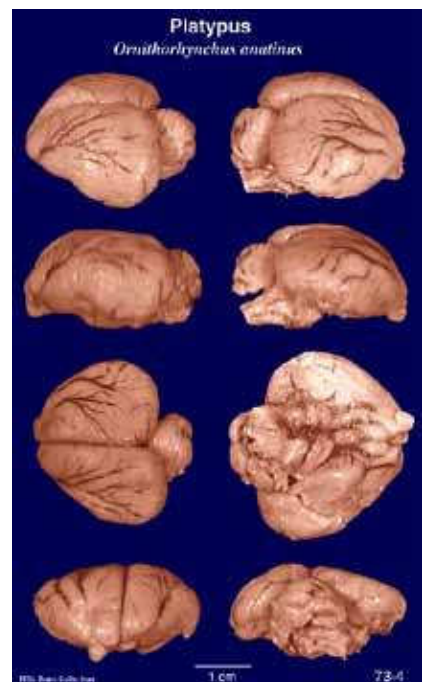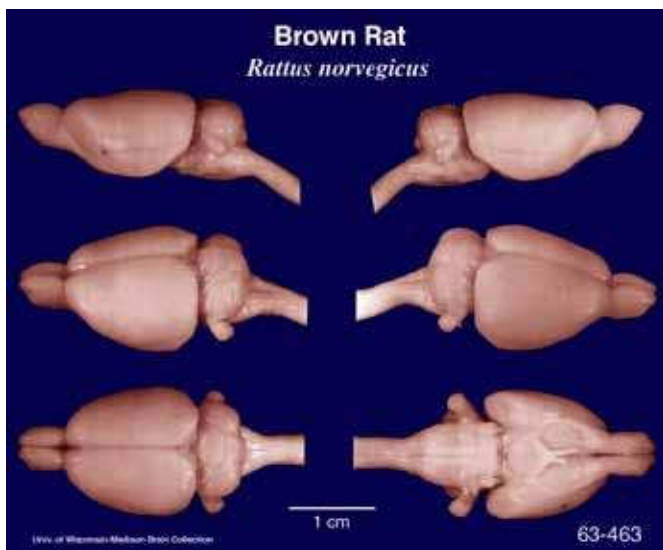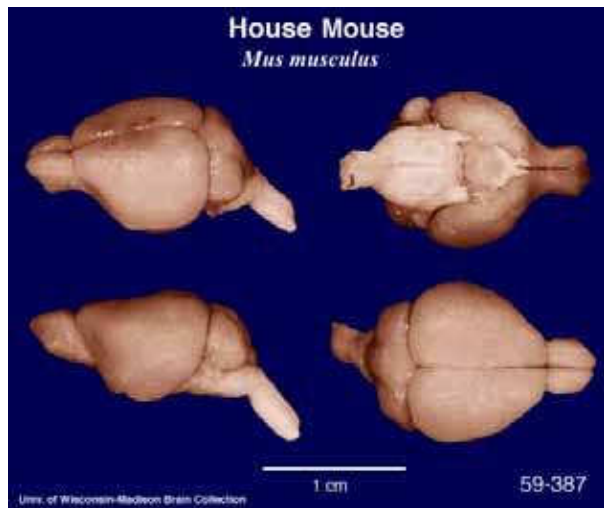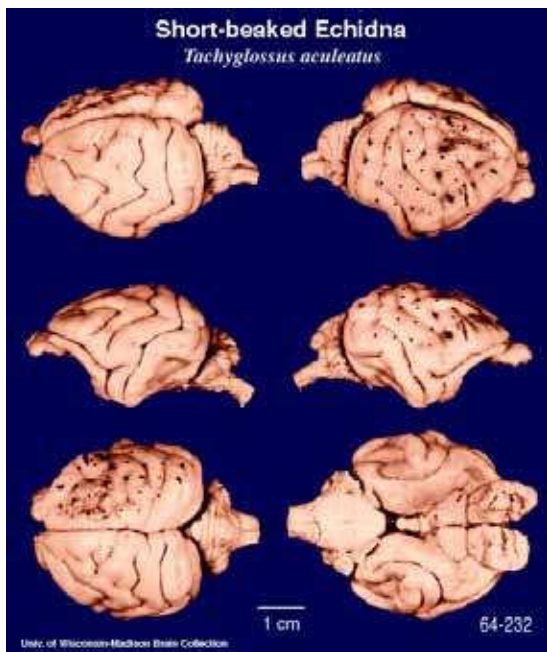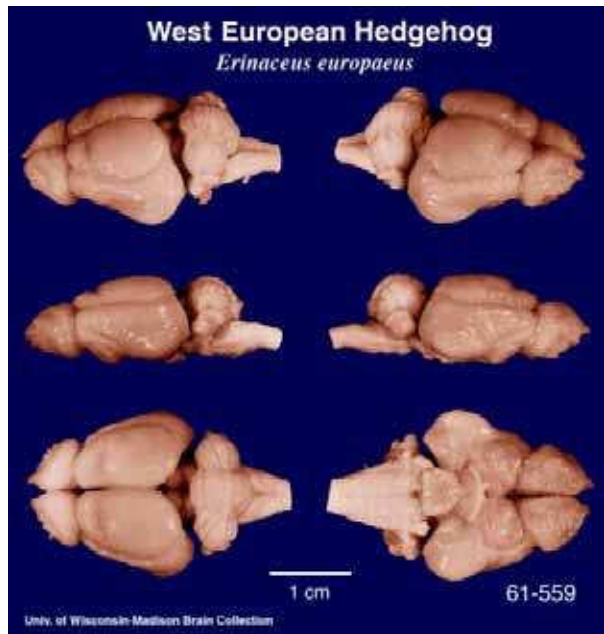
Fig. 10/6: Brain of different modern Carnivora. Reproduced with permission from http://www.brains.rad.msu.edu, and http://brainmuseum.org, supported by the US National Science Foundation.
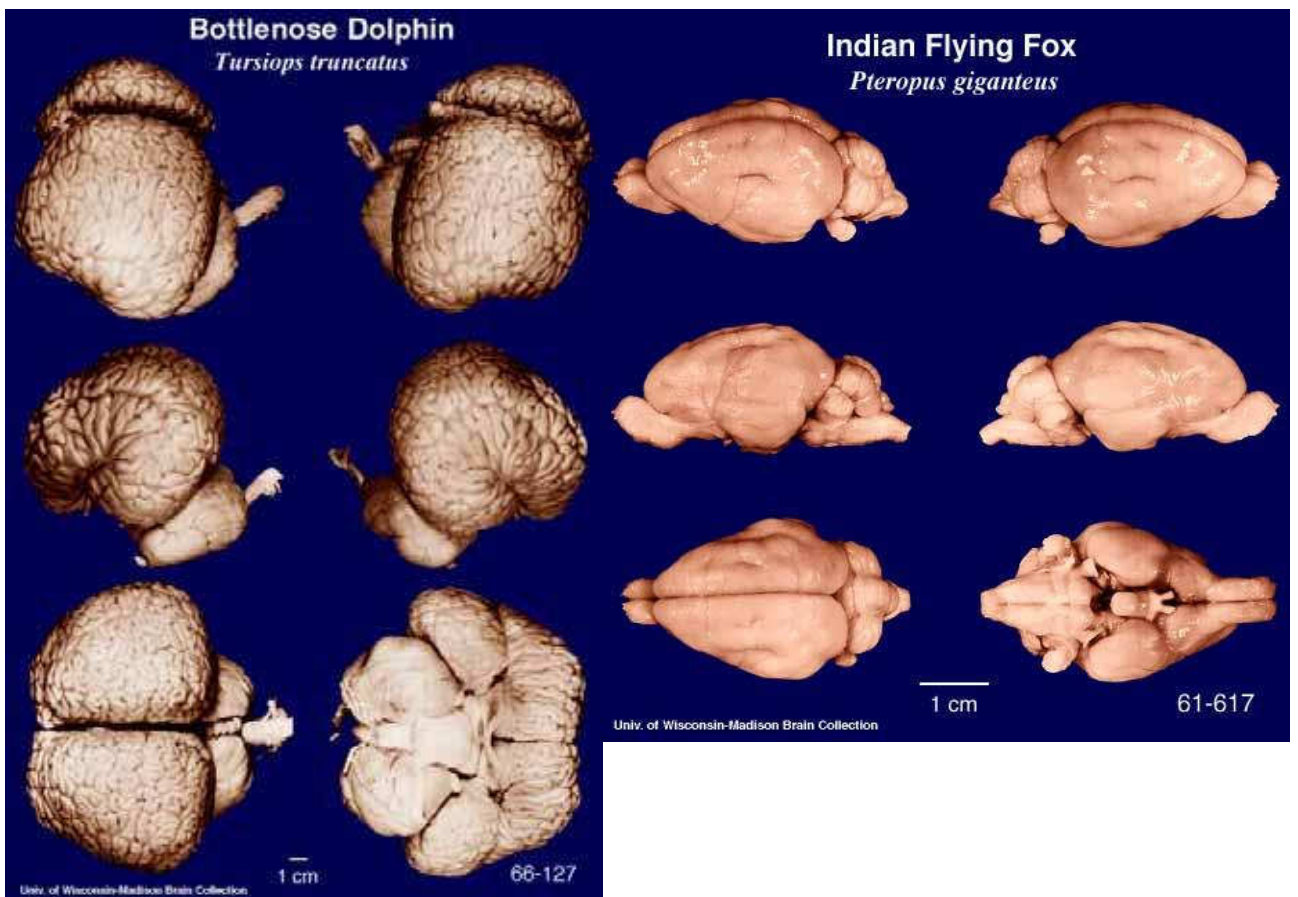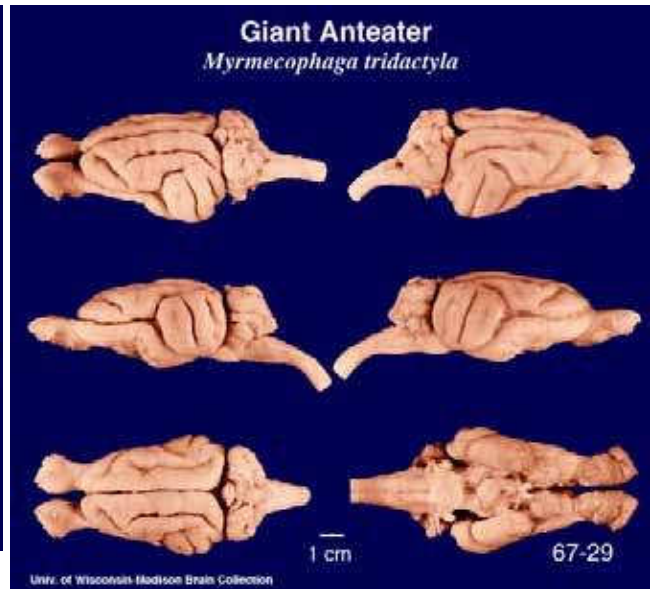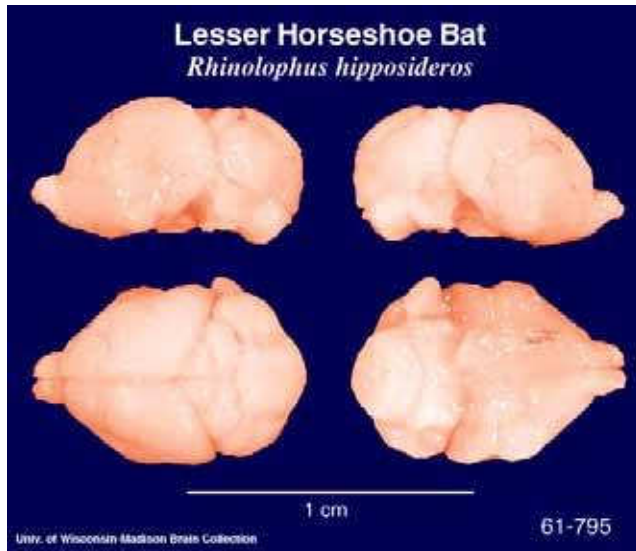
Fig. 10/7: Brain of different modern Carnivora. Reproduced with permission from http://www.brains.rad.msu.edu, and http://brainmuseum.org, supported by the US National Science Foundation.

Chapter 11

11. On the hearing apparatus

11.1 Introduction

The hearing apparatus is made up by the outer ear (pinna, auditory meatus), the middle ear (bulla, auditory ossicles) and the inner ear (including the cochlea; Getty, 1964; Gulya 2007; Toth and Csillag, 2005). Toth and Csillag (2005) provided a great comprehensive work on the human sensory organs. Information about soft tissues, blood supply and nerves is given therein too (Toth and Csillag, 2005). Gulya (2007) gave a great study based on the human hearing apparatus, including its embryology. Concerning Carnivora, the domestic dog was extensively studied and detailed description is given in Getty (1964). Evolution of the mammalian middle ear (e.g. radiation of the malleus-incus complex) and its function is discussed in Fleischer (1973; 1978). Herein, the focus is on the auditory bulla and the auditory ossicles. However, the introduction contains information on other structures too.

The auditory ossicles

The auditory ossicles are also called ossicula tympani (Sarrat et al., 1988) and comprehend the malleus (hammer), the incus (anvil) and the stapes (stirrup). If there are more terms for the same structure, then these are mentioned in brackets the first time they appear in the text.

Other bones can be found associated with the auditory ossicles. Van der Klaauw (1923) gave a revision on two additional bones within the hearing apparatus that were constantly confused in literature. There is a small bone within the tendon of the musculus stapedius. This bone was previously thought to be a vestige of the extracolumella (Van Kampen, 1915), often confused with the os lenticulare and named "ossiculum quartum" or interhyale or orbiculare or infrastapediale (Van der Klaauw, 1923). Thus, Van der Klaauw (1923) named it "bone of Paauw", after its first discoverer. The second small bone is situated near the chorda tympani, where the nervus facialis originates. It is often completely or partly cartilaginous, small and rod shaped. It was called process of the chorda and renamed by Van der Klaauw (1923) as "bone of Spence", after its discoverer. The bone of Spence is later developed than the bone of Paauw, although both are of late embryonic origin. Van der Klaauw (1923) thus speculated that they are new acquisitions and unrelated to structures seen in reptiles.

Topology of the hearing apparatus

As mentioned above, the ear comprehends the external (outer), the middle and the inner ear (e.g. Toth and Csillag, 2005). The organs of hearing and equilibrium are embedded in the petrous part of the temporal bone. Fig. 11/1 A-B gives an overview of the topology of the hearing apparatus.

The external ear includes the pinna, the external acoustic pore and meatus and the tympanic membrane (eardrum) (Toth and Csillag, 2005). The pinna (auricle) focuses and localises sounds (Gulya, 2007). Herein, the pinna is not further discussed as it is rarely preserved in the fossil record. The external acoustic meatus is composed of cartilage (the external one third) and bone (the internal two thirds) in human (Toth and Csillag, 2005). It follows a gentle S-curve. The tympanic membrane is funnel-shaped with its concave side facing exterior. It is inclined at an 50° angle with the inferior margin being farther away from the external acoustic pore. In newborns the membrane is still horizontal. The largest part of the tympanic membrane is taut and called pars tensa. A smaller part is adjacent to the squamous temporal above and lax, thus called pars flaccida (Toth and Csillag, 2005; Shrapnell´s membrane in Gulya, 2007; membrana Shrapnelli in Van der Klaauw, 1931). It is triangular and bordered by the anterior and posterior mallear folds (Toth and Csillag, 2005). The umbo marks the approximate center of the tympanic membrane (Gulya, 2007). The tympanic membrane is associated with (1) the manubrium mallei attaching to the internal side of the membrane at the umbo and (2) the lateral process of the malleus contacting the border between pars tensa and pars flaccida called proeminentia mallearis (Toth and Csillag, 2005). The tympanic annulus (limbus) anchors the tympanic membrane in the tympanic sulcus (Gulya, 2007). The pars tensa consists of three different layers, the lateral

epidermal, the medial mucosal and the intermediate fibrous layer (pars propria). Within the last, there are circular and radial arranged strata of fibrous tissue. The pars flaccida basically consists also of the same three layers, with the exception that the fibrous layer shows irregularly arranged fibrous tissue. The cavity superior to the tympanic membrane is called Prussak´s space. The pars flaccida borders it laterally and attaches to the tympanic incisura (notch of Rivinus). Opposite to the tympanic membrane the promontory is found, an elevation or eminence, that represents the basal turn of the cochlea (Getty, 1964; Toth and Csillag, 2005). The oval or vestibular window is located on the dorso-lateral surface of the promontory (Getty, 1964). The oval window (fenestra vestibuli) is leading to the inner ear (Toth and Csillag, 2005). That is were the footplate of the stapes is situated. After branching off the facial nerve, the tympanic nerve (chorda tympanii) passes through the tympanic cavity medial to the malleus and joins the lingual nerve (Getty, 1964). A short canal extends from the nasal pharynx to the tympanic cavity proper and is called auditory or Eustachian tube (tuba auditiva). The tympanic cavity (cavum tympani) contains the auditory ossicles, the chorda tympani nerve, the muscles and the auditory tube, which communicates with the nasal pharynx (Getty, 1964). The middle ear air space is divided into the mesotympanum (medial to the tympanic membrane and the bony tympanic annulus), the epitympanum (area that lies superior to a horizontal plane at the superior border of the tympanic membrane), the protympanum (anterior of the frontal plane through the anterior margin of the tympanic annulus) and the hypotympanum (inferior to a horizontal plane through the inferior border of the tympanic annulus; Gulya, 2007). The hypotympanicum corresponds to the bulla tympanica (Getty, 1964). The tympanic cavity proper contains the secondary tympanic membrane closing the round window (= fenestra cochlea) — this is in its posterior portion facing anteriorly. The ventral portion is the space within the tympanic bulla. It shows an elliptical opening that faces dorsally. Through this opening it communicates with the tympanic cavity (Getty, 1964).

The auditory ossicle chain serves the mechanical transmission and amplification of sound energy to the inner ear (Toth and Csillag, 2005). The chain is connected via synovial joints and held in position by ligaments. Nomenclature of the malleus is additionally explained in Fig. 11/2 A. The head of the malleus lies in the epitympanic recess (evagination of the tegmen tympani) and shows the facet for the incus. The epitympanic recess is occupied almost entirely by the head of the malleus and the incus at their articulation (Getty, 1964). The manubrium (handle) is attached to the umbo (Toth and Csillag, 2005; umbo membranae tympani in Getty, 1964). Fig. 11/4 A shows the malleus within the bulla of a cat, still attached to the tympanic membrane. There are processi present, the anterior and the lateral processus (Toth and Csillag, 2005). The anterior process (processus gracilis, processus Folianus) of the malleus is thin and projects to the petrotympanic (Glasserian) fissure and is accompanied by the chorda tympani nerve (Gulya, 2007). The anterior process is often fractured or resorbed in adults (without hearing loss), thus Gulya (2007) doubts it has some important function.

The superior ligament attaches the head of the malleus to the epitympanic recess (Toth and Csillag, 2005). The anterior ligament connects the anterior process with the petrotympanic fissure. The lateral ligament joins the neck of the malleus to the tympanic notch (incisura tympanica). A cartilaginous cap of the lateral process joins to the pars tensa of the tympanic membrane (Gulya, 2007). The inferior end of the manubrium, the pars propria (tunica propria in Getty, 1964), is firmly attached to the tympanic membrane and envelops the umbo (Gulya, 2007). Most of the ligaments attached to the malleus are well outside the axis of rotation and serve only for suspensory. The malleus is also bound due to the capsule of the incudomalleal articulation, which includes the medial and lateral incudomalleal ligaments. The tendon of the tensor tympani muscle extends from the cochlearform process to the neck and manubrium of the malleus. Contracted it exerts tension on the tympanic membrane. Fusion of the malleus to the epitympanic wall is seen in some mammals, e.g. the fruit bat. Ankylosis of the head of the malleus is found in 15 of 1200 individuals in humans and causes the same functional problems as stapes fixation (Gulya, 2007). Special remarks concerning this ossicle in the dog are (Getty, 1964): The malleus is the largest ossicle and the most lateral one. The handle is triangular in cross section. The muscular process of the malleus provides a tiny hook as attachment site for the tensor tympani muscle. The anterior or long process is in large contact with the tympanic membrane (Getty, 1964).

The incus (Fig. 11/2 A) consists of the body, the articulation facet, the long and the short process and the

lenticular process (Gulya, 2007). The shape often reminded researchers of a human bicuspid tooth with diverging roots (Getty, 1964). Due to the saddle-shaped articulation between the malleus and the incus, the latter is matched to the movements of the former (Gulya, 2007). The body of the incus shows the facet for the malleus (Gulya, 2007; Toth and Csillag, 2005). The incus is situated in the epitympanic recess, with the short crus (short process, crus breve) connected via the posterior ligament to the fossa incudis (a depression in the posterolateral wall of the tympanic cavity; Toth and Csillag, 2005; = the posterior incudal recess in Gulya, 2007). The long crus (long process, crus longum) joins to the head of the stapes (Toth and Csillag, 2005). More detailed, the long process ends in the lenticular process, which provides a convex surface for the concave head of the stapes (Gulya, 2007). This bone can be ossified to the crus and then forms the processus lenticularis (Getty, 1964). The incus and the malleus are formed by Meckel´s cartilage (more specifically: the incus body and short crus; and the head of the malleus) and by Reichert´s cartilage (long crus of incus; manubrium of malleus; Toth and Csillag, 2005). The superior ligament connects the body of the incus to the epitympanic recess, but Gulya (2007) did not find this ligament. The posterior incudal ligament holds the short crus and the medial and lateral incudomallear ligaments hold the body to the head of the malleus (Gulya, 2007). The long process of the incus is sensitive to osteitic resorption caused by chronic otitis media. In infants the marrow spaces in the malleus and the incus are large. A pit present on the long process of the incus is common and a sign of slight pneumatisation. The incus is in the dog about 4 mm long and 3 mm high (Getty, 1964). It is much smaller than the malleus.

The stapes (Fig. 11/2 A) is composed of the head (caput), the footplate (basis stapedis) and two crura or legs (Gulya, 2007; Toth and Csillag, 2005). One is more straight — called the anterior limb (crus rectilineum; Toth and Csillag, 2005) and more delicate (Gulya, 2007). The other one is more curved and called posterior limb (crus curvilineum; Toth and Csillag, 2005). The posterior crus is slightly shorter than the anterior one (Getty, 1964). The area between the crura is called obturator foramen and is sometimes bridged by a mucous membrane (Gulya, 2007), named obturator or stapedial membrane (membrana stapedis; Getty, 1964). The footplate is held in place by the annular ligament (Gulya, 2007), but ensures sufficient mobility too (Toth and Csillag, 2005). Toth and Csillag (2005) stated, that calcification of the annular ligament diminishes ossicular movements, which is a common cause of hearing defects in old age. The footplate is morphologically variable and differs in shape, thickness and curvature (the same is true for the crura; Gulya, 2007). On its lateral surface there is a ridge called the crista stapedis. A muscular process can be present and serves as attachment site for the stapedius tendon (Gulya, 2007) or stapedius muscle (Getty, 1964). The stapes is the smallest bone and about 2 mm in length in the dog (Getty, 1964). This ossicle is the most conservative one (Fleischer, 1978). The stapes complex is a semi-independent part of the ossiculat chain, because it is separated from the malleus-incus complex by a thin layer of cartilage or other soft tissues in all mammals. Furthermore, it is a mass-spring system with the annular ligament being the spring (Fleischer, 1978).

The tensor tympani muscle inserts at the base of the manubrium of the malleus (Toth and Csillag, 2005). It diminishes the pressure exerted by the tympanic membrane on the malleus, when contracted. In this way, vibration of the ossicle can be absorbed. The stapedius muscle inserts on the head of the stapes. When contracted, it retracts the stapes and thus attenuates movements of the stapes inside the oval window. These muscles protect the ossicles from excessive vibration caused by loud sounds (Toth and Csillag, 2005).

The inner ear is a system of membranous ducts containing the receptor structures for hearing and balance (called membranous labyrinth; Toth and Csillag, 2005). These ducts are enclosed by osseus canals (the cochlea), that are embedded in the petrous temporal bone. The membranous labyrinth consists of the cochlear part (cochlear duct) and the vestibular part (the three semicircular ducts, utricule and saccule). These two parts are connected via the ductus reuniens. The basilar membrane widens towards the apex of the cochlea. A specialised band of neuroepithelium, the spiral organ (organ of Corti), is situated on the basilar membrane. In the organ of Corti sustentacular and receptor cells are situated. The tectorial membrane borders the spiral organ and contains the hair cells (microvilli, "stereocilia"; Toth and Csillag, 2005).

The inner ear consists of the cochlea, the vestibule and the semicircular canals (Getty, 1964; see Fig. 11/1 C herein). The cochlea is anterior and converts the mechanical stimuli into nerve pulses (Getty, 1964).

The posterior part comprehends the semicircular canals, of which each lies in a different plane. The vestibule contains the utricle and the saccule. The utricle and the semicircular canals are important for the equilibrium. The whole labyrinth is about 15 mm long in the dog. The cochlea shows three and one quarter turns in the dog. It is located in the promontorium and points ventrolaterally and slightly laterally. The scala vestibuli communicates with the vestibule and is in contact with the base of the stapes at the fenestra vestibuli (oval window). The other scala, the scala tympani, is in contact with the round window, which is closed by the secondary tympanic membrane. A small opening, the helicotrema, at the apex connects the scalae. The diameter of the basal turn of the cochlea measures 4 mm and the height about 7 mm (in the dog). The vestibule is an oval space of about 3 mm diameter and is connected with the cochlea rostrally and the semicircular canals caudally (in the dog). The recesses for the saccule and the utricle show groups of foramina (maculae cribrosae). The semicircular canals lie caudal and slightly dorsal to the vestibule. Each of them describes about two thirds of a circle in a single plane, that is arranged at a 90° angle to the other canals. The diameter of these canals is 0.5 mm, except near the vestibule, where this part is twice as large (in the dog). This section is called crus and contains per canal a dilation, the ampulla. The anterior canal is the largest one. The lateral canal lies in a horizontal plane. In medium sized dogs the arcs of the anterior canal measures 6 mm, of the lateral canal 4.5 mm and of the posterior canal 3.5 mm (in the dog). The measurements vary with the size of the dog (Getty, 1964).

General information on the hearing apparatus

The ear originated in the lateral line canals of early aquatic vertebrates (Toth and Csillag, 2005). Takechi and Kuratani (2010) gave an excellent and recent review of the evolution of the mammalian middle ear. Interesting details of the ontogeny are discussed, e.g. the fact that marsupials are born as "reptiles", because they suck to the mother´s nipples with the primary jaw joint (Takechi and Kuratani, 2010): the squamosal and the dentary bones are too premature at that time. In non-mammalian amniotes the hyomandibular was released from the quadrate and the tympanic membrane evolved at a region inbetween them. In tetrapods the lamina of the angular served as an attachment site for the tympanic membrane. In the early therapsids the sound was transmitted through the angular-articular-quadrate-hyomandibular route (Takechi and Kuratani, 2010). The outer ear often follows phylogenetic patterns (Coleman and Ross, 2004; e.g. the cartilaginous ear canal). Webster (1966) stated, that the pinna is peculiar to mammals and is important for hearing and as heat dissipator. Environmental pressures operate more on the external and middle ear than on the inner ear. The most obvious variation in the inner ear is the number of turns of the cochlea coil, which ranges from two to five turns. He found it obvious that the number of turns does not correlate with frequency or intensity ranges. Whales have a long, narrow external auditory meatus (Webster, 1966).

Bats use ultrasonic sounds and have a very small tympanic membrane (less than 3 mm^2 surface area; Webster, 1966). The manubrium of the malleus is unusually long and the malleo-incudal joint is particularly complex. The latter possesses superior and inferior facets at sharp angles to each other. Cochlear size in recent and fossil bats was examined by Habersetzer and Storch (1992). A recent study concerning echolocation in bats was performed by Simmons et al. (2010).

Sarrat et al. (1988) state that the auditory ossicles are morphologically variable, particularly in humans. They found the incus to be the least variable ossicle. Sarrat et al. (1992) added that there is great diversity of bone density in human auditory ossicles. The cavitation increases with aging (Sarrat et al., 1992). Wilkins et al. (1999) state that the malleo-incudal joint is tight and that the incudo-stapedial joint is loose (allows rocking motion of the stapes in response to contraction of the stapedius muscle, if present) in Geomyidae. Nummela (1995) confirms that regardless to animal size, a given ossicular cross-sectional area is exposed to similar sound induced stress.

Lannigan et al. (1995) found the incus to be the most frequently deseased ossicle. Its long process is remodelled through life (Anson and Bast, 1959 in Lannigan et al., 1995), because of the paucity of blood and vascular supply. Roberto et al. (1993, in Lannigan et al., 1995) reported that disarticulated incudes in dogs showed

new bone formation and random organisation of new secondary osteoms. Thus, the incus is capable to react to variations in mechanical stimulations (Lannigan et al., 1995). They concluded that small biomechanical loadings cause resorption and speculated the cause to eventually be industrial noise. Finally, Lannigan et al. (1995) stated that females show this effect less than males.

Willi et al. (2002) worked on the topic of the incudo-malleolar joint, which is a synovial joint and answered the question if this is rigid or not. They found that articulation occurs at this joint. The most important vibrational component of the ossicular chain is the rotation around the axis through the short process of the incus and the head of the malleus. Relative motion in the incudo-malleolar joint occurs at 1-3 kHz (Willi et al., 2002).

High frequencies rapidly fade away due to atmospheric attenuation, whereas low frequencies undergo only small amounts of atmospheric attenuation and travel farther (Fleischer, 1978). This fundamental relation influences the connection of frequency with informational content: the amount of information increases with the frequency. Thus, high frequencies carry a lot of information. Furthermore, a compromise between a lot of information transferred/received over a small distance and a small amount of information transferred/received over a large distance has to be made. Desert mammals are adapted to low frequencies.

The stapes bears another indication for the frequency adaptation: taxa adapted to high frequencies or high ultrasonic sound have a very light stapes with a large area of attachment (for the ligament) and taxa adapted to low frequencies have a massive stapes with only a small area for attachment (Fleischer, 1978).

The normal range of human hearing is between 2 kHz and 4 kHz (Martinez et al., 2004).

Puria and Steele (2008) gave a great study on the mechano-acoustical transformations and the physics behind the hearing apparatus. When there is a change in impedance, then the energy transformation through mechanical levers improves the sound transmission. The impedance is low in air and high in the fluid filled cochlea. First, the sound pressure is increased due to a decrease in area, from the concha of the pinna to the ear canal and from the tympanic membrane to the stapes footplate. The lever ratio in the ossicular chain increases the force. The decrease of surface area from the stapes footplate to the basilar membrane results in an increase in velocity. The tympanic membrane is composed of several layers. Inbetween there are layers containing collagen fibers, radially oriented in one and circumferentially oriented in another layer. This is unique to mammals and might have a consequence: "Among vertebrates, a great majority of mammals are sensitive to ultrasonic sounds (above 20 kHz), while non-mammals are not" (p. 176 in Puria and Steele, 2008). The incorporation of the malleus-incus complex helped to specialize on high frequencies. The malleus-incus joint is fused together and rotates as one, but slippage occurs above about 8 kHz (in the cat). The displacement of the lenticular process serves to protect the cochlea from large motions at high static pressures. The most common pathologies are a missing or eroded incus and an ossified stapes. An elongated, coiled cochlea is present in marsupials and mammals, but not in Monotremata. Many features of vertebrate hearing evolved independently: the development of tympanic ears for aerial hearing; the development of two categories of hair cells; the three-boned middle ear of mammals; the inner ear organs themselves in fish, amphibians, archosaurs and mammals; the mechanisms for frequency selectivity; the cochlear amplification (Puria and Steele, 2008);

The middle ear in terrestrial vertebrates brings about a mechanical impedance matching when the air-borne sound is translated into changing pressure gradients in the cochlear fluid (Nummela et al., 1999). This air/fluid transformer is not advantageous when dwelling in water, so cetaceans developed a different system. In odonocetes the tympano-periotic complex is well isolated from the skull, whereas in mysticetes there is contact through the mastoid process. The tympanic bone is bowl-shaped and ectotympanic in origin. The tympanic membrane is modified and elongated into a conical structure, the tympanic conus. Some forms lost this and possess a tympanic wall, the tympanic plate (Fleischer, 1978; Nummela et al., 1999). The auditory ossicles are thick and hearing functions by vibration (Nummela et al., 1999). Fleischer (1978) gave information on the function of the middle ear of whales.

Hemilä et al. (1995) contributed to the topic of size impact on the ears. They found that middle ears are from small to large mammals — from bats to elephants — geometrically similar and that the ossicular bones are largely isometric to the ear. Additionally, the specific acoustic input impedance of the inner ear is independent of animal size. The parameter limiting high frequency sensitivity is ossicle inertia. A wide frequency range is characteristic for carnivores. They emphasize the exceptional high frequency hearing of the cat (Hemilä, 1995). Another important question has always been if the size of the tympanic membrane improves the hearing sensibility. Heffner (1983) stated that there is no correlation between the tympanic membrane size and the hearing sensitivity in different sized dogs.

Holz (1931) stated that the middle ear is variable in humans and animals, due to age and constitution. The bulla is the most variable component of the hypotympanicum. The greatest influence on hearing sensitivity of low and high frequencies in dogs is due to age rather than race. The articular surface of the malleo-incudal joint in Carnivora is often made up by four differently sized areas that are of tectiform shape. This allows less movement than in saddle-shaped articular surfaces as in the seal, the horse or in cattle. The incus is for every species characteristic, especially, the short and the long crus. The crus breve is frequently shorter than the long crus. In ruminants the state is vice versa. Holz (1931) examined pathologies of the stapes frequently. The angle between the stapes and the incus is acute in ruminants and carnivores. In the marmoset it is perpendicular and in humans it is often slightly obtuse angled. The position of the malleo-incudal complex is more important for mechanics. Movements between the malleus and the incus are reduced in the dog due to a ligament that runs from the crus longum to the opposing neck of the malleus (Holz, 1931).

Quam and Rak (2008) provided measurements of the malleus and the incus and information on paleopathologies in humans: deep pits on the bony surface of ossicles, named pockmarks, correspond to otitis media (an erosive pathological process). The morphological variation in the incus is greater than in the malleus, e.g. in details of the short process, the curvature of the long process and the depth of the excavated area on the medial aspect of the body. Neanderthals are less variable than modern humans (Quam and Rak, 2008). The notch along the inferior margin of the short process is the attachment site for the posterior incudal ligament. The ossicles of modern humans and Neanderthals differ, but the latter are within the range of the former. Quam and Rak (2008) interpreted this as phylogenetic information.

Rak and Clarke (1979) found *Australopithecus robustus* to differ in the morphology of the incus compared to modern humans, chimpanzees and gorillas. They found the incus to be important for phylogenetic reconstructions, as the ontogeny of this bone is an undisturbed expression of basic controlling genetic factors. A fossil human stapes was described by Moggi-Cecchi and Collard (2002).

Adaptations found within the hearing apparatus

Adaptations of the hearing apparatus are a well-discussed topic in the case of small mammals depending on low frequencies (e.g. Argyle and Mason, 2008; Burda et al., 1992; Coleman and Colbert, 2010; Lange et al., 2004, Lange et al., 2005; Lay, 1972; Mason et al., 2010; Webster and Webster, 1975; Webster, 1961; Webster, 1966). Argyle and Mason (2008) state that adaptations to low frequencies in rodents are: increased bulla volume, large eardrum without a pars flaccida, a large stapes footplate area and loosely suspended ossicles (due to loosened ligaments). Additionally, they mention that another adaptation seen in rodents is a synostosed malleus-incus-complex.

Burda et al. (1992) mentioned the following features as specialisations of subterranean insectivores and rodents: a rather round and large eardrum without a pars flaccida, a loose or no connection between the malleus and the tympanic bone, reduced and straightened transversal part of the malleus, an enlarged incus, an increased and rather flat incudo-mallear joint, a rather parallel position of the mallear manubrium and incudal crus longum in some cases and reduced or even missing middle ear muscles. Additionally, they stated, that the shape of the stapes is not adaptive and is incredibly variable in some taxa (Burda et al., 1992).

Coleman and Colbert (2010) found that an increase in size of middle ear structures (cavity volumes, tympanic

membrane, stapedial footplate area, ossicular mass) are associated with heightened low frequency sensitivity, because these features reduce the stiffness or elastic reactance. Further, they reported that the cochlear length is associated with the low frequency sensitivity (in contrast to the statement of Lange et al., 2004, see below) and that the malleus and incus are important to protect the inner ear from being overstimulated by loud sounds rather than for increasing the pressure.

Lange et al. (2004) stated that the middle ear morphology of the fossorial rodents *Microtus arvalis* and *Arvicola terrestris* is intermediate between subterranean rodents like the mole-vole and surface dwellers like the house mouse. The higher coiling of the cochlea in subterranean mammals (Fleischer, 1973) is in no direct relation to the auditory range (Lange et al., 2004). However, large ossicles and a large eardrum indicate a higher sensitivity for low frequencies. A specialisation to high frequencies is indicated by a small eardrum, a gonial of the malleus fused to the tympanic ring and strong middle ear muscles.

Lange et al. (2005) found the mallear and incudal lever to be independent of body size in African mole-rats (Bathyergidae). Species-specific differences could be identified: attachment site of the tensor tympani muscle, attachment site of the stapedial muscle and shape of the stapes; Especially interesting is the malleo-incudal complex — it shows no inter-individual variability, but differs between species. The incus size is independent from the body size (Lange et al., 2005).

Lay (1972) stated that in gerbiline rodents the total volume of the middle ear air space plays a significant, but passive role in the actual transformer efficiency and thus gives greater sensitivity for lower frequencies. Gerbillinae and Dipodidae possess an accessory tympanic membrane that is not a modified pars tensa of the tympanic membrane. The malleoincudal joint is hold together by a capsular ligament and rigified by fine intercapsular, medial, central and lateral ligaments. This construction reduces the energy loss through mechanical deformation. With the presence of an accessory tympanum, the malleus was modified in the following way: the neck is lengthened, the manubrium is rotated mediad, the process brevi manubrii is lengthened and a laterally directed ridge is developed on the upper third to half of the neck (there, the accessory tympanum attaches); All specimens with reduced middle ear volumes were quickly caught by owls (*Otus asia*) and rattlesnakes (*Crotalus cerastes*). Tape recordings revealed that the attack flight of an owl produced frequencies up to 1200 Hz and that a weak burst of up to 2200 Hz was produced by a struck of a rattlesnake. Thus, an increased middle ear air space is a predator avoidance structure (Lay, 1972).

Mason et al. (2010) found that Spalacidae use seismic signaling with conspecifics and show a "jaw listening" behaviour. *Spalax* thumps the anterodorsal part of the head on the burrow roof and holds its cheek and lower jaw in close contact with the burrow wall, when a neighbour is doing that head thumping. They possess a pseudoglenoid (= postglenoid) fossa and a periotic lamina through which the incus articulates with the skull (Mason et al., 2010). Rado et al. (1989) explained the procedure in more detail: the vibrations of the mandible are directly coupled to the auditory bulla and the incudo-periotic articulation; the short process of the incus is firmly anchored within a bony cup and that cup is attached to the skull via a thin periotic lamina (Rado et al., 1989).

Webster and Webster (1975) examined Heteromyidae and found that they are adapted to predator avoidance. Environment has a great influence on the middle ear, but there is no firm relationship between the habitat and the modifications in Heteromyidae (Webster and Webster, 1975).

Other groups examined respective to their adaptations are bats: Bruns et al. (1989) reported on the frog-eating bat *Trachops*, which is specialised on low frequencies. The basillar membrane is long and wide and there is an increase in innervation of the apical portion of the cochlea. The crus breve of the incus is very long, almost as long as the crus longum (Bruns et al., 1989).

The hearing apparatus in different taxa with special regards on Carnivora

A large study was performed by Bondy (1907) on the hearing apparaturs of many taxa including Monotremata, Insectivora, Rodentia, Chiroptera, Edentata, Carnivora, Pinnipedia, Perissodactyla, Artiodactyla and Primates. Another important publication included Monotremata, Marsupialia, Insectivora, Dermoptera, Chiroptera, Primates, Edentata, Pholidota, Lagomorpha, Rodentia, Cetacea, Tubulidentata, Proboscidea, Hyracoidea, Sirenia, Artiodactlya, Perissodactyla and Carnivora (Fleischer, 1973). All these groups cannot be described here. Various authors focused on a single species: Saunders and Summers (1982) examined the mouse middle ear. Hellström et al. (1982) reported about the rat. Wysocki (2005) described the ear of the guinea pig. Giannini et al. (2006) performed an extensive study on a bat, including the ossicles. Meng et al. (2001) even reported on fossil petrosals of gliriforms.

Aitkin and Johnstone (1972) researched upon the echidna *Tachyglossus aculeatus*. They concluded that the Monotremata show a plesiomorphic state: the malleus is larger, the incus is tightly attached to the malleus, the stapes is columelliform, the middle ear chain is stiff and no tympanic bulla is present. Therefore, echidna is similar to lizards (Aitkin and Johnstone, 1972). They speculate that they lay their snout on the ground to hear.

Botti et al. (2006) examined ruminants and compared them to the horse. They concluded that auditory ossicles differ in the head and the processi of the malleus, in the length of the processi of the incus and in the shape and topography of the processi on the stapes.

Bouetel and Muizon (2006) gave information on the mysticete *Piscobalaena nana* including the hearing apparatus. The ossicles are here of a completely different morphology. The malleus is stout, the incus too with a short and thin crus brevis and a very thick crus longum (Bouetel and Muizon, 2006).

Miller (1964) gave a great overview of the whole hearing apparatus of the dog. The cochlea of *Canis* shows 3 ¼ turns. Cole (2009) also worked on the dog and gave a good recent overview. Eom et al. (2008) performed a virtual CT otoskopy in the dog.

Solntseva (2007) gave an overview of the ears in mammals with emphasis on whales. Measurements and weights of ossicles of select Carnivora can be found therein (Table 5, p. 66, in Solntseva, 2007). She stated, that different types of structures in the middle ear are found in taxa with different ecologies.

Hunt (1991) pointed out, that within Carnivora Herpestidae and Hyaenidae show a modern arrangement and morphology of the auditory ossicles. Both show mallei with a reduced lamina and a short anterior process. Felids and viverrids have mallei with a well-developed pocketed lamina. If these features provide phylogenetic information is doubted (Hunt, 1991).

Huang et al. (1997) stated that the bony septum in the domestic cat divides the middle ear air space into two distinct compartments, the tympanic and the bullar cavity. They are connected via a narrow foramen. Similar frequency dependance was detected in the lion and the domestic cat. Sound pressures are smaller in the lion (Huang et al., 1997).

Huang et al. (2002) examined the specialisations concerning the ear in the sand cat *Felis margarita*. Larger auditory bullae are known in Gerbillinae and Heteromyidae that live in deserts. This feature is seen as an adaptation to increase the sensitivity for lower frequencies. This is evidenced by the fact that individuals with artificially reduced middle ear air volume of the kangaroo rat *Dipodomys* are more likely to by catched by owls and snakes (Webster and Webster, 1972). In the sand cat the following (Huang et al., 2002) was observed: the bony ear canal is unusually prominent; the region between the bullae is narrow; the bulla is extremely wide; the anterior part of the bulla is extended more anterior than the jaw joint; *Felis margarita* uses long distance communication, which is based on low frequencies. Additionally, high frequencies are largely absorbed by the atmosphere in low humidity. Huang et al. (2002) concluded, that the coupling of structural variations of the ear with the habitat is not evident in all species that live in the same habitat. They applied this concept to felids in the savannah and found that the cheetah is an exception. Furthermore, they proposed that the cheetah could be seen as special case, as it differs from all other felids in body structure, activity pattern and predation style (Huang et al., 2002).

Petter (1959) described the ossicles of the lion. He found that the malleus is becoming more mobile with age. The anterior process is undergoing resorption. The incus is quite large in relation to the malleus (Petter, 1959).

Ray (1976) described the incus of *Phoca wymani* as thick and with a small, saddle-shaped articulation surface. Salles (1992) used in his phylogenetic study on felids the auditory ossicles. The processus muscularis on the malleus is the attachment site for the tendon tympani muscle. Its enlargement is synapomorphic for *Panthera leo*, *Panthera pardus* and *onca*. *Panthera tigris* is plesiomorphic in this respect as it shows a process with a large base, that gradually becomes pointed. An anteriorly oriented reflection of the processus brevis on the malleus is a unique feature in *Acinonyx jubatus*. The only character of the incus used was the distinct outward projection of the inferior head of the incus with the malleus. This is apomorphic and found e.g. in *Otocolobus manul*. The plesiomorphic state is a smooth surface with less projection, e.g. in *Panthera leo* (Salles, 1992).

11.2 Auditory bulla

11.2.1 Introduction

The auditory bulla (or bulla auditiva) provides important information on phylogenetic relationships in fossil and living Carnivora (Hunt, 1987; Hunt and Tedford, 1993; Polly et al., 2006). As an example the Asian *Tungurictis spocki* (middle Miocene) was identified based on bulla remains as a hyaenid instead of being related to viverrids, as previously thought (Hunt, 1991). The auditory bulla patterns of felids and viverrids have evolved by the early Miocene in Europe, although the aeluroid hearing apparatus must have developed in the Oligocene (Hunt, 1991). The bulla provided evidence for the monophyly of the aeluroids (Hunt and Tedford, 1993). Hunt and Tedford (1993) also gave a morphological spectrum for adult aeluroid carnivores (Fig. 5.6, p. 58 therein). In general, this pattern ranges from an extreme inflation of the posterior chamber (as in felids) to an extreme inflation of the anterior chamber (as in hyaenids; Hunt and Tedford, 1993). The different pathways of the ontogenetic elements forming the bulla was also provided for arctoid (ursid), cynoid (canid) and aeluroid (felid) carnivorans (Fig. 5.5, p. 58, in Hunt and Tedford, 1993). The earlist known auditory bulla of Carnivora is known from the Eocene: *Viverravus acutus* (Viverravidae) from the Clarks Fork Basin in Wyoming (Polly et al., 2006). Interestingly, this bulla was most probable exclusively composed by the ectotympanic (Polly et al., 2006). This led the authors to the conclusion that viverravids lie outside the crown-group Carnivora (Feliformia, Caniformia).

The plesiomorph therian middle ear, common to marsupials and placentals, does not surround the middle ear cavity with a rigid wall, but to a great extent with soft connective tissues (Fleischer, 1978). The problem of this constellation is the slight deformation of the middle ear cavity during motions of the head (chewing, gnawing, swallowing, vocalizing, licking etc.; Fleischer, 1978): pressure inside the cavity is altered and causes changes of the sensitivity of the ear including changed stiffness of the ossicular chain. These disturbances affect the low frequencies and thus nearly all groups of mammals developed a closed middle ear cavity. Animals with extensive gnawing activities (e.g. rodents) or using echolocation (e.g. bats, dolphins) evolved an isolation of their middle ears to protect them from inevitable vibrations (Fleischer, 1978).
The bulla encloses and protects a defined middle ear space within which a bony ossicular system operates (Hunt and Tedford, 1993). The elements that contribute to the adult bulla are the ectotympanic, the rostral entotympanic and the caudal entotympanic(s) (Mickoleit, 2004; Hunt, 1987; Hunt and Tedford, 1993). These parts are unfused in neonate and juvenile individuals (Hunt, 1987). Thus, the contribution of the bulla elements can be better confirmed with the knowledge of the non-adult material. As mentioned above, morphological features of this region give phylogenetic information: the presence of the septum bullae characterizes the family Felidae. This septum is defined by its ontogeny: it is formed by the joining of the entotympanic and ectotympanic elements during early ontogeny and it is thus bilaminar in origin. A smaller anterolateral chamber of the ectotympanic is present. The details of how the septum bullae is formed point to lineages within a group (Hunt, 1987). The septum in canids is formed by the caudal entotympanic alone and in felids by the ectoympanic and the caudal entotympanic (Fig. 565, p. 502 in Mickoleit, 2004).

Hunt (1987) concluded, that the bulla shape does not significantly influence hearing quality, but each pattern is useful over a wide range of environments.

Tedford and Hunt (1993) gave an overview on the different compositions of the auditory bulla in carnivorous mammals (Fig. 5.4, p. 57). Tedford et al. (1995) described the characters of the auditory region that define the Canidae: a large ectotympanic (that ossifies from at least two centers); a partial septum (formed by the entotympanic); an internal carotid artery that lies in a groove on the medial side of the caudal entotympanic (Tedford et al., 1995). Ivanoff (2000) gave additional information on the septum in the canid bulla: it is product of the ventral entotympanic sinus (which is an additional cavity within the hypotympanicum). This is — according to Ivanoff (2000) — the only argument against the homology with the felid septum, since the dorsal septum is formed exclusively by the caudal entotympanic, whereas the ventral septum is bilaminar (formed by the growth of the caudal entotympanic over the ectotympanic; Ivanoff, 2000).

The hyaenid auditory region was described by Hunt (1991). The anterior chamber of the bulla (made up mostly by the ectotympanic) extends backwards and covers the posterior chamber (Hunt, 1991). The posterior chamber is made up by the caudal entotympanic and remains small in volume, especially compared to the anterior chamber (Hunt, 1991). This is true for all fossil and living hyaenids, except *Proteles* (Hunt, 1991). The eutherian Carnivora are characterized by the employment of entotympanics in conjunction with the ectotympanic (Hunt and Tedford, 1993). In metatherian carnivores the ectotympanic is combined with the alisphenoid, the exoccipital and the petrosal (Hunt and Tedford, 1993). Oligocene and younger carnivorans commonly show ossified bullae, but most early Cenozoic eutherian carnivores lacked ossified bullae except for a simple ectotympanic (Hunt and Tedford, 1993). For most of them a fibrous membrane or a cartilaginous capsule partially of fully enclosing a small tympanic cavity is assumed (Hunt and Tedford, 1993). The auditory region in nimravids was examined by Joeckel et al. (2002). The development of the ectotympanic in Nimravidae and the phylogenetic consequences were an important discovery of Peigné and De Bonis (2003). Van der Klaauw (1931) described the auditory bulla of some fossil mammals, including the North American *Hyaenodon*. He stated that the ectotympanic developed in early mammals. A ringlike tympanic is considered as plesiomorphic and seen in monotremes and marsupials. The tympanic of "creodonts" is horseshoe-like and comparable to that seen in *Nandinia*. A flat bulla is the rule in insectivores. Ususally, the bulla is not completely ossified in "creodonts", though it commonly is in hyaenodontids. He incorrectly stated that no ossified bulla is present in *Neohyaenodon*. The bony cylindrical auditory meatus is just a lip in Felidae, but long in Hyaenidae. *Nandinia* is considered primitive, because of its small entotympanic and the missing septum bullae (Van der Klaauw, 1931).

11.2.2 The auditory bulla of *Hyaenodon*

The bulla of *Hyaenodon* was already described by Filhol (1883) and Piveteau (1935). Filhol (1883) stated that there is no depression present posterior and medial to the bulla (as seen in the cat) and that no septum is present.

Mellett (1977) described the bulla of *Hyaenodon* as follows (the following thus is valid for the North American taxa): The auditory bulla is distinct and ossified. A separate tympanic ring is present. The bulla itself is bean shaped. Its long axis is tilted mediad. In general the bulla looks aeluroid-like (felid-viverrid). The posteromedial portion of the bulla is entotympanic in origin, confirming the statement of Van der Klaauw (1931; Mellett, 1977). The entotympanic contacts the skull between the carotid foramen and the posterior lacerate foramen (Mellett, 1977). The glenoid foramen is present. A number of bony septae appear on the roof and medial walls of the entotympanic. The bulla is composed of the entotympanic and an extension of the petrosal bone. Van der Klaauw (1931) considered this extension to be part of the entotympanic septum. The entotympanic bulla does not extend far enough laterally to enclose the middle ear. Thus, it was assumed by Mellett (1977), that the middle ear was covered by a tympanic ring and a cartilaginous cap. Concluding from this state the ear cavity had two compartments: a globular hypotympanic sinus enclosed by the entotympanic and the petrosal

bones and an epitympanic sinus enclosed ventrolaterally by the tympanic ring and dorsally by the petrosal and probably by squamosal bones. Functionally it was judged to work as in aeluroid carnivorans (Mellett, 1977). Comments upon the petrosal and other parts of the ear region are summarized here, following again Mellett (1977): Lateral to the entotympanic-petrosal suture the surface of the promontorium contains two grooves. One groove accomodated the promontory (= internal carotid of the Carnivora) and the other one probably accomodated the tensor tympani muscle. The promontorium tympani is a swelling of the basal cochlea coil and is located between the round and the oval foramen. It shows small grooves for the plexus tympanicus. The groove for the stapedial artery is running dorsolaterally across the promontorium towards the fenestra ovalis. The cochlea shows three complete turns. The fenestra rotunda lies in a deep socket facing posteriorly and slightly mediad. The condition in Carnivora is different: the socket faces posterolaterally. A conspicuous projection of the rest of the bony labyrinth was exposed posterodorsal to the cochlear (petrosal) eminence. That is strikingly different from modern Carnivora and also primitive Hyaenodontidae. The exposure is related to the great foreshortening of the basicranial region. The stylomastoid foramen exits in a canal through the mastoid bone, not between the mastoid and the tympanohyal, which is the usual configuration in Carnivora. In life the ectotympanic ring probably contacted the facial nerve leaving the ear region (Mellett, 1977).

Following Lange-Badré (1979) the specimen Qu 8593 shows that the septum is build by the entotympanic. There is no contribution by the ectotympanic as described for the North American species *Hyaenodon crucians* and *horridus* by Van der Klaauw (1931) and proposed for European species by Piveteau (1935) (Lange-Badré, 1979). Schlosser (1887) stated that there is no ectotympanic present in *Hyaenodon brachyrhynchus* and *Pterodon dasyuroides*. The bulla auditiva is composed of a posteromedial chamber made up by the entotympanic and the anterolateral, half ossified chamber made up by the ectotympanic (which is not preserved; Lange-Badré, 1979). The reconstruction of the ectotympanic as small ring (Fig. 22, p. 104 in Lange-Badré, 1979) can be doubted. There is no indication for exactly this shape and configuration. Furthermore, there is no ectotympanic preserved. She assumed, that is was only half-ossified. On the other hand, Mellett (1977) also assumed that the ectotympanic was a ring-like structure.
The stylomastoid canal is the outlet of the nervus facialis. Below the stylomastoid canal there is the fossa muscularis for the stapes muscle (Lange-Badré, 1979). The foramen lacerum posterius is very large, but has the same location as in Carnivora. The condyloid foramen (= foramina condyloidea, hypoglossal foramen in Mellett, 1977) is doubled, so there are two present (Lange-Badré, 1979).
The condition in *Pterodon* is completely different (Lange-Badré, 1979): the petrosum is isolated through a circumferential channel (= lacune circumpetreuse) from the neighbouring bones, the basispenoid, basioccitpital, exoccipital and alispenoid.

11.2.3 New description of a European specimen

Qu 8594 is a left skull fragment with a very well preserved bulla auditiva (Fig. 11/3 A-C). A right skull fragment, belonging to the same individual, is preserved too (Qu 8593; Fig. 11/3 D-F) and shows the petrosal.

It has already been described by Lange-Badré (1979). Herein, it is figured in detail and described again, including a review of the former description.
Fig. 11/3 A-B shows the following characters: the bulla is bean-shaped and its tip is anteromedially. There is a large space between the bulla and the auditory meatus. It can be assumed that the auditory canal was cartilaginous. However, it is clear, that a part is missing: the ectotympanic. Its shape remains unknown. Thus, the preserved bullar part is entotympanic in origin. A part of the petrosal bone can be viewed too — it forms together with the entotympanic a structure that looks like a parrot´s beak. The large foramen ovale (not the foramen ovale of the inner ear) anterior to the bulla is very large. Right behind the glenoid there is the foramen postglenoideum. The fissure of Glaser is between the medial border of the glenoid and the lateral border of the

foramen ovale. The carotid foramen is located on the medial side of the bulla. The anterior lacerate foramen is anterior and the posterior lacerate foramen is posterior of the entotympanic bulla. The latter one is large. On the lateral side of the bulla, the foramen stylomastoideum is present. The mastoid process is conspicuous. It is not fused to the bulla, well-developed and curved inwards (mediad).

Fig. 11/3 D-E shows some additional details: the alisphenoid canal is present. The bulla is not preserved, thus the inner structures are revealed: the petrosal and the round foramen can be seen. The strong ridge on the petrosal is for the promontory artery. As Lange-Badré (1979) already described the fossa muscularis is present. The facial canal ("aqueduct de Fallope" in Lange-Badré, 1979) runs anteroventrally.

The length (antero-posterior axis) of the entotymanic bulla mesures 9.99 mm and its width is 6.97 mm.

In order to gather additional information, the inner ear was examined. A computer tomography was performed together with Gerhard Weber and Martin Dockner on the microCT-device Viscom X8060 (tube: X9225-XD) at the Department of Anthropology (University Vienna). 696 slices with a resolution of 696 x 843 x 792 voxels with a voxel size of 20 x 20 x 20 μm were produced. The reconstruction of the CT-data, including the pictures (Fig. 11/4 B-F), was performed together with Gerhard Withalm at his working station with the software Osirix. The bulla clearly shows chambers (Fig. 11/4 B-C). There are two small posterior chambers and one large, anterior chamber. The lateral, posterior chamber is globular. There is a connection, a small channel, to the medial, posterior chamber. This chamber is the smallest one and elongated antero-posteriorly. It is connected with the anterior, large chamber through a narrow channel. Interestingly, when going through the slices, there is no connection present between the anterior, large chamber and the lateral, posterior, globular chamber. The cochlea (Fig. 11/4 D-E) makes at least three full turns. Semicircular canals could also be successfully reconstructed (Fig. 11/4 F).

11.2.4 Conclusions on the bulla

Apart from the bulla the mastoid process should be mentioned: it is very conspicuous and unfused with the bulla.

This feature is known from the North American taxa too (Mellett, 1977).

Tedford et al. (1995) described the mastoid process and used its development as character in the phylogenetic analysis of recent Caninae. They found the mastoid process to be large in *Pseudalopex*, but it does not exceed the bulla as in *Hyaenodon*. A small, crestlike mastoid process is the plesiomorph and an enlarged, knob- or ridgelike mastoid process is the apomorph condition in Caninae (character 33 in Tedford et al., 1995). It is apparent in *Hyaenodon* due to its conspicuous development and probably is a more plesiomorph character (at least compared to Carnivora).

The description of the bulla largely confirms Lange-Badré (1979) and Mellett (1977). The most important remaining question is the morphology of the ectotympanic. Depending on its development, either planar and crescentic (plesiomorph) or chambered and inflated (apomorph) (in Caninae; Hunt, 1987), it would contribute to evolutional and phylogenetic knowledge of *Hyaenodon*. Based on the knowledge that the ectotympanic is ring-like in plesiomorphic Carnivora (e.g. *Nandinia binotata*), it could be assumed (as Mellett, 1977 and Lange-Badré, 1979 did), that it was shaped like that also in *Hyaenodon*. On the other hand, viverravids show that the ectotympanic was the more important part in the bulla of sister taxa of the crown-group Carnivora (Polly et al., 2006). In Tedford and Hunt (1993: Fig. 5.4, p. 57) a small ectotympanic was figured for modern hyaenodonts (and *Hyaenodon*).

It is interesting, that the entotympanic is chambered, unlike the different patterns within Carnivora (Hunt, 1987; 1991). There are septa present within the bulla, correcting the view of Filhol (1883) and confirming Mellett (1977). Nevertheless, these partitions are not like the felid septum (between the ecto- and entotympanic). The chambered entotympanic seems to be a result of convergent evolution, as Carnivora

evolved partitioned bullae too (Hunt and Tedford, 1993). Also, it shall be mentioned, that *Nandina binotata* shows a plesiomorphic aeluroid auditory bulla composed of a single chamber, with no inflation during ontogeny of both, ectotympanic and entotympanic, and no internal septum.

The turns of the cochlea are comparable to that in the dog (Getty, 1964). The same number of turns is known from the North American *Hyaenodon* (Mellett, 1977).

Concluding from this, the bulla is structural the same in North American and European *Hyaenodon*.

11.3 First description of the inner ear of *Hyaenodon*

The inner ear of *Hyaenodon* was hitherto not documented, although it was included in the hitherto unpublished CT-scan of the brain of a North American species (see Chapter 10). The same specimen that gave information on the auditory bulla (Qu 8594, *Hyaenodon exiguus*, Quercy, see above) contributes to this topic. The whole structure of the inner ear can be found in fossils, because it is enclosed by osseous canals and embedded in the petrosum (Toth and Csillag, 2005). The same micro CT-scan (as described above for the bulla) was used for the reconstruction of the cochlea and the labyrinth. The software Amira 5.3 was available at the Department of Anthropology as well as a working station. Due to preservation simple tools, which automatically mark the area of interest (e.g. working with the threshold, greyscales) could not be used. Instead the label field was marked with the lasso-tool on a drawing panel in each slice of interest in two cutting planes. The surface generation was created with the option unconstrained smoothing. Measurements were performed directly in Amira with the 2D measurement tool (see Fig. 11/9 F). Dimensions are usually simple width and height distances and were performed according to Spoor and Zonneveld (1995).

The cochlea has a different position than in the dog. In *Hyaenodon* (Fig. 11/9 A) the cochlea points rostrally, whereas it is known to point ventrolaterally in the dog (Getty, 1964). The coiling of the cochlea — three turns — is comparable to the coiling in the dog (three and one quarter turns; Getty, 1964). However, the cochlea in *Hyaenodon* is low (see Tab. 11/2), not as high as in the dog (compare to Fig. 11/1 C). The diameter of the basal turn of the cochlea measures 4 mm and the height about 7 mm in the dog (Getty, 1964). That is contrasted by a height of about 4.3 mm in *Hyaenodon* and a comparable width of about 4.4 mm. Thus, the cochlea appears flattened and compressed. The oval window (fenestra vestibuli) can be seen as well as the round window, which is the larger one (Fig. 11/9 F, Fig. 11/10 A-F). All the semicircular canals are extensive (see Tab. 11/1). Each of them describes about two thirds of a circle in a single plane, that is arranged at a 90° angle to the other canals as seen in *Hyaenodon* and the dog too. The anterior one does not appear clearly as the largest one (as it does in the dog). The lateral semicircular canal lies in a horizontal plane (this is known in the dog; Getty, 1964).

semicircular canal	height	width
lateral	2.94 mm	2.73 mm
anterior	3.24 mm	3.31 mm
posterior	4.41 mm	2.78 mm

Tab. 11/1: Dimensions of the semicircular canals.

additional measurements	value
cochlea width	4.49 mm
cochlea height	4.34 mm
length of common crus	2.50 mm
ampulla width	2.65 mm

Tab. 11/2: Dimensions of the cochlea and other structures.

Gray (1907) gave an overview of the labyrinth of several animal groups: mammals, birds, reptiles and amphibians. His dataset of carnivores was quite extensive with description of the inner ear of the tiger, the lion, the domestic cat, the puma the aardwolf and the mongoose (*Herpestes griseus*). The number of cochlear coils is ranging from two and a quarter (seal) to nearly four (weasel) in carnivores. Gray (1907) considered the inner ear of carnivores — comparatively large number of turns of the cochlea, absence of perilymph space in the canals (except for aquatic carnivores) and general absence of pigment — to be one of the most advanced types within mammals. A common feature of the labyrinth among carnivores and other orders is the presence of a distinct "bulging outwards of the floor of the scala tympani in the region of the aqueduct of the cochlea" (p. 77 in Gray, 1907). Fleischer (1973) provided descriptions of the osseous cochlea of placentals.

The reconstruction of the labyrinth of *Hyaenodon* was performed on the preserved osseous structures, thus the amount of perilymph space cannot be judged. The bulging outwards of the cochlear aqueduct (= endolymphatic duct), seen in recent carnivores (Gray, 1907), is not present in *Hyaenodon*. The aqueduct is quite straight and narrow (Fig. 11/9 and 11/10 A-F). The lateral semicircular canal (horizontal canal in Gray, 1907) is the smallest one of the three ducts in *Hyaenodon* and as in the recent carnivores. The proportion of the cochlea to the rest of the labyrinth is about the same in *Hyaenodon* (compared to the carnivores; Gray, 1907, e.g. Plate XI). The most striking difference of the inner ear of the recent carnivore and that of *Hyaenodon* is the type of cochlea: the sharp-pointed cochlea is a main feature of the carnivore labyrinth. The cochlea of *Hyaenodon* is the opposite — it´s obtuse and compressed. Each semicircular canal lies in one plane (Fig. 11/10 A-F) as in the lion. Gray (1907) stated that the ducts are proportionally larger in canids than in felids. The cochlea width is in the domestic cat larger (6 mm; Gray, 1907): the turns of the cochlea are about three — this is the same as in the domestic dog (Getty, 1964) and cat (Gray, 1907). The round window is larger than the oval window (Fig. 11/9 F and 11/10 A-F). The oval window is compared to the round window significantly larger in *Hyaenodon* than in canids (Getty, 1964).

Measurements are known to vary with size at least in the dog (Getty, 1964), so the values herein should be considered keeping in mind they were found in a small sized form (fox size) of *Hyaenodon*.

The most obvious variation of the inner ear is the coiling of the cochlea, although it cannot be correlated with frequency or intensity ranges (Webster, 1966).

Therefore, it is proposed here that the inner ear could give a clue on the phylogeny. Thus, the documentation of the cochlea and the labyrinth in *Hyaenodon* shall raise the interest in this topic to make proper comparisons possible.

11.4 New descriptions of select auditory ossicles

The photos were made with the digital microscope Keyence VHX-1000 D (connected to a profile measurement unit, the Keyence VHX-S15).

Most of the measurements were taken from Quam and Rak (2008). They themselves modified measurements from Masali (1964) and provided figures and tables to describe them. In the following these measurements are explicated herein (Fig. 11/2 B-C). Before performing the measurements the ossicles are oriented: the incus is lying on its medial aspect, thus in most cases most of the facet is visible and the long process is pointing downwards; the malleus was not oriented as in Quam and Rak (2008; lying on its posterior aspect), but was orientated in a way that its articular facet could be fully viewed, lying on its anterior aspect.

In hitherto detailed publications, e.g. (Fleischer 1973; 1978) the articulation surface between the malleus and the incus was not the main topic. Herein, the first known auditory ossicle of *Hyaenodon* is described: an incus. Due to a lack of knowledge of some clue features for hearing inference (e.g. Fleischer, 1973) — this joint surface became an interesting point.

Explication of measurements

Incus (Table 2 and Fig. 2, both p. 418 in Quam and Rak, 2008; Fig. 11/2 B herein):

"Short process length" (9 in Quam and Rak, 2008) comprehends the maximum distance from the most salient point of the body to the opposite lying tip of the short process.

"Long process length" (10 in Quam and Rak, 2008) comprehends the maximum distance from the most salient point of the body to the opposite lying tip of the long process.

"Height of articular facet" (11 in Quam and Rak, 2008) comprehends the maximum distance of the facet.

"Functional length" (12 in Quam and Rak, 2008) was modified: herein it is the maximum distance between the tip of the long process and the lowermost point of the articular facet.

"Depth of long process" (13 in Quam and Rak, 2008) comprehends the maximum depth of the arc of the long process, measured perpendicular to a line connecting the outermost part of the lower part of the articular facet to the tip of the long process.

"Intercrural length" (14 in Quam and Rak, 2008) comprehends the maximum distance between the most salient point of the superior border of the short process to the tip of the long process.

"Intercrural arc depth" (15 in Quam and Rak, 2008) comprehends the maximum depth of the curvature, measured perpendicular to a line drawn from the tip of the short process to the tip of the long process.

"Angle between the axes" (16 in Quam and Rak, 2008) comprehends the angle between the short and long process with those transformed into straight lines.

"Facet length" is measured, when the articular facet is in full view. This comprehends the maximum distance from the upper to the lower border of the articular facet (the same axis as from the short to the long process).

"Facet width" is measured in the same position as the former. It comprehends the maximum width of the articular facet.

"Intercrural angle" is measured in the normal orientation as most of the measurements (incus lying on its medial aspect). It comprehends the angle between the short and the long process.

Malleus (Table 1, p. 417 and Fig. 1, p. 416 in Quam and Rak, 2008; Fig. 11/2 C herein):

"Malleus length" (1 in Quam and Rak, 2008) comprehends the maximum distance from the tip of the manubrium to the most salient point of the head.

"Manubrium length" (2 in Quam and Rak, 2008) comprehends the maximum distance from the tip of the short process to the tip of the manubrium.

"Manubrium thickness" (3 in Quam and Rak, 2008) comprehends the thickness of the manubrium at mid-manubrium length.

"Depth of manubrium" (4 in Quam and Rak, 2008) comprehends the maximum depth of the curvature of the manubrium, measured perpendicular to a line connecting the tip of the short process to the tip of the manubrium.

"Corpus length" (5 in Quam and Rak, 2008) comprehends the maximum distance between the tip of the head to the lower border of the manubrium.

"Head width" (6 in Quam and Rak, 2008) comprehends the maximum width of the head.

"Neck width" (7 in Quam and Rak, 2008) comprehends the minimum width of the neck.

"Length of the facet" comprehends the length of the articular facet.

"Width of the facet" comprehends the width of the articular facet.

11.4.1 Incus

Hyaenodon exiguus (Qu 8594; Fig. 11/5 A)

The specimen is a nearly complete, left incus. It was found together with two skull fragments, one exhibiting a beautifully preserved bulla (Qu 8594 left fragment; Qu 8593 right fragment). No more precise information than Quercy is indicated for the findings.

The lenticular process is missing, which is not unusual (see below). The incus itself appears small. The body is stout and compact, but the processi are short and rather fragile. Both crura are not thick. The long process is even slimmer than the short process. The superior border of the crus breve is not straight: it is concave with the tip of the crus breve curved upwards. The long process is very short, comparable to the crus breve. The former is twisted. In lateral view much of the facet is seen. The facet is very long, occupying most of the length of the whole incus. It is divided into two main articular surfaces. The superior one is larger. The lower one is quite small and oval in outline. A narrow groove separates the two surfaces. A striking feature is seen in medial view: the facet is not simply saddle-shaped (with the two areas mentioned above), it is rather arranged in a downward slope — showing an additional, broadened and lower articulation surface. The lower joint surface is projecting.

measurements of the incus	value in mm
short process length	2.40
long process length	2.90
height of articular facet	1.50
functional length	1.24
depth of long process	0.27
intercrural length	2.18
intercrural arc depth	0.48
angle between the axes	44°
facet length	1.43
facet width	0.98
intercrural angle	139.8°

Felis catus (IUPW 2073/1; Fig. 11/5 B)
The specimen is a nearly complete (except for the lenticular process), left incus. It comes from a 4 weeks old, female domestic cat. The bullae are not yet fused (Fig. 11/4 A). The large process shows a flat surface for the lenticular process. The crus breve is long. It has a straight, superior border. The intercrural depth is deep, partly due to the long crura. The long process is strongly curved and twisted. Its tip is distally pointed. The facet is made up by two articular surfaces. The superior one is large and convex. The lower one is very broad and more concave, thus providing a depression for the complimentary surface on the malleus. In medial aspect the straight outline of the border of the crus breve is emphasized. The long process is the thicker one. The facet appears saddle-shaped and of triangular outline.

measurements of the incus	value in mm
short process length	2.58
long process length	2.99
height of articular facet	1.40
functional length	1.50
depth of long process	0.21
intercrural length	2.81
intercrural arc depth	0.93
angle between the axes	58.4°
facet length	1.38
facet width	1.21
intercrural angle	109.5°

Crocuta crocuta (IUPW without number; Fig. 11/5 C)

The specimen is a nearly complete, left incus. It misses only the lenticular process. The articular surface is large and broad. The facet in general is saddle shaped and divided into two main articular surfaces. The superior one (near the crus breve) is the more extensive one. The lower one fades towards the lateral side and decreases in length. There is a strongly developed projection below the facet for the malleo-incudal joint. On the whole the incus is thick and extremely robust. The excavation between the crura is deep. The crus breve is quite long and thick as well. Its superior border shows a straight border. The long process is thick and exceeds in this aspect the crus breve. A conspicuous tip is present on the distal side of the terminal long process. Due to the process below the articular surface, the medial border of the long process gets a strongly curved border. In medial view the flattened surface of the end of the long process shows up clearly. That is where the lenticular process attaches. The medial aspect shows that the superior part of the facet is the more extensive one. The tip of the crus breve is eroded. The specimen comes from a neonate individual. The overall surface shows small pits and eroded areas. These are indicators for pathology (Quam and Rak, 2008). The described symptoms match with otitis media (Quam and Rak, 2008). However, the impact of the early ontogenetic stage has to be taken into account too.

Another specimen of *Crocuta crocuta* shows a very broad articulation surface with a vertical split of the lower surface (pers. obs). It is much similar to the state in *Hyaena hyaena* (pers. obs.) — both are much different from the hyaenid *Proteles* (see below).

measurements of the incus	value in mm
short process length	3.58
long process length	5.13
height of articular facet	2.70
functional length	2.56
depth of long process	0.42
intercrural length	5.24
intercrural arc depth	1.40
angle between the axes	66.6°
facet length	2.96
facet width	2.48
intercrural angle	141.8°

Proteles cristatus (IUPW 2398; Fig. 11/5 D)

It should be noted that *Proteles* shows enlarged bullae (ventrally strongly inflated). A septum divides the bulla into an anterior and a posterior chamber.

The specimen is a nearly complete, left incus. Only the lenticular process is not preserved. The short crus is clearly shorter than the long crus and also slimmer. Its border is almost straight in outline – except for a small tubercle above the facet and the fact that the crus breve is pointing diagonally upwards. The long process is long, thick and only slightly twisted. The facet is divided into three articular surfaces. The superior one is connected with the lateral lower one. The medial lower articular surface is separated by a groove. This area is isolated and circular in outline. In medial view it is obvious that this surface and the superior articular surface are convex (the corresponding areas on the malleus are distinct concave). The lateral, lower articular surface slopes downwards extending on the long process. The facet is very broad and long too. From a medial view the facet appears saddle shaped.

measurements of the incus	value in mm
short process length	2.61
long process length	3.59
height of articular facet	2.41
functional length	1.40
depth of long process	0.07
intercrural length	3.53
intercrural arc depth	0.92
angle between the axes	65.4°
facet length	2.09
facet width	1.81
intercrural angle	142.8°

Vulpes vulpes (NMW 1073; Fig. 11/6 A)

The specimen is a nearly complete, left incus. The lenticular process is missing. The crus breve is curved upwards. The superior border of the incus body is strongly convex and leads into a strongly concave curve of the crus breve. In medial view the crus breve shows a long facet. The long process is rather short and much thicker than the short process. A groove is present on the long process. Two distinct articular surfaces of the malleo-incudal joint are present on the medial side. The lower one of these is circular. The lateral articular surface is saddle-shaped. A vertical groove separates the lateral und medial articular surfaces. In general the facet is twisted laterad with all articular surfaces facing laterad except for the lower, circular one on the medial side.

measurements of the incus	value in mm
short process length	2.48
long process length	3.21
height of articular facet	1.58
functional length	1.28
depth of long process	0.20
intercrural length	3.12
intercrural arc depth	0.81
angle between the axes	65°
facet length	1.70
facet width	1.58
intercrural angle	119.3°

Vulpes lagopus (NMW 4007; Fig. 11/6 B)

The specimen is a nearly complete, left incus. The lenticular process is missing. The superior border is first convex (body) and then concave (crus breve). The crus breve is curved upwards and thick. It is as thick as the long process, when viewed medially. A groove is present on the long process. The facet is facing laterad and is divided. The lower, medial articular surface is circular, but not as perfectly as in *Vulpes vulpes*. The superior, medial facet is large, extensive and connected with the lateral articular surface. A groove separates only the circular facet from the rest of the articular surface of the malleo-incudal joint. In medial view the facet is saddle-shaped and a constriction is present below the facet.

measurements of the incus	value in mm
short process length	2.17
long process length	2.89
height of articular facet	1.82
functional length	1.07
depth of long process	0.14
intercrural length	2.95
intercrural arc depth	0.63
angle between the axes	70.1°
facet length	1.46
facet width	1.37
intercrural angle	122°

Vulpes zerda (NMW B4817; Fig. 11/6 C)

The specimen is a nearly complete, right incus. The lenticular process is missing. The crus breve is strongly curved and its superior border is strongly concave. The long process is very thick, short, somewhat twisted and shows a smooth surface for the lenticular process. The facet is indented and saddle-shaped. This facet is more complicated and is divided in two lateral articular surfaces and one medial articular surface. The lateral ones are distinct from each other and a groove separates them. They are rounded. Above them there is a bulge of the body present. The medial articular surface is not divided. In fact the superior one connects to the superior lateral surface.

measurements of the incus	value in mm
short process length	1.88
long process length	2.54
height of articular facet	1.68
functional length	0.89
depth of long process	0.15
intercrural length	2.34
intercrural arc depth	0.57
angle between the axes	54.1°
facet length	1.93
facet width	1.64
intercrural angle	129.8°

Speothos venaticus (NMW 1287; Fig. 11/7 A)

The specimen is a nearly complete, left incus. Just the lenticular process is missing. The crus breve is considerably shorter than the long process. Both are thick. The long process is twisted and long. The superior border of the crus breve is straight. The facet of the malleo-incudal joint is made up by a clearly smaller lateral articular surface and a medial articular surface. The groove between the lateral and the medial part is very long. The lateral articular surface is facing laterad, the medial articular surface is facing upwards and slightly mediad. In medial view the facet appears saddle-shaped.

measurements of the incus	value in mm
short process length	2.37
long process length	3.58
height of articular facet	1.93
functional length	1.48
depth of long process	0.28
intercrural length	3.24
intercrural arc depth	0.75
angle between the axes	62.2°
facet length	1.80
facet width	1.71
intercrural angle	109.7°

Urocyon cinereoargenteus (NMW 2876; Fig. 11/7 B)

The specimen is a nearly complete, left incus. The lenticular process is missing. The superior border is a convex curve (body), leading into a concave curve (short process). The crus breve is curved upward. The long process is thicker. The facet of the malleo-incudal joint is facing laterad. The articular surfaces are arranged like a four-leaf clover. No groove is present. A constriction is present below the facet. In medial view the facet is saddle-shaped.

measurements of the incus	value in mm
short process length	2.28
long process length	3.03
height of articular facet	1.78
functional length	1.21
depth of long process	0.15
intercrural length	2.97
intercrural arc depth	0.95
angle between the axes	70.2°
facet length	1.53
facet width	1.53
intercrural angle	135.4°

Cuon alpinus (NMW 4254/B4719; Fig. 11/7 C)

The specimen is a nearly complete, left incus. The lenticular process is missing. The crus breve is terminally curved upwards and thick. The short process shows an elongated tip. Its superior border is convex. A flattened surface is present on the crus breve in medial view, maybe as attachment site for a ligament. The long process is not long, but thick and twisted. A flat facet is present for the lenticular process. The facet is quadratic in shape. In medial view it is saddle-shaped. The articular surfaces are not clearly separated. There is no groove present. The lower, lateral articular surfaces face strongly laterad and are convex.

measurements of the incus	value in mm
short process length	2.35
long process length	3.19
height of articular facet	1.75
functional length	1.30
depth of long process	0.16
intercrural length	2.84
intercrural arc depth	0.90
angle between the axes	61.3°
facet length	1.61
facet width	1.62
intercrural angle	126.4°

11.4.2 Malleus

Felis catus (IUPW 20731, Fig. 11/8 A)

No measurements were performed on this specimen, because it is too fragmented. Just the head with the articulation facet is discussed herein. The neck of the left malleus is strongly curved. The articulation facet is composed by three surfaces. The uppermost of the two upper surfaces is concave.

Crocuta crocuta (IUPW without number, Fig. 11/8 B)

The specimen has a strange appearance. It is very different from all the other observed mallei. It is thick and very robust. Furthermore, its coarse surface displays small pits — a possible indication for otitis media (Quam and Rak, 2008). Its manubrium is broken. Both, anterior and muscular processi are equally well-developed. The muscular process is strong. A small lateral process seems to be present. The articulation facet is deeply excavated.

measurements of the malleus	value in mm
malleus length	7.55*
manubrium length	/
manubrium thickness	2.22
depth of manubrium	/
corpus length	7.47
head width	3.66
neck width	1.10
length of the facet	3.03
width of the facet	2.71

*manubrium is broken, thus the measurement was made until the line of breakage valid for all tables in this section.

Proteles cristatus (IUPW 2398, Fig. 11/8 C)

The specimen is a left malleus and shows a slightly curved manubrium. The anterior process is broken. The muscular process is strongly developed and pointed. The lateral process is large. The neck is curved. The articular facet shows a peculiar shape. There is a u-shaped band present, instead of more simple surfaces as in e.g. canids or the human.

measurements of the malleus	value in mm
malleus length	9.58
manubrium length	4.90
manubrium thickness	0.74
depth of manubrium	1.49
corpus length	4.30
head width	2.23
neck width	0.71
length of the facet	2.27
width of the facet	1.84

Vulpes vulpes (NMW 1073, Fig. 11/8 D)

The right malleus shows a long, curved manubrium. A crest is running on it and ends in a broadened tip of the manubrium. The anterior process is small. The muscular process is more developed. A small lateral process is present. The articulation facet is indented by a deep groove. Four surfaces make up the articulation facet. These are connected by an u-shaped band. A small groove indents the facet.

measurements of the malleus	value in mm
malleus length	8.45
manubrium length	5.18
manubrium thickness	0.80
depth of manubrium	1.52
corpus length	3.64
head width	2.14
neck width	1.80
length of the facet	1.70
width of the facet	1.86

Vulpes lagopus (NMW 4007, Fig. 11/8 E)

The right malleus shows a broken manubrium. It is similar to the malleus in *Vulpes vulpes*. The crest runs along the manubrium, assumingly also ending in a broadened tip. The anterior process is small. The muscular process is strong and its tip is shaped like a hook. A small lateral process is present. The head shows an articulation facet composed by four surfaces. These are connected by an u-shaped band and a small groove indents the facet.

measurements of the malleus	value in mm
malleus length	6.53*
manubrium length	2.86*
manubrium thickness	0.73
depth of manubrium	1.36*
corpus length	3.55
head width	1.80
neck width	1.00
length of the facet	1.62
width of the facet	1.73

Vulpes zerda (NMW B 4817, Fig. 11/8 F)

The right malleus shows a broken manubrium (for measurements the left malleus with a complete manubrium was available). The neck and the manubrium are slightly curved. The anterior process is broken. The muscular process is well developed. Its tip is curved and shaped like a hook. A small lateral process is present. The head shows the articulation facet. There is no groove indenting the facet. The four surfaces are all in contact with each other, making up a complex facet.

measurements of the malleus	value in mm
malleus length	7.48
manubrium length	3.17
manubrium thickness	0.98
depth of manubrium	1.34
corpus length	3.82
head width	2.03
neck width	1.08
length of the facet	1.83
width of the facet	1.90

Speothos venaticus (NMW 1287, Fig. 11/8 G)

The right malleus is quite robust. The manubrium is short and thick. As observed in other canids, the manubrium shows a crest ending in a broadened tip. The anterior process is broken. The muscular process is strong. A small lateral process is present. The neck is curved. The head displays an articulation facet with four surfaces for the corresponding area on the incus. A shallow groove divides the upper and the lower half of the facet.

measurements of the malleus	value in mm
malleus length	7.91
manubrium length	3.88
manubrium thickness	0.74
depth of manubrium	1.26
corpus length	4.07
head width	1.83
neck width	1.36
length of the facet	1.70
width of the facet	1.85

Urocyon cinereoargenteus (NMW 2876, Fig. 11/8 H)

The left malleus shows a curved neck and a curved manubrium. A crest runs along the manubrium, ending in a broadened tip. Associated with the crest is a deep groove. The anterior process is small. The muscular process is strong and its tip is curved, shaped like a small hook. The head displays the articulation facet: the four surfaces are arranged like a four-leaved cloverleaf as already seen on the incus.

measurements of the malleus	value in mm
malleus length	8.54
manubrium length	4.59
manubrium thickness	0.77
depth of manubrium	1.52
corpus length	3.88
head width	1.85
neck width	1.63
length of the facet	1.79
width of the facet	1.42

Cuon alpinus (NMW 4254/B4719, Fig. 11/8 I)

The left malleus shows a long manubrium with a crest ending in a broadened tip. It is quite robust. The anterior and the muscular processi are well-developed. The anterior process is long and thin. The muscular process is more robust, showing a curved tip. The lateral process is small. A thin ossified surface, the lamina, connects these with the head. The neck and the manubrium are slightly curved. The head shows the usual composition of a canid articulation facet: a small groove indents the facet. The four articulation surfaces are connected in an u-shaped band.

measurements of the malleus	value in mm
malleus length	9.35
manubrium length	4.12
manubrium thickness	0.82
depth of manubrium	1.76
corpus length	0.46
head width	2.05
neck width	1.32
length of the facet	1.75
width of the facet	1.83

Nandinia binotata (NMW 1164/B2097, Fig. 11/8 J)

The left malleus shows a very strongly curved neck and a rather large body in relation to the manubrium. The manubrium is straight and thin, ending in a broadened tip. The anterior process is broken. The muscular process is very long and pointed. The lateral process is a small bump. There is thin ossified surface, the lamina, connecting the anterior process with the head. The head displays a large articulation facet, which is clearly divided into two surfaces: a lower and an upper articulation surface; they compose an acute angle.

measurements of the malleus	value in mm
malleus length	5.19*
manubrium length	1.99*
manubrium thickness	0.38
depth of manubrium	0.58
corpus length	3.58
head width	1.46
neck width	1.04
length of the facet	1.12
width of the facet	1.18

11.4.3 Discussion of the auditory ossicles and inferences on hearing

Alas, the only ossicle known so far in *Hyaenodon* is the incus. However, this is the first known auditory ossicle in this taxon and probably also the first known within Hyaenodontidae. The articulation facet gives a clue on the counterpart on the malleus. It should be generally saddle-shaped, showing two main articulation surfaces. The articulation facet of *Hyaenodon* is completely unlike those seen in canids: all the canid specimens show a facet composed in various types by four articulation surfaces. In *Hyaenodon*, the incus shows a large upper articulation surface and a lower circular area. The hyaenids are also showing a different formed facet. From this sample, a felid, the domestic cat, is comparable in some aspects to *Hyaenodon*. It shows three articulation surfaces of the facet in equal development. The upper one is convex and the lower two are concave. The lateral one is sloping and the other one is circular. The latter is similar in *Hyaenodon* — but the lower articulation is not as broad as in the cat. Both, in the cat and in *Hyaenodon* the incus is small and delicate. The long process is short in relation to the crus breve in *Hyaenodon* — that is not seen in the comparative carnivore set. The crus breve is curved and in this character the *Hyaenodon* incus is most similar to the fox *Vulpes vulpes*. Thus, as no other hyaenodontid ossicle is known up to now, this *Hyaenodon* incus appears to be unique.
The incus of *Hyaenodon* is not unusually small compared to the body size of the individual. Although the incus size is approaching the incus size of the smaller cat and is smaller than the incus of *Vulpes vulpes* which is of approximate same body size. However, the incus is known to be geometrically similar with the body size (Hemilä et al., 1995; Lange et al., 2005).

The cochlea length is important for the low frequencies (Coleman and Colbert, 2010). Concerning the turns of the cochlea *Hyaenodon* is similar to the modern dog.

Holz (1931) stated that the incus is specific for each species. This statement seems to be true. A comparison to taxa more related to *Hyaenodon* would be of great interest, because the incus provides phylogenetic information (Rak and Clarke, 1979; Quam and Rak, 2008). As a comparative set of hyaenodontid ossicles is hitherto not available, this topic awaits future discussion.

As the impact of phylogeny and ecology is known, but not too well documented in the aspect of what influence results in what development — it can not be decided by now, how the morphology of the incus in *Hyaenodon* should be interpreted in detail.

However, some significant clues give information on the hearing in *Hyaenodon*. There is no sign of an adaptation to low frequency hearing, as none of the characteristics like a large, inflated bulla, an enlarged incus,

a flat articular surface of the incus or a synostosed malleus-incus-complex (Argyle and Mason, 2008; Burda et al., 1992) is present in *Hyaenodon*. The bulla is not greatly inflated like in the fennec fox or the hyaenid *Proteles*.

Carnivora are known to have a wide frequency range (Hemilä et al., 1995). This makes sense for a predator. Cats are known to show a great sensitivity to high frequencies (Hemilä et al., 1995). The incus of *Hyaenodon* is most comparable to the cat, also concerning the measurements. This infers a similar adaptation. It is most probable that *Hyaenodon* had as a predator a relatively wide frequency range and rather an adaptation to high frequencies than to low frequencies.

A

semicircular ducts

utricle

saccule

endolymphatic duct

endolymphatic sac

scala vestibuli

scala tympani

cochlear duct

auditory tube

petrous temporal bone

perilymphatic space of vestibule

base of stapes in oval window

stapes

incus

malleus

round window

external acoustic meatus

tympanic membrane

tympanic cavity

tympanic bulla

B

epitympanum

superior ligament

lateral ligament

Prussak´s space

head of the malleus

incus

tensor tympani tendon

facial nerve

stapes

pars flaccida

lateral process

anterior process

manubrium

promontory

external auditory canal

pars tensa

round window

hypotympanum

semicanal for the tensor tympani muscle

Eustachian tube

C

cupula of cochlea

oval window

anterior ampulla

lateral ampulla

site of secondary spiral lamina

round window

cochlear aqueduct

vestibule

vestibular aqueduct

common crus

posterior semiciruclar canal

anterior semicircular canal

lateral semicircular canal

Fig. 11/1: Drawings for explanation of the hearing apparatus (see text). Topology of the middle and the inner ear. A, section through the middle ear of the dog, redrawn from Getty (1964: Fig.17-11, p. 852) ; B, human middle ear, redrawn from Gulya (2007; Fig. 82, p. 86); C, inner ear of the dog, redrawn from Getty (1964; Fig. 17-17, p.861).

A — malleus in medial aspect

- head
- articular surface for the incus
- osseus lamina
- neck
- anterior process
- muscular process
- lateral process
- manubrium

malleus in posterior aspect

- muscular process

incus in medial anterior aspect

- short crus
- articular surface for the malleus
- os lenticularis
- long crus

stapes in medial posterior aspect

- base
- posterior crus
- obturator foramen
- anterior crus
- muscular process
- head

B

- short process length (9)
- angle between the axes (16)
- intercrural arc depth (15)
- intercrural length (14)
- intercrural angle
- long process length (10)
- heigth of articular facet (11)
- functional length (12)
- depth of long process (13)
- facet width
- facet length

C

- malleus length (1)
- manubrium thickness (3)
- depth of manubrium (4)
- manubrium length (2)
- facet width
- neck width (7)
- facet length
- head width (6)
- corpus length (5)

Fig. 11/2: Drawings for explanation of the auditory ossicles and performed measurements (see text). A, topology of the auditory ossicles of the dog, redrawn from Getty (1964: Fig.17-14, p. 858) ; B, measurments performed on the incus (most after Quam and Rak, 2008; indicated with their numbers, see text); C, measurements performed on the malleus (as for the incus, most of them follow Quam and Rak, 2008; see text).
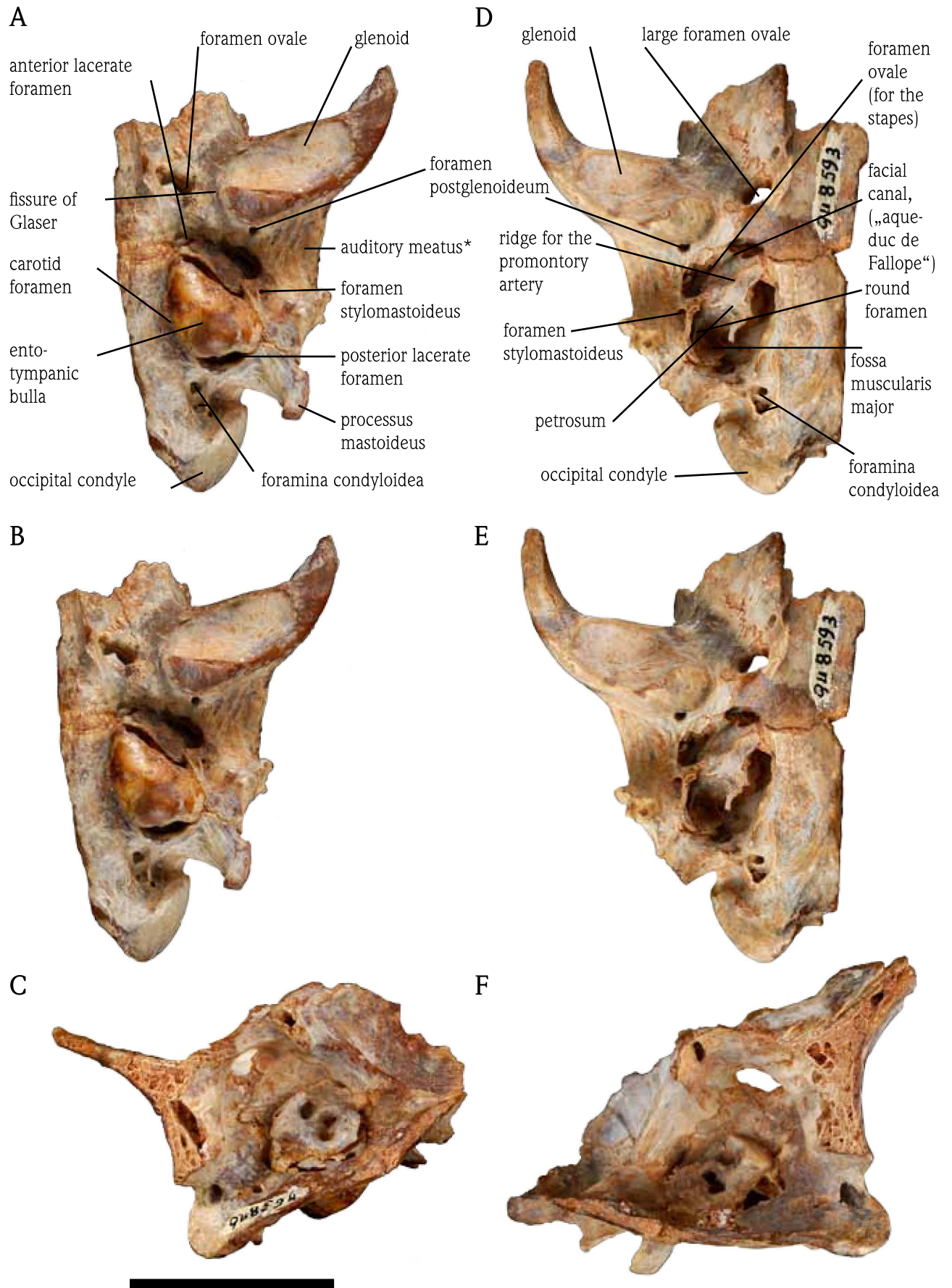
Fig. 11/3: Disto-ventral fragments of the skull of *H. exiguus* from Quercy. Bar equals 1cm. A, Qu 8594, left skull fragment with bulla in ventral view; B, the same as A, but without labels; C, Qu 8594, internal view with petrosum; D, Qu 8593, right skull fragment of the same individual in ventral view, bulla has broken away; E, the same as D, but without labels; F, Qu 8593, internal view with petrosum. *indicates where the auditory meatus, presumably cartilaginous, must have been.
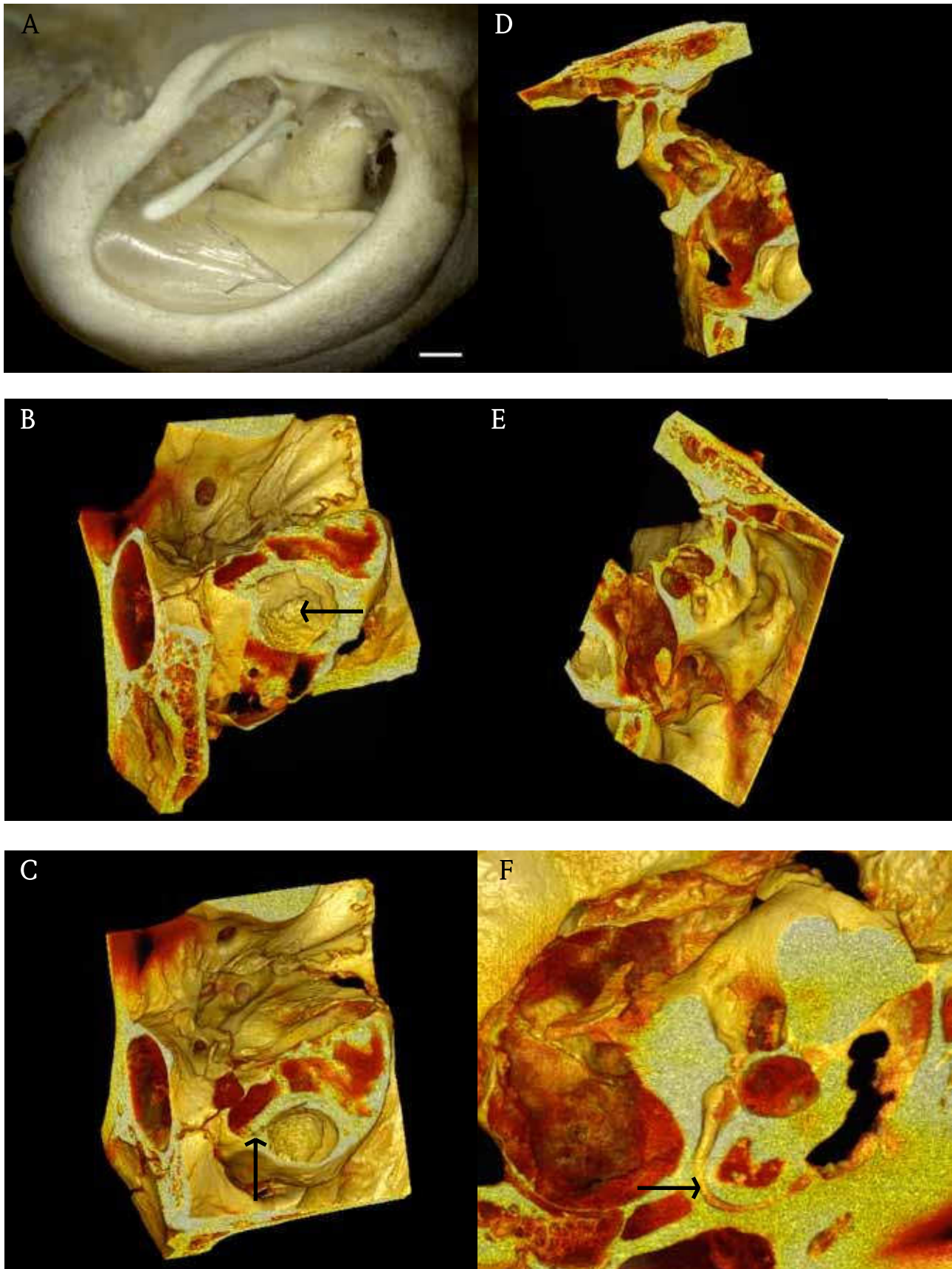
Fig. 11/4: Malleus in situ in a cat (**A**, bar equals 1 mm) and sections of the CT-data of a skull fragment of *Hyaenodon exiguus* (Qu 8594, **B**-**F**). **A**, IUPW 2073, *Felis catus*, left side of the skull with bulla and the malleus associated with the tympanic membrane; **B**, section of the bulla, revealing a large circular chamber (arrow); **C**, section of the bulla, showing the connection (arrow) between the posterior two chambers ; **D**, section of the cochlea; **E**, section of the cochlea in a different plane (both suggest about three turns); **F**, section revealing a semicircular duct (arrow).
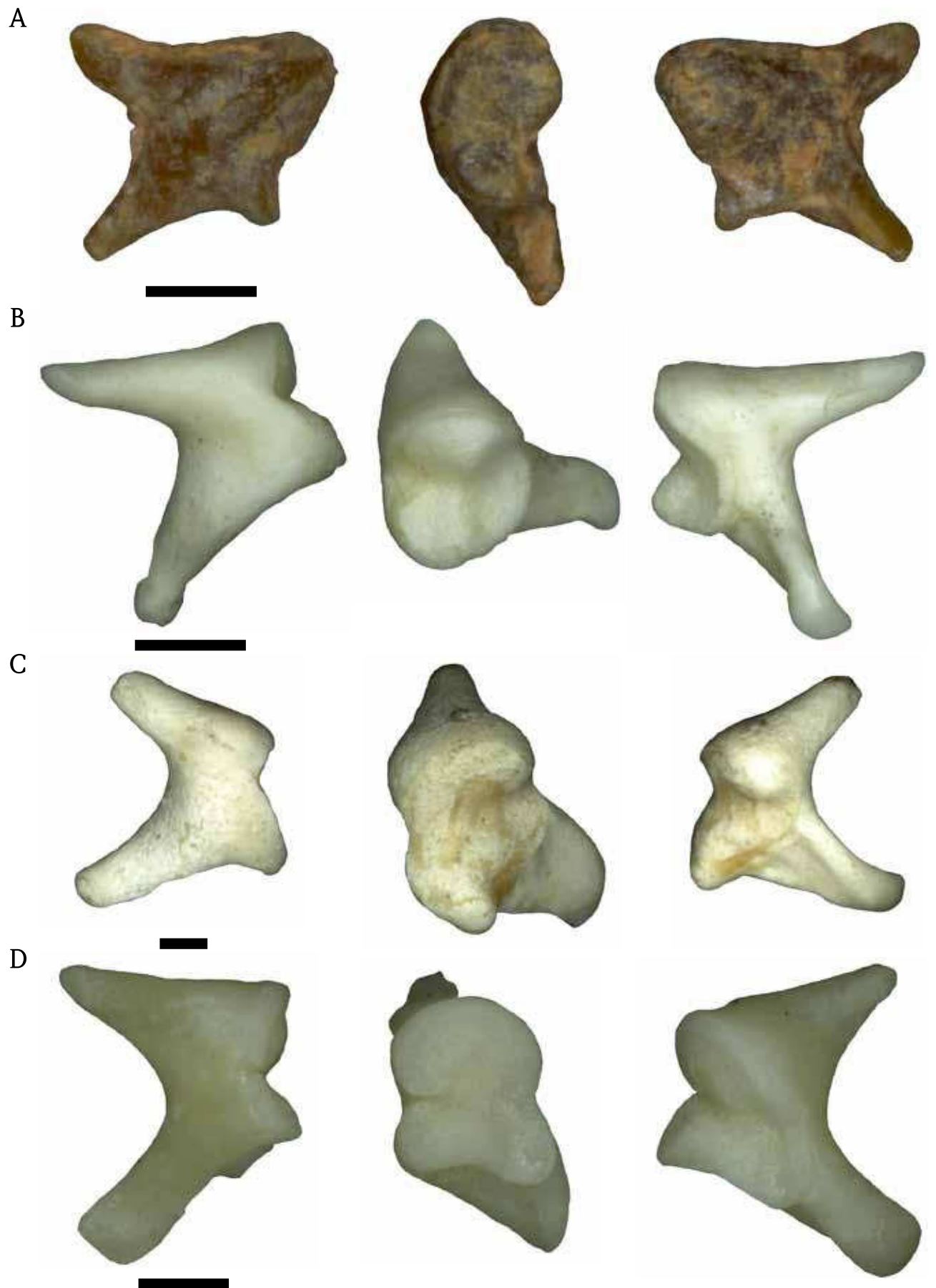
Fig. 11/5: Incus of *Hyaenodon* and felid and hyaenid Carnivora in medial (left) and lateral (right) view, with view of the articulation facet for the malleo-incudal joint (middle). Bar equals 1 mm. **A**, Qu 8594, left incus of *Hyaenodon exiguus*; **B**, IUPW 2073, incus of *Felis catus*; **C**, IUPW without number, incus of *Crocuta crocuta*; **D**, IUPW 2398, left incus of *Proteles cristatus*.
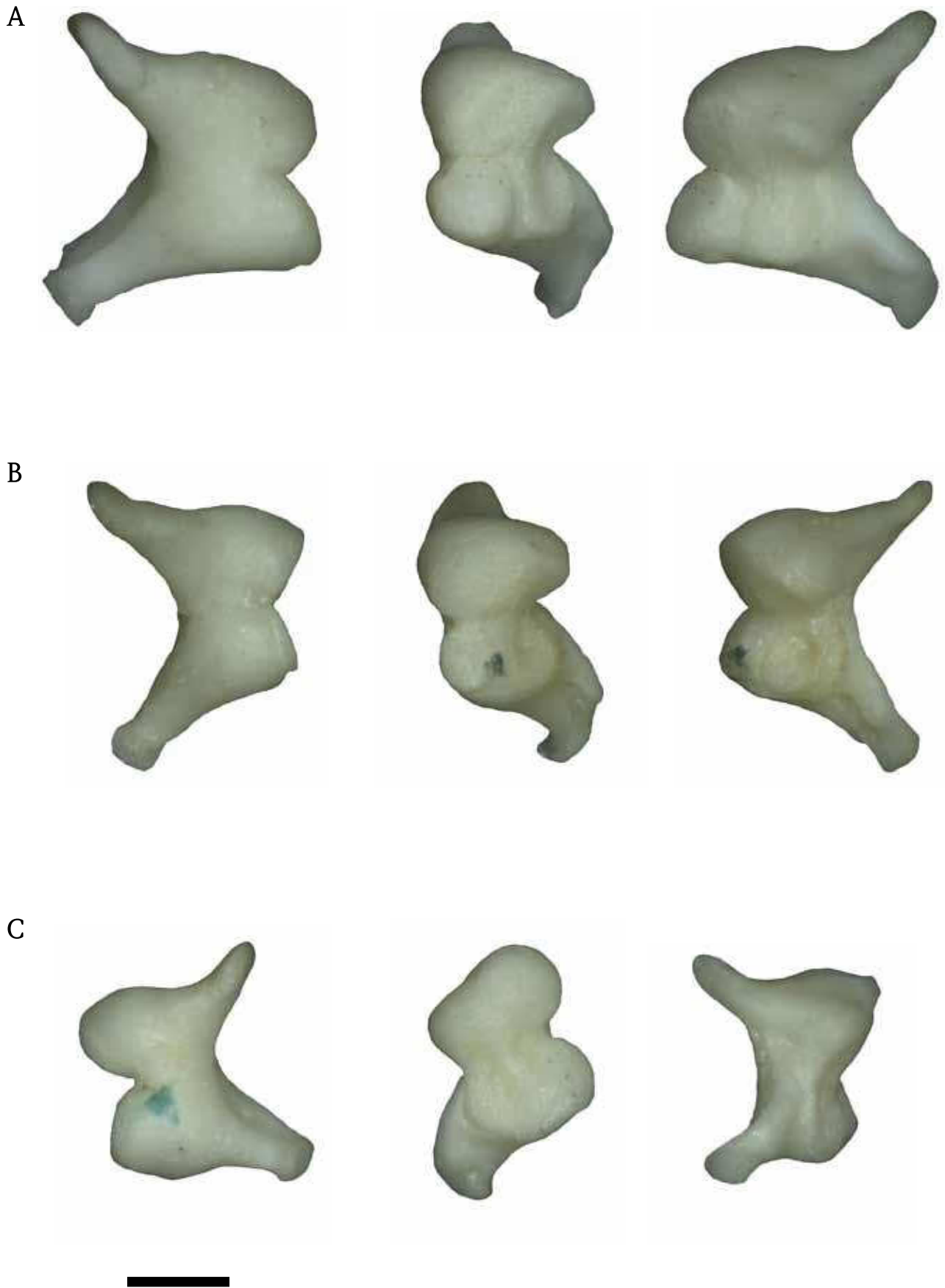
Fig. 11/6: Incus of select canid Carnivora in medial (left) and lateral (right) view, with view of the articulation facet for the malleo-incudal joint (middle). Bar equals 1 mm. **A**, NMW 1073, left incus of *Vulpes vulpes*; **B**, NMW 4007, left incus of *Vulpes lagopus*; **C**, NMW B4817, right incus of *Vulpes zerda*. Note that the morphological differences are greater in the fennec fox, *Vulpes zerda*.
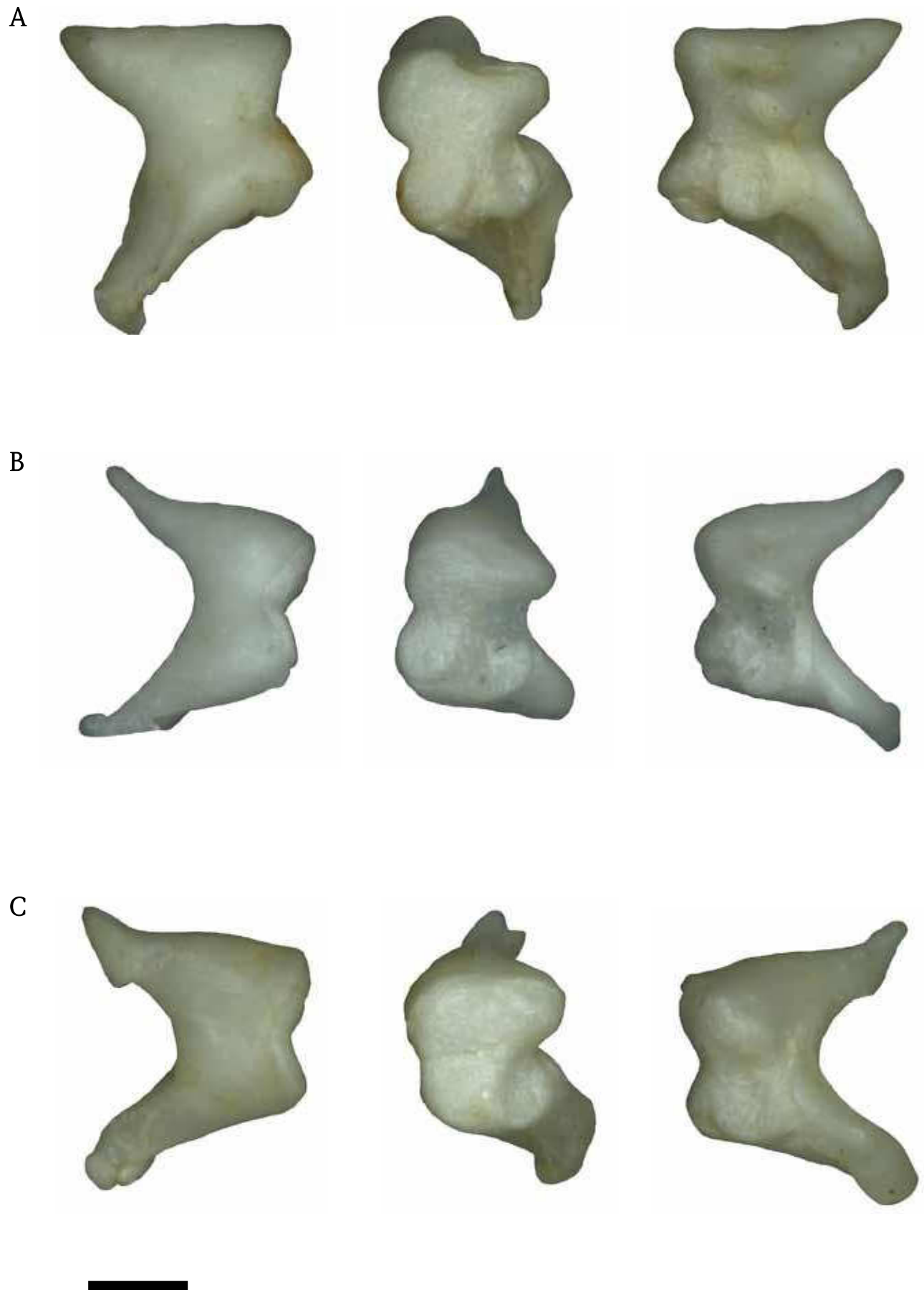
Fig. 11/ 7: Incus of select canid Carnivora in medial (left) and lateral (right) view, with view of the articulation facet for the malleo-incudal joint (middle). Bar equals 1 mm. **A**, NMW 1287, left incus of *Speothos venaticus*; **B**, NMW 2876, left incus of *Urocyon cinereoargenteus*; **C**, NMW 4254 B4719, left incus of *Cuon alpinus*.
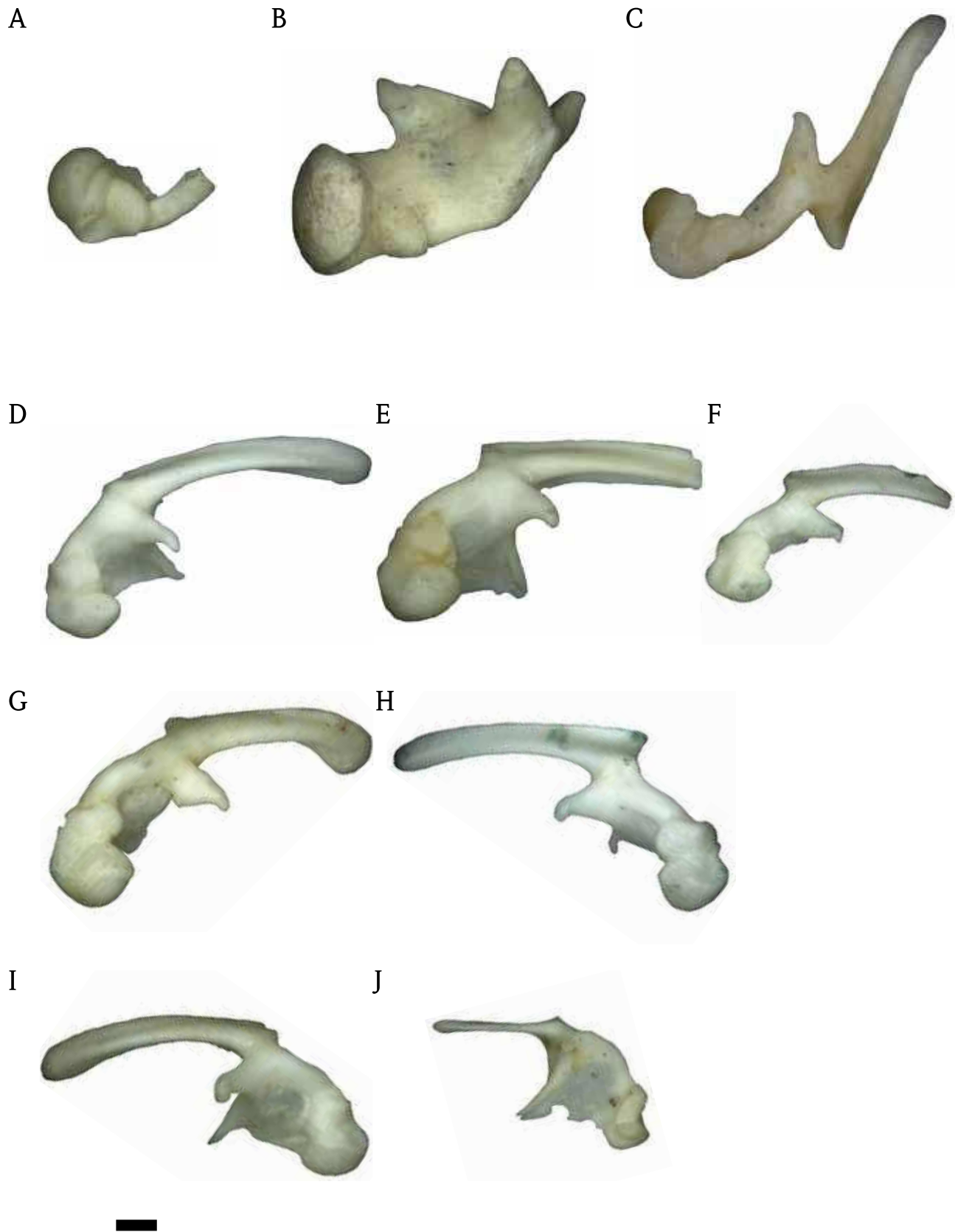
Fig. 11/ 8: Malleus of select Carnivora, lying on the anterior aspect, showing the articulation facet for the malleo-incudal joint. Bar equals 1 mm. **A**, IUPW 20731, *Felis catus*, left malleus; **B**, IUPW without number, *Crocuta crocuta*, right malleus; **C**, IUPW 2398, *Proteles cristatus*, left malleus; **D**, IUPW 1073, *Vulpes vulpes*, right malleus; **E**, IUPW 4007, *Vulpes lagopus*, right malleus; **F**, IUPW B4817, *Vulpes zerda*, right malleus; **G**, IUPW 1287, *Speothus venaticus*, right malleus; **H**, IUPW 2876, *Urocyon cinereoargenteus*, left malleus; **I**, IUPW 4254/B4719, *Cuon alpinus*, left malleus; **J**, IUPW 1164/B2097, *Nandinia binotata*, left malleus.
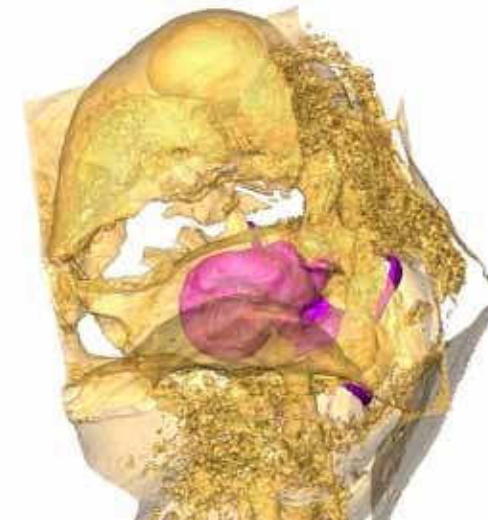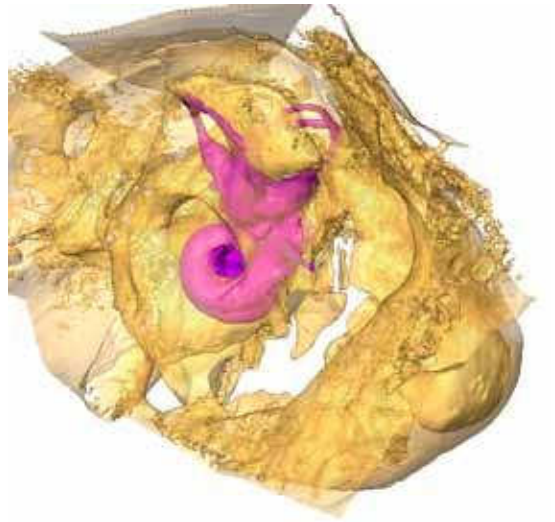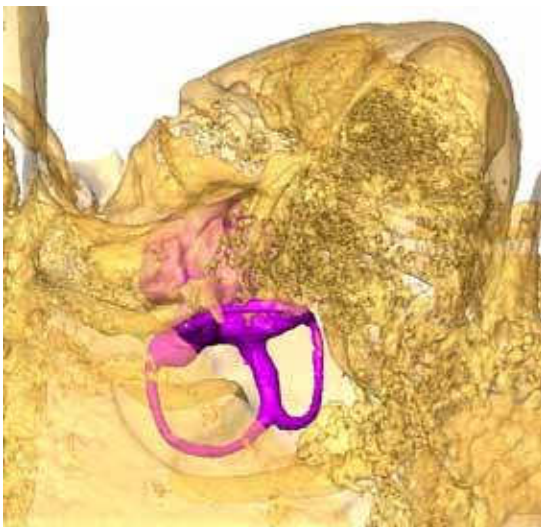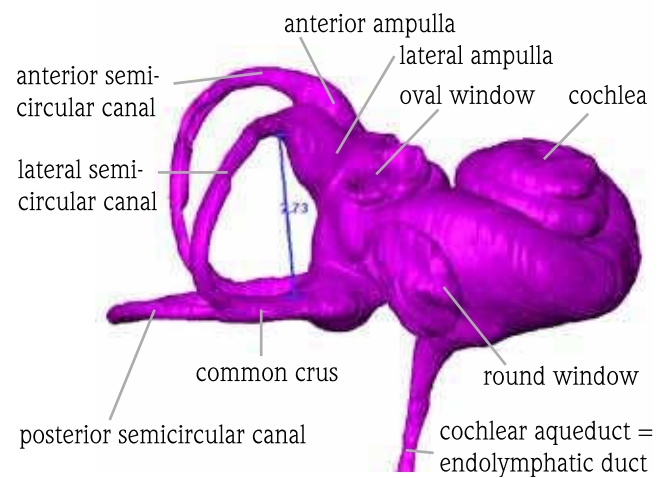
Fig. 11/9 : Reconstruction of the inner ear inside the bulla of *H. exiguus* (Qu 8594) from Quercy. A, bulla with cochlea in tilted ventral view; B, the same as A in ventral view; C, in internal view, note the semicircular ducts; D, inner ear with the petrosum in dorsal view, note the cochlear duct and the semicircular ducts; E, the same as D in tilted dorsal view; F, the inner ear itself with the example of a width measurement and the termini used in the text.
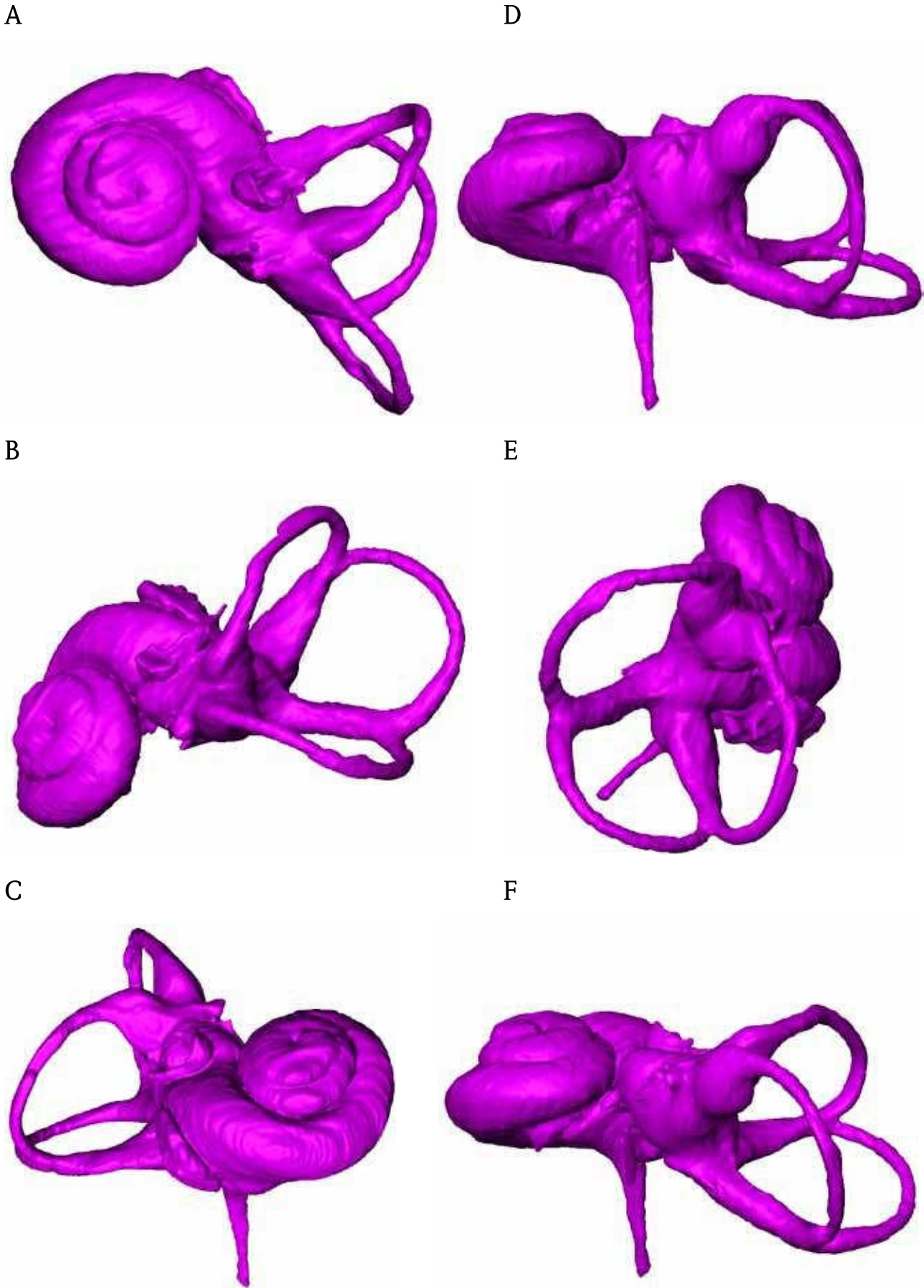
Fig. 11/10 : **A-F,** Reconstruction of the inner ear (cochlea and semicircular ducts) of *Hyaenodon exiguus* (Qu 8594) from Quercy in different views. Note the coiling of the cochlea and the widely expanding semicircular ducts.

Chapter 12

12. Summary

Hyaenodon is a genus with a wide temporal and geographic range (e.g. Tsubamoto et al., 2008). It was distributed over the whole Northern Hemisphere (Europe, North America and Asia) and present from the late Eocene to the early Miocene. Although Quercy is a fossil rich complex of fissure fillings, skeletal material is rare in Europe. Evidence is even sparser in Asia, concerning even dental material.

Due to the good fossil record in North America detailed descriptions were published early (e.g. Osborn and Wortman, 1894; Scott, 1895; Scott and Jepsen, 1936). A taxonomic revision including the paleoecology was performed by Mellett (1977) for the North American *Hyaenodon*. Morlo (1999) classified the European Eocene species of *Hyaenodon* as cursorial, as meat/bone consumer and depending on the species as belonging to the 10-30 or 30-100 kg body mass class. A detailed work as Mellett´s (1977) is missing for the European *Hyaenodon*, because Lange-Badré (1979) provided indeed a revision of the European species, but neither postcranial material was discussed, nor details on the ecomorphology were given.

This thesis focuses now on the topic of ecomorphology and should not be comprehended as revision of systematics, although taxonomical valuable information is discussed. The paleoecology of *Hyaenodon* is based herein on three main topics: diet, sensory capabilities and locomotion pattern with all relevant fields (e.g. ontogeny, brain morphology or hunting strategy).

12.1 Diet

Various authors remarked that *Hyaenodon* had ossiphagous tendencies (e.g. Mellett, 1977; Morlo 1999). Similar to the recent spotted hyena, its premolars show plateaus. Furthermore, *Hyaenodon* shows very extreme wear, with large slicing facets on the molars and an m1 worn down to its stumps (e.g. Mellett, 1977; Schlosser, 1887). The morphology of the teeth gives also significant clues: the molars are cutting blades — exclusively for cutting of meet; these carnassials were more numerous than in Carnivora and two in the upper jaw (M1-2) and even three in the lower jaw (m1-3) — thus *Hyaenodon* possessed a large slicing area. However, in most species all four premolars were present. Especially the third and the fourth premolar show the plateau-wear and leave no doubt that they were used. Summarizing, *Hyaenodon* was assumed to occupy the hyena-niche (Mellett, 1977).

This hypothesis was tested with two methods to gain additional information.
One method is the analysis of the ultrastructure of the enamel. The ultrastructure is the same in European (Chapter 8) as in the North American forms (Stefen, 1997b): the prisms are of (hexagonal)-polgygonal to polymorph shape, with nearly no prisms of rounded shape; the sheaths are frequently closed; crystallites within the prisms are oriented parallel to the axis of the prism; the interprismatic matrix surrounds the prisms in equal thickness; zigzag Hunter-Schreger-bands can be observed under the light microscope.
The change from undulating via the acute-angled type to the zigzag HSB is observed in various European and Asian species (pers. obs., Fig. 8/3 G). This is true for the North American taxa too (Stefen, 1997b), except for *Hyaenodon horridus* that shows exclusively zigzag HSB (Stefen, 1997b). I had not the possibility to observe HSB in the North American specimens and thus cannot confirm or refute this finding. However, there is no explanation for a different HSB-pattern in *Hyaenodon horridus*, it does not exhibit more wear than other species and appears also in the microwear pattern not more adapted to bone (see below).

The enamel thickness of a small European *Hyaenodon* was compared to the same tooth positions in a fox. The enamel of *Hyaenodon* is thicker in the milk tooth as well as in the permanent tooth.

The stereomicrowear results indicate that the genus occupied a broad dietary niche. In general, its pattern shows a high count of scratches, a high count of pits and gouges (an evidence for tough food on its own). Pits separate carnivorous mammals better (see Fig. 8/1 A-D). *Hyaenodon* overlaps with the spotted hyaena (meat/bone diet) and the lion (meat with a varying addition of bone). Interestingly, the European taxa plot more with the bone-cracker *Crocuta crocuta* and the North American taxa plot more with the lion. It should be noted, that within the North American forms it is *Hyaenodon crucians* overlapping with the spotted hyena and not *Hyaenodon horridus*, which stays in the morphospace of the lion. Interestingly, within the European forms *Hyaenodon exiguus* and *Hyaenodon rossignoli* plot nearest with the spotted hyena. Those species are small sized taxa. Additionally, brachyrhynch forms do not appear more ossiphagous than longirhynch forms.

For the first time the HSB pattern of European and Asian *Hyaenodon* species was examined, as well as the ultrastructure of the enamel of a European taxon. Furthermore, this study is the first that applies stereomicrowear to *Hyaenodon* from all continents. It revealed as well for the first time different dietary niches of taxa of different continents.

The ossiphagous tendencies of *Hyaenodon* can be confirmed: the heavy wear, the thicker enamel, the presence of zigzag HSB and the highly pitted microwear pattern indicate the procession of tough food. A surprising result is the slightly different niche of the North American compared to the European *Hyaenodon*. *Pterodon* disappears at the Eocene-Oligocene border from Europe and findings of *Entelodon* are rare in Europe. Concludingly, bone crackers were rarer in Europe than in North America and *Hyaenodon* could have been adapted more into that niche in Europe.

12.2 Sensory capabilities

Main points concerning this topic were the sense of hearing, the sense of touch and the brain.

Touch

The sense of touch was comparable to other Carnivora, except felids — judging the whiskers. Felids possess specialized whiskers to apply a killing bite (Turner and Antón, 1997). To supply these sensitive vibrissae, a large infraorbital foramen is essential (Turner and Antón, 1997).

For the first time this foramen was studied in *Hyaenodon*: it is relative small and comparable to that of canids. Thus, it is inferred herein, that the sense of touch was developed as in recent canids and not as excellent as in felids.

Brain and smell

The brain of *Hyaenodon* shows a small cerebellum with three folds on each side (e.g. Lange-Badré, 1979). The pyriform lobe is developed as a bulge (Lange-Badré, 1979) and is large. Its presence is an indication for good olfactory capabilities (Lawrence Witmer, pers. comm.). The olfactory bulbs are large in relation to the other parts of the brain. The characteristics of the *Hyaenodon* brain are: large olfactory bulbs, large pyriform lobe, low neocortex and a moderately folded neocortex are shared with the marsupial Tasmanian devil *Sarcophilus harrisii* and the giant anteater *Myrmecophaga tridactyla*. The simplicity of the ethmoturbinates and the smaller size of the olfactory compartment leaded Joeckel et al. (1997) to the contradicting conclusion of less acute olfactory capabilities in *Hyaenodon*. However, the soft tissue anatomy of the turbinate structure is unknown and the brain structure (relative size of the olfactory bulbs and the pyriform lobe) indicates that the sense of smell was relatively important in *Hyaenodon* (Lawrence Witmer, pers. comm.).

For the first time the brain of *Hyaenodon* was compared to a larger set of therian brains and combined with the available results on its olfactory capabilities. The shared features (large olfactory bulbs and a large pyriform lobe) with two therians of known well-developed olfactory capabilites, *Sarcophilus harrisii* and the *Myrmecophaga*

tridactyla, indicate a distinct sense of smell. This sense is judged herein as well-developed, especially regarding to its other senses.

Hearing

The reconstruction of the sense of hearing is based on examination of the bulla auditiva, the first known auditory ossicle (an incus) and the inner ear (cochlea and semicircular ducts). The bulla of *Hyaenodon* is rather small, bean-shaped and inflated, although not much. Alas, no hitherto known specimen is preserved with the ectotympanic — so the final state of the bulla remains unknown. However, the entotympanic is preserved in some North American and in one European specimen: it is chambered. A septum bullae is present, confirming Mellett (1977) and correcting Filhol (1883). This "septum" cannot be compared to the septum bullae of felids (build by ecto- and entotympanic; Hunt, 1987; Mickoleit, 2004). The canid septum is more comparable as it is made up exclusively by the caudal ectotympanic alone (Hunt, 1987; Mickoleit, 2004). The bulla is structurally the same in the North American and the European forms.

The cochlea of *Hyaenodon* points rostrally and not ventrolaterally as in the dog. The inner ear of *Hyaenodon* is on the other hand comparable to the dog: its cochlea makes three turns. The coiling of the cochlea is not correlated with frequency or intensity ranges (Webster, 1966).

For the first time an auditory ossicle of *Hyaenodon* is described: the incus. Its saddle-shaped facet is divided in a larger superior articulation surface and a smaller, lower and circular articulation surface. It is most similar to the incus of the cat. Due to the fact that the incus should be specific for each species (Holz, 1931). A comparative set (other species or hyaenodontids) would be ideal. Nevertheless, the incus also provides ecological signals. It is clear, that *Hyaenodon* was not adapted to low frequencies.

The first description of an *Hyaenodon* auditory ossicle could be given herein. Results concerning the hearing apparatus are: small, but bony bulla; bulla of entotympanic origin and chambered; cochlea makes three turns; small and delicate incus; incudo-mallear joint on the incus with rather simple articulation facets. Concluding from these structures of the hearing apparatus, *Hyaenodon* shows no adaptation to low frequencies. It most probably had a wide frequency range (as predators commonly do) and if the inference of the morphological similarity of the *Hyaenodon* incus to the incus of the cat is allowed, an adaptation to high frequencies is indicated.

Sight

The eye sockets were laterally positioned and the eye socket points of to the side ("Razorjaws", 2009). The consequence was, that there is only little overlap between the two visual fields. The depth perception was only in a small field right in the front of the snout and little binocular view ("Razorjaws", 2009). The vision also determined how *Hyaenodon* attacked its prey ("Razorjaws", 2009): it came up to the side of the prey animal and clamped down with its jaws. Thus, it is implied that sight was not the main sense for prey detection.

12.3 Skeleton and locomotion pattern including hunting behavior

Skeleton and Locomotion

The basis for inferences of the locomotion pattern and the predation style was the skeleton. European remains of the postcranial skeleton are rare and isolated. The problem of misidentifications should not be neglected. The head was compared to recent carnivorans proportionally oversized. Canine dogs possess a ligamentum nuchae to reduce energy loss of the neck muscles (Wang et al., 2008), as well as ungulates. It inserts in dogs on the epistropheus and in ungulates on the posterior aspect of the skull (Wang et al., 2008). The epistropheus in *Hyaenodon* shows no broadening of the caudal part of the neural spine. Thus, the nuchal ligament, if present in *Hyaenodon* (Mellett, 1977), did not insert on the epistropheus. It rather inserted on the posterior aspect of the skull as in ungulates.

No scapholunatum is present in European forms. This statement was based on a misidentification. Alas, up to now, no European specimen is preserved with the carpus of *Hyaenodon*. Concluding from the distal radial facet, it should have articulated with a scaphoid and a lunatum as in North American taxa.

There is no European specimen of a scapula. The North American forms show a rectangular outline of the corpus. The humerus shows a fossa anconeus, as well as an epicondylar foramen. The olecranon of the ulna is posteriorly inclined. The femur possesses a deep patellar groove with high marginal ridges and a laterally oriented fovea capitis. The tibial crest is well developed. The metapodials are closely adjoined. These features are all interpreted as cursorial features (Chapter 9; e.g. Andersson, 2003; Gunnell, 1998; Laborde, 1987; Taylor, 1974; Taylor 1989; Wang, 1993). The skeleton shows terrestrial features as well (e.g. spherical astragalar caput, short femoral neck, concave distal articulation surface on the radius, deep tibio-tarsal joint, narrow and deep femoral trochlea; e.g. Ginsburg, 1961; Laborde, 1987; see Chapter 9). The fibula shows large articulation facets and a semilunar shape of the distal articulation facet — this infers progression over uneven surface at high speeds (Barnett and Napier, 1953).

Summarizing, *Hyaenodon* was primarily dwelling on the ground and adapted to running and is in this sense cursorial. Mellett´s experiment ("Razorjaws", 2009) reminds that a strong musculature can speed up also a short-legged body. Especially the forelimb was powerful, most probable convenient to hold down prey.

For the first time the epistropheus was examined in detail to find the attachment site for the assumed ligamentum nuchae. It can now confidently be stated, that such a ligament could not have inserted on the epistropheus. The posterior aspect of the skull should bear an attachment site.

The finding that the European specimens of *Hyaenodon* scapholunata are misidentifications, is important. It can now be assumed that the European species also possessed an unfused scaphoid and lunatum as did the North American taxa.

Hunting behavior

The canines of *Hyaenodon* are mediolaterally compressed. Canids possess the same type of canines, in contrast to felids which have rounded canines (Van Valkenburgh, 1995). The mediolaterally compressed canines are ideal for slashing (Werdelin, 1996). Thus, *Hyaenodon* inflicted its prey with shallow wounds and not with a killing bite like recent felids do. Additional evidence comes from the non-specialized whiskers — they too infer that there was no precise killing bite. On the whole, the most important weapon was the head for *Hyaenodon* ("Razorjaws", 2009): a row of slicing teeth and a biting power of 270 kg (three times greater at the rear teeth — the carnassials — than at the canines). *Hyaenodon* "crushed" its prey. The presence of coprolithes with e.g. an incisor of a horse ("Razorjaws", 2009) shows that the whole carcass was consumed.

The predation style of *Hyaenodon* was ambushing, although it was not underlying in a chase with most contemporaneous prey animals ("Razorjaws,", 2009). Werdelin (1996) characterized the hunting behavior of "creodonts" as "ambush-and-slash": the prey was killed by slashing, inflicting it with shallow wounds. *Hyaenodon* was a powerful predator in the forests of the Eocene as well as in the more open landscape of the Oligocene.

12.4 Ontogeny and pathologies

Growth rates (measured on dental material) show that the growth from juvenile to adult was below 30% and in most cases around 15%. This shows, that small juveniles could not grow into significantly larger adults. It gave evidence that a juvenile figured in Lange-Badré (1979: Planche XX, Fig. 6) was misidentified as *Hyaenodon brachyrhynchus*.

For the first time a section of a milk canine of the North American *Hyaenodon horridus* was examined and four dental rings were counted. The tooth replacement is usually finished after half a year or latest after one year in

modern Carnivora (Miles and Grigson, 1990). Concluding from this observation and the assumption that one line per year is formed as in recent Carnivora (Spinage, 1976), the ontogeny of *Hyaenodon* would have lasted considerably longer.

The juvenile individuals of *Hyaenodon* start to process food early, namely during the tooth replacement. Wear facets and microwear patterns provide evidence: the dp4 in a European specimen (M4498) and the dp4 in a North American specimen (YPM-PU 136674) show microwear (pers. obs). However, it is also known from modern Carnivora, that they use their milk dentition (NMW 1275, *Crocuta crocuta* with P4 and p4 erupting, shows microwear on m1, pers. obs.). FAM 75725 (*Hyaenodon horridus*) shows that the dp4 shows the first wear facet buccally on the anterior accessory cusp. The successor, the p4, shows the first facet on the talonid (e.g. in AMNH 1009, *H. horridus*; YPM-PU 10010).

During its life *Hyaenodon* possessed teeth in perfect alignment (Mellett, 1977), which was a definite advantage even to modern Carnivora: the upper teeth rotated inward and the lower teeth rotated outwards. In this way, there was always a cutting edge available for slicing meat. This procedure resulted in senile individuals in extreme conditions, where the cutting edge is going across the roots (Mellett, 1977; "Razorjaws", 2009). Pathologies in *Hyaenodon* are known, but rare — as in modern wildstate Carnivora (Miles and Grigson, 1990). All known varieties of abnormalities observed in Carnivora like extra teeth, loss of teeth, anomalous tooth morphology, root variations and fractures have also been found in *Hyaenodon* too (Mellett, 1977). I could not find pathologies in the European material (rotated teeth (P3 or p2) are no pathology).

Tooth replacement is an important part of the ontogeny of a mammal. Especially concerning *Hyaenodon* the tooth replacement is an important topic: It was a major argument to place "creodonts" in Placentalia and not in Marsupialia (Filhol, 1876; Schlosser, 1887). The tooth eruption sequence of the lower jaw in *Hyaenodon* was discussed in Bastl (2008) and published in detail in Bastl et al. (2011). Herein, further juvenile material was studied and the tooth eruption sequence of the upper jaw was reconstructed as detailed as possible. Alas, juvenile upper jaws are even more rare than juvenile lower jaws. The difference in the tooth eruption sequence of the lower jaw (concerning the p3, the p4, the m3 and the canine) can be confirmed here and additional evidence is presented (Chapter 7). Interestingly, the tooth eruption sequence of the upper jaw shows only a minor difference (concerning the eruption of the P1) between the taxa from Europe and North America. However, the difference in the eruption of the upper teeth was noted for the first time.

The European *Hyaenodon* follows the pattern (Fig. 7/6):
M1+m1 – P1+p1 – m2 – I+I – P2+p2 – P4+c+p3+m3 – M2 – P3+p4 – C.
It is unclear why the canines of the upper jaw start their eruption later.

The North American *Hyaenodon* follows the pattern (Fig. 7/6):
M1+m2 – I+I – P2+p2 – P4+p4 – M2+m3 – P3+p3 – C+c.
It is unclear whether the p1 or the m1 erupts earlier in the North American forms.

The questions if these differences follow functional pressures cannot be answered. However, there is no obvious advantage of e.g. earlier/later erupted p4. If the lactation period was longer in the European or the North American *Hyaenodon* can only be speculated. The difference in the tooth eruption sequences is therefore seen as primarily phylogenetic signal indicating divergence.

The juvenile material yielded even further information: the milk dentition in European *Hyaenodon* shows interspecific different morphologies. Interestingly, the Oligocene species *Hyaenodon exiguus* and *filholi* show differences in the morphology of the upper milk teeth DP3 and DP4 (development of the anterior cusp and the cutting blade) and the lower milk teeth dp3 and dp4 (development of the anterior cuspid and the talonid). Compared with other known juvenile material from North America and Asia, the morphology of *Hyaenodon exiguus* (talonid with cuspids) appears to be a product of European evolution.

Salles (1992) and Guanfang and Schmidt-Kittler (1983) used milk teeth morphology as phylogenetic characters.

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North American (e.g. *Hyaenodon mustelinus* YPM PU 13674) taxa and Asian taxa (pers. obs.) show a dp4 with a cutting blade. The assumption that *Hyaenodon filholi* was an Asian immigrant (Lange-Badré, 1979) is emphasized here. Although, BiochroM´97 (1997) suggested, that *Hyaenodon exiguus* was an Asian immigrant too, the survival and evolution of an own European lineage is hypothesized here: not all Oligocene species in Europe must be of Asiatic origin.

For the first time an indication for an European Oligocene lineage was found: the different milk tooth morphologies evidence a not as close relationship between *Hyaenodon filholi* and *exiguus* as their permanent tooth morphology would propose. Therefore, not all Oligocene European *Hyaenodon* species should be regarded as Asian immigrants.

12.5 New taxonomic evidence

The species *Hyaenodon cayluxi* is now included in *Hyaenodon leptorhynchus*. The material attributed to *Hyaenodon cayluxi* was limited to a few specimens and consisted of exclusively lower jaws. Lange-Badré (1979) already proposed the designation *Hyaenodon* aff. *leptorhynchus*. Here it is proposed to take the next step and designate it as proper *Hyaenodon leptorhynchus*.
Divergence within the genus was found during this thesis. Some differences between the North American and the European *Hyaenodon* hitherto described in literature (Scott, 1895) turned out to be not valid, e.g. the presence of a scapholunatum in the European taxa (based on misidentifications). However, there are differences:

1) the tooth eruption sequence

2) the more plesiomorphic morphology of the M1 in North American forms

3) the root development (single- or double-rooted) of the p1

The tooth eruption pattern is a consistent difference between the European and the North American forms. The M1 of the North American taxa is more plesiomorphic as the fusion of the anterior cusps is not complete. This state is known in Eocene European *Hyaenodon* too, but most species show the modern fused state in the Oligocene. The root development is varying and does not give distinct clues: the oldest species shows a single-rooted p1 (Asian *H. yuanchensis*) and the Oligocene species in Europe possess a double-rooted p1. The skeleton of the European *Hyaenodon* shows differences between Eocene and Oligocene material (e.g. the tuberculum major on the femur and the distal radial articulation area), not between European and North American forms. The evolution of the North American *Hyaenodon* is acknowledged as an own lineage, following Mellett (1977).

For the first time an evolutionary change of postcranial material of *Hyaenodon* could be described. It is obvious in Eocene and Oligocene material from Europe on certain long bones (radius and femur).
The divergence within the genus is described here, but not used up to now for higher systematics awaiting the evaluation of the Asian taxa.

13. Acknowledgements

14. References

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Aitkin L. M. and B. M. Johnstone. Middle-ear function in a Monotreme: The echidna (*Tachyglossus aculeatus*). Journal of Experimental Zoology 180: 245-250.

Andersson, K. 2003. Aspects of locomotor evolution in the Carnivora (Mammalia). Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 877, Acta Universitatis Upsaliensis, Uppsala 2003: 20 pp.

Andersson K. 2004. Predicting carnivoran body mass from a weight-bearing joint. Journal of Zoology, London 262: 161-172.

Anson B. J. and T. H. Bast. 1959. Development of the incus of the human ear. Quarterly Bulletin of the NUM School 33: 110-119.

Argot C. 2010. Morphofunctional analysis of the postcranium of *Amphicyon major* (Mammalia, Carnivora, Amphicyonidae) from the Miocene of Sansan (Gers, France) compared to three extant carnivores: *Ursus arctos, Panthera leo,* and *Canis lupus*. Geodiversitas 32(1): 65-106.

Argyle E. C. and M. J. Mason. 2008. Middle ear structures of *Octodon degus* (Rodentia: Octodontidae), in comparison with those of subterreanean caviomorphs. Journal of Mammalogy 89(6): 1447-1455.

Asher R. J. and T. Lehmann. 2008. Dental eruption in afrotherian mammals. BioMed Central (BMC) Biology 6: 1-11.

Aulerich R. J. and D. R. Swindler. 1968. The dentition of the mink (*Mustela vison*). Journal of Mammalogy, 49: 488-494.

Barnet C. H. and J. R. Napier. 1953. The rotary mobility of the fibula in eutherian mammals. Journal of Anatomy 87: 11-21.

Bastl K. 2008. New information on the tooth eruption sequence in European *Hyaenodon*. Master thesis, University Vienna: 42 pp.

Bastl K., Morlo M., Nagel D. and E. Heizmann. 2011. Differences in the tooth eruption sequence in *Hyaenodon* („Creodonta", Mammalia) and implications for the systematics of the genus. Journal of Vertebrate Paleontology 31(1): 181-192.

Biknevicius A. R. and B. Van Valkenburgh. 1996. Design for Killing: Craniodental Adaptations of Predators, in: Carnivore behaviour, ecology and evolution, Gittleman, J. L. (ed.). Ithaca, New York: Cornell University Press, Vol 2: 393-428.

BiochroM´97 (1997): Synthèses et Tableaux de Corrélations. In: Aguilar J.-P., Legendre S., Michaux J. (eds.): Actes du Congrès BiochroM´97, Mémoires et Travaux de l´institute, École Pratique des Hautes Études 21: 769-805.

Blainville, H. M. D. De. 1841-1842. Ostéographie ou description iconographique compare du squelette et du sytéme dentaire des mammiféres récents et fossils. Tome 2: Secondates et Suburus. 123 pp. (Viverras) in Baillère (ed.), Paris, 100 pp., atlas, and 117 pl.

Bodingbauer J. 1949. Die Staupe-Schmelzhypoplasien (Staupegebiss) des Hundes. Schweizer Archiv für Tierheilkunde, 91: 84-116.

Bondy G. 1907. Beiträge zur vergleichenden Anatomie des Gehörorgans der Säuger. (Tympanicum, Membrana Shrapnelli und Chordaverlauf). Anatomische Hefte, 1. Abteilung, 106. Heft (35. Band, Heft 2): 295-408.

Bonis L. De. 1964. Étude de quelques mammifères du Ludien de la Débruge (Vaucluse). Annales de Paléontologie (Vertébrés), 50(2): 121-154.

Botti M., Secci F., Ragionieri L., Dessole A. A. and F. Acone. Auditory ossicles in the ruminants: comparative morphological analysis with the analogues formations of horse. Ann. Fac. Medic. Vet. di Parma, Vol. XXVI: 91-96.

Bouetel V. and C. de Muizon. 2006. The anatomy and relationships of *Piscobalaena nana* (Cetacea, Mysticeti), a Cetotheriidae s.s. from the early Pliocene of Peru. Geodiversitas 28(2): 319-395.

Breuer, R. 1932. Ein seltener Fall von Selbsthilfe der Natur. Zeitschrift für Stomatologie, 30: 334-343.

Bruns V., Burda H. and M. J. Ryan. 1989. Ear morphology of the frog-eating bat (*Trachops cirrhosus*, Family: Phyllostomidae): Apparent Specialisations for Low-Requency Hearing. Journal of Morphology 199: 103-118.

Burda H., Bruns V. and G. C. Hickman. 1992. The ear in subterranean Insectivora and Rodentia in comparison with ground-dwelling representatives. I. Sound conducting system of the middle ear. Journal of Morphology 214: 49-61.

Carbone C., Mace G. M., Roberts S. C. and D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402: 286-288.

Cohen J. E., Pimm S. L., Yodzis P. and J. Saldana. 1993. Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology 62: 67-78.

Cole L. K. 2009. Anatomy and physiology of the canine ear. Veterinary Dermatology 20: 412-421.

Coleman M. N. and M. W. Colbert. 2010. Correlations between auditory structures and hearing sensitivity in non-human primates. Journal of Morphology 271: 511-532.

Coleman M. N. and C. F. Ross. 2004. Primated auditory diversity and its influence on hearing performance. The anatmical record Part A 281A: 1123-1137.

Dashzeveg D. 1964. On two Oligocene Hyaenodontidae from Erghilyin-Dzo (Mongolian People´s Republic). Acta Paleontologica Polonica 9: 263-274.

Dashzeveg D. 1985. Nouveaux Hyaenodontidae (Creodonta, Mammalia) du Paleogéne de Mongolie. Annales de Paleontologie (Vert.-Invert.), 71 (4): 223-256.

Dayan, T. and D. Simberloff. 1996. Patterns of size seperation in carnivore communities. In Carnivore behaviour, ecology, and evolution, Vol. 2: 243-266. Gittleman, J. L. (ed.) Ithaca: Cornell University Press.

Denison R. 1938. The broad-skulled Pseudocreodi. Annals of the New York Academy of Sciences, 37: 163-257.

Dewar, E.W. 2004. Microwear of carnivorous mammals described with low-magnification dental stereomicroscopy. Journal of Vertebrate Paleontology 24(3): 52A.

Diaz J. I. 2002. Differential scaling of locomotor performance in small and large terrestrial mammals. The Journal of Experimental Biology 205: 2897-2908.

Douglass, E. 1901. Fossil Mammalia of the White River beds of Montana. Transactions of the American Philosophical Society, NS 20: 237-278.

Dujardin F. 1840. Note sur un tete fossile d´Hyaenodon trouvée au bord du Tarn, prés du Rabastens. Comptes rendus de l´Academie des Sciences de Paris, 10(4): 134-135.

Egi N. 2001. Body mass estimates in extinct mammals from limb bone dimensions: the case of North American hyaendontids. Paleontology 44(3): 497-528.

Egi N., P. A. Holroyd, T. Tsubamoto, A. N. Soe, M. Takai and R. L. Ciochon. 2005. Proviverrine Hyaenodontids (Creodonta: Mammalia) from the Eocene of Myaenmar and a phylogenetic analysis of the Proviverrines from the Para-Tethys Area. Journal of Systematic Paleontology 3 (4): 337-358.

Egi N., Tsubamoto T. and M. Takai. 2007. Systematic status of Asian "*Pterodon*" and early evolution of hyaenaelurine hyaenodontid creodonts. Journal of Paleontology 81: 4770-4778.

Eklund C. M., Hadlow W. J., Kennedy R. C., Boyle C. C. and T. A. Jackson. 1968. Aleutian disease of mink: properties of the etiologic agent and the host responses. Journal of Infectious Disease, 118: 510-526.

Eom K., Kwak H., Kang H., Park S., Lee H., Kang H., Kwon J., Kim I., Kim N. and K. Lee. 2008. Virtual CT otoscopy of the middle ear and ossicles in dogs. Veterinary Radiology and Ultrasound 49(6): 545-550.

Fabian H. 1933. Merkmale und Grenzen in Domestikationsfrage am Gebiss. Deutsche Zahnheilkunde, 84: 1-99.

Fancy S. G. 1980. Preparation of mammalian teeth for age determination by cementum layers: a review. Wildlife Society Bulletin 8(3): 242-248.

Filhol H. 1873. Sur les Vertebrés fossils trouvés dans les dépôts de phosphate de chaux du Quercy. Bulletin de Sciences de la Société Philomatique de Paris 10: 85-89.

Filhol H. 1882. Mémoires sur quelques Mammiféres Fossiles. Toulouse, Imprimerie Vialelle et Cie 1882, Serie 4: 9-24.

Filhol, H. 1883. Description de la base du crane des Hyaenodon. Bull. Soc. philo. Paris, 1882-1883, 7(7): 96-98.

Filhol H. 1876. Recherches sur les phosphorites du Quercy. Étude des fossiles qu´on y rencontre et specialement des Mammiféres. – Annales sciénces géologiques, Paris, G. Masson, 7(7): 1-561.

Fleischer G. 1973. Studien am Skelett des Gehörorgans der Säugetiere einschließlich des Menschen. Säugetierkundliche Mitteilungen 21: 131-239.

Fleischer G. 1978. Evolutionary principles of the mammalian middle ear. Advances in Anatomy, Embryology and Cell Biology 55(5): 7-69.

Forster Cooper C. 1926. *Hyaenodon aimi* sp. n. from the Headon beds at Hordle. Annals and Magazine of Natural History, London 18: 370-373.

Fostowicz-Frelik L. 2007. The hind limb skeleton and cursorial adaptation of the Plio-Pleistocene rabbit *Hypolagus beremendensis*. Acta Palaeontologica Polonica 52(3): 447-476.

Gaudry A. 1878. Les enchainements du monde animal dans les temps géologiques. Mammiféres tertiaires. Paris, Librairie F. Savy: 1-28.

Gray A. A. 1907. The labyrinth of animals – including mammals, birds, reptiles and amphibians. J. and A. Churchill (eds.), London.

Gebo D. L. and K. D. Rose. 1993. Skeletal morphology and locomotor adaptation in *Prolimnocyon atavus*. An early eocene hyaenodontid creodont. Journal of Vertebrate Paleontology 13(1): 125-144.

Gervais P. 1848-1852. Zoologie et paleontologie francaises (animaux vertébrés) òu nouvelles recherches sur les animaux vivantes et fossils de la France. 146 pp. (Tome I), 146 pp. (Tome II) in Arthus Bertrand (ed.), Paris.

Gervais P. 1870. Memoires sur les formes cérébrales propres aux carnivores vivants et fossiles. Nouv. Arch. Mus. D´Hist. Nat. Paris. 6: 103-162.

Gervais P. 1873. Mammifère don't les ossements accompagnent les dépôts de chaux phosphate des départements du Tarn-et-Garonne et du Lot. Journal de Zoologie (Paris) 2: 356-380.

Getty R. 1964. The ear. In: Anatomy of the Dog. M. Miller, G. C. Christensen and H. E. Evans (eds.), W. B. Saunders Company, USA: 847-863.

Gheerbrant E. 1990. On the early biogeographical history of the African placentals. Historical Biology 4: 107-116.

Gheerbrant E., Iarochene M., Amaghzaz M. and B. Bouya. 2006. Early African hyaenodontid mammals and their bearing on the origin of the Creodonta. Geological Magazine 143(4): 475-489.

Giannini N. P., Wible J. R. and N. B. Simmons. 2006. On the cranial osteology of Chiroptera. I. *Pteropus* (Megachiroptera: Pteropodidae). Bulletin of the American Museum of Natural History, New York, 295: 1-134.

Gingerich P. D. 1980. *Tytthaena parrisi*, oldest known oxyaenid (Mammalia, Creodonta) from the Late Paleocene of Western North America. Journal of Paleontology 54(3): 570-576.

Gingerich P. D. and H. A. Deutsch. 1989. Systematics and evolution of Early Eocene Hyaenodontidae (Mammalia, Creodonta) in the Clarks Fork Basin, Wyoming. Contributions from the Museum of Paleontology, the University of Michigan 27(13): 327-391.

Ginsburg L. 1961. Plantigradie et digitigradie chez les carnivores fissipedes. Mammalia 25: 1-21.

Ginsburg L. 1999. Order Creodonta. In: Rössner G. E. and K. Heissig (eds.): The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München: 105-108.

Gittleman J. L. 1986. Carnivore brain size, behavioural ecology and phylogeny. Journal of Mammalogy 67: 23-36.

Glass G. E. and N. B. Todd. 1977. Quasi-continuous variation of the second upper premolar in *Felis bengalensis* Kerr 1792 and its significance for some fossil lynxes. Zeitschrift für Säugetierkunde, 42: 36-44.

Graf M., Grundbacher B., Gschwendtner J. and P. Lüps. 1976. Grössen- und Lagevariation des zweiten Prämolaren bei der Hauskatze *Felis sylvestris* f. *catus*. Revue Suisse de Zoologie, 83: 952-956.

Granger W. 1938. A giant oxyaenid from the upper Eocene of Mongolia. American Museum Novitates 969: 1-5.

Gray J. 1968. Animal Locomotion. Norton, New York: 479pp.

Gromova V. 1952. [On primitive carnivores of the Paleogene of Mongolia and Kazakhstan]. Trudy Paleontologichesksogo Instituta, Akademiya Nauk SSSR (= Transactions of the Palaeontological Institute, Academy of Sciences of the USSR) 41: 151-177. [Russian]

Godfrey, L. R., Semprebon, G. M., Jungers, W. L., Sutherland, M. R., Simons, E. L. and N. Solounias. 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. Journal of Human evolution 47: 145-169.

Goillot C., Blondel C. and S. Peigné. 2009. Relationships between dental microwear and diet in Carnivora (Mammalia) – Implications for the reconstruction of the diet of extinct taxa. Palaeogeography, Palaeoclimatology, Palaeoecology 271: 13-23.

Green J. L., Semprebon G. M. and N. Solounias. 2005. Reconstructing the palaeodiet of Florida Mammut americanum via low-magnification stereomicroscopy. Palaeogeography, Palaeoclimatology, Palaeoecology 223: 34-48.

Guanfang C. and N. Schmidt-Kittler. 1983. The deciduous dentition of *Percrocuta* Kretzoi and the diphyletic origin of the hyaenas (Carnivora, Mammalia). Paläontologische Zeitschrift 57: 159-169.

Gulya A. J. 2007. Gulya´s and Schuhknecht´s Anatomy of the temporal bone with surgical implications. Informa Healthcare USA, New York, Third edition: 1-356.

Gunnell G. F. and P. D. Gingerich. 1991. Systematics and evolution of late Paleocene and early Eocene Oxyaenidae (Mammalia, Creodonta) in the Clarks Fork Basin, Wyoming. Contributions from the Museum of Paleontology, the University of Michigan 28(7): 141-180.

Gunnell G. F. 1998. Creodonta. in: Evolution of tertiary mammals of North America – Volume 1: Terrestrial Carnivores, Ungulates, and ungulatelike mammals. In Janis C. J., Scott K. M. and L. L. Jacobs (eds.). Cambridge University Press: 91-109.

Gustafson E. P. 1986. Carnivorous mammals of the late Eocene and early Oligocene of Trans Pecos Texas. Texas Memorial Museum Bulletin 33: 1-66.

Habermehl K. H. 1975. Die Altersbestimmung bei Haus- und Labortieren. Paul Parey, Berlin und Hamburg: 1-216.

Habersetzer J. and G. Storch. 1992. Cochlea size in extant Chiroptera and middle Eocene microchiropterans from Messel. Naturwissenschaften 79(10): 462-466.

Hall E. R. 1940. Supernumerary and missing teeth in wild mammals of the orders Insectivora and Carnivora, with some notes on disease. Journal of Dental Research, 19: 103-143.

Hancox M. 1988. Dental anomalies in the Eurasian badger. Journal of Zoology, London, 216: 606-608.

Handschin E. 1944. Insekten aus den Phosphoriten des Quercy. Schweizerische Paläontologische Abhandlungen, Band 64: 1-23.

Heffner H. E. 1983. Hearing in Large and Small Dogs: Absolute Threshold and size of the tympanic membrane. Behavioural Neuroscience 97: 310-318.

Heinrich R. E. and A. R. Biknevicius. 1998. Skeletal allometry and interlimb scaling patterns in mustelid carnivorans. Journal of Morphology 235: 121-134.

Heinrich R. E. and K. D. Rose. 1997. Postcranial morphology and locomotor behaviour of two early Eocene miacoid carnivorans, Vulpavus and Didymictis. Paleontology 40(2): 279-305.

Helbing H. 1926. Über ein Tibiafragment (*Hyaenodon*) aus dem Oliogcaen von Belfort. Eclogae geologica Helvetica 19(3): 763-768.

Helbing H. 1928. Carnivoren des oberen Stampien. Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft, 47: 1-83.

Hellström S., Salén B. and L.-E. Stenfors. 1982. Anatomy of the Rat Middle Ear. Acta anatomica 112: 346-352.

Hemilä S., Nummela S. and T. Reuter. 1995. What middle ear parameters tell about impedance matching and high frequency hearing. Hearing Research 85: 31-44.

Holroyd P. A. 1999. New Pterodontinae (Creodonta: Hyaenodontidae) from the late Eocene-early Oligocene Jebel Quatrani Formation, Fayum Province, Egypt. PaleoBios 19(2): 1-18.

Holz K. 1931. Vergleichende anatomische und topographische Studien über das Mittelohr der Säugetiere. Zeitschrift für die gesamte Anatomie I. Abt, Bd. 4: 757-791.

Hopwood A. T. 1947. Contributions to the study of some African mammals. III: Adaptation in the bones of the fore limb in the lion, leopard and cheetah. Zoological Journal of the Linnean Society 41: 259-271.

Huang G. T., Rosowski J: J., Flandermeyer D. T., Lynch III T. J. and W. T. Peake. 1997. The middle ear of a lion: Comparison of structure and function to domestic cat. Journal of the Acoustical Society of America 101(3): 1532-1549.

Huang G. T., Rosowski J. J., Ravicz M. E. and W. T. Peake. 2002. Mammalian ear specializations in arid habitats: structural and functional evidence from sand cat (*Felis margarita*). Journal of Comparative Physiology A, 188: 663-681.

Huang X.-S. and B.-C. Zhu. 2002. Creodont (Mammalia) remains from the Early Oligocene of Ulantatal, Nei Mongol. Vertebrata Palasiatica 40: 17-22.

Hunt R. M. Jr. 1987. Evolution of the aeluroid Carnivora: significance of auditory structure in the nimravid cat *Dinictis*. American Museum Novitates 2886: 1-74.

Hunt R. M. Jr. 1991. Evolution of the aeluroid Carnivora: viverrid affinities of the Miocene carnivoran *Herpestides*. American Musem Novitates 3023: 1-34.

Hunt R. M. Jr. and R. H. Tedford. 1993. Phylogenetic relationships within the aeluroid Carnivora and implications of their temporal and geographic distribution. Chapter 5 in: Mammal Phylogeny: placentals. F. S. Szalay, M. J. Novacek and M. C. McKenna (eds.), Springer, New York: 53-73.

Ivanoff D. V. 2000. Origin of the septum in the canid auditory bulla: Evidence from morphogenesis. Acta Theriologica 45(2): 253-270.

Janis C. M. and P. B. Wilhelm. 1993. Were there mammalian pursuit predators in the Tertiary? Dances with wolf avatars. Journal of Mammalian Evolution 1: 103-25.

Joeckel R. M., Bond H. W. and G. W. Kabalka. 1997. Internal anatomy of the snout and parnasal sinuses of *Hyaenodon* (Mammalia, Creodonta). Journal of Vertebrate Paleontology 17(2): 440-446.

Joeckel R. M., Peigné S., Skolnick R. I. and R. M. Hunt Jr. 2002. The auditory region and nasal cavity of Oligocene Nimravidae (Mammalia: Carnivora). Journal of Vertebrate Paleontology 22: 830-847.

Jones M. 2003. Convergence in ecomorphology and guild structure amoung marsupial and placental carnivores. In: Predators with pouches, Jones M., Dickman C. and M. Archer (eds.), Collingwoog, Australia, CSIRO Publishing: 285-296.

Klatt B. 1921. Mendelismus, Domestikation and Kraniologie. Archiv für Anthropologie, neue Folge, 18, Heft 3 und 4: 225-250.

Klinghardt, F. 1934. Gehirnrelief- und Schädelstudien über Hyaenodon und Dinictis. Zeitschrift für Säugetierkunde (9): 76-86.

Koenigswald, W. and W. A. Clemens. 1992. Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. Scanning Microscopy 6(1): 195-218.

Koenigswald, W. v. 1992. Tooth enamel of the cave bear (Ursus spelaeus) and the relationship between diet and enamel structure. Acta Zoologica Fennica 28: 217-227.

Kurtén B. 1963. Return of a lost structure in the evolution of a felid dentition. Societas Scientarum Fennica Commentationes Biologicae, 26, part 4: 1-12.

Kvam T. 1985. Supernumerary teeth in the European lynx, *Lynx lynx lynx*, and their evolutionary significance. Journal of Zoology, London, 206: 17-22.

Laborde C. 1987. Caractéres d´adaption des membres au mode de vie aboricole chez Cryptoprocta ferox par comparaison d´autres Carnivores Viverridés. Annales des Sciences Naturelles, Zoologie, Série 13(8): 25-39.

Laizier L. and J. de Parieu. 1838. Description et determination d´une machoire fossile appurtenant à un mammifère jusqu´à present inconnu, *Hyaenodon leptorhynchus*. Comptes-rendus hebdomadaires des séances de l´Academie des Sciences, Paris 7:442.

Lange-Badré B. 1979. Les Créodontes (Mammalia) d´Europe occidentale de l´Éocéne supérieur à l´Oligocéne supérieur. Mémoires du muséum national d´histoire naturelle, Série C, Sciences de la terre, Tome XLII: 1-249.

Lange-Badré B. and D. Dashzeveg. 1989. On some Oligocene carnivorous mammals from Central Asia. Acta Palaeontologica Polonica 34 : 125-148.

Lange-Badré B. and M. Böhme. 2005. *Apterodon intermedius*, sp. nov., a new European Creodont Mammal from MP22 of Espenhain (Germany). Annales de Paléontologie 91: 311-328.

Lange S., Stalleicken J. and H. Burda. 2004. Functional morphology of the ear in fossorial rodents, *Microtus arvalis* and *Arvicola terrestris*. Journal of Morphology 262: 770-779.

Lange S., Burda H., Bennett N. C. and P. Nemec. 2005. Middle ear ossicles as a diagnostic trait in African mole-rats (Rodentia: Bathyergidae). African Biodiversity, Molecules, Organisms, Ecosystems, Springer Science and Business Media: 329-337.

Lannigan F. J., Higgins P. O., Oxnard C. E. and P. McPhie. 1995. Age-related resorption in the normal incus: a case of maladaptive remodelling? Journal of Anatomy 186: 651-655.

Lavrov A. V. and R. J. Emry. 1998. *Hyaenodon venturae* (Hyaenodontidae, Creodonta, Mammalia) from the early Chadronian (latest Eocene) of Wyoming. Journal of Paleontology 72(4): 752-757.

Lavrov A. V. 1999. New Material on the Hyaenodontidae (Mammalia, Creodonta) from the Ergiliyn Dzo Formation (Late Eocene of Mongolia) and Some Notes on the System of the Hyaenodontidae. Paleontological Journal 33(3): 321-329.

Lay D. M. 1972. The anatomy, physiology, functional significance and evolution of specialized hearing organs of gerbiline rodents. Journal of Morphology 138: 41-120.

Leidy J. 1853. Remarks on a collection of fossil Mammalia from Nebraska. Proceedings of the Academy of Natural Sciences Philadelphia 6: 392-394.

Legendre S., Sigé B., Astruc J. G., De Bonis L., Crochet J.-Y., Denys C., Godinot M., Hartenberger J.-L., Lévèque F., Marandat B., Mourer-Chauviré C., Rage J.-C., Remy J. A., Sudre J., Vianey-Liaud M. 1997. Les phosphorites du Quercy: 30 ans de recherche. Bilan et prespectives. Géobios MS 20: 331-345.

Lewis M. E. and M. Morlo. 2010. Creodonta. In : Cenozoic mammals of Africa. Werdelin L. and W. J. Sanders (eds.), University of California Press: 543-560.

Loughlin T. R. 1982. Functional adaptation of eruption sequence in pinniped postcanine teeth. Journal of Mammalogy, 63: 523-525.

Lüps P. 1980. Vergleichende Untersuchung am zweiten oberen Vorbackenzahn P^2 der Hauskatze *Felis sylvestris* f. *catus*. Zeitschrift für Säugetierkunde, 45: 245-249.

Lydekker R. 1885. Catalogue of the fossil Mammalia in the British Museum (Natural History). Part I Primates, Chiroptera, Insectivora, Carnivora and Rodentia. British Museum, London: 20-41.

Lyras G. 2009. The evolution of the brain in Canidae (Mammalia: Carnivora). Scripta Geologica 139: 1-93.

Macdonald J. R. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bulletin of the Los Angeles City Museum 8: 1-82.

MacLeod N. and K. D. Rose. 1993. Inferring locomotor behaviour in Paleogene mammals via Eigenshape analysis. American Journal of Sciences 293-A: 300-355.

Maitre E., Escarguel G. and B. Sigé. 2006a. Amphilemuridae (Lipotyphla, Mammalia) éocènes d´Europe occidentale: nouvelles données taxonomiques. Palevol 5(2006): 813-820.

Maitre E., Hugueney M., Astruc J. G., Crochet J.-Y., Escarguel G., Godinot M., Legendre S., Marandat B., Mourer-Chauviré C., Rage J.-C., Rémy J. A., Simon-Coinçon R., Sudre J., Valette P. and B. Sigé. 2006b. Huit nouvelles faunes éocènes et oligocènes des phosphorites du Quercy. Strata Série 1, Vol. 13: 113-127.

Marandat B., Mourer-Chauviré C., Rage J.-C., Rémy J. A., Simon-Coinçon R., Sudre J., Valette P. and B. Sigé. 2006b. Huit nouvelles faunes éocènes et oligocènes des phosphorites du Quercy. Strata Série 1, Vol. 13: 113-127.

Marandat B., Crochet J.-Y., Godinot M., Hartenberger J.-L., Legendre S., Remy J. A., Sigé B., Sudre J. and M.Vianey-Liaud. 1993. Une nouvelle faune à mammiféres d´âge éocène moyen (Lutétien supérieur) dans les phosphorites du Quercy. Geobios 26 (5): 617-623.

Marshall W. H. 1952. Note on missing teeth in *Martes americana*. Journal of Mammalogy, 33: 116-117.

Martin R. 1906. Revision der obereocaenen und unteroligecaenen Creodonten Europas. Revue suisse de Zoologie 14(3): 405-600.

Martinez I., Rosa M., Arsuaga J.-L., Jarabo P., Quam R., Lorenzo C., Gracia A., Carretero J.-M., Bermúdez de Castro J.-M. and E. Carbonell. 2004. Auditory capacities in middle Pleistocene humans from the Sierra de Atapuerca in Spain. PNAS 101(27): 9976-9981.

Masali M. 1964. Dati sulla variabilitá morfometrica e ponderale degli ossicini dell´udito nell´Uomo. Archivio Italiano di Anatomia e di Embriologia 69: 435-446.

Mason M. J., Lai F. W. S., Li J.-G. and E. Nevo. 2010. Middle ear structure and bone conduction in *Spalax*, *Eospalax,* and *Tachyoryctes* mole-rats (Rodentia: Spalacidae). Journal of Morphology 271: 462-472.

Matthew W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Memoirs of the American Museum of Natural History 9: 289-567.

Matthew W. D. andW. Granger. 1924. New Carnivora from the Tertiary of Mongolia. American Museum Novitates 104: 1-9.

Matthew W. D. and W. Granger. 1925a. New Creodonts and rodents from the Ardyn Obo formation of Mongolia. American Museum Novitates 193: 1-7.

Matthew W. D. and W. Granger. 1925b. New mammals from the Shara Murun Eocene of Mongolia. American Museum Novitates 196: 1-11.

Matthew W. D. and W. Granger1925c. New mammals from the Irdin Manha Eocene of Mongolia. American Museum Novitates 198: 1-10.

McKenna M. C. 1975. Toward a phylogenetic classification of the Mammalia. In: Phylogeny of Primates, W. P. Luckett and F. S. Szalay (eds.), Academic Press, New York: 21-46.

Mellanby M. 1929. Diet and the Teeth: An Experimental Study. Part I. Dental Structure in Dogs. Medical Research Council, Special Report Series, No. 140, His Majesty's Stationary Office, London, 308pp.

Mellett J. S. 1977. Paleobiology of North American Hyaenodon (Mammalia, Creodonta). Contributions to Vertebrate Evolution, 1: 1-133.

Meng J., Wu W.-Y., Ye J. and S.-D. Bi. 2001. Two petrosals of gliriform mammals from late Oligocene of Tieersihabahe, Xinjiang Uygur autonomous region, China. Vertebrate PalAsiatica: 43-53.

Merceron G., Viriot L. and C. Blondel. 2004. Tooth microwear pattern in roe deer (*Capreolus capreolus*, L.) from Chizé (Western France) and relation to food composition. Small Ruminant Research 53(1): 125-132.

Mickoleit G. 2004. Phylogenetische Systematik der Wirbeltiere. Verlag Dr. Friedrich Pfeil, München: 1-671.

Miles A. E. W. and C. Grigson. 1990. Colyer's Variations and diseases of the teeth of animals. – Cambridge University Press: 62-100; 238-281; 339-342; 371-402; 444-448; 476-479; 511-512; 543-546.

Moggi-Cecchi J. and M. Collard. 2002. A fossil stapes from Sterkfontein, South Africa, and the hearing capabilities of early hominids. Journal of Human Evolution 42: 259-265.

Morales J., Pickford M. and D. Soria. 1998. A new creodont *Metapterodon stromeri* nov. sp. (Hyaenodontidae, Mammalia) from the Early Miocene of Langental (Sperrgebiet, Namibia). Comptes Rendus de l'Academie des Sciences de Paris 327: 633-638.

Morlo M. 1999. Niche structure and evolution in creodont (Mammalia) faunas of the European and North American Eocene. Geobios 32(2): 297-305.

Morlo M. and J. Habersetzer. 1999. The Hyaenodontidae (Creodonta, Mammalia) from the lower Middle Eocene (MP 11) of Messel (Germany) with special remarks on new x-ray methods. Courier Forschungsinstitut Senckenberg 216: 31-73.

Morlo M. and G. F. Gunnell. 2003. Small Limnocyonines (Hyaenodontidae, Mammalia) from the Bridgerian Middle Eocene of Wyoming: *Thinocyon*, *Prolimnocyon*, and *Iridodon*, new genus. Contributions from the Museum of Paleontology, the University of Michigan 31(2): 43-78.

Morlo M. and D. Nagel. 2006. New remains of Hyaenodontidae (Creodonta, Mammalia) from the Oligocene of Central Mongolia. Annales de Paléontologie 92: 305-321.

Morlo M., Gunnell G. and P. D. Polly. 2009. What, if not nothing, is a creodont? Phylogeny and classification of Hyaenodontida and other former creodonts. Journal of Vertebrate Paleontology 29(3, Supplement): 152A.

Morlo M., Gunnell G. F. and D. Nagel. 2011. Ecomorphological Analysis of carnivore guilds in the Eocene through the Miocene of Laurasia. In: Carnivoran Evolution: New Views on Phylogeny, Form, and Function. A. Goswami and A. R. Friscia (eds.), Cambridge University Press, Cambridge: 269-311.

Müller H. J. 1967. Form und Funktion der Scapula. Vergleichend-analytische Studien bei Carnivora und Ungulaten. Zeitschrift für Anatomie und Entwicklungsgeschichte 126: 205-263.

Muizon C. De and B. Lange-Badré. 1997. Carnivorous dental adaptations in tribosphenic mammals and phylogenetic reconstruction. Lethaia 30: 353-366.

Nègre G. 1908. Contribution à l'étude de la formation des Phosphorites du Midi de la France. Buelletin de la Société Géologiques de France Paris 4(8): 490-505.

Nehring A. 1884. Über eine grosse Wolfsähnliche Hunderasse der Vorzeit (*Canis fam. decumanus*) und über ihre Abstammung. Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin, 1884(9): 153-165.

Neuenschwander A. and R. Lüps. 1975. Zahnvariationen bei einer Mauswiesel-Population, *Mustela nivalis* Linné 1766, aus Hessen. Säugetierkundliche Mitteilungen 23(2): 85-93.

Nummela S. 1995. Scaling of the mammalian middle ear. Hearing Research 85: 18-30.

Nummela S., Reuter T., Hemilä S., Homberg P. and P. Paukku. 1999. The anatomy of the killer whale middle ear (*Orcinus orca*). Hearing Research 133: 61-70.

O'Harra C. C. 1920. The White River Badlands. South Dakota School of Mines, Bulletin No. 13, Department of Geology, Rapid City, South Dakota, November 1920: 78.

Ooë T. and S. Esaka. 1981. Le chevauchement des dents jugales chez les phocques: modalities et evolution postnatale. Mammalia, 45: 497-503.

Osborn H. F. and J. L. Wortman.1894. Fossil mammals of the lower Miocene River beds. Collection of 1892. Bulletin of the American Museum of Natural History 6, Article 7: 199-228.

Pales L. and C. Lambert. 1971. Atlas ostéologique pour servir à l'identification des mammifères du Quaternaire. I. Les membres. Carnivores. Editions du centre national de la recherche scientifique, Paris: 1-57.

Parris D. C. and J. A. Holman. 1978. An Oligocene snake from a coprolite. Herpetlogica 34(3): 258-264.

Peigné S. and L. De Bonis. 2003. Juvenile cranial anatomy of Nimravidae (Mammalia, Carnivora): biological and phylogenetic implications. Zoological Journal of the Linnean Society 138(4): 477-493.

Petter G. 1959. Evolution de la forme du marteau (malleus) chez le lion de la naissance a l'age adulte. Mammalia — International Journal of the Systematics, Biology and Ecology of Mammals 23(3): 350-356.

Piveteau, J. 1935. Études sur quelques créodontes des phosphorites du Quercy. Annales de Paléontologie XXIV, Masson et Cie (eds.), Paris: 75-95.

Piveteau J. 1961. Carnivora. In: Traité de Paléontologie. 6(1), Masson (ed.), Paris: 641-820.

Pohle H. 1923. Über den Zahnwechsel der Bären. Zoologischer Anzeiger, 55: 266-277.

Polly P. D. 1993. Hyaenodontidae (Creodonta, Mammalia) from the Early Eocene Four Mile Fauna and Their Biostratigraphic Implications. PaleoBios 14(4): 1-10.

Polly P. D. 1996. The skeleton of *Gazinocyon vulpeculus* gen. et comb. nov. and the cladisitic relationships of Hyaenodontidae (Eutheria, Mammalia). Journal of Vertebrate Paleontology 16: 303-319.

Polly P. D., Wesley-Hunt G. D., Heinrich R. E., Davis G. and P. Houde. 2006. Earliest known carnivoran auditory bulla and support of a recent origin of crown-group Carnivora (Eutheria, Mammalia). Paleontology 49(5): 1019-1027.

Polly P. D. and N. MacLeod. 2008. Locomotion in Fossil Carnivora: An Application of Eigensurface analysis for Morphometric Comparison of 3D Surfaces. Paleontologica Electronica 11(2), 10A: 1-13.

Puria S. and C. R. Steele. 2008. Mechano-Acoustical Transformations. Chapter 3.10 in The senses. A comprehensive reference. Vol. 3, Academic Press:165-201.

Quam R. and Y. Rak. 2008. Auditory ossicles from southwest Asian Mousterian sites. Journal of Human Evolution 54: 414-433.

Radinsky L. 1969. Outlines of canid and felid brain evolution. Annals of the New York Academy of Sciences 167: 277-288.

Radinsky L. 1973. Evolution of the canid brain. Brain Behaviour and Evolution 7: 169-202.

Radinsky, L. 1977. Brains of early carnivores. Paleobiology 3: 333-349.

Rado R., Himelfarb M., Arensburg B., Terkel J. and Z. Wolberg. 1989. Are seismic communication signals transmitted by bone conduction in the blind mole rat? Hear Research 41: 23-30.

Rak Y. and R. J. Clarke. 1979. Ear ossicle of *Australopithecus robustus*. Nature 279: 62-63.

Rausch R. L. 1961. Notes on the black bear, *Ursus americanus* Pallas, in Alaska, with particular reference to dentition and growth. Zeitschrift für Säugetierkunde, 26: 77-107.

Ray C. E. 1976. *Phoca wymani* and other tertiary seals (Mammalia: Phocidae) described from the Eastern Seaboard of North America. Smithsonian Contributions to Palaeobiology 28: 1-36.

Razor jaws: Prehistoric Predators. Razor Jaws. Season 1: Episode6 National Geographic Channel 2009. Supervising Producer John Joseph, Produced and Directed by John Joseph.

Reif, W. E. 1974. REM Beobachtungen am Schmelz eines rezenten und eines fossilen Caniden. Biomineralisation 7: 56-68.

Remy J. A., Crochet J.-Y., Sigé B., Sudre J., De Bonis L., Vianey-Liaud M., Godinot M., Hartenberger J.-L., Lange-Badré B. and B. Comte. 1987. Biochronologie des phosphorites du Quercy: Misa à jour des listes fauniques et nouveaux gisements de mammifères fossiles. Münchner Geowissenschaftliche Abhandlungen A10: 169-188.

Remy J. A., Aguilar J.-P., Crochet J.-Y., Duffaud S., Escarguel G., Godinot M., Marandat B., Michaux J., Rage J.-C., Sigé B., Sudre J. and M. Wiénin. 1997. Les remplissages karstiques polyphasés (Éocène, Oligocène, Pliocène) de Saint-Maximin (Phosphorites du Gard) et leur apport à la connaissance des faunes européennes, notamment pour l′Éocène moyen (MP 13). In: Aguilar J.-P., Legendre S., Michaux J. (eds.): Actes du Congrès BiochroM′97, Mémoires et Travaux de l′institute, École Pratique des Hautes Études 21: 711-728.

Roberto M., Favia A. and E. Lozupone. 1993. Bone tissue kinetics in the surgically disarticulated incus. Acta Otologica (Stockholm) 113: 181-186.

Salles L. O. 1992. Felid Phylogenetics: Extant taxa and skull morphology (Felidae, Aeluroidea). American Museum Novitates 3047: 1-67.

Sarrat R., Guzmán A. G. and A. Torres. 1988. Morphological Variations of Human Ossicula Tympani. Acta anatomica 131: 146-149.

Sarrat R., Torres A., Guzman A. G., Lostalé F. and J. Whyte. Functional structure of human auditory ossicles. Acta anatomica 144: 189-195.

Saunders J. C. and R. M. Summers. 1982. Auditory structure and function in the mouse middle ear: an evaluation by SEM and capacitive probe. Journal of Comparative Physiology 146: 517-525.

Savage R. J. G. 1965. Fossil mammals of Africa: 19 The Miocene Carnivora of East Africa. Bulletin of the British Museum (Natural History), Geology, 10 (8): 242-316.

Scherzinger A., Franz M., Heizmann E. P. J. and F. Hofmann. 2005. Neue Spaltenfüllungen aus dem nördlichen Hegau und der Umgebung von Sigmaringen (Westliche Schwäbische Alb). – Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie), Nummer 354, ed.: Staatliches Museum für Naturkunde, Rosenstein 1, Stuttgart: 1-45.

Schlosser M. 1887. Die Affen, Lemuren, Chiropteren, Insektivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten, 1. Teil. — Beiträge zur Paläontologie Österreich-Ungarns und des Orients, Mojisisovics E. v. and M. Neumayr (eds.), Band 6: 1-224.

Schmidt-Kittler N. 1987. Correlation tables. In Schmidt-Kittler (ed.) International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene. Mainz, February 18th-21st 1987. Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie, Friedrich Pfeil Verlag: 17-19.

Schneider K. M. 1959. Zum Zahndurchbruch des Löwen (*Panthera leo*) nebst Bemerkungen über das Zahnen einiger anderer Grosskatzen und der Hauskatze (*Felis catus*). Der Zoologische Garten, 22: 240-361.

Schubert B. W., Ungar P. S. and L. R. G. DeSantis. 2010. Carnassial microwear and dietary behavior in large Carnivorans. Journal of Zoology 280: 257-263.

Scott W. B. 1888. On some new and little known creodonts. Journal of the Academy of Natural Sciences of Philadelphia, 9: 155-185.

Scott W. B. 1895. The osteology of *Hyaenodon*. Journal of the Academy of Natural Sciences of Philadelphia, 9: 499-535.

Scott W. B. and G. Jepsen. 1936. The Mammalian fauna of the White River Oligocene. Part I — Insectivora and Carnivora. Transactions of the American Philosophical Society, Volume 28, Part 1: 1-153.

Semprebon G. M., Godfrey L. R., Solounias N., Sutherland M. R. and W. L. Jungers. 2004a. Can low-magnification stereomicroscopy reveal diet? Journal of Human Evolution 47, 115-144.

Semprebon G. M., Janis C., N. Solounias. 2004b. The diets of the Dromomerycidae (Mammalia: Artiodactyla) and their response to Miocene vegetational change. Journal of Vertebrate Paleontology 24(2): 427-444.

Semprebon, G. M. and F. Rivals. 2007. Was grass more prevalent in the pronghorn past? An assessment of the dietary adaptations of Miocene to Recent Antilocapridae (Mammalia: Artiodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology 253: 332-347.

Shires, P. K. 2003. Atlantoaxial Instability. In Chapter 79: Atlantoaxial conditions and Wobbler Syndroms in: Textbook of small animal surgery. 3rd edition, Saunders, Elsevier Science (USA), Volume 1: 1173-1180.

Sigé B., Aguilar J.-P., Marandat B. and J.-B. Astruc. 1991. Extension au Miocène inférieur des remplissages phosphates du Quercy. La faune vértébrés de Cémat (Lot, Franche). Geobios 24(4): 497-502.

Simmons N. B., Seymour K. L., Habersetzer J. and G. F. Gunnell. 2010. Inferring echolocation in ancient bats. Nature 466: 7309.

Skobe, Z., Prostak, K. S. and P. L. Trombly. 1985. Scanning electron microscope study of cat and dog enamel structure. Journal of Morphology 184: 195-203.

Slaughter B. H., Pine R. H. and N. E. Pine. 1974. Eruption of cheek teeth in Insectivora and Carnivora. Journal of Mammalogy, 55: 115-125.

Solntseva G. N. 2007. Morphology of the auditory and vestibular organs in mammals, with emphasis on marine species. Russian Academic Monographs 4, V. M. Belkovitch (ed.): 1-244.

Smith B. H. 2000. Schultz´s rule and the evolution of tooth emergence and replacement patterns in primates and ungulates. In: Development, Function and Evolution of Teeth. M. F. Teaford, M. M. Smith and M. W. J. Ferguson (eds.), Cambridge University Press, Cambridge U.K.: 212-217.

Smith T. and R. Smith. 2001. The creodonts (Mammalia, Ferae) from the Paleocene-Eocene transition in Belgium (Tienen Formation, MP7). Belgian Journal of Zoology 131: 117-135.

Solé F., Gheerbrant E., Amaghzaz M. and B. Bouya. 2009. Further evidence of the African antiquity of hyaenodontid ("Creodonta", Mammalia) evolution. Zoological Journal of the Linnean Society 156: 827-846.

Solé F. 2010. Les premiers placentaires carnassiers européen (Oxaenodonta, Hyaenodontida et Carnivora): origine, évolution, paléoècologie et plaéobiogéographie; apport des faunes de l´Éocene inferieur du Bassin de Paris. Muséum National d´Histoire Naturelle: 883 pp.

Solé F. 2011. New data on the Oxyaenidae from the Early Eocene of Europe; biostratigraphic, paleobiogeographic and paleoecologic implications. Palaeontologica Electronica 14(2), 13A: 1-41.

Solounias N. and G. Semprebon. 2002. Advances in the Reconstruction of Ungulate Ecomorphology with Application to Early Fossil Equids. American Museum Novitates 3366: 1-49.

Spinage C. A. 1976. Incremental cementum lines in the teeth of tropical African mammals. Journal of Zoology, London 178: 117-131.

Spoor F. and F. Zonneveld. 1995. Morphometry of the primate bony labyrinth: a new method based on high-resolution computed tomography. Journal of Anatomy 186: 271-286.

Stefen, C. (1997a): Differentiations in Hunter-Schreger bands of carnivores. Chapter 7 in: Tooth enamel microstructure. W. v. Köngiswald and P. M. Sander (eds.), Balkema, Rotterdam: 123-136.

Stefen, C. (1997b): The enamel of Creodonta, Arctocyonidae, and Mesonychidae (Mammalia), with special reference to the appearance of Hunter-Schreger-Bands. Paläontologische Zeitschrift 71(3/4): 291-303.

Stock C. 1933. Hyaenodontidae of the upper Eocene of California. Proceedings of the National Academy of Sciences (USA) 19: 434-440.

Stubbe M and F. Krapp. 1993. Handbuch der Säugetiere Europas. Band 5: Raubsäuger- Carnivora (Fissipedia). Teil 1: Canidae, Ursidae, Procyonidae, Mustelidae I. AULA Verlag Wiesbaden, J. Niethammer and Franz Krapp (ed.).

Sudre J. 1977. L´Évolution du genre Robiacinia Sudre 1969, et l´origine des Cainotheriidae; Implications sytématiques. Geobios 10(1): 213-231.

Sudre J., De Bonis L., Brunet M., Crochet J.-Y., Duranthon F., Godinot M., Hartenberger J.-L., Jehenne Y., Legendre S., Marandat B., Remy J. A., Ringeade M., Sigé B. and M. Vianey-Liaud. 1992. La biochronologie mammalienne du Paléogène au Nord et au Sud des Pyrénées: état de la question. Comptes Rendus de l´Académie des Sciences, Paris 314, Série II: 631-636.

Sudre J. and M. Vianey-Liaud. 1997. Les phosphorites du Quercy: 30 ans de recherche. Bilan et perspectives. Geobios 20: 331-345.

Takechi M. and S. Kuratani. 2010. History of studies on mammalian middle ear evolution: a comparative morphological and developmentyl biology perspective. Journal of Experimental Zoology, Part B, Molecular and Developmental Evolution 314: 417-433.

Taylor M. E. 1974. The functional anatomy of the forelimb of some African Viverridae (Carnivora). Journal of Morphology 143: 307-336.

Taylor M. E. 1976. The functional anatomy of the hindlimb of some African Viverridae (Carnivora). Journal of Morphology 148: 227-253.

Taylor M. E. 1989. Locomotor adaptations by carnivores. In: J. L. Gittleman (Ed.) Carnivore Behaviour, Ecology, and Evolution: 382-409. Comstock Publication Association, Ithaca.

Tedford R. H., Taylor B. E. and X. Wang. 1995. Phylogeny of the Caninae (Carnivora: Canidae): the living taxa. American Museum Novitates 3146: 1-37.

Thorpe M. R. 1922. A new genus of Oligocene Hyaenodontidae. American Journal of Science 3: 277-287.

Tomes, C. S. 1906. On the minute structure of the teeth of creodonts with special reference to their suggested resemblance in marsupials. Proceedings of the Zoological Society London 1906(1): 45-58.

Toth M. and Csillag A. 2005. The organ of hearing and equilibrum. Chapter 1 in: Atlas of the Sensory Organs. Functional and Clinical Anatomy. Human Press, Totowa (New Jersey): 1-85.

Tsubamoto T., Watabe M. and K. Tsogtbaatar. 2008. *Hyaenodon chunkhtensis* and the hyaenodontid fauna from the upper Eocene Ergilin Dzo Formation of Mongolia. Journal of Vertebrate Paleontology 28: 559-564.

Turner A. (text) and Antón M. (illustrations). 1997. The big cats and their fossil relatives: an illustrated guide to their evolution and natural history. Columbia University Press, New York: 234 pp.

Ungar P. S., Scott J. R., Schubert B. W. and D. D. Stynder. 2010. Carnivoran dental microwear textures: comparability of carnassial facets and functional differentiation of postcanine teeth. Mammalia 74: 219-224.

Valentin S. and B. Lange-Badré. 1991. Morphologie de la mandibule et usure dentaire chez *Hyaenodon* (Creodonta, Mammalia): un compromise fonctionnel singulier. Geobios 13: 201-206.

Van Kampen P. N. 1915. Over het homologon van de colomella auris der reptilien bij zoogdieren. Nederlandsch tijdschr. v. geneesk 59, 2. Heft B, No. 22: 2444-2446.

Van der Klaauw C. J. 1923. Die Skelettstückchen in der Sehne des Musculus stapedius und nahe dem Ursprung der Chorda tympani. Zeitschrift für Anatomie und Entwicklungsgeschichte 69: 32-83.

Van der Klaauw C. J. 1931. On the auditory bulla in some fossil mammals, with a general introduction to this region of the skull. Bulletin of the American Museum of Natural History, Vol. LXII: 1-352.

Van Valen L. 1967. New Paleogene insectivores and insectivore classification. Bulletin of the American Museum of Natural History 135: 5217-5284.

Van Valen L. M. 1994. Serial homology: the crests and cusps of mammalian teeth. Acta Palaeontologica Polonica 38(3/4): 145-158.

Van Valkenburgh B. 1987. Skeletal indicators of locomotor behaviour in living and extinct carnivores. Journal of Vertebrate Paleontology 7(2): 162-182.

Van Valkenburgh B. 1988. Trophic diversity in past and present guilds of large predatory mammals. Paleobiology, 14(2): 155-173.

Van Valkenburgh B., Teaford M. F. and A. Walker. 1990. Molar microwear and diet in large carnivores: inferences concerning diet in the sabretooth cat, *Smilodon fatalis*. Journal of Zoology, London 222: 319-340.

Van Valkenburgh B. 1995. Tracking ecology over geologic time: evolution within guilds of vertebrates. Trends in Ecology and Evolution 10(2): 71-76.

Van Valkenburgh B. 1999. Major patterns in the history of carnivorous mammals. – Annual Review of Earth and Planetary Sciences 27: 463-493.

Van Valkenburgh, B., Wang, X. and J. Damuth. 2004: Cope´s rule, hypercarnivory, and extinction in North American canids. Science 306: 101-104.

Wang X. 1993. Transformation from plantigrady to digitigrady: Functional morphology of locomotion in Hesperocyon (Canidae: Carnivora). American Museum Novitates, 3069: 1-23.

Wang X., Qiu Z. and B. Wang. 2005. Hyaenodonts and carnivorans from the early Oligocene to early Miocene of Xianshuihe Formation, Lanzhou Basin, Gansu Province, China. Paleontologica Electronica 8(1:6A): 1-14.

Wang X. and Tedford R. H. (illustrations by Mauricio Antón). 2008. Dogs: their fossil relatives and evolutionary history. Columbia University Press: 1-219.

Webster D. B. 1961. The ear apparatus of the kangaroo rat, *Dipodomys*. American Journal of Anatomy 108: 123-147.

Webster D. B. 1966. Ear structure and function in modern mammals. American Zoologist 6: 451-466.

Webster D. B. and M. Webster. 1975. Auditory systems of Heteromyidae: Functional morphology and evolution of the middle ear. Journal of Morphology 146: 343-376.

Werdelin L. 1987. Supernumerary teeth in *Lynx lynx* and the irreversibility of evolution. Journal of Zoology, London, 211: 259-266.

Werdelin L. 1996. Carnivoran ecomorphology: a phylogenetic perspective. In Carnivore behaviour, ecology, and evolution: 582-624. Gittleman, J. L. (ed.). Ithaca, New York: Cornell University Press.

Wesley-Hunt G. D. 2005. The morphological diversification of carnivores in North America, carnivore evolution. Paleobiology 31(1): 35-55.

Wilkins K. T., Roberts J. C. Roorda C. S. and J. E. Hawkins. Morphometrics and functional morphology of middle ears of extant pocket gophers (Rodentia: Geomyidae). Journal of Mammalogy 80(1): 180-189.

Willi U. B., Ferrazzini M. A. and A. M. Huber. 2002. The incudo-malleolar joint and sound transmission losses. Hearing Research 174: 32-44.

Wilson D. E. and R. A. Mittermeier (eds.). 2009. Handbook of the mammals of the world. Volume 1: Carnivores. Lynx Edicions, Barcelona: 1-727.

Wysocki J. 2005. Topographical anatomy of the guinea pig temporal bone. Hearing Research 199: 103-110.

Yalden D. 1970. The functional morphology of the carpal bones in carnivores. Acta Anatomica 77, No. 4: 481-500.

Young C. C. 1937. An early Tertiary vertebrate fauna from Yuanchu. Bulletin of the Geological Society of China 17: 413-438.

Zhao, Z. and Li, Y. 1987. The ultrastructure of the enamel in the giant panda of the Pleistocene. Vertebrata Palasiatica 25(4): 297-305.

15. Appendix

The first table contains the counts of the microwear features.

Abbreviations used:
sm. p.: average count of the small pits
l. p.: average count of the large pits
sm. p. p.: average count of the small puncture pits (0.03 mm or <0.03 mm)
m. p. p.: average count of the medium puncture pits (0.04-0.09 mm)
l. p. p.: average count of the large puncture pits (>0.09 mm)
f. scr.: average count of the fine scratches
c. scr.: average count of the coarse scratches
n. hyp. s.: average count of the narrow hypercoarse scratches
w. hyp. s.: average count of the wide hypercoarse scratches (>0.025 mm in width)
cross scr.: average count of the cross scratches
total scr.: average count of the total scratches
NA: North America
The genus is abbreviated. *H.* stands for *Hyaena* (*H. hyaena*) at the top and for *Hyaenodon* (various species) in the lower part.

The second table contains the standardized values used in the PCA-Analysis (performed in PAST)

Abrreviations used for taxa:	PB	*Parahyaena brunnea*
	HH	*Hyaena hyaena*
	CC	*Crocuta crocuta*
	AJ	*Acinonyx jubatus*
	PL	*Panthera leo*
	LL	*Lutra lutra*
	VV	*Vulpes vulpes*
	NB	*Nandinia binotata*
	GG	*Genetta genetta*
	HNA	*Hyaenodon* (from North America)
	HEU	*Hyaenodon* (from Europe)

specimen number	taxon	conti-nent	tooth	sm. pits	l. pits	sm. p. p.	m. p. p.	l. p. p.	total pits	f. scr.	c. scr.	n. hyp. scr.	w. hyp. scr.	cross scr.	gouges	total scr.
AMNH 83589	*P. brunnea*	Africa	P4 dex.	110,5	5,5	0	0	0	116	0	4,5	1	0,5	0,5	2	6
AMNH 85390	*P. brunnea*	Africa	m1 dex.	110	6	0	0	0	116	0	4,5	1	1	0	2	6,5
AMNH 83589	*P. brunnea*	Africa	m1 dex.	110	7,5	0	0	0	117,5	0	4,5	1,5	0,5	0	2	6,5
AMNH 81834	*P. brunnea*	Africa	m1 dex.	109,5	6,5	0	0	0	116	0	5	1	0,5	0,5	2	6,5
NMW 21494	*P. brunnea*	Africa	P4 sin.	107	4	0	0	0	111	0	6,5	0,5	0,5	0	1	7,5
NMW 21494	*P. brunnea*	Africa	m1 dex.	109,5	5	0	0	0	114,5	0	4,5	1	0	0	1	5,5
species average				109,41	5,75	0	0	0	115,16	0	4,91	1	0,5	0,16	1,66	6,41
standard deviation				1,24	1,21	0	0	0	2,25	0	0,8	0,31	0,31	0,25	0,51	0,66
AMNH 67	*H. hyaena*	Africa	P4 dex.	119,5	7,5	0	0	0	127	0	6,5	1,5	0	0,5	1	8
AMNH 187784	*H. hyaena*	Africa	DP4 dex.	105	7	0	0	0	112	1,5	5,5	1	0,5	1,5	2	8,5
AMNH 179144	*H. hyaena*	Africa	P4 sin.	114,5	5	0	0	0	119,5	1	5,5	0,5	1	2	2	8
AMNH 1544	*H. hyaena*	Asia	P4 sin.	119	8,5	0	0	0	127,5	0	6,5	1	0	0	2	7,5
AMNH 67	*H. hyaena*	Africa	m1 dex.	120	8,5	0	0	0	128,5	0	6,5	1,5	0	1,5	2	8
AMNH 1544	*H. hyaena*	Asia	m1 dex.	102	7,5	0	0	0	109,5	0	7	0,5	0	0	2	7,5
NMW 1756	*H. hyaena*	Africa	P4 sin.	113,5	4,5	0	0	0	118	0	5,5	1	0,5	0	2	7
species average				113,35	6,92	0	0	0	120,28	0,35	6,14	1	0,28	0,78	1,85	7,78
standard deviation				7,23	1,59	0	0	0	7,69	0,62	0,62	0,4	0,39	0,85	0,85	0,48
AMNH 187771	*C. crocuta*	Africa	P4 dex.	131,5	5	0	0	0	136,5	0	6	2	1,5	0	2	9,5
AMNH 187775	*C. crocuta*	Africa	m1 dex.	133	5	0	0	0	138	0	9	2,5	0	1	1	11,5
NMW 1244	*C. crocuta*	Africa	m1 dex.	129	5,5	0	0	0	134,5	0	8,5	1,5	0	0	2	10
NMW 1244	*C. crocuta*	Africa	P4 dex.	139	5	0	0	0	144	0	8	0,5	0,5	0	2	9
NMW 21495	*C. crocuta*	Africa	m1 dex.	131	4,5	0	0	0	135,5	0	8	1,5	0,5	0	2	10
NMW 1755	*C. crocuta*	Africa	P4 dex.	132,5	6,5	0	0	0	139	0	7	0,5	1	0	2	8,5
NMW 1755	*C. crocuta*	Africa	m1 dex.	139,5	5,5	0	0	0	145	0	6,5	1,5	1,5	0	2	9,5
NMW 7392	*C. crocuta*	Africa	m1 dex.	132	5	0	0	0	137	0	7,5	1	0	0	2	8,5
NMW 1150	*C. crocuta*	Africa	m1 dex.	138,5	6	0	0	0	144,5	0	7,5	1	0,5	0	2	9
NMW 6064	*C. crocuta*	Africa	P4 sin.	129,5	5,5	0	0	0	135	0	5,5	2,5	1,5	0	2	9,5
NMW 6064	*C. crocuta*	Africa	m1 dex.	131,5	5,5	0	0	0	137	0	7	2	0	0	2	9
NMW 6062	*C. crocuta*	Africa	P4 dex.	131,5	5,5	0	0	0	137	0	7	0	0,5	0	2	7,5
NMW 6062	*C. crocuta*	Africa	m1 sin.	132,5	5	0	0	0	137,5	0	5,5	0,5	1,5	0	2	7,5

NMW 3919	C. crocuta	Africa	m1 dex.	136	4,5	0	0	0	140,5	0	5	0,5	1,5	0	2	7
NMW 3919	C. crocuta	Africa	P4 sin.	130,5	6,5	0	0	0	137	0	7,5	0,5	1	0	2	9
NMW 5584	C. crocuta	Africa	P4 dex.	131	4	0	0	0	135	0	6,5	1	1	0	2	8,5
NMW 5584	C. crocuta	Africa	m1 dex.	132,5	3,5	0	0	0	136	0	6	1	1	0	2	8
NMW 1744b	C. crocuta	Africa	P4 dex.	141	4,5	0	0	0	145,5	0	6,5	1,5	0,5	0	2	8,5
NMW 1744b	C. crocuta	Africa	m1 dex.	134,5	7	0	0	0	141,5	0	8,5	1	0	0	2	9,5
NMW 6063	C. crocuta	Africa	P4 sin.	134	5	0	0	0	139	0	5,5	2	0	0	2	9,5
NMW 6063	C. crocuta	Africa	m1 dex.	139,5	7,5	0	0	0	147	0	5	2,5	1,5	1	2	11,5
NMW 7393	C. crocuta	Africa	P4 sin.	130	6,5	0	0	0	136,5	0	7	0,5	0,5	0	2	8
NMW 7393	C. crocuta	Africa	m1 dex.	131	6	0	0	0	137	0	7	1,5	0	0	2	8,5
NMW 6061	C. crocuta	Africa	m1 dex.	127	8,5	0	0	0	135,5	0	7	1	0	0	2	8
NMW 6061	C. crocuta	Africa	P4 sin.	130	8	0	0	0	138	0	9,5	0,5	0	0	2	10
species average				133,12	5,64	0	0	0	138,76	0	6,96	1,22	0,64	0,08	1,96	9
standard deviation				3,73	1,21	0	0	0	3,69	0	1,2	0,72	0,6	0,27	0,2	1,1
AMNH 119656	A. jubatus	Africa	P4 dex.	85	13,5	0	0	0	98,5	1,5	3,5	1,5	0	1,5	0	6,5
AMNH 119655	A. jubatus	Africa	P4 sin.	86	11,5	0	0	0	97,5	0,5	4,5	1	0	1	0	6
AMNH 35998	A. jubatus	Africa	P4 dex.	85,5	17,5	0	0	0	103	0	3,5	0	0	0	0	3,5
AMNH 27897	A. jubatus	Africa	P4 dex.	85,5	16,5	0	0	0	102	0	4	0,5	0	0,5	0	4,5
AMNH 35997	A. jubatus	Africa	P4 sin.	98	16	0	0	0	114	0	4	1	0	1	0	5
AMNH 119656	A. jubatus	Africa	m1 sin.	85	16,5	0	0	0	101,5	0,5	6	0,5	0	1,5	0	7
AMNH 35998	A. jubatus	Africa	m1 dex.	79,5	13	0	0	0	92,5	0	5,5	1,5	0	1,5	0	7
AMNH 27897	A. jubatus	Africa	m1 dex.	89	14,5	0	0	0	103,5	0,5	7	0	0	0,5	0	7,5
AMNH 35997	A. jubatus	Africa	m1 dex.	87,5	12,5	0	0	0	100	0	4,5	0,5	0	0,5	0	5
AMNH 161139	A. jubatus	Africa	m1 dex.	87	12,5	0	0	0	99,5	3,5	3,5	0	0	0,5	0	7
NMW 64961	A. jubatus	Africa	m1 dex.	109	10,5	0	0	0	119,5	0	3,5	0,5	0	0,5	1	4
NMW 64961	A. jubatus	Africa	P4 sin.	97	12	0	0	0	109	0	3,5	1,5	0	0	1	5
NMW 62175	A. jubatus	Africa	m1 dex.	102,5	14	0	0	0	116,5	0	3	0	0,5	0	1	3,5
NMW 62175	A. jubatus	Africa	P4 dex.	93,5	11	0	0	0	104,5	0	5	0,5	0	0	0	5,5
NMW 12071	A. jubatus	Africa	P4 dex.	101,5	13	0	0	0	114,5	0	3,5	1	0	0	0	4,5
NMW 12071	A. jubatus	Africa	m1 dex.	91	12,5	0	0	0	103,5	0	4	0,5	0	0	0	4,5
NMW 12070	A. jubatus	Africa	P4 dex.	100,5	13	0	0	0	113,5	0	4,5	0,5	0	0	0	5
NMW 12070	A. jubatus	Africa	m1 sin.	94,5	10,5	0	0	0	105	0	3	1	0,5	0	1	4,5
NMW 61336	A. jubatus	Africa	P4 dex.	93,5	11	0	0	0	104,5	0	3,5	0	0,5	0	0	4
species average				92,15	13,23	0	0	0	105,39	0,34	4,18	0,63	0,07	0,47	0,21	5,23
standard deviation				7,68	2,11	0	0	0	7,22	0,85	1,05	0,52	0,18	0,56	0,41	1,25

NMW 6055	*P. leo*	Africa	m1 dex.	134	9,5	0	0	0	143,5	0	8	0,5	1,5	0	1	10
NMW 6058	*P. leo*	Africa	m1 dex.	133	10,5	0	0	0	143,5	0	9,5	1	0	0	1	10,5
NMW 6058	*P. leo*	Africa	P4 dex.	110,5	9,5	0	0	0	120	0	9	1	0,5	0,5	1	10,5
NMW 62154	*P. leo*	Africa	P4 dex.	115	10	0	0	0	125	0	8	0,5	0,5	0	0	9
NMW 62154	*P. leo*	Africa	m1 dex.	111	10	0	0	0	121	0	10	0,5	1	0	1	11,5
NMW 1241	*P. leo*	Africa	m1 dex.	135	9,5	0	0	0	144,5	0	8	2	0,5	0	0	10,5
NMW 6056	*P. leo*	Africa	P4 dex.	135,5	12,5	0	0	0	148	0	11,5	0,5	0	0	0	12
NMW 6056	*P. leo*	Africa	m1 dex.	133,5	11,5	0	0	0	145	0	12	1	0	0	0	13
species average				125,93	10,37	0	0	0	136,31	0	9,5	0,875	0,5	0,06	0,5	10,87
standard deviation				11,5	1,09	0	0	0	12,01	0	1,58	0,51	0,53	0,17	0,53	1,24
NMW 43391	*L. lutra*	Europe	m1 dex.	112	9,5	0	0	0	121,5	1	4	0,5	1	2	1	6,5
NMW 43391	*L. lutra*	Europe	P4 dex.	109,5	11,5	0	0	0	121	0	4,5	0,5	0	1,5	1	5
NMW 3719	*L. lutra*	Europe	m1 dex.	111,5	10,5	0	0	0	122	0	3	0,5	0,5	0,5	1	4
NMW 3719	*L. lutra*	Europe	P4 dex.	102,5	9,5	0	0	0	112	0	4,5	0	0	0,5	1	4,5
NMW 3676	*L. lutra*	Europe	m1 sin.	112,5	9	0	0	0	121,5	0	5,5	0	1	1,5	1	6,5
NMW 3676	*L. lutra*	Europe	P4 dex.	106,5	9,5	0	0	0	116	0	5	0,5	0,5	1	1	6
NMW 55257	*L. lutra*	Europe	m1 dex.	109,5	10,5	0	0	0	120	0	5	1,5	0	0	1	6,5
NMW 55257	*L. lutra*	Europe	P4 dex.	108,5	10,5	0	0	0	119	0	4	1	0,5	1,5	1	5,5
NMW 65174	*L. lutra*	Europe	m1 dex.	112,5	9,5	0	0	0	122	0	5	1	0	0,5	1	6
NMW 65174	*L. lutra*	Europe	P4 dex.	111,5	10	0	0	0	121,5	0	4,5	0,5	1	1	1	6
NMW 66690	*L. lutra*	Europe	P4 dex.	116	8	0	0	0	124	0	4	0,5	0,5	0	0	5
NMW 66690	*L. lutra*	Europe	m1 dex.	118,5	8,5	0	0	0	127	0	3	1	1,5	1	0	5,5
NMW 43394	*L. lutra*	Europe	P4 dex.	118,5	8,5	0	0	0	127	0	5	0,5	0,5	0	0	6
NMW 43394	*L. lutra*	Europe	m1 dex.	115	8,5	0	0	0	123,5	0	5,5	1	0	0,5	1	6,5
NMW 43392	*L. lutra*	Europe	P4 dex.	115,5	8	0	0	0	123,5	0	3	1	0,5	1	1	4,5
NMW 43392	*L. lutra*	Europe	m1 dex.	114	8,5	0	0	0	122,5	0	3	1	1,5	2	1	5,5
NMW 57485	*L. lutra*	Europe	m1 dex.	110,5	8	0	0	0	118,5	0	3,5	2	0	2	1	5,5
NMW 57480	*L. lutra*	Europe	dp4 sin.	109,5	8,5	0	0	0	118	0	3	2	0	1,5	0	5
NMW 65757	*L. lutra*	Europe	m1 sin.	115	9,5	0	0	0	124,5	0	2,5	1	0	0	1	3,5
NMW 57484	*L. lutra*	Europe	m1 dex.	109	10,5	0	0	0	119,5	0	2,5	1	1	1,5	1	4,5
NMW 57484	*L. lutra*	Europe	P4 dex.	114	9	0	0	0	123	0	2	1,5	0	0,5	1	3,5
NMW 3511	*L. lutra*	Europe	m1 dex.	111	8	0	0	0	119	0	2,5	1	1,5	1	0	5
NMW 64125	*L. lutra*	Europe	m1 sin.	109	9	0	0	0	118	0	2,5	1	0,5	0,5	0	4
NMW 64125	*L. lutra*	Europe	P4 dex.	109	8	0	0	0	117	0	3	0,5	0	0	0	3,5
species average				111,7	9,18	0	0	0	120,89	0,041	3,75	0,87	0,5	0,89	0,7	5,16
standard deviation				3,72	0,99	0	0	0	3,43	0,2	1,08	0,51	0,53	0,67	0,46	0,99

AMNH 60130	*V. vulpes*	Asia	m1 dex.	79,5	8	0	0	0	87,5	0,5	5,5	1	0	1,5	0	7
AMNH 60098	*V. vulpes*	Asia	m1 dex.	82,5	8,5	0	0	0	91	0	5,5	0,5	0	1	0	6
AMNH 117630	*V. vulpes*	Asia	P4 dex.	71	8,5	0	0	0	79,5	0,5	6,5	0	0	1,5	0	7
AMNH 60130	*V. vulpes*	Asia	P4 dex.	90	6	0	0	0	96	0	6	0,5	0	2,5	0	6,5
AMNH 59312	*V. vulpes*	Asia	m1 dex.	91	5	0,5	2	0,5	99	0	4,5	0	0,5	0,5	0	5
species average				82,8	7,2	0,1	0,4	0,1	90,6	0,2	5,6	0,4	0,1	1,4		6,3
standard deviation				8,2	1,6	0,22	0,89	0,22	7,62	0,27	0,74	0,41	0,22	0,74	0	0,83
NMW 44311	*V. vulpes*	Europe	m1 dex.	99,5	6	1,5	0	0	107	0	6	0	0	2,5	1	6
NMW 44311	*V. vulpes*	Europe	P4 dex.	99	5,5	1	1,5	0	107	0	4	1	0	1	1	5
NMW 41043	*V. vulpes*	Europe	m1 dex.	92,5	3,5	0	1,5	0	97,5	0	4,5	0	0	0,5	1	4,5
NMW 41043	*V. vulpes*	Europe	P4 dex.	99,5	4,5	0	0	0	104	0	3	1,5	0,5	0,5	1	5
NMW 42643	*V. vulpes*	Europe	P4 dex.	101,5	4	1,5	0	0	107	0	6,5	0	0	1	1	6,5
NMW 42643	*V. vulpes*	Europe	m1 dex.	95,5	4	0	0,5	0	100	1	4,5	0,5	0	1,5	1	6
NMW 41051	*V. vulpes*	Europe	P4 dex.	100,5	3,5	1	1,5	0	106,5	0	3,5	1	0,5	1	1	5
NMW 42638	*V. vulpes*	Europe	m1 dex.	97	2,5	0	0,5	0	100	0	5,5	0	1	2,5	1	6,5
NMW 42638	*V. vulpes*	Europe	P4 dex.	92,5	3,5	0	0	0	96	0	5,5	0	0	2	1	5,5
NMW 43461	*V. vulpes*	Europe	m1 dex.	96	3,5	0	0	0	99,5	3	2,5	0,5	0	2	1	6
NMW 43461	*V. vulpes*	Europe	P4 dex.	94	1,5	0	0	0	95,5	1	3,5	1,5	0,5	2,5	1	6,5
NMW 42278	*V. vulpes*	Europe	P4 dex.	95,5	3	0	0,5	0	98,5	0,5	6	0,5	0	1,5	1	7
NMW 43462	*V. vulpes*	Europe	m1 dex.	101	5	1,5	0	0	107,5	0,5	5	0	0	1,5	1	5,5
NMW 43462	*V. vulpes*	Europe	P4 dex.	91,5	7,5	0	0	0	99	0	5	0,5	0	2	1	5,5
NMW 41042	*V. vulpes*	Europe	m1 dex.	98,5	6,5	0	0	0	105	1	4	1	0,5	0	0	6,5
NMW 41047	*V. vulpes*	Europe	m1 dex.	97	6,5	0	0	0	103,5	0	4	1	0	0	0	5
NMW 36305	*V. vulpes*	Europe	P4 dex.	93	5,5	0	0	0	98,5	0	8	0	0	2,5	0	8
NMW 36305	*V. vulpes*	Europe	m1 dex.	93,5	5,5	0	0	0	99	0	5,5	0,5	0,5	0,5	0	6,5
NMW 38094	*V. vulpes*	Europe	P4 dex.	97	6	0	0	0	103	0	5,5	0	0	0,5	1	5,5
NMW 38094	*V. vulpes*	Europe	m1 dex.	102	5	0	0	0	107	1	5,5	1	0	2	1	7,5
NMW 44310	*V. vulpes*	Europe	m1 dex.	90	5,5	0	0	0	95,5	0	5	1	0	2	0	6
NMW 44310	*V. vulpes*	Europe	P4 dex.	93	5	0	0	0	98	0	3,5	2,5	0	2,5	0	6
NMW 41054	*V. vulpes*	Europe	P4 dex.	93	3	0	0	0	96	0	3	0,5	0	0,5	1	3,5
NMW 41054	*V. vulpes*	Europe	m1 dex.	88,5	3	0	0	0	91,5	0	2,5	1	0,5	0,5	1	4
NMW 42647	*V. vulpes*	Europe	P4 dex.	100,5	2	1	1,5	0	105	0	1,5	1	1,5	1,5	1	4
NMW 42647	*V. vulpes*	Europe	m1 dex.	104	3	1	0	0	108	0	3	0,5	0,5	1	1	4
NMW 25194	*V. vulpes*	Europe	P4 dex.	92,5	4	0	0	0	96,5	0	3	2,5	0	1,5	0	5,5
NMW 25194	*V. vulpes*	Europe	m1 dex.	92,5	4,5	0	0	0	97	1	4,5	1,5	0	1,5	0	7
NMW 41041	*V. vulpes*	Europe	m1 dex.	104,5	4,5	0	0	0	109	0,5	4	1	0	1,5	0	5,5

NMW 41041	*V. vulpes*	Europe	P4 dex.	101,5	3	0	0	0	104,5	0	3,5	1	0,5	1,5	0	5
NMW 42641	*V. vulpes*	Europe	m1 dex.	102,5	4	0	0	0	106,5	0	5	1,5	0	1,5	1	6,5
NMW 42641	*V. vulpes*	Europe	P4 dex.	101	4,5	0	0	0	105,5	0,5	5	0	0,5	0,5	1	6
species average				96,87	4,32	0,26	0,23	0	101,68	0,31	4,4	0,76	0,21	1,35	0,68	5,7
standard deviation				4,33	1,4	0,52	0,5	0	4,79	0,61	1,36	0,68	0,35	0,76	0,47	1,04
Nandinia binotata																
AMNH 51494	*N. binotata*	Africa	P4 dex.	150,5	13	4	0,5	0	168	1	7,5	1,5	0	1,5	0	10
AMNH 51491	*N. binotata*	Africa	P4 dex.	143	10	3	0	0	156	0	7	1	0	2	0	8
AMNH 51498	*N. binotata*	Africa	P4 dex.	163,5	10	1,5	2	0	177	5	6	0,5	0	2	0	11,5
AMNH 51500	*N. binotata*	Africa	P4 dex.	138	10,5	2,5	2,5	0	153,5	1,5	9,5	1	0	2,5	0	12
AMNH 51494	*N. binotata*	Africa	m1 dex.	159	12	3	1	0	175	4	5	0	0	2	0	9
AMNH 51501	*N. binotata*	Africa	m1 dex.	139,5	11	4	0	0	154,5	0,5	9,5	2	1	3	0	13
species average				148,91	11,08	3	1	0	164	2	7,41	1	0,16	2,16	0	10,58
standard deviation				10,58	1,2	0,94	1,04	0	10,68	2,02	1,82	0,7	0,4	0,51	0	1,9
NMW B2145	*G. genetta*	Africa	m1 sin.	110	6	3	0	0	119	0	5	0	0	2	0	5
NMW B2145	*G. genetta*	Africa	P4 sin.	107,5	6,5	1,5	0	0	115,5	0	6	0	0	1	0	6
NMW 19005	*G. genetta*	Europe	m1 dex.	108	7	2	0,5	0,5	118	0	5	0	0	1	0	5
NMW 1162	*G. genetta*		m1 dex.	108	7	0,5	2	0	117,5	0	2,5	1,5	0,5	0,5	0	4,5
NMW 2913/B2464	*G. genetta*		m1 dex.	105,5	7	2	1	0	115,5	0	4,5	0	2	1,5	0	6,5
NMW 2913/B2464	*G. genetta*		P4 dex.	103	8	1,5	1	0	113,5	0	4,5	0	0,5	1	0	5
NMW 41579	*G. genetta*	Africa	P4 dex.	102	6,5	1,5	1,5	0	111,5	0	5	1	0,5	0,5	0	6,5
NMW 41579	*G. genetta*	Africa	m1 dex.	109	8	2	1,5	0	120,5	0	3,5	1,5	0,5	0,5	0	5,5
NMW 41583	*G. genetta*	Africa	m1 dex.	108,5	8	3	0	0	119,5	0	3,5	2,5	0	1,5	0	6
NMW 41583	*G. genetta*	Africa	P4 dex.	106	8	2	0	0	116	0	5	0,5	1	1	0	6,5
NMW 41586	*G. genetta*		m1 dex.	108,5	10	2,5	0,5	0	121,5	0	4	0,5	0	0	0	4,5
NMW 2911/B2467	*G. genetta*		m1 dex.	109	12	0	0	0	121	0	7,5	0,5	0	0,5	0	8
species average				107,08	7,83	1,79	0,66	0,04	117,41	0	4,66	0,66	0,41	0,91		5,75
standard deviation				2,48	1,68	0,89	0,71	0,14	3,1	0	1,28	0,8	0,59	0,55	0	1,03
FAM 75644	*H.* sp.	NA	P4 dex.	133,5	10	0	0	0	143,5	0	9,5	1,5	0	0	0	11
FAM 75639	*H.* sp.	NA	DP4 dex.	130,5	11,5	0	0	0	142	0,5	7,5	1,5	0	2,5	0	9,5
AMNH 12233	*H. crucians*	NA	P4 dex.	137,5	10	0	0	0	147,5	0,5	7,5	1	0,5	0	1	9,5
AMNH 647	*H. crucians*	NA	P4 dex.	109,5	8	0	0	0	117,5	0,5	6	1	0,5	0,5	0	8
YPM 10075	*H. leptocephalus*	NA	P4 dex.	116,5	10,5	0	0	0	127	0	6	3	1,5	0	2	10,5
FAM 75608	*H. crucians*	NA	P4 dex.	121	9,5	0	0	0	130,5	2	8	0,5	0	3	0	10,5

FAM 75569	H. crucians	NA	M1 sin.	124	10,5	0	0	0	134,5	2	7,5	2	0	1,5	2	11,5
FAM 75746	H. sp.	NA	M1 sin.	128,5	8,5	0	0	0	137	1	10,5	0	0	0,5	0	11,5
AMNH 39430	H. horridus	NA	M1 dex.	120	10	0	0	0	130	0	8	0,5	0,5	0	1	9
AMNH 647	H. crucians	NA	M1 dex.	118	10	0	0	0	128	0	7	1	0,5	0	0	8,5
AMNH 94745	H. crucians	NA	M1 dex.	126,5	9	0	0	0	135,5	0,5	8	0	0	0,5	1	8,5
FAM 75608	H. crucians	NA	M1 dex.	115	12	0	0	0	127	1,5	9	0,5	0,5	1,5	1	11,5
YPM PU 13801	H. horridus	NA	M1 dex.	123	12	0	0	0	135	0	7	2	1	0	1	10
YPM 56780	H. crucians	NA	M1 dex.	119,5	9	0	0	0	128,5	0	11	0,5	0,5	0	0	12
FAM 75730	H. horridus	NA	M1 dex.	132,5	11,5	0	0	0	144	0	7	1,5	0,5	0	2	9
Qu 8308	H. heberti	Europe	M1 dex.	126	5,5	0	0	0	131,5	0	7,5	2	2	0	2	11,5
Qu 8307	H. dubius	Europe	M1 sin.	131	10	0	0	0	141	2,5	8,5	0,5	0	3	2	11,5
Qu 8650	H. brachyrhynchus	Europe	M1 dex.	129	5	0	0	0	134	0	8,5	0,5	1	0,5	2	10
YPM PU 11462	H. exiguus	Europe	M1 dex.	130	6,5	0	0	0	136,5	0	7	2	0,5	0	2	9,5
Qu 16524	H. sp.	Europe	M1 sin.	135,5	8	0	0	0	143,5	0	9	0	1	1	1	10
FAM 75746	H. sp.	NA	M2 sin.	121,5	9	0	0	0	130,5	5,5	7	3	0	5,5	0	15,5
AMNH 12233	H. crucians	NA	M2 dex.	137	8	0	0	0	145	1	8	1	1,5	0,5	2	11,5
YPM PU 10010	H. horridus	NA	M2 dex.	121,5	11,5	0	0	0	133	0	11,5	1	0,5	0	1	13
FAM 75608	H. crucians	NA	M2 dex.	124	8	0	0	0	132	0	7,5	1	0	0	0	8,5
Qu 8308	H. heberti	Europe	M2 dex.	130,5	6,5	0	0	0	137	0	8,5	1,5	2,5	0	2	12,5
Qu 8307	H. dubius	Europe	M2 sin.	125	6	0	0	0	131	2,5	6,5	1,5	0	2,5	2	10,5
Qu 16524	H. sp.	Europe	M2 sin.	124,5	8	0	0	0	132,5	0	8,5	1	0	0	1	9,5
FAM 75644	H. sp.	NA	p4 dex.	132	9,5	0	0	0	141,5	0	10	1,5	0,5	1,5	0	12
FAM 75639	H. sp.	NA	dp4 sin.	116	8,5	0	0	0	124,5	0,5	7	1	0	1,5	0	8,5
AMNH 1379	H. crucians	NA	p4 sin.	112	9	0	0	0	121	2	6	1	1,5	3,5	1	10,5
AMNH 649	H. crucians	NA	dp4 sin	143,5	9,5	0	0	0	153	1	5,5	2	1	0,5	2	9,5
FAM 75725	H. horridus	NA	dp4 sin.	120,5	10,5	0	0	0	131	0,5	6	1	1,5	2,5	0	9
FAM 75575	H. crucians	NA	dp4 dex.	102,5	2	0	0	0	104,5	0	7,5	3	0	3,5	0	10,5
AMNH 19125	H. pervagus	Asia	dp4 sin.	111,5	8	0	0	0	119,5	0,5	12	1	0	5,5	0	13,5
MNHN No.29-15	H. sp.	Asia	p4 sin.	120	5,5	0	0	0	125,5	0	6	0	0	2,5	0	6
NMHW 2005z0224/0006	H. pervagus	Asia	p4 sin.	125,5	4	0	0	0	129,5	0	9,5	0	0	0	0	9,5
GMM A5.103	H. brachyrhynchus	Europe	dp4 dex.	107	4	0	0	0	111	0	4,5	0,5	0,5	2,5	0	5,5
M 4498	H. leptorhynchus	Europe	dp4 sin.	113,5	6	0	0	0	119,5	0,5	5,5	0,5	0	2	1	6,5
PD 487	H. exiguus	Europe	dp4 sin.	163,5	11	0	0	0	174,5	0	5	4	1	1,5	2	10

YPM PU 11462	*H. exiguus*	Europe	p4 dex.	126,5	7,5	0	0	0	134	0	6,5	2,5	2	0	2	11
Qu 8403	*H. rossignoli*	Europe	p4	84	3,5	0	0	0	87,5	0	5	2,5	0,5	2,5	0	8
Qu 8431	*H. sp.*	Europe	p4 sin.	123	7,5	0	0	0	130,5	0	6,5	1,5	0	2,5	2	8
PD 314	*H. exiguus*	Europe	p4 sin.	145	6	0	0	0	151	0	8,5	1	0,5	3,5	1	10
FAM 75641	*H. crucians*	NA	m1 dex.	140	10	0	0	0	150	0,5	10,5	1,5	0,5	2,5	1	13
FAM 75573	*H. crucians*	NA	m1 sin.	117,5	7,5	0	0	0	125	2	10,5	0,5	0	0	0	13
AMNH 1379	*H. crucians*	NA	m1 sin.	104,5	8,5	0	0	0	113	1	8	1,5	0	2,5	1	10,5
FAM 75739	*H. crucians*	NA	m1 dex.	139,5	8,5	0	0	0	148	0	14,5	1	0	6,5	1	15,5
AMNH 649	*H. crucians*	NA	m1 sin	133,5	17,5	0	0	0	151	0	7	2	1,5	1	2	10,5
FAM 75629	*H. brevirostris*	NA	m1 sin.	115,5	11	0	0	0	126,5	0	7	1,5	0,5	0,5	1	9
FAM 75725	*H. horridus*	NA	m1 sin.	124	11	0	0	0	135	0,5	9	1,5	0	0,5	0	11
AMNH 647	*H. crucians*	NA	m1 dex.	119,5	8,5	0	0	0	128	0	7	4	1,5	0	0	12,5
YPM PU 10916	*H. horridus*	NA	m1 dex.	122,5	13	0	0	0	135,5	1	5	2,5	1	1,5	1	9,5
FAM 75575	*H. crucians*	NA	m1 dex.	117,5	14,5	0	0	0	132	1,5	9,5	0	0	1	0	11
AMNH 26066	*H. sp.*	Asia	m1 dex.	152,5	9	0	0	0	161,5	1	7,5	1	0	0	1	9,5
AMNH 19125	*H. pervagus*	Asia	m1 sin.	111	7,5	0	0	0	118,5	0	7	1	1,5	0,5	1	9,5
A 4478	*H. filholi*	Europe	m1 sin.	128	9,5	0	0	0	137,5	0,5	11	2	0	5	1	13,5
Qu 8385	*H. filholi*	Europe	m1 dex.	122,5	8,5	0	0	0	131	2	6,5	0,5	0	3	1	9
Qu 8342	*H. sp.*	Europe	m1 dex.	107	7	0	0	0	114	0	7,5	1	1	3	1	9,5
Qu 8382	*H. sp.*	Europe	m1 sin.	119	6,5	0	0	0	125,5	1,5	6,5	2	0,5	4,5	1	10,5
Qu 8465	*H. filholi*	Europe	m1 sin.	103	7	0	0	0	110	0	9	1,5	0,5	1,5	1	11
Qu 8367	*H. sp.*	Europe	m1 dex.	149	6	0	0	0	155	1	8	1,5	0,5	3,5	1	11
Qu 8431	*H. sp.*	Europe	m1 sin.	131	5,5	0	0	0	136,5	0	8,5	1	1,5	3,5	1	11
PD 314	*H. exiguus*	Europe	m1 sin.	131,5	5	0	0	0	136,5	0	8,5	0,5	1	4	1	10
M 9622	*H. sp.*	Europe	m1 dex.	124	8,5	0	0	0	132,5	0,5	6	0,5	1,5	2	1	8,5
M 9621	*H. sp.*	Europe	m1 sin.	145,5	8	0	0	0	153,5	0	6,5	2,5	0,5	2,5	2	9,5
YPM PU 11462	*H. sp.*	Europe	m1 dex.	125	6,5	0	0	0	131,5	0	7	2	2	3	2	11
M 7486	*H. heberti*	Europe	m1 sin.	138,5	6,5	0	0	0	145	0	9	1,5	0	2	2	10,5
FAM 75641	*H. crucians*	NA	m2 dex.	143,5	9	0	0	0	152,5	0	10	0,5	1	0	2	11,5
FAM 75613	*H. crucians*	NA	m2 dex.	136,5	13,5	0	0	0	150	0,5	12	0	1	4	2	13,5
FAM 75634	*H. sp.*	NA	m2 dex.	108,5	12	0	0	0	120,5	1	8,5	0,5	0	0,5	1	10
FAM 75749	*H. crucians*	NA	m2 sin.	114	15,5	0	0	0	129,5	0	9	0,5	0	0,5	0	9,5
AMNH 38810	*H. crucians*	NA	m2 sin.	147	12,5	0	0	0	159,5	1	9	0,5	0	1	1	10,5
AMNH 12233	*H. crucians*	NA	m2 dex.	138,5	11	0	0	0	149,5	0,5	8	2	1,5	0	2	12
FAM 75614	*H. crucians*	NA	m2 dex.	146,5	9	0	0	0	155,5	3	5	1,5	1	2,5	1	10,5

FAM 75725	*H. horridus*	NA	m2 sin.	122,5	9,5	0	0	0	132	0	9	2	0,5	0	0	11,5
AMNH 39430	*H. horridus*	NA	m2 dex.	121	11,5	0	0	0	132,5	0,5	7	3	0	2	1	10,5
YPM-PU 12694	*H. mustelinus*	NA	m2 sin.	123,5	7,5	0	0	0	131	0	8,5	1,5	0,5	0	2	10,5
YPM 12769	*H. crucians*	NA	m2 dex.	125,5	8	0	0	0	133,5	0	5	3,5	1,5	0	1	10
YPM PU 13801	*H. horridus*	NA	m2 sin.	120	8,5	0	0	0	128,5	0	7,5	0,5	1,5	0	2	9,5
YPM 10075	*H. leptocephalus*	NA	m2 dex.	116	11,5	0	0	0	127,5	0	7	1,5	0,5	0,5	2	9
taxon average				127,92	10,69					0,5	8,11	1,34	0,69	0,84	1,3	10,65
standard deviation				12,96	2,35	0	0	0	12,79	0,84	1,9	1,06	0,59	1,24	0,75	1,21
MNHN No.29-15	*H. sp.*	Asia	m2 sin.	122,5	10	0	0	0	132,5	1,5	9,5	1	0	1	2	12
No. 29-15	*H. sp.*	Asia	m2 dex.	148	6,5	0	0	0	154,5	3	7	1,5	1	3	2	12,5
taxon average				135,25	8,25					2,25	8,25	1,25	0,5	2		12,25
standard deviation				18,03	2,47	0	0	0	15,55	1,06	1,76	0,35	0,7	1,41	0	0,35
A 4478	*H. filholi*	Europe	m2 sin.	121	8,5	0	0	0	129,5	0	8,5	1	1	0	2	10,5
Qu 8385	*H. filholi*	Europe	m2 dex.	128,5	9	0	0	0	137,5	1	7,5	1	0	2	2	9,5
Qu 8391	*H. rossignoli*	Europe	m2 dex.	119,5	8,5	0	0	0	128	0	7,5	0,5	1	0,5	1	9
Qu 8367	*H. sp.*	Europe	m2 dex.	144	8,5	0	0	0	152,5	1	9,5	1	1,5	0	2	13
?Quercy	*H. leptorhynchus*	Europe	m2 dex.	135	9,5	0	0	0	144,5	0	7,5	1,5	1	0,5	2	10
A 4472	*H. filholi*	Europe	m2 dex.	121,5	6	0	0	0	127,5	0	7	1	0	0	2	8
Qu 8431	*H. sp.*	Europe	m2 sin.	110,5	11,5	0	0	0	122	0,5	7,5	1,5	0,5	0,5	2	10
Qu 8355	*H. leptorhynchus*	Europe	m2 sin.	124	8,5	0	0	0	132,5	0	6,5	0	1	0,5	2	7,5
Mo 39	*H. rossignoli*	Europe	m2 sin.	139,5	6,5	0	0	0	146	0,5	6	0,5	0	0,5	1	7
PD 314	*H. exiguus*	Europe	m2 sin.	134	6	0	0	0	140	0	8	1	0	2,5	1	9
NMHW 2009z0084/0004a	*H. exiguus*	Europe	m2 sin.	128	7	0	0	0	135	0	7	2	1	0	2	10
M 9622	*H. sp.*	Europe	m2 dex.	115,5	5,5	0	0	0	121	0	6	1	1,5	0	2	8,5
M 1669	*H. brachyrhynchus*	Europe	m2 dex.	118,5	6,5	0	0	0	125	0	6,5	1	1	1,5	2	8,5
YPM PU 11462	*H. sp.*	Europe	m2 dex.	120,5	7	0	0	0	127,5	0	8	1,5	1	0,5	2	10,5
M 9621	*H. sp.*	Europe	m2 sin.	140	8,5	0	0	0	148,5	0	7	2,5	1	0,5	2	10,5
taxon average				126,66	7,8					0,2	7,33	1,13	0,76	0,63	1,8	9,43
standard deviation				9,95	1,62	0	0	0	9,96	0,36	0,93	0,61	0,53	0,76	0,41	1,48
FAM 75641	*H. crucians*	NA	m3 dex.	138,5	10	0	0	0	148,5	0	8	0,5	0	0,5	1	8,5
FAM 75630	*H. horridus*	NA	m3 sin.	139,5	8,5	0	0	0	148	0	4	4,5	0,5	0	1	9
AMNH 1379	*H. crucians*	NA	m3 sin.	118	12,5	0	0	0	130,5	1,5	7	0,5	0	0,5	1	9
AMNH 12233	*H. crucians*	NA	m3 dex.	131	10,5	0	0	0	141,5	1	9	0,5	0,5	1	2	11
YPM 10075	*H. leptocephalus*	NA	m3 dex.	120,5	11,5	0	0	0	132	0	13	0	0	0,5	1	13

YPM PU 13801	*H. horridus*	NA	m3 sin.	119	8	0	0	0	127	0	6	0,5	1	0	1	7,5
FAM 75720	*H. horridus*	NA	m3 dex.	148	10,5	0	0	0	158,5	0,5	7,5	2	2	0	1	12
NMHW 2005z0229/0001	*H. incertus*	Asia	m3 sin.	124	5,5	0	0	0	129,5	0	6	2	1	0	0	9
NMHW 2005z0229/0002	*H. incertus*	Asia	m3 sin.	110	3,5	0	0	0	113,5	0	9	2	0	0	0	11
Qu 8416	*H.* sp.	Europe	m3 sin.	113,5	13	0	0	0	126,5	1	7	1	0,5	1,5	2	9,5
Qu 8367	*H.* sp.	Europe	m3 dex.	149	9,5	0	0	0	158,5	0	6	1,5	1	0,5	2	8,5
?Quercy	*H. leptorhynchus*	Europe	m3 dex.	120	8	0	0	0	128	0	7	0	2	0	2	9
PD 314	*H. exiguus*	Europe	m3 sin.	132	5	0	0	0	137	0	7,5	1	0,5	0	1	9
NMHW 2009z0084/0004a	*H. exiguus*	Europe	m3 sin.	125,5	8	0	0	0	133,5	0	5,5	1	1,5	0	2	8
M 2347	*H. leptorhynchus*	Europe	m3 sin.	117	6	0	0	0	123	0	6	0	0	0	1	6
M 1669	*H. brachyrhynchus*	Europe	m3 dex.	114	6,5	0	0	0	120,5	0	7	0,5	1,5	1	2	9
M 9621	*H.* sp.	Europe	m3 sin.	140,5	8,5	0	0	0	149	0	7	1	1	0	2	9
BMNH 29752	*H. minor*	Europe	m3 dex.	144,5	7,5	0	0	0	152	0	7,5	1,5	2,5	0	2	11,5

0	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	Axis 11	Axis 12	Axis 13
PB	-0.22748	-1.3548	0.87433	-0.33472	-0.23965	-0.07982	0.024432	-0.44005	-0.40698	0.36526	0.45797	0.017288	-0.00017031
PB	0.10789	-1.6798	1.1417	-0.041403	0.0083568	-0.68386	0.1539	-0.0041129	-0.056166	-0.043568	0.70208	0.017476	-4.07E-05
PB	0.087671	-1.5266	0.51909	-0.13549	0.52469	0.055204	0.50569	-0.44528	-0.17672	0.3119	0.82932	0.026214	4.38E-06
PB	-0.061161	-1.278	0.58597	-0.21054	-0.25534	-0.046167	0.027939	-0.29569	-0.24389	0.42444	0.58404	0.015948	-0.00015535
PB	-0.27454	-1.1195	0.44816	0.38841	-0.77932	0.060391	-0.55141	-0.42766	0.3408	-0.96967	-0.048272	-0.0052762	-0.00041384
PB	-0.92843	-1.0932	0.28819	0.075556	0.13377	0.36596	0.051879	-1.1368	-0.38214	-0.39689	-0.17292	0.0086663	-0.00022711
HH	0.58866	-0.49053	-0.42825	-0.013909	0.40706	0.97819	0.1075	-0.55614	-0.080845	-0.011772	-0.28529	0.019153	-0.00012968
HH	0.2579	0.090664	0.11024	-1.5247	-1.3772	-0.065747	0.85101	0.098453	-0.022869	0.065546	1.0983	0.011012	-0.0003647
HH	0.55163	-0.031204	0.99271	-1.4492	-1.7102	-0.65536	0.021267	0.70348	-0.28931	0.2808	0.28485	0.008051	-0.00034696
HH	0.80299	-1.0099	-0.38243	0.53343	-0.11928	0.31663	0.12588	-1.0266	-0.33432	0.54503	0.48981	0.014687	-9.03E-05
HH	0.93391	-0.38459	-0.31072	-0.64263	-0.1278	1.0589	0.024592	-0.19846	-0.42486	1.283	0.19498	0.027318	-0.00015055
HH	-0.14372	-1.2409	-0.43361	0.63262	-1.0073	0.33106	-0.29735	-0.88832	0.16804	0.22684	0.9867	-0.0028723	-0.00038032
HH	0.31868	-1.5205	0.90774	0.010316	-0.35168	0.081206	-0.075829	-0.72631	-0.16831	-0.1284	0.4792	0.015352	-0.00024516
CC	2.4949	-1.5401	1.6826	-0.39058	0.82975	-0.16481	0.35965	0.53763	0.23923	-0.47114	0.24377	0.043141	0.00011855
CC	2.5459	-0.14806	-0.19182	-0.70817	0.54199	2.532	-0.062135	-0.31192	0.38365	-0.38139	-0.66043	0.039039	-0.00031932
CC	2.1991	-0.94989	-0.0362	0.29386	-0.2594	1.3196	-0.1352	-1.1523	0.028245	-0.068611	0.19354	0.023656	-0.0003011
CC	2.3485	-0.86536	0.50238	0.76878	-0.83621	-0.18162	-0.52682	-0.90227	-0.42963	-0.067027	-0.40059	0.010307	-0.00017375
CC	2.3799	-1.1349	0.63387	0.12812	-0.17147	0.81828	-0.15121	-0.66897	0.10158	-0.3272	0.10292	0.026551	-0.0002341
CC	1.9836	-1.0714	0.71617	0.69322	-0.52272	-0.90539	-0.30686	-0.13578	-0.22633	-0.01304	-0.065401	0.011258	1.34E-06
CC	2.8792	-1.2943	1.508	0.031562	0.4827	-0.63146	0.13369	0.42997	-0.016151	-0.33106	-0.11115	0.035541	0.00016638
CC	1.7355	-0.94273	0.21148	0.44552	-0.47935	0.67956	-0.24321	-1.4107	-0.47082	0.079932	-0.12796	0.017195	-0.00025303

CC	2.3962	-0.90702	0.43574	0.53049	-0.21969	0.044849	-0.16055	-0.78218	-0.40025	0.071205	-0.24234	0.021024	-5.54E-05
CC	2.45	-1.6342	1.7031	-0.6822	1.372	0.12796	0.68241	0.63882	0.31356	-0.4154	0.43014	0.053209	0.00019134
CC	1.9965	-1.0714	0.28614	-0.10202	0.50609	1.3737	0.30457	-1.2536	-0.29769	0.095678	0.11828	0.037567	-0.00014102
CC	1.3765	-0.96357	0.48489	0.91979	-1.117	-0.76845	-0.59175	-0.92366	-0.60839	0.10767	-0.27294	-0.00013669	-0.00016689
CC	1.6729	-1.385	1.6443	0.37156	-0.31235	-1.5559	-0.22702	0.24099	-0.35575	-0.22993	-0.17431	0.015453	9.19E-05
CC	1.6505	-1.3938	1.8523	0.30867	-0.20683	-1.6697	-0.18376	0.10077	-0.59417	-0.19633	-0.36594	0.017833	0.00013232
CC	2.0675	-1.0684	0.61556	0.72663	-0.656	-0.76668	-0.38386	-0.058748	-0.034108	-0.098274	0.042037	0.0094036	-5.53E-05
CC	1.8712	-1.3324	1.3235	0.15711	-0.27897	-0.34563	-0.21425	-0.28824	-0.17096	-0.35454	-0.065949	0.021153	-0.0001063
CC	1.7461	-1.3723	1.518	0.07832	-0.20449	-0.43181	-0.1775	-0.39893	-0.34862	-0.34151	-0.1827	0.02275	-8.55E-05
CC	2.3337	-1.0816	0.96265	0.059692	0.29044	0.34707	0.092832	-0.95911	-0.59661	-0.030365	-0.36913	0.033678	-2.50E-05
CC	2.2993	-0.71903	-0.33495	0.72964	-0.44091	0.68493	-0.22154	-1.1885	-0.28137	0.24456	-0.044284	0.016275	-0.00017899
CC	1.9287	-1.0775	0.55612	-0.29314	0.67918	1.2285	0.48224	-1.3464	-0.51665	0.073124	0.0069298	-0.54508	-0.00021096
CC	3.2136	-0.84291	1.3506	-1.1243	1.3857	0.14056	0.71935	1.2772	0.059381	0.32346	0.021356	-0.67336	0.00016867
CC	1.5594	-0.98662	0.32436	0.72286	-0.61824	-0.41703	-0.29923	-0.7413	-0.41718	0.17095	-0.044695	0.0091167	-9.53E-05
CC	1.7574	-0.99218	0.14147	0.20325	0.12942	0.91292	0.12144	-1.2833	-0.42625	0.21302	0.049007	0.027716	-0.00013954
CC	1.4006	-0.8511	-0.41571	0.64633	-0.097412	0.31768	0.081423	-1.0971	-0.44595	0.56263	0.22289	0.016743	-4.88E-05
CC	2.2435	-0.60468	-0.77808	1.1431	-1.0331	0.45588	-0.52007	-1.023	-0.02486	0.2585	0.12935	0.0027767	-0.00025988
AJ	-2.1574	0.8968	-1.8603	-1.3515	0.44563	0.13496	1.6967	0.62661	0.3322	-0.12224	0.74057	0.0045044	-9.87E-06
AJ	-2.2724	0.079398	-1.5066	-0.33177	0.25041	0.23923	0.56847	0.3901	0.42696	-0.1571	0.30848	-0.0054876	-0.00012661
AJ	-2.9926	-0.28701	-2.5129	1.4618	0.75062	-1.4676	0.58556	0.21912	0.0048644	0.63964	0.43731	-0.022634	0.00035924
AJ	-2.6578	-0.14638	-2.3546	0.85505	0.81826	-0.73169	0.54971	0.51759	0.21126	0.64648	0.40536	-0.013271	0.00025342
AJ	-1.852	0.1839	-2.1221	0.33978	1.2331	-0.32472	0.66368	0.62506	-0.09298	0.91359	-0.099066	0.0021129	0.00033811
AJ	-1.8873	0.73778	-2.7842	0.18473	-0.12944	-0.18066	0.41165	1.1346	0.64541	0.62573	0.48344	-0.017356	5.39E-06
AJ	-2.1565	-0.011684	-1.8737	-0.48104	0.60507	1.0708	0.27211	1.1275	0.93592	0.33259	0.51456	0.0018517	-0.00014675
AJ	-1.5	0.36486	-2.6006	1.0281	-0.59999	-0.4755	0.12548	0.41846	0.77624	-0.19741	0.41962	-0.029581	-0.00011441
AJ	-2.4926	-0.31383	-1.6503	0.58898	0.33874	-0.28287	0.17669	0.20723	0.27691	0.065864	0.13879	-0.014054	-1.11E-05
AJ	-2.076	1.8389	-2.1651	-1.0153	-1.529	-1.7831	2.63	-0.59009	0.091496	-1.7078	1.2227	-0.0308	-0.00019051
AJ	-1.4354	-0.56881	-0.6476	0.39091	0.32397	-0.66236	0.2878	-0.59619	-0.8355	0.78148	-0.15147	0.0024159	0.00012576
AJ	-1.4976	-1.0068	-0.93897	0.18948	1.2788	0.098676	0.91314	-0.39459	-0.11205	0.48738	0.73839	0.016501	0.00018127
AJ	-1.7307	-0.78894	-0.96095	1.1035	0.4674	-1.9909	0.47988	0.048938	-0.57443	0.83343	0.33686	-0.0080176	0.00039442
AJ	-1.9945	-0.49603	-1.4123	0.86715	0.32447	-0.22867	0.11806	-0.21188	0.29235	-0.39935	-0.012882	-0.013805	-5.04E-05
AJ	-1.8524	-0.41544	-1.4419	0.68063	1.3794	-0.43287	0.73025	-0.2302	-0.19819	0.089758	-0.18191	0.0025022	0.00028718
AJ	-2.4497	-0.51604	-1.5466	0.87289	0.64329	-0.55356	0.36681	-0.14686	0.1073	-0.094528	0.099675	-0.012454	9.18E-05
AJ	-1.7594	-0.30477	-1.667	1.0391	0.73947	-0.6188	0.36586	-0.19854	-0.049281	0.0055616	-0.19537	-0.00975	0.00017884
AJ	-1.7925	-1.233	-0.24602	0.21439	0.82593	-0.71716	0.62371	0.035978	-0.04699	0.17087	0.67217	0.0078576	0.00014873
AJ	-2.4877	-0.66443	-0.81995	0.93755	0.26799	-1.4382	0.093649	0.20989	0.020434	-0.35962	-0.15372	-0.019142	0.00010829
PL	2.4348	-0.52371	0.048811	1.1074	0.0077057	-1.3877	-0.28161	1.0526	0.4553	-0.56771	-0.50722	0.0050683	0.000224
PL	2.3161	-0.065213	-1.4947	1.2109	0.037276	0.65217	-0.15167	-0.55714	0.22523	-0.064195	-0.41864	0.0078099	-2.70E-05
PL	1.1884	-0.40928	-0.98263	0.54504	-0.40291	0.5994	-0.35566	0.54274	0.97482	-0.31368	0.28345	0.0019661	-0.00023184
PL	0.49458	-0.13797	-1.221	1.2016	-0.00080492	-0.22019	-0.32796	0.31615	0.69333	-0.91008	-0.60554	-0.010791	-5.13E-05
PL	1.7195	-0.59243	-0.92686	1.2127	-0.76384	-0.21811	-0.58407	0.9808	1.4138	-0.78614	0.43922	-0.0093158	-0.00019091

PL	2.1934	-0.029184	-0.85694	0.51563	1.5183	0.81632	0.35893	0.21425	0.51815	-0.93774	-1.0342	0.026119	0.00018753
PL	2.6362	0.68986	-2.5542	1.9662	-0.20004	0.50159	-0.5458	-0.091106	0.72692	-0.60692	-1.0777	-0.011136	-2.70E-05
PL	2.9179	0.5768	-2.4163	1.649	-0.015444	1.1537	-0.47993	-0.018034	1.0623	-0.88171	-0.91034	-0.0033966	-0.0001209
LL	-0.38512	0.49433	0.067472	-1.1395	-0.63422	-1.3216	0.51763	1.1941	-0.40832	0.41922	-0.15883	0.0046792	4.21E-05
LL	-1.1049	0.010624	-0.99907	-0.034475	-0.066694	-0.31551	0.009242	0.083362	-0.72289	1.3135	-0.29793	0.0022725	5.54E-05
LL	-1.1978	-0.68779	-0.16864	0.31196	0.52174	-1.2619	0.35068	-0.038178	-0.77609	0.66216	-0.20474	0.0056292	0.00025944
LL	-1.656	-0.60201	-0.71524	0.62286	-0.50341	-0.68129	-0.17175	-0.56543	-0.52073	0.5066	-0.015096	-0.01211	-9.83E-05
LL	-0.29261	-0.20938	0.038926	0.049743	-0.78633	-1.2362	-0.5668	1.1356	-0.16504	0.51575	-0.45554	-0.006396	-2.39E-05
LL	-0.78898	-0.46461	-0.34945	0.081228	-0.21491	-0.54572	-0.13307	0.39849	-0.16781	0.479	-0.067835	0.00010365	-3.10E-05
LL	-0.34207	-0.79679	-0.82454	0.31253	1.0129	0.39709	0.62645	-0.55971	-0.099397	0.22073	0.28404	0.017987	0.00010015
LL	-0.84933	-0.27896	-0.30514	-0.49189	0.39465	-0.35351	0.2036	0.68908	-0.41402	0.96866	-0.16022	0.013711	0.00011743
LL	-0.49773	-0.52783	-0.64695	0.216	0.3894	0.13636	0.23059	-0.50929	-0.40437	0.43392	-0.12484	0.010162	1.18E-05
LL	-0.40749	-0.51554	0.049098	0.063563	0.072681	-1.2253	-0.023433	0.96065	-0.18374	0.45245	-0.18666	0.004356	0.00015812
LL	-1.0093	-0.51224	-0.12812	0.64942	0.62857	-0.94083	0.084752	-0.24286	-0.39116	-0.65071	-1.0156	-0.0020685	0.00013113
LL	-0.5178	-0.37284	0.77373	-0.36556	1.1603	-1.5064	0.24468	1.5391	-0.18775	-0.38132	-1.1335	0.014841	0.0003663
LL	-0.49205	-0.37583	-0.38282	0.80931	0.51389	-0.79852	-0.0094746	-0.1437	-0.2036	-0.68728	-1.0161	-0.0031738	0.00011251
LL	-0.2137	-0.5129	-0.52279	0.20236	0.22386	0.30442	0.090968	-0.58077	-0.35014	0.26084	-0.24193	0.0099442	-6.25E-05
LL	-0.89082	-0.60632	0.39552	-0.43651	0.60057	-0.55534	0.28246	0.030599	-0.82457	0.57361	-0.50309	0.017444	0.0001372
LL	-0.46048	-0.40298	1.0521	-1.1168	0.4458	-1.2656	0.06823	1.8885	-0.3811	0.72795	-0.52208	0.020928	0.00023461
LL	-0.8985	-0.19697	0.0017878	-1.5239	0.90793	1.1454	0.43528	0.17557	-0.65561	1.0785	-0.37312	0.034369	-3.50E-05
LL	-1.4593	-0.035043	-0.31671	-1.1296	1.5424	0.93477	0.59472	0.1558	-0.49415	0.30543	-0.90762	0.028106	7.91E-05
LL	-1.2527	-0.88233	-0.20134	0.29473	1.0874	-0.5653	0.69944	-1.0387	-1.0694	0.52192	-0.25678	0.015659	0.0002529
LL	-1.0878	-0.49745	0.33465	-0.68535	0.76589	-1.1479	0.40096	1.1816	-0.55675	0.95811	-0.20375	0.018287	0.00030553
LL	-1.3271	-0.79653	0.027347	-0.37716	1.3951	-0.083672	0.83996	-0.7794	-1.0949	0.71487	-0.28839	0.026837	0.00024219
LL	-1.1053	-0.55295	0.90763	-0.51589	1.0952	-1.4687	0.25213	1.5612	-0.09194	-0.46084	-0.9133	0.012919	0.00029887
LL	-1.7187	-0.50096	-0.057246	-0.04455	1.2007	-0.73591	0.46263	0.13306	-0.49536	-0.18894	-0.80366	0.009092	0.00022828
LL	-2.038	-0.5659	-0.37592	0.54467	0.66773	-0.61288	0.21872	-0.87698	-0.70818	-0.38367	-0.8916	-0.0038249	6.44E-05
VV	-2.3915	0.065353	-1.037	-0.88009	-0.5602	0.98193	0.027683	0.54868	0.81478	-0.56167	0.29625	-0.0097628	-0.00051215
VV	-2.5502	-0.33361	-1.0734	0.011181	-0.49963	0.48484	-0.39785	0.30262	0.61853	-0.39035	0.04237	-0.017804	-0.00041281
VV	-2.8973	0.14618	-1.4539	-0.27197	-1.6854	0.43153	-0.54263	0.65396	1.0478	-0.60051	0.47556	-0.034603	-0.00068767
VV	-2.2053	0.33953	-0.60292	-1.0031	-1.1847	1.055	-0.96176	0.79894	0.31441	0.069947	-0.71942	-0.013727	-0.00062529
VV	-3.5715	2.9741	4.8838	6.1754	-2.0373	2.7324	3.6303	1.999	0.18672	0.28746	-0.18873	-0.0011539	-0.00035659
VV	-1.5415	1.1388	0.036551	-0.57969	-1.2013	0.4577	-2.0508	0.30182	-0.87237	0.53031	0.47077	-0.01666	-0.00043904
VV	-1.9397	1.2934	1.7937	0.11545	0.48415	0.37793	-0.37265	-1.51	1.4597	1.1375	0.35609	0.005204	-0.0006521
VV	-2.5682	0.33747	1.7401	0.6653	-1.0181	-0.19381	-0.31454	-1.9073	1.9389	0.80499	-0.23438	-0.016867	-0.00098863
VV	-1.5428	-1.3397	1.0056	-0.816	0.56302	0.29517	0.28834	-0.19731	-0.13025	-0.37685	0.14015	0.019633	-0.00017992
VV	-1.1648	0.42009	0.33091	0.23606	-1.0326	0.38994	-1.9447	-0.6091	-0.59966	-0.5652	0.68975	-0.01972	-0.00048541
VV	-1.8293	0.45782	0.63386	-1.0662	-1.4351	0.24945	0.22602	-0.83837	0.47324	0.0075143	0.076021	-0.0067261	-0.00074984
VV	-1.8157	1.0424	2.6549	-0.13708	0.46226	-0.02526	-0.46755	-1.1014	1.547	0.73964	0.22812	0.0077803	-0.00065179
VV	-1.4611	0.097448	1.6645	-1.0163	-1.902	-0.27269	-1.2181	1.0084	0.88252	0.40862	-0.5744	-0.01161	-0.00078109
VV	-2.1322	-0.37099	0.23093	-0.7711	-1.9195	0.56049	-1.1335	-0.050577	-0.16606	0.25282	-0.28542	-0.016379	-0.00073568

VV	-1.9479	1.2814	0.27147	-2.8237	-2.2414	-0.47217	1.6931	-0.8505	-0.73958	-1.0528	0.57247	-0.0065565	-0.00064679
VV	-1.6326	-0.055318	1.3094	-2.786	-0.99265	0.9548	0.25928	0.52434	-0.049129	-0.41433	0.068622	0.016841	-0.00064635
VV	-1.4623	0.18739	0.65817	-0.75098	-1.6136	0.80154	-0.42588	-0.68469	0.84408	-0.045084	-0.05208	-0.0088811	0.018435
VV	-1.62	0.90064	0.30982	-0.3912	-1.0145	-0.039926	-1.4038	-0.49747	-1.0162	-0.2602	0.72041	-0.017017	-0.00038102
VV	-2.017	-0.24584	-0.42252	-0.76492	-1.0045	0.51996	-0.53711	0.32315	-0.11772	0.78829	0.059744	-0.0054887	-0.00043685
VV	-1.4275	-0.30974	-0.09349	-0.38732	0.15402	-0.38741	0.85606	-0.20998	0.34212	-1.6454	0.027515	-0.0019443	-0.00017269
VV	-2.0988	-0.82965	-0.29524	0.15584	0.54389	0.33367	0.14292	-0.64982	0.061829	-0.89302	-0.34531	-0.001129	-0.00019553
VV	-1.549	0.55177	-0.87814	-0.55563	-2.0181	1.082	-1.4928	0.82553	0.60405	-0.16951	-0.84552	-0.026621	-0.00079932
VV	-1.7327	-0.68314	-0.047881	0.10605	-0.43046	0.042017	-0.50135	0.2815	0.61552	-1.1504	-0.34027	-0.013549	-0.00038658
VV	-1.674	-0.82302	-0.24589	0.38789	-1.1505	-0.063688	-0.60105	-0.67653	-0.095113	-0.14874	0.059704	-0.016835	-0.00044251
VV	-0.84119	0.3688	-0.092042	-1.6126	-1.249	0.89042	0.17758	-0.091872	-0.10503	-0.11722	0.031188	0.0043888	-0.00056484
VV	-2.3154	-0.038362	-0.2943	-1.1056	-0.46328	1.189	-0.53103	0.48609	0.26344	-0.18426	-0.57208	-0.0027686	-0.00052612
VV	-2.0997	-0.074388	0.22373	-2.3799	0.95085	2.2373	0.20379	0.74753	0.14227	0.06832	-0.58651	0.031551	-0.00037455
VV	-2.6769	-1.2887	0.79042	-0.40672	-0.58758	0.13141	-0.27323	-1.0232	-0.49021	-0.32435	-0.0055494	-0.0036906	-0.00045749
VV	-2.57	-1.5746	1.2663	-0.80914	-0.078465	0.050293	-0.012998	-0.2837	-0.073736	-0.57107	0.31926	0.0065024	-0.00036797
VV	-2.0672	0.79346	4.0521	-0.86295	0.68362	-1.1296	-0.4412	0.12521	1.4848	0.63878	0.035057	0.015053	-0.00048364
VV	-1.8548	-0.35289	1.463	-0.55098	-0.10504	-0.3631	-0.99775	-0.32281	-0.99916	-0.37734	0.17772	0.00055201	-0.00021427
VV	-2.2435	-0.61964	0.48805	-1.9053	1.2393	2.0017	0.41185	0.11549	0.16112	-0.52839	-0.40748	0.030623	-0.00034116
VV	-1.8274	0.24806	-0.14208	-1.6858	-0.32624	1.199	0.52274	-0.037636	0.32639	-1.1026	-0.15771	0.0054684	-0.00053434
VV	-1.7757	0.14855	0.073471	-1.1191	-0.22282	0.62377	0.050142	-0.25019	-0.34359	-0.58003	-0.93358	0.0027986	-0.00037212
VV	-2.0166	-0.45354	0.89878	-1.1133	-0.028559	0.36013	-0.38279	0.3561	-0.14848	-0.67806	-1.0431	0.0049595	-0.00035305
VV	-1.0529	-0.6165	0.41337	-1.1976	-0.2032	1.4209	-0.22321	-0.2252	-0.099412	0.060067	-0.19175	0.016975	-0.00046465
VV	-1.2567	-0.69579	0.44322	-0.056145	-1.3175	-0.67018	-0.28717	-0.35401	-0.053648	-0.73287	0.044226	-0.014503	-0.00041879
NB	2.5094	4.9955	-0.60931	0.4741	2.5246	0.22376	-1.4823	-0.38174	-1.4088	-0.22189	0.84381	0.01447	0.00057591
NB	1.3269	3.1829	-0.51148	0.25524	1.6188	0.49192	-2.2019	0.15935	-1.9355	0.053285	-0.23368	0.0080301	0.00040782
NB	2.9706	7.5206	0.32295	-1.3002	-0.89555	-1.9303	2.8315	-2.4959	0.77403	-0.40734	-0.71478	-0.0014045	-0.00036583
NB	2.0574	6.5325	0.80514	0.40947	0.44804	0.48295	-0.64715	-1.1482	2.6869	1.2883	-0.19804	-0.0013818	-0.00067295
NB	2.0588	6.9717	-0.3617	-0.72324	-0.070668	-2.3177	0.97809	-1.6453	-1.5553	-0.57272	0.17003	-0.010947	0.00025026
NB	3.2213	4.4151	-0.18834	-0.81828	1.9809	1.0399	-2.5705	2.3567	-0.82849	-0.67655	1.0698	0.021521	0.00044313
GG	-1.6972	2.4151	0.30474	9.35E-05	0.26756	0.022511	-2.7766	-0.028159	-1.7524	-0.45307	0.41513	-0.02051	-6.39E-05
GG	-1.3537	1.03	-0.32244	0.54622	-0.2334	0.011687	-1.7161	-0.31311	-0.71656	-0.73696	-0.11915	-0.022158	-0.0002106
GG	-2.5662	3.2898	3.1233	5.8356	-1.5245	3.1895	2.3694	2.5172	-3.2542	-0.39557	0.34942	0.0013592	0.00035667
GG	-1.8806	1.5679	2.285	0.40075	1.9398	-0.38165	0.67792	-1.2847	2.3747	0.97636	-0.782	0.016994	-0.00039532
GG	-1.0037	1.9488	2.3473	0.39453	0.54243	-2.1766	-1.7264	1.7576	1.2051	-0.37893	0.20495	-0.015271	-6.49E-05
GG	-1.944	1.7839	0.8958	0.8498	0.38195	-0.98276	-1.1836	-0.28827	0.73676	0.20626	-0.062896	-0.019426	-0.00025992
GG	-1.4183	1.8584	1.6267	0.74294	1.1833	-0.054057	-0.70698	-0.7801	1.9748	-0.039779	0.19379	-0.0025178	-0.0004594
GG	-1.3376	2.2271	1.7959	0.56867	2.3733	-0.19908	-0.45485	-0.84201	1.3273	0.26325	0.35749	0.012306	-0.00011516
GG	-1.0775	1.8936	0.38045	-1.0279	3.003	1.526	-1.2066	0.15134	-1.3086	-0.5444	1.1903	0.030109	0.00031003
GG	-0.93156	1.053	0.45234	0.25466	0.83592	-0.81303	-1.5937	1.0828	-0.44066	-1.0054	0.5411	-0.0094036	0.00015754
GG	-1.6714	1.7567	0.050818	1.3192	1.7518	-0.63339	-1.2425	-1.0292	-0.63983	-0.39155	0.83526	-0.011113	0.00020526
GG	-0.28375	0.19706	-1.9312	1.0143	0.0077757	0.13391	-0.21494	0.13387	0.41171	-0.16811	-0.49872	-0.012141	-5.32E-05

HNA	3.7462	-0.54949	-0.21886	1.2835	-0.71037	-0.61796	-0.50089	0.19212	0.23128	0.047395	-0.14164	0.0094334	4.16E-05
HNA	3.7948	1.8884	-1.5697	-0.6303	-2.6075	-0.14233	-1.1819	2.7258	0.31513	2.1851	-0.43079	-0.0013088	-0.00020588
HNA	0.75041	0.47279	-1.9975	0.49865	-1.0231	0.07291	0.42112	-0.17103	0.55513	-0.22722	0.6331	-0.010882	-0.00022065
HNA	0.64173	0.58118	-2.8397	1.4918	0.13586	0.079096	-0.13975	0.48989	0.65853	0.15876	-0.39197	-0.012972	0.00010102
HNA	2.8807	1.3583	-1.9157	0.59	-0.62493	-0.2802	0.40634	-0.39588	-0.55079	0.43215	-0.87206	0.0040024	0.00011931
HNA	3.9367	-0.63496	0.1226	0.10641	0.90686	-0.48745	0.92602	1.0266	0.5894	-0.1321	0.62642	0.041045	0.0003778
HNA	2.75	2.4184	-0.04887	-2.6603	-0.60232	-1.066	2.2304	0.78908	-0.85564	-0.38834	-0.59351	0.031108	0.00016499
HNA	1.9245	-0.15554	-1.1154	0.51488	1.1199	1.2108	0.17725	0.49379	1.1609	-1.1956	-0.50113	0.019087	-9.10E-06
HNA	1.6632	0.60392	-1.2218	-1.5939	1.3173	2.1805	1.0487	0.70647	0.26818	0.81335	0.068091	0.049551	4.20E-05
HNA	2.2744	-1.0429	-0.087214	0.36627	-0.083859	0.75882	-0.014341	-0.26449	0.46469	-0.066611	0.58446	0.022915	-0.00015934
HNA	2.2053	-1.2958	1.0705	-0.98719	2.8559	0.73149	1.3187	1.2387	0.78927	-0.80083	0.22766	0.066295	0.00041708
HNA	1.8859	-1.2393	0.53088	0.75929	-0.55803	-1.2587	-0.27929	0.90284	0.55426	-0.14769	0.62013	0.0067075	3.74E-05
HNA	1.4035	-0.80695	-0.64721	0.18461	0.36683	0.27468	0.37355	0.28696	0.23507	0.84783	0.86732	0.024532	9.37E-05
HNA	2.4973	0.71251	-1.4345	-0.38783	-1.5262	0.65154	0.69976	-0.43088	0.30213	0.079198	0.92347	0.0076413	-0.00034446
HEU	1.7791	0.74599	-0.74544	-0.97818	-1.1872	0.56142	0.34555	-0.19152	-0.57312	1.0666	0.085534	0.017118	-0.00023037
HEU	1.1266	-0.49568	-0.13519	0.60416	-0.42182	-0.64275	-0.42804	0.74957	0.42818	-0.31553	-0.25038	2.54E-05	-4.67E-05
HEU	4.3929	-0.16633	0.2046	0.37388	-0.64459	-0.96874	0.46101	0.63629	0.55425	-0.77306	0.32405	0.018955	8.52E-05
HEU	2.7999	-0.71694	0.1575	0.1698	0.41195	-0.14705	0.19462	0.53225	0.053511	0.50059	0.14935	0.031807	0.00019166
HEU	1.0404	-1.0823	0.033455	0.39557	-0.43793	0.62163	-0.12963	-1.2212	-0.28197	0.17075	0.28862	0.014285	-0.00025722
HEU	1.4569	-0.5483	-0.86305	-0.062589	-0.055694	0.33833	0.64716	0.32543	0.56316	0.44756	1.2838	0.020027	-2.92E-05
HEU	1.1437	-0.84119	0.32005	0.70442	-0.91615	-1.3929	-0.43788	0.28314	-0.30955	0.54895	0.09187	0.00037664	2.25E-05
HEU	1.0898	0.15455	-0.19174	0.29582	-0.3573	-0.28438	0.087572	-1.2274	-1.0805	-0.043758	-1.1767	0.0072063	-3.93E-05
HEU	1.4188	0.69864	-0.31652	-0.8287	-0.83977	1.2723	-0.82573	0.19075	-0.54606	0.84178	-1.4284	0.01507	-0.00034179
HEU	2.4548	-1.2861	0.72081	-0.10463	0.71836	0.37709	0.37755	0.20607	0.34417	-0.15852	0.47918	0.03871	6.16E-05
HEU	1.2306	-1.6444	1.3895	0.059313	-0.20737	-0.83433	-0.09408	0.65861	0.43725	-0.45777	0.63873	0.017512	-5.65E-05
HEU	1.1573	-0.71395	0.77404	-0.65138	-0.66172	-0.067791	-0.38647	0.86624	0.0074491	0.63539	0.16875	0.019096	-0.00016904
HEU	2.164	-1.0541	0.45893	-0.1032	-0.17046	0.39197	-0.11623	0.58858	0.6224	-0.048503	0.58458	0.024758	-0.00014203
HEU	3.297	-0.8472	0.56091	-0.45824	1.3296	0.60836	0.64441	0.4851	0.057642	0.37171	0.1056	0.054145	0.00026494

CURRICULUM VITAE

Personal data

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Birthdate and -place:	13. 05. 1986 in Wiener Neustadt

Education

1996	Graduation of the elementary school Herzog-Leopold-Straße-Ost, Wiener Neustadt
2004	Final examination passed with honors at the secondary school Babenbergerring,Wiener Neustadt

Academic studies

WS 2004/05	Matrikulation, Diploma study Biology
SS 2006	Beginning of the second term with field of study Paleobiology
June 2008	Final graduation of the diploma study Paleobiology, Diploma examination with honors: basic subject Paleozoology, optional subject Paleobotany, title of the Master Thesis: "New information on the tooth eruption sequence of European *Hyaenodon*"
October 2008	Immatrikulation for the PhD study Natural science with field of dissertation: Paleobiology, topic: Ecomorphology of European *Hyaenodon*

Awards

2007-08	Awards of a merit scholarship of the University of Vienna for academic success, award of a grant from the capital of donations and special assets from the University of Vienna;
July 2009	Award of the Jackson School of Geosciences Student Member Travel Grant for the SVP (Society of Vertebrate Paleontology) conference in September 2009 in Bristol
2009-10	Awards of advancement scholarships of the University of Vienna (used for travel costs)
October 2009	Award of the **Erich Thenius-Stipendium** (Erich Thenius scholarship) 2009 for the master thesis
September 2011	One of the best ranked at the competition "Zukunftspreis" at the PalGes conference 2011 in Vienna

Relevant Professional Experience

WS 2007/08; 08/09; 09/10	Tutor in the lectures: "Morphologie und Paläodiversität der Vertebraten" ("Morphology and Paleodiversity of Vertebrates") "Paläobiologie der Tiere" ("Paleobiology of animals") "Übungen zur Paläodiversität der Vertebrata" ("Course about the Paleodiversity of the Vertebrates")

SS 2010; 2011	Lector in the lectures: "Palaeobiology of vertebrates — Darwin Award for animals" "Terrestrische Aktuopaläontologie: Rezentversuche für Interpretation paläobiologischer Muster" ("Terrestrial actuopalaeontology — recent experiments for interpretation of paleobiological patterns")
2008-2011	Attendence of meetings and presentation (talk or poster) at: SVP (Society of Vertebrate Paleontology, 2009-2011); PalGes (Paläontologische Gesellschaft, 2011); "Arbeitskreis für Wirbeltierpaläontologie" (2008-2011); ÖPG (Österreichische Paläontologische Gesellschaft (2008-2010);
2009-2010	Several service contracts at the Naturhistorisches Museum Wien (Geologisch-Paläontologische Abteilung) for curatory work (e.g. organisation and inventory of the evertebrate paleozoic collection and parts of the vertebrate collection including Fayum (Egypt), Dévinská Nová Vés (= Neudorf an der March, Slovakia), Hájnacskö (Slovakia), Pikermi (Greece)) and preparation of thin-sections in course of the FWF-Project P20018-N10 (project manager Dr. Alexander Lukeneder)
2010	Service contract at the Institute of Palaeontology (University of Vienna) for organisation and curatory work (reorganisation and inventory of the collection Pikermi)
2010-2011	Conference assistent at: Arbeitskreis Wirbeltierpaläontologie (Paläontologische Gesellschaft) in Vienna organised by Ursula Göhlich 2010; EGU (European Geosciences Union) conference in Vienna in the Austria Center Vienna, 2011; PalGes (Paläontologische Gesellschat) conference in Vienna at the Department for Paleontology (University Vienna), 2011;
2008-2010	Participation in field trips to South Germany and the USA; Excavation in Kryopigi (Greece);

Affiliations

since 2008	student member of the ÖPG (Austrian Paleontological Society)
since 2009	student member of the SVP (Society of Vertebrate Paleontology)

Publications

Bastl K., Morlo M., Nagel D. and E. Heizmann. 2011. Differences in the tooth eruption sequence in *Hyaenodon* ("Creodonta", Mammalia) and implications for the systematics of the genus. Journal of Vertebrate Paleontology 31(1): 181-192.

Bastl K. and T. Neubauer. 2010. Tagungsbericht zum 37. Treffen des Arbeitskreises Wirbeltierpaläontologie in der Paläontologischen Gesellschaft in Wien. Gmit, Nr. 40: 62-64. http://www.palaeontologische-gesellschaft. de/palges/publikationen/akwpal.pdf