universität wien

DISSERTATION

Titel der Dissertation

„Floral evolution in the sarracenioid clade (Actinidiaceae, Roridulaceae and Sarraceniaceae) of Ericales“

Verfasser

Stefan Löfstrand, MSc

angestrebter akademischer Grad

Doctor of Philosophy (PhD)

Wien, 2015

Studienkennzahl lt. Studienblatt:	A 794 685 437
Dissertationsgebiet lt. Studienblatt:	Biologie
Betreuerin / Betreuer:	Univ.Prof. Dr. Jürg Schönenberger

PREFACE

After three years of working with floral structure and development, through the inhalation of alcohol and FAA fumes, ruining days of work because the f*****g block I was cutting cracked in the middle of the floral base after hundreds of slides prepared, the frustration of not finding the developmental stage I'm looking for after what feels like the 1.000th bud I dissect of the same species, struggling to find even one decent, unequivocally synapomorphic trait for my flowers, *et cetera,* I sometimes feel inclined to use Ambrose Bierce's definition of botany:

> BOTANY. The science of vegetables, those that are not good to eat, as well as those that are. It deals largely with their flowers, which are commonly badly designed, inartistic in color, and ill-smelling.
>
> **Bierce, A. 1906.** *The Cynic's Word Book*. New York: Doubleday, Page & Company.

Then I take a day off… or take a walk through the greenhouses and the botanical garden… or think about what I would do if I were to choose another career… and suddenly I feel much more inclined to go by sir Joseph Paxton's, perhaps overly enthusiastic, definition:

> BOTANY. The science of the vegetable kingdom, is one of the most attractive, most useful and most extensive departments of human knowledge. It is, above every other, the science of beauty.
>
> **Paxton, J. 1838.** *Peter Parley's Cyclopedia of Botany.* Boston: Otis, Broaders & Company.

Which leads me to the people I want to thank for my time here in Vienna, and for laying down the path that led me here:

Above all, I want to thank my supervisor Jürg Schönenberger for all the help and support offered during my doctoral studies. I am eternally grateful for the opportunity and everything you have taught me.

Other co-workers to whom I want to express my sincere gratitude are Maria von Balthazar, Marion Chartier, Susanne Sontag, Susanne Pamperl, Ursula Schachner, Andrea Frosch-Radivo, Perica Brodaric, Yannick Städler, and, of course, everyone else at the division of structural and functional botany. Your continuous help, support and encouragement have been vital and much appreciated. I cannot imagine a better group of people to work with.

Current and previous students that deserve special mention are Thomas Kreisberger, Agnes Dellinger, Kerstin Friesenbichler, Lisa Maurer, Stefanie Forster, Anna Franchitz, Florian Etl, Maximilian Nepel, Felix Oberhauser and Sandra Fleck.

Other co-workers at the institute I would like to thank are Michael Barfuss, Elfriede Grasserbauer and Barbara Turner at the molecular systematic division and Walter Till at the herbarium.

For providing material for my studies, I would like to thank Agneta Julia Borg, Peter Endress, Åsa Krüger, Peter Brownless and Eric La Fountaine; the herbaria E, MO and W; and the botanical gardens of University of Vienna, University of British Columbia and University of Zurich, National Botanical Gardens – Castle Garden Schönbrunn, Royal Botanic Garden of Edinburgh and Bergius Botanical Garden.

Previous tutors and co-workers that especially inspired me to pursue a career in botanic research are, in no particular order: Sylvain Razafimandimbison, Åsa Krüger, Annika Bengtson, Frida Stångberg, Per-Ola 'P-O' Karis, Barbro 'Kajsa' Axelius, Birgitta Bremer, Agneta Julia Borg, Kent Kainulainen, Magnus Lundberg, Jenny Smedmark, Torsten Eriksson and Markus Englund.

On a more personal note, I would like to especially thank some people for making my stay in Vienna a time to remember fondly.

Marion – for dinners and rum and whisky and beer, for patiently explaining ecological and statistical theories, for being calm when I'm a nervous wreck or stressed out, for joining in laughter, tears, despair and hope, and most of all, for your friendship. I would never have survived this past year without you.

Agnes – for sharing my office, reminiscing about Sweden – both the good and the bad, for agreeing that Swedish coffee surely is a lot better than Austrian, and for friendship both at the university and outside. You're going to do a splendid job as Jürgs next Ph.D. student!

Thomas – for filling the office happiness and laughter (and the occasional muttered curse), for 'L-T' (something only you, I and Marion will understand), for warm beer, for being a friend both at the university and out in the real world. Vienna felt terribly empty when you went to India and I think we're all glad to have you back, even if you finished your studies and won't hang out at the university.

Yannick – for putting up with (and sometimes joining in) my frustrated ranting, when I was half delirious from writing non-stop for 15+ hours. For talks and laughs on late nights and weekends, when we seem to be the only people left in the building

Michi – for helping to turn this alien city into my home, for providing a safe haven outside the university, and your dear friendship after we decided our lives were taking different paths.

Och några på svenska:

Jürg och Maria – för att ni genast fick mig att känna mig välkommen på jobbet och i Wien, för allt annat ni gjort för mig, från hjälp med studier till flytthjälp och bankkontakter, för trevliga middagar ute i Gumpoldskirchen.

Givetvis vill jag även tacka de vänner jag lämnade bakom mig i Sverige: Emelie, Helder, Henrik och Åsa, för er vänskap och ert stöd. Jag har saknat er i min frånvaro från Stockholm!

Min underbara familj: mamma & pappa, Micke & Nemie, Martina, Andreas & Agnes, Sebastian, Sara & Hugo, My, Mimmi & Fredrik, Anders, morfar & Siw, mormor, farmor (även farfar, som dessvärre inte fick se mig avsluta min doktorsexamen), samt Ulla-Britt & Christian. För att ni alltid finns där för mig genom skratt, tårar, motgångar och framgångar. Det har varit tomt att inte ha er nära.

For everyone I have forgotten and everything I cannot put into words– Thank you. I might not remember now, in the haze of finishing up my thesis, but you have a place in my mind and in my heart. So a final thanks, danke, tack, merci, obrigado, misaotra and kiitos to everyone, in any way, involved in my path towards the completion of this thesis!

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Development status of manuscripts:

Chapter II

Published – Löfstrand SD, Schönenberger J. 2015. Comparative floral structure and systematics in the sarracenioid clade (Actinidiaceae, Roridulaceae and Sarraceniaceae) of Ericales. *Botanical Journal of the Linnean Society* 178: 1–46.

Chapter III

Submitted for publishing in *Botanical Journal of the Linnean Society* (6 July 2015).

Chapter IV

Accepted for publishing with minor revision in *TAXON* (6 July 2015).
Revised manuscript submitted (13 July 2015).

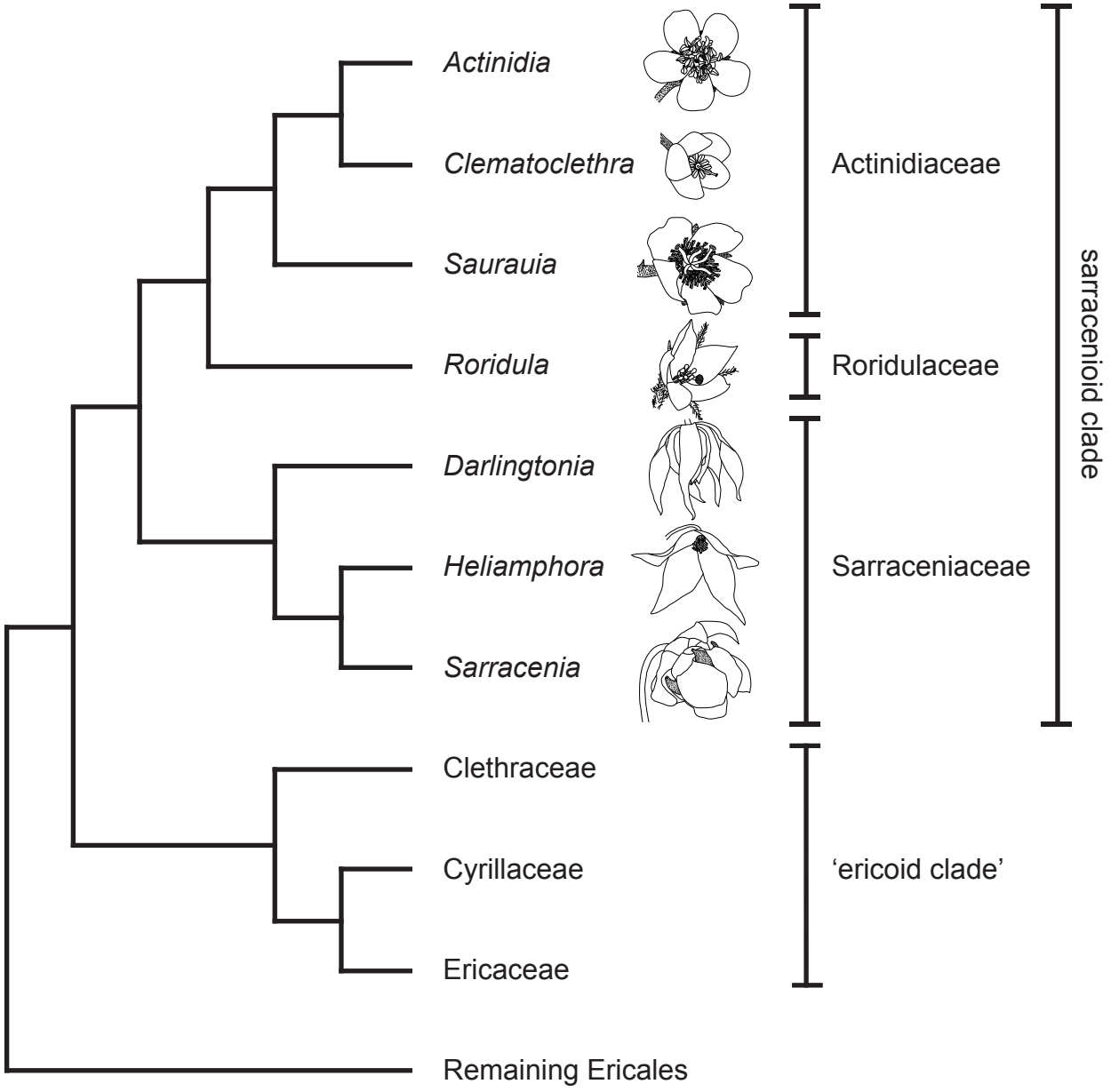
ABSTRACT

The sarracenioid families (Actinidiaceae, Roridulaceae and Sarraceniaceae) form a strongly supported clade in the asterid order Ericales. Together with its sister clade (the ericoids; consisting of Clethraceae, Cyrillaceae and Ericaceae), the sarracenioids constitute the so-called core Ericales. Actinidiaceae comprise *Actinidia*, *Clematoclethra* and *Saurauia*, Roridulaceae consists of the single, proto-carnivorous genus *Roridula*, and Sarraceniaceae are composed of the three carnivorous genera *Darlingtonia*, *Heliamphora* and *Sarracenia*. In pre-molecular classifications, the sarracenioids were often neither affiliated with other ericalean taxa nor were they considered closely related with each other as they differ conspicuously in their habit, way of nutrient uptake and superficial floral structure. In order to analyse floral diversity and infer floral evolution in the clade, a detailed comparative study of floral structure (Chapter II), a study of floral development (Chapter III) and a molecular phylogenetic analysis with ancestral state reconstructions of floral traits (Chapter IV) are presented. Chapter II indicates the following characters as synapomorphic for the sarracenioids: proximally thick petals, polystemony, ovules with a nucellar hypostase, vesicles that appear to contain condensed tannins in floral tissue, and the presence of iridoid compounds in leaves. For the subclade of Actinidiaceae–Roridulaceae, potential synapomorphies include the presence of raphides and mucilage cells in floral tissue, a secretory inner surface in the gynoecium and the absence of synlateral vasculature in the ovary. Chapter III indicates spirally initiated perianth organs and polystemony based on ring primordia with alternipetalous leading stamens as synapomorphic for the clade. Chapter IV strongly supports the monophyly of all sarracenioid families, subclades and genera. Additionally, two distinct geographical lineages are identified in *Saurauia*. The ancestral state reconstructions further support proximally thick petals, polystemonous androecia, and the presence of a nucellar hypostase as synapomorphic for the sarracenioids. Furthermore, all synapomorphies proposed for the Actinidiaceae–Roridulaceae clade in Chapter II are supported.

ZUSAMMENFASSUNG

Die Familien Actinidiaceae, Roridulaceae und Sarraceniaceae bilden eine phylogenetisch klar umschriebene monophyletische Gruppe (*sarracenioids*) innerhalb der Asteridenordung Ericales. Mit ihrer Schwestergruppe den *ericoids*, bestehend aus Clethraceae, Cyrillaceae und Ericaceae, bilden die drei sarracenioiden Familien die sogenannten *core Ericales*. Den Actinidiaceae werden die Gattungen *Actinidia*, *Clematoclethra* und *Saurauia* zugeordnet, die Roridulaceae bestehen aus der einzigen, protokarnivoren Gattung *Roridula* und die Sarraceniaceae umfassen die drei karnivoren Gattungen *Darlingtonia*, *Heliamphora* und *Sarracenia*. Bevor molekulare Klassifikationen in die Systematik einbezogen wurden, wurden die sarracenioiden Familien weder mit anderen Taxa der Ericales assoziiert, noch als untereinander nahe verwandt betrachtet, da sie sich auffällig in ihrer Wuchsform, in ihrer Nährstoffaufnahme und in ihrem oberflächlichen Blütenbau unterscheiden. Um die Diversität der Blüten analysieren und die Evolution der Blütenmerkmale in dieser Gruppe rekonstruieren zu können, wurden eine detaillierte, vergleichende Studie der Blütenstruktur (Chapter II), ein Studie der Blütenontogenie (Chapter III) sowie eine molekularphylogenetische Analyse mit Rekonstruktion der Merkmalsevolution (Chapter IV) durchgeführt. In Chapter II werden die folgenden Merkmale als synapomorph für die Untersuchungsgruppe identifiziert: proximal verdickte Kronblätter, Polystemonie, Samenanlagen mit einer Hypostase im Nucellus, im Blütengewebe auftretende Vesikel mit kondensierten Tanninen und das Vorkommen von Iridoid-Verbindungen in den Blättern. Das Auftreten von Raphiden und Schleimzellen im Blütengewebe, eine sekretorische innere Epidermis des Gynoeciums, und das Fehlen von synlateralen Gefäßbündeln im Ovar, zählen zu potentiellen Synapomorphien für die aus den Actinidiaceae und Roridulaceae bestehende monophyletische Untergruppe. In Chapter III werden spiral initiierte Perianthorgane und Polystemonie basierend auf Ringprimordien mit alternipetalen *leading stamens* als synapomorph für die sarracenioiden Familien identifiziert. Die Analysen in Chapter IV unterstützen die jeweilige Monophylie der drei Familien sowie aller Untergruppen und Gattungen. Im Weiteren werden innerhalb der Gattung *Saurauia* zwei geographisch abgegrenzte Abstammungslinien identifiziert. Die Merkmalsrekonstruktionsanalysen bestätigen die in Chapter II für die *sarracenioids* identifizierten Synapomorphien (verdickte Petalen, Polystemonie, Hypostase). Dasselbe gilt für die in Chapter II vorgeschlagenen Synapomorphien für die monophyletische Gruppe, die aus Actinidiaceae und Roridulaceae besteht.

PREAMBLE



Cladogram of the families and genera in the sarracenioid clade, showing the sister group relationship with the ericoid clade (*i.e.* core Ericales; based on Fig. 1 in Chapter IV) with flower illustrations representing all genera (based on Fig. 1 in Chapter II; not to scale).

BACKGROUND AND AIMS

This Ph.D. project is part of a broader project on floral structure and evolution on the flowering plant order Ericales lead by Univ.-Prof. Dr. Jürg Schönenberger, University of Vienna, Department of Botany and Biodiversity Research, Division of Structural and Functional Botany.

Several recent molecular phylogenetic studies (*e.g.* Geuten *et al.,* 2004; Schönenberger *et al*., 2005; Soltis *et al*., 2011; Magallón *et al*., 2015) have provided a clearer picture of the suprafamilial relationship in Ericales, which is in sharp contrast to what has lately been achieved at the morphological level. Comparative structural studies of suprafamilial clades in Ericales were, before my studies, only available for the balsaminoid clade (Balsaminaceae, Marcgraviaceae and Tetrameristaceae; von Balthazar & Schönenberger, 2013) and the polemonioid clade (Fouquieriaceae and Polemoniaceae; Schönenberger, 2009). It is therefore not surprising that non-molecular synapomorphies are currently lacking for many of the suprafamilial clades in Ericales. The progress in terms of molecular systematics has led to the paradoxical situation that we now have clear phylogenetic hypotheses for the groups, yet we do not know any morphological features that characterise the respective clades.

My studies are focused on the sarracenioid clade, comprising the three families Actinidiaceae, Roridulaceae and Sarraceniaceae. The main goal of the project is to investigate and compare floral structure and development in the sarracenioid clade and its subclades to characterise them at the morphological level and identify potential synapomorphies. On a broader scale this will allow me to test recent hypotheses on floral evolution and phylogenetic relationships in Ericales as a whole, and to contribute to an order-wide morphological dataset that may subsequently be used for various phylogenetic analyses involving extant and fossil taxa, reconstructions of character evolution as well as morphospace analyses.

INTRODUCTION

Ericales are one of the eudicot orders that have undergone major systematic changes due to advances in molecular systematics. The order now comprises 22 families and more than 11,500 species (Stevens, 2001 onwards; Angiosperm Phylogeny Group, 2009). A couple studies aimed at resolving the phylogenetic relationships in Ericales (Anderberg *et al*., 2002; Schönenberger *et al*., 2005) have succeeded in providing a framework of the suprafamilial relationship in the order, but several deeper nodes remain unresolved. In pre-molecular classification systems (*e.g*. Cronquist, 1981; Dahlgren, 1983), the families now classified in Ericales were placed in three different flowering plant subclasses (Dilleniidae, Rosidae and Asteridae) and up to 12 different plant orders. The families and genera of Ericales are highly diverse at all levels of their structure and biology, particularly at the level of floral structure and function, where the evolution of many characters shows extensive homoplasy (Schönenberger *et al.,* 2005).

The sarracenioid clade comprises seven extant genera, classified in three families: Actinidiaceae is the largest family with around 350 species in three genera (52 species in *Actinidia* Lindl., the monotypic *Clematoclethra* (Franch.) Maxim. and around 300 species in *Saurauia* Willd.; Li *et al.,* 2007), followed by Sarraceniaceae with 35 species in three genera (the monotypic *Darlingtonia* Torr., 23 species in *Heliamphora* Benth. and 11 species in *Sarracenia* L.; McPherson *et al*., 2011; Mellichamp, 2009) and Roridulaceae with two species in a single genus (*Roridula* Burm. ex L.; Conran, 2004). The geographical distribution is disjunct, with Actinidiaceae present in the Neotropics (*Saurauia*), temperate to tropical Asia (*Actinidia*, *Clematoclethra* and *Saurauia*) and tropical Oceania (*Saurauia*; Li *et al*., 2007; Tropicos, 2015), Roridulaceae endemic to South Africa (Conran, 2004), and Sarraceniaceae restricted to temperate North America (*Darlingtonia* and *Sarracenia*) and the Guiana Highlands of South America (*Heliamphora*; McPherson *et al*., 2011; Mellichamp, 2009).

VEGETATIVE MORPHOLOGY AND HABIT

The vegetative morphology in the sarracenioid clade is diverse, ranging from herbaceous, rosettiform perennials with an underground rhizome in Sarraceniaceae (*e.g*. Macfarlane, 1908; Berry *et al*., 2005; Mellichamp, 2009), through shrublets, densely covered in glandular (resin secreting) hairs in Roridulaceae (*e.g.* Diels, 1930; Conran, 1996), to trees (*Saurauia*) and lianas (*Actinidia* and *Clematoclethra*) in Actinidiaceae (*e.g*. Gilg & Werdermann, 1925; Soejarto, 1980; Cuong *et al*., 2007; Li *et al*., 2007).

In terms of nutrient uptake, Actinidiaceae are autotrophic (*e.g.* Lechner, 1915), Roridulaceae are proto-carnivorous with mutualistic relationships with hemipteran bugs (*e.g*. Ellis & Midgley, 1996; Anderson, 2005) and Sarraceniaceae are carnivorous (Macfarlane, 1908). Although both Roridulaceae and Sarraceniaceae have an insectivorous habit, they display vastly different pathways of nutrient uptake: Sarraceniaceae attracts insects by secreting a sugary liquid, luring insects to fall into the pitcher leaves, thereafter the insects are digested by enzymes (*e.g*. Hepburn *et al*., 1920, 1927; Jaffé *et al.,* 1992; Pietropalo & Pietropalo, 2005; Karagatzides *et al*., 2009); the digestion of the prey is further assisted by insect larvae and various microorganisms inhabiting the pitchers (*e.g*. Hepburn *et al*., 1927; Karagatzides *et al.*, 2009). Roridulaceae, contrastingly, depend on mutualistic hemipterans (and possibly spiders) inhabiting the plants to eat and digest the insects trapped on the resin-secreting, glandular hairs, thereafter nutrient adsorption takes place from the insect faeces takes place on the leaf lamina (Anderson, 2005). Resin-secreting glandular hairs on vegetative organs are also present in some members of Actinidiaceae (*e.g.* Dressler & Bayer, 2004; Li *et al*., 2007), presenting a potential evolutionary origin of the glandular hairs in Roridulaceae.

FLORAL MORPHOLOGY AND POLLINATION

Flowers in the sarracenioid clade range from less than a centimetre (*Clematoclethra* and *Saurauia p.p.*), through a couple centimetres (*Actinidia p.p.*, *Saurauia p.p.*, *Roridula* and *Sarracenia p.p.*), to several centimetres (*Actinidia p.p.*, *Saurauia p.p.* and most Sarraceniaceae) in diameter (*e.g*. Diels, 1930; Li *et al*., 2007; Mellichamp, 2009). They either have flowers with open access to the floral centre (Actinidiaceae, *Roridula* and *Heliamphora*) or flowers with synorganised organs and more canalised access (*Darlingtonia* and *Sarracenia; e.g*. Diels, 1930; Li *et al*., 2007; Mellichamp, 2009). Flowers are predominately pendant in all genera, and presented either on cymose flowering branches (*Actinidiaceae* and *Heliamphora*; botryoid branches in *Roridula*) or solitary on tall scapes (*Darlingtonia* and *Sarracenia*; Macfarlane, 1908; Hunter, 1966; Soejarto, 1980; Andersson *et al*., 2003; Cuong *et al*., 2007; Li *et al.,* 2007).

The pollination systems are diverse among the sarracenioids, although pollen-collecting bees are generally the main pollinators (*e.g*. Hunter, 1966; Schmid, 1978; Renner, 1989; Ne'eman *et al.*, 2006; Meindl & Mesler, 2011). Some more specialised pollination systems have also been described: *Saurauia* (Actinidiaceae) and *Heliamphora* (Sarraceniaceae) have been described as buzz-pollinated (Renner, 1987; Cane, 1993; Berry *et al*., 2005). *Roridula* (Roridulaceae) are mainly self-pollinated, assisted by the mutualistic hemipterans; juvenile hemipterans feed on the swollen anther connective, upon which the anther rapidly inverts and expels a cloud of pollen, covering both the insects and the stigma (Marloth, 1903; Anderson *et al*., 2003). Solitary bees are the main pollinators of *Darlingtonia and Sarracenia*, brushing the stigmas with pollen upon entry to and exit from the flowers (as a result of the synorganised perianth and styles; *e.g*. Ne'eman *et al*., 2006; Meindl & Mesler, 2011). Flies are potentially significant contributors to the pollination of *Sarracenia* (they often roost in the flowers at night and are commonly covered in *Sarracenia* pollen; Jones, 1908; Mandossian, 1965; Ne'eman *et al*., 2006). The pollination has not been studied in *Clematoclethra* (Actinidiaceae), but Gilg & Werdermann (1925) assume bee pollination.

EARLY FLORAL DEVELOPMENT

Studies of floral development have helped to clarify many controversial interpretations of floral structures (*e.g*. the calyptra of Eupomatiaceae, Endress 2003; the perianth of Penaeaceae, Schönenberger & Conti 2003; the androecium of Malvaceae, von Balthazar *et al*. 2004, 2006). In polystemonous flowers, as present in the sarracenioid clade, a developmental study is the only way to unequivocally determine the organisation of the androecium. Although some detailed developmental studies are at hand for *Actinidia* (Brundell, 1975; van Heel, 1987; Caris, 2013) and, in part, *Saurauia subspinosa* J.Anthony (Brown, 1935) and *Sarracenia purpurea* L. (Shreve, 1906), very little is known about the floral development in *Clematoclethra*, *Roridula*, *Darlingtonia* and *Heliamphora*. Early floral development and androecium organisation has been investigated for many groups in Ericales, providing a good basis for comparison with the sarracenioids (*e.g*. Tsou, 1998; Zhang *et al*., 2007, 2008; Wang *et al*., 2010; Caris, 2013; Zhang & Schönenberger, 2014).

The early perianth development has only been investigated in detail for one species (*Actinidia chinensis* Planch.), indicating a spiral insertion of both perianth whorls (Caris, 2013). Other studies in the clade have focused on androecium development and late floral development (Shreve, 1906; Brown, 1935; Brundell, 1975; van Heel, 1987). In *Actinidia*, the stamens are borne on a ring primordium with leading secondary stamens in alternipetalous positions (van Heel, 1987), thereafter the primordia, depending on the species, continue proliferating centripetally, centrifugally and/or laterally (Brundell, 1975; van Heel 1987; Caris, 2013). In *Saurauia*, Brown's (1935) study indicates a two-whorled androecium with secondary, centrifugal proliferation in the central whorl of stamens. In *Sarracenia*, Shreve's (1906) study indicates a one-whorled androecium with two groups of stamens in every alternipetalous position, but the limited material did not allow for more detailed observations. In later stages the stamens are organised in 10–17 vaguely defined groups (Mellichamp, 2009), but the developmental origin of these groups is unclear. An interesting character occurring in the late floral development of all sarracenioids is inversion of the anthers (*i.e*. anthers that were extrorse during the earlier floral development invert to an introrse orientation and *vice versa*; Schönenberger *et al*., 2012).

ANTHER INVERSION

In Ericales, anther inversion is only present in core Ericales (comprised of the ericoid and sarracenioid clades) and has been suggested to be a potential synapomorphy for the clade (with a secondary loss of the phenomenon in Cyrillaceae; Schönenberger *et al*., 2012). Actinidiaceae, Roridulaceae, Clethraceae and the subfamilies Arbutoideae, Enkianthoideae and Monotropoideae of Ericaceae all have anthers that invert late during the floral development from an extrorse anther orientation to an introrse anther orientation, 'Late anther inversion type A' (Matthews & Knox, 1926; Leins, 1964; Hermann & Palser, 2000; Schönenberger *et al*., 2012; Caris, 2013). The anther inversion in Sarraceniaceae has been described to the opposite direction at anthesis, from an introrse to an extrorse orientation, 'Late anther inversion type B' (Macfarlane, 1908; Berry *et al*., 2005; Mellichamp, 2009; Schönenberger *et al*., 2012). However, the anthers of *Darlingtonia* can be assigned neither an extrorse orientation nor an introrse orientation, due to its peculiar anther shape, hence it does not conform to 'Late anther inversion type B' as currently defined (Macfarlane, 1909; Mellichamp, 2009; Schönenberger *et al*., 2012). Crown group Ericaceae (subfamilies Cassiopoideae, Ericoideae, Harrimanelloideae, Styphelioideae and Vaccinioideae), unlike the sarracenioids, have anthers that invert from an extrorse orientation to an introrse orientation early during floral development, referred to as 'Early anther inversion' (Matthews & Knox, 1926; Leins, 1964; Hermann & Palser, 2000; Schönenberger, 2012; Caris, 2013).

FLORAL MESOFOSSILS

Two fossil genera from the late Cretaceous of North America are tentatively placed in the sarracenioid clade with most morphological similarities shared with extant Actinidiaceae (mainly *Saurauia*): *Glandulocalyx* Schönenberger, von Balthazar, Takahashi, Xiao, Crane & Herendeen and *Parasaurauia* Keller, Herendeen & Crane (Keller *et al.,* 1996; Schönenberger *et al*., 2012). Keller *et al*. (1996) suggest a close relationship between *Parasaurauia* and Actinidiaceae based in part on the prominent, multicellular hairs on the calyx (similar to *Saurauia*), an androecium consisting of ten stamens (similar to *Clematoclethra*), deeply sagittate, basifixed anthers (similar to *Saurauia*), a trimerous gynoecium with fully free styles emerging from a depression on the ovary top (similar to *Saurauia*). Schönenberger *et al*. (2012) suggest a close relationship between *Glandulocalyx* and core Ericales (*i.e*. the sarracenioid and ericoid clades), based mainly on the presence of ventrifixed, extrorse anthers (in Ericales only present in Actinidiaceae, Roridulaceae, Clethraceae and Ericaceae). They further hypothesise the potential of 'Late anther inversion type A' in the genus, as it appears to be closely linked to ventrifixed anthers (Schönenberger *et al*., 2012). Within core Ericales, *Glandulocalyx* shares the strongest similarities with Actinidiaceae, particularly with *Saurauia*. Similarities between Actinidiaceae and *Glandulocalyx* include a polystemonous androecium and largely free styles. The proposed close relationship with *Saurauia* was based mainly on the protruding-diffuse and pendant placentae (Schönenberger *et al*., 2012). Clethraceae also has protruding-diffuse placentae, but unlike Actinidiaceae, Clethraceae is diplostemonous and has largely united styles (Schönenberger *et al*., 2012).

PREVIOUSLY SUGGESTED SYNAPOMORPHIES

Before the studies included in this thesis, very few non-molecular synapomorphic characters have been proposed for the sarracenioid clade. Among them are free styles (with reversals in *Clematoclethra*, *Roridula* and *Heliamphora*) and the presence of a nucellar hypostase in the ovules (Anderberg *et al.*, 2002). Schönenberger *et al.* (2005) discussed polystemony as a potential synapomorphy for the clade (with a reversal in the haplostemonous Roridulaceae). One potentially synapomorphic phytochemical character is the presence of iridoid compounds in leaf tissue (Jensen *et al*., 1975; Albach *et al*., 2002).

TAXONOMIC HISTORY AND SYSTEMATICS

The taxonomic history of the sarracenioid families is complicated, particularly regarding the suprafamiliar affiliations and taxonomic ranks of Roridulaceae and the genera in Actinidiaceae (Kubitzki, 2004). In pre-molecular classifications, much weight was put on superficial floral structure, insectivory and vegetative structures to determine the systematic positions of the sarracenioid genera and families (*e.g*. Netolitzky, 1926; Melchior, 1964; Cronquist, 1981). The widely accepted classification system by Cronquist (1981) placed Actinidiaceae in Theales (Dilleniidae), Roridulaceae in Rosales (Rosidae) and Sarraceniaceae in Nepenthales (Dilleniidae). Actinidiaceae have been variably treated as a natural group, or as a part of, among others, Dilleniaceae or Clethraceae (*e.g*. Lechner, 1915; Hunter, 1966; Cronquist, 1968). *Saurauia* has additionally been treated as the monogeneric family Saurauiaceae, thus restricting Actinidiaceae to *Actinidia* and *Clematoclethra* (*e.g*. Takhtajan, 1966). Roridulaceae have, mostly based on the peculiar vegetative morphology and carnivory, been variably placed in Byblidaceae, Clethraceae, Droseraceae and Ochnaceae, or treated as the natural group Roridulaceae (*e.g*. Engler, 1907; Hallier, 1912; Netolitzky, 1926; Cronquist, 1981; Takhtajan, 1987). Among the sarracenioid families, Sarraceniaceae have the least complicated history and were generally undisputed as a natural group (*e.g*. Macfarlane, 1908; Uphof, 1936; Cronquist, 1981).

Roridulaceae (as a part of Byblidaceae or Droseraceae) and Sarraceniaceae were often considered closely related (together with Nepenthaceae) in early systematic treatments, based on their carnivorous nature (*e.g*. Warming, 1878; Hallier, 1905). However, even before the rise of

molecular systematics, carnivory was disproved as a useful character in suprafamilial systematics (Uphof, 1936; DeBuhr, 1975; Conran & Dowd, 1993). Actinidiaceae was first proposed to be closely related to Ericaceae and Clethraceae by Hunter (1966), based on floral and vegetative morphology. Hufford (1992) again demonstrated their close relationship using morphological and phytochemical data. Dahlhgren & van Wyk (1988) first placed, albeit with expressed uncertainty, Roridulaceae in Ericales using morphological data, followed by Anderberg's (1992, 1993) cladistic analyses, demonstrating the ericalean affinity and close relationships of the sarracenioid families. Based on molecular data, Chase *et al*. (1993) first found a close relationship of the sarracenioids in their angiosperm-wide phylogenetic analysis, but the families did not form a monophyletic group. Anderberg *et al*. (2002) first placed the sarracenioids in a well-supported clade, as sister to the ericoid clade (Clethraceae, Cyrillaceae and Ericaceae *s.l*.). These relationships were continuously recovered in subsequent molecular phylogenetic studies (*e.g*. Schönenberger *et al*., 2005; Soltis *et al*., 2011).

Before this thesis, no study has included all sarracenioid genera in a single molecular phylogenetic analysis. In addition, suprageneric relationships and monophyly of the genera in Actinidiaceae and the infrageneric relationships in *Saurauia* had never been tested. Earlier molecular phylogenetic studies in Actinidiaceae mainly focused on the classification of *Actinidia*, utilising *Clematoclethra* and *Saurauia* solely as outgroups (*e.g*. Li *et al*., 2002; Chat *et al*., 2004). Ellison et al. (2012) investigated the phylogenetic relationships of Sarraceniaceae and demonstrated the suprageneric relationships in the family, but the infrageneric relationships in *Heliamphora* and *Sarracenia* remained largely unresolved. More recently, Stephens *et al*. (2015) investigated the complex evolutionary history and infrageneric relationships of *Sarracenia*, finally presenting a reasonably well-resolved phylogenetic tree of the genus.

RESEARCH OUTLINE

CHAPTER II – COMPARATIVE FLORAL STRUCTURE AND SYSTEMATICS IN THE SARRACENIOID CLADE (ACTINIDIACEAE, RORIDULACEAE AND SARRACENIACEAE) OF ERICALES

As previously stated, the sarracenioid clade has been widely accepted using a molecular systematics approach, but not yet studied morphologically as an entity. Before this study, only the balsaminoid clade (Balsaminaceae, Marcgraviaceae and Tetrameristaceae; von Balthazar & Schönenberger, 2013) and the clade comprised of Fouquieriaceae and Polemoniaceae (Schönenberger, 2009) have been comparatively studied in detail at the floral morphological level in Ericales.

The morphology, anatomy and histology of floral structures are investigated in detail, using techniques such as microtome sectioning, light microscopy (LM), scanning electron microscopy (SEM) and microcomputer X-ray tomography (Micro CT). Additionally, an extensive review of earlier literature is performed.

The aim of Chapter II is to perform a critical comparison of the morphological, anatomical and histological floral characters of the sarracenioid families and genera, as well as to contribute to a more comprehensive understanding of the evolutionary history of Ericales. Secondarily, it attempts to identify potential morphological, anatomical and histological synapomorphies for the sarracenioid clade.

CHAPTER III – EARLY FLORAL DEVELOPMENT AND ANDROECIUM STRUCTURE IN THE SARRACENIOID CLADE (ACTINIDIACEAE, RORIDULACEAE AND SARRACENIACEAE) OF ERICALES

As previously stated, earlier floral developmental studies in the sarracenioid clade have mainly focused on *Actinidia* (Brundell, 1975; van Heel, 1987; Caris, 2013), with some limited studies also performed in *Saurauia* (Brown, 1935) and *Sarracenia* (Shreve, 1906). The early floral development is investigated for additional species of *Actinidia* and *Saurauia*, as well as *Roridula* and *Heliamphora*. Additionally, the later developmental stages of *Clematoclethra*, *Darlingtonia* and *Sarracenia* are investigated. Earlier interpretations of floral development and androecium organisation in the sarracenioid families are complemented and tested with special attention to androecium development. Of additional interest is the perianth development of *Heliamphora*, traditionally interpreted as apetalous (*e.g.* Macfarlane, 1908; Berry *et al*., 2005) and tetramerous to hexamerous. The comparative structural study (Chapter II) challenges that view, and based on the anatomy, histology and morphology of mature flowers indicates a two-whorled, dimerous perianth.

The morphological techniques used in the comparative structural study (Chapter II) are employed to investigate different stages of floral development and compare them to other plant families in the Ericales.

The aim of Chapter III is to increase our understanding of the floral development and evolution in the sarracenioid clade and, potentially, identify previously unknown floral developmental synapomorphies, as well as determine the perianth organisation in *Heliamphora*.

CHAPTER IV – MOLECULAR PHYLOGENETICS AND FLORAL EVOLUTION IN THE SARRACENIOID CLADE (ACTINIDIACEAE, RORIDULACEAE AND SARRACENIACEAE) OF ERICALES

As previously stated, up until this point no single molecular phylogenetic analysis has included all genera of the sarracenioid clade. Particularly problematic are Actinidiaceae, where previous studies have been restricted almost exclusively to *Actinidia*, whereas *Saurauia*, the largest genus of the family, has received very little attention. Hence, a larger scale analysis of the entire clade is needed to affirm the monophyly of *Actinidia*, *Clematoclethra* and *Saurauia* and to investigate their suprageneric relationships.

Standard techniques in molecular phylogenetics are employed (polymerase chain reaction, sequencing and phylogenetic analyses using Bayesian, maximum likelihood bootstrap and parsimony bootstrap diagnostics). Using the phylogenetic relationships in the family as a backbone, ancestral state reconstructions are performed. The reconstructions focus mainly on the findings from the comparative structural study (Chapter II) and previously suggested synapomorphic characters. Phylogenetic reconstructions are performed in RAxML (Stamatakis, 2006), PAUP* (Swofford, 2002) and MrBayes (Ronquist *et al*., 2012). Ancestral state reconstructions are performed with likelihood in Mesquite (Maddison & Maddison 2015).

The aim of Chapter IV is to provide a well-resolved phylogenetic tree of the sarracenioid clade, to test the monophyly of Actinidiaceae and its genera, and to test the potentially synapomorphic characters suggested for the sarracenioids and its subclades suggested in the comparative structural study (Chapter II) and by previous authors (Albach *et al*., 2002; Anderberg *et al*., 2002; Schönenberger *et al*., 2005). This provides a much stronger foundation for evolutionary hypotheses.

CONTEXTUAL LINK BETWEEN THE THREE STUDIES

The research presented in this thesis allows discussion of floral evolution in the sarracenioid clade on a broad scale. Detailed knowledge about the anatomy, histology and morphology of the seemingly disparate flowers of the sarracenioid genera is needed to identify potential floral synapomorphies for the clade and its subclades (Chapter II). Paired with a broad literature review to identify potential non-floral synapomorphies for the clade, Chapter II provides a solid basis for further studies of the sarracenioids. Detailed knowledge about floral development in the sarracenioid genera is needed to identify potential floral developmental synapomorphies for the clade and its subclades (Chapter III). Perhaps most of all, detailed knowledge of androecium development is needed to understand the basic organisation of the polystemonous androecia present in Actinidiaceae and Sarraceniaceae (Chapter III). To interpret the findings of Chapters II and III, a better understanding of the phylogenetic relationships in the sarracenioid clade is needed, particularly in Actinidiaceae (Chapter IV). Only once a solid phylogenetic hypothesis has been formed can the potential synapomorphic characters be tested by means of ancestral state reconstructions (Chapters II–IV).

On a broader scale, the findings of this thesis provide a key component for further studies of floral evolution in Ericales and its suprafamilial subclades, as well as angiosperms as a whole. In addition, the detailed knowledge of floral structure will allow explicit phylogenetic analyses and placement analysis of the floral mesofossils previously associated with Actinidiaceae. This, in turn, allows for well-founded dating analyses and biogeographical analyses, which provides a solid basis for discussions on of both floral and non-floral evolution.

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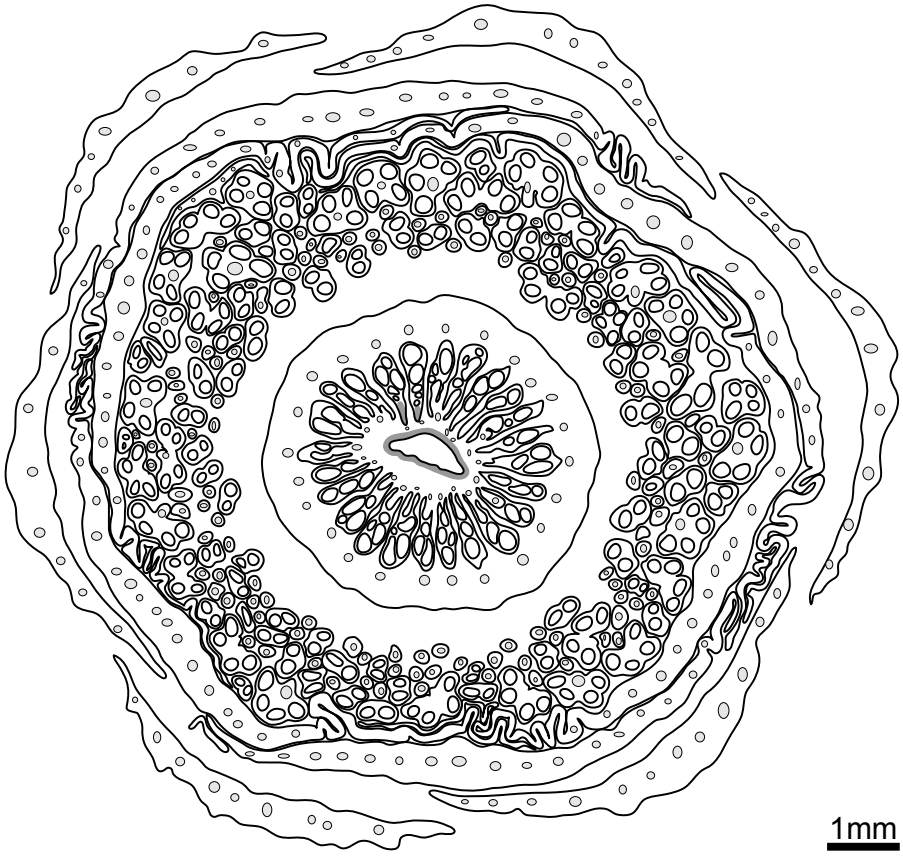
CHAPTER II

COMPARATIVE FLORAL STRUCTURE AND SYSTEMATICS IN THE SARRACENIOID CLADE (ACTINIDIACEAE, RORIDULACEAE AND SARRACENIACEAE) OF ERICALES

Published: Löfstrand SD, Schönenberger J. 2015. Comparative floral structure and systematics in the sarracenioid clade (Actinidiaceae, Roridulaceae and Sarraceniaceae) of Ericales. *Botanical Journal of the Linnean Society* 178: 1–46.

Authors' contributions: conceptualisation, laboratory work, writing and correspondence by Stefan D. Löfstrand; conceptualisation and comments on writing by Jürg Schönenberger.



Line drawing based on light micrograph of functionally female *Actinidia arguta.*

Botanical Journal of the Linnean Society, 2015, **178**, 1–46. With 14 figures

Comparative floral structure and systematics in the sarracenioid clade (Actinidiaceae, Roridulaceae and Sarraceniaceae) of Ericales

STEFAN D. LÖFSTRAND* and JÜRG SCHÖNENBERGER

Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, AT-1030 Vienna, Austria

Received 27 October 2014; revised 6 January 2015; accepted for publication 10 January 2015

In molecular phylogenetic studies, Actinidiaceae, Roridulaceae and Sarraceniaceae form a strongly supported clade, which is sister to the ericoid clade (Clethraceae, Cyrillaceae and Ericaceae). In pre-molecular classifications, the sarracenioid families were often not affiliated with other ericalean taxa or considered to be closely related with each other, as they differ conspicuously in their habit, mode of nutrient uptake and/or superficial floral structure. In order to interpret the findings of molecular phylogenetic analyses from a morphological point of view, a detailed comparative study of floral morphology, anatomy and histology of these three families is presented. In addition, earlier literature is reviewed. The three families share a series of general and, at the level of Ericales, most likely plesiomorphic floral features, including pentamery, actinomorphy and hypogyny. Other, more specialized features, such as polystemony, choripetaly and integument number, turn out to be homoplasious in the sarracenioid clade. A floral feature shared by the three families is late anther inversion, which, in Ericales, is restricted to the sarracenioids and ericoids. Potential synapomorphies for the sarracenioids include vesicles that appear to contain condensed tannins in floral tissue, proximally thick petals, ovules with a nucellar hypostase and the presence of iridoid compounds. For the subclade of Actinidiaceae and Roridulaceae, potential synapomorphies include the presence of raphides and mucilage cells in floral tissue, a secretory inner surface in the gynoecium and the absence of synlateral vasculature in the ovary. Floral features in the clade are discussed and compared with the other families of Ericales. Further structural studies in other clades of Ericales and a well-resolved molecular phylogeny of the order are needed to test the systematic value of these features further. Some features may turn out to be true synapomorphies, whereas others may turn out to be widespread in Ericales and therefore plesiomorphic for the order. *Botanical Journal of the Linnean Society*, 2015, **178**, 1–46.

ADDITIONAL KEYWORDS: anatomy – androecium – anther inversion – asterids – gynoecium – histology – morphology – perianth.

INTRODUCTION

Ericales is one of the eudicot orders that has undergone major systematic changes as a result of advances in molecular systematics. It now comprises 22 families and more than 11 500 species (Stevens, 2001 onwards; APG III, 2009). Several recent molecular phylogenetic studies have provided a framework for the interfamilial relationships in the order, but the backbone of the phylogenetic tree remains partly unresolved (e.g. Geuten *et al*., 2004; Schönenberger, Anderberg & Sytsma, 2005; Soltis *et al*., 2011). In pre-molecular classification systems (Cronquist, 1981; Dahlgren, 1983), the families now classified in Ericales were placed in three different flowering plant subclasses (Dilleniidae, Rosidae and Asteridae) and in up to 12 different orders. Advances in the circumscription and delimitation of the taxonomic composition of Ericales and interfamilial relationships based on molecular phylogenetics are in sharp contrast with what has lately been achieved at the morphological level. It is therefore not surprising that non-molecular synapomorphies for many of the ericalean clades comprising more than one family are currently lacking. This has led to the paradoxical situation that there

*Corresponding author. E-mail: stefan.loefstrand@univie.ac.at

are now clear phylogenetic hypotheses for many suprafamilial clades of Ericales, but no unequivocal morphological features to characterize these clades are known.

The families and genera of Ericales are highly diverse at all levels of their structure and biology, particularly so at the level of floral structure and function, for which the evolution of many characters shows extensive homoplasy (Schönenberger *et al*., 2005). So far, only the clades comprising Balsaminaceae, Marcgraviaceae and Tetrameristaceae (von Balthazar & Schönenberger, 2013) and Fouquieriaceae and Polemoniaceae (Schönenberger, 2009) have been comparatively studied in detail at the floral morphological level.

As a fourth in a series of studies dealing with comparative floral morphology, anatomy and histology (Schönenberger, 2009; Schönenberger, von Balthazar & Sytsma, 2010; von Balthazar & Schönenberger, 2013), the present study focuses on the sarracenioid clade, comprising the families Actinidiaceae, Roridulaceae and Sarraceniaceae. In pre-molecular times, the three families were considered to belong to three different plant orders, in two different subclasses of angiosperms: Actinidiaceae in Theales of Dilleniidae, Roridulaceae in Rosales of Rosidae and Sarraceniaceae in Nepenthales of Dilleniidae (Cronquist, 1981). The monophyly, interfamilial relationships (Sarraceniaceae sister to a clade formed by Actinidiaceae and Roridulaceae) and systematic position of the sarracenioid clade in Ericales have only relatively recently been established and are well supported on the basis of molecular phylogenetic analyses (Anderberg, Rydin & Källersjö, 2002; Schönenberger *et al*., 2005; Soltis *et al*., 2011). The sarracenioids are the sister group of a clade formed by Clethraceae, Cyrillaceae and Ericaceae, one of the suprafamilial groups in Ericales in which the interfamilial relationships are well supported (e.g. Anderberg *et al*., 2002; Schönenberger *et al*., 2005; Soltis *et al*., 2011).

The sarracenioid clade comprises seven genera (*c*. 400 species): Actinidiaceae is the largest of the families with *c*. 360 species in three genera [*Actinidia* Lindl., *Clematoclethra* (Franch.) Maxim. and *Saurauia* Willd.; Li, Li & Soejarto, 2007], followed by Sarraceniaceae with *c*. 35 species in three genera (*Darlingtonia* Torr., *Heliamphora* Benth. and *Sarracenia* L.; McPherson & Schnell, 2011; McPherson *et al*., 2011), and lastly Roridulaceae with two species in a single genus (*Roridula* Burm. ex L.; Conran, 2004). At a macroscopic scale, the vegetative morphology in these families is diverse, ranging from herbaceous perennials with conspicuous pitcher leaves in Sarraceniaceae (Macfarlane, 1908), to shrublets, densely covered in glandular hairs in Roridulaceae (Diels, 1930), and several metres tall lianas and trees in Actinidiaceae (e.g. Hunter, 1966; Soejarto, 1980; Li *et al*., 2007). The geographical distribution is disjunct, with Actinidiaceae present in the Neotropics, temperate to tropical Asia and tropical Oceania, Roridulaceae endemic to the Cape region in South Africa, and Sarraceniaceae restricted to temperate North America and the Guiana Highlands in South America (Tropicos.org, 2014). The families also exhibit great diversity in habit and nutrient uptake: autotrophy in Actinidiaceae (Dressler & Bayer, 2004); protocarnivory in Roridulaceae (Conran, 2004); and carnivory in Sarraceniaceae (Kubitzki, 2004b). The flowers range in size from a few millimetres to several centimetres at anthesis (Fig. 1), and plants may be dioecious, subdioecious or bisexual (Kubitzki, 2004a). The sarracenioids are well represented in the fossil record with well-preserved floral mesofossils from the Late Cretaceous suggested to belong to Actinidiaceae (Keller, Herendeen & Crane, 1996; Schönenberger *et al*., 2012).

To date, a few non-molecular synapomorphic characters for the sarracenioids have been proposed. Among these are free styles (with exceptions) and the presence of a nucellar hypostase in the ovules (Anderberg *et al*., 2002). Additionally, Schönenberger *et al*. (2005) discussed polystemony as a potential synapomorphy for the clade, with a reversal in the haplostemonous Roridulaceae.

The aim of this study is to attempt a critical comparison of the morphological, anatomical and histological floral characters of the sarracenioid families and genera, and to contribute to a more comprehensive understanding of the evolutionary history of Ericales. Confirmed structural synapomorphies will allow for the incorporation of fossil taxa in phylogenetic analyses, detailed reconstructions of character evolution and reliable estimations of the age of the ericalean clades and families.

MATERIAL AND METHODS

The morphology, anatomy and histology of floral buds or anthetic flowers of the following taxa are included in the study.

Actinidiaceae

Actinidia arguta (Siebold & Zucc.) Planch. ex Miq.; JS714 (functionally female floral buds); cult. University of Zurich Botanic Garden, Switzerland.

Actinidia arguta (Siebold & Zucc.) Planch. ex Miq.; SL035 (functionally male floral buds); cult. private garden in Baden, Austria.

Actinidia chinensis Planch.; JS715 (functionally female and functionally male floral buds); cult. University of Zurich Botanic Garden, Switzerland.

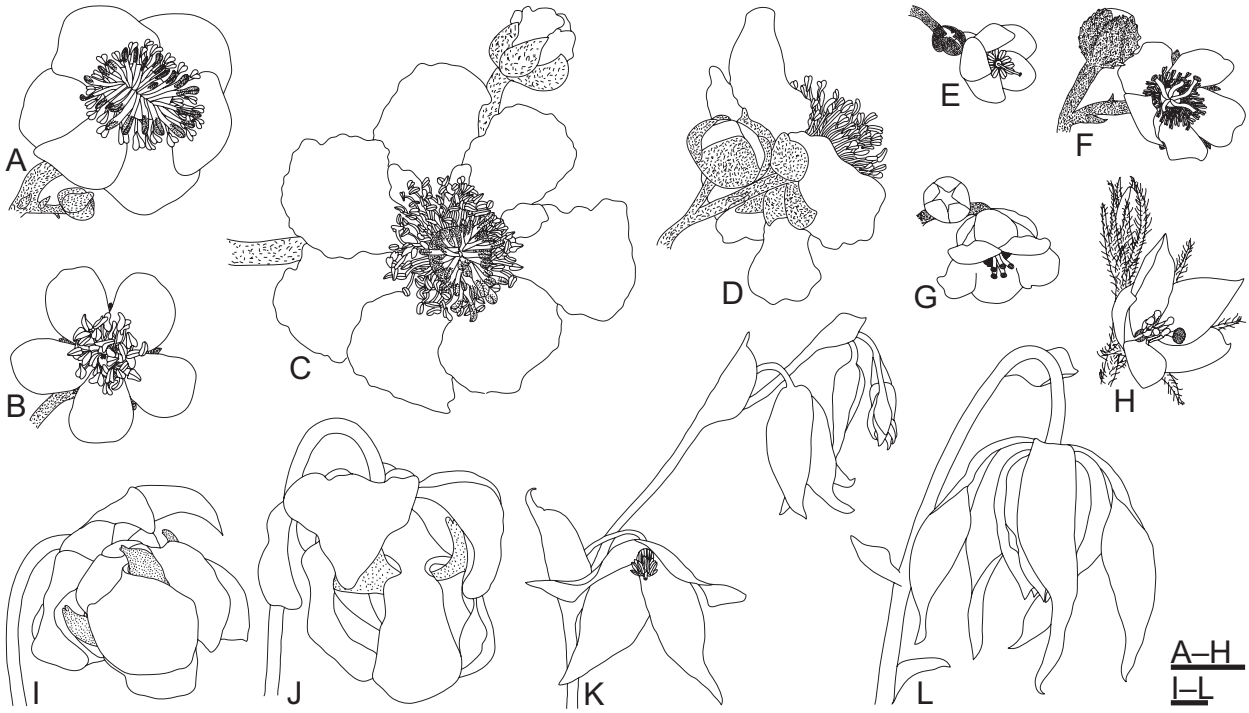


Figure 1. Half-schematic line drawings of flowers and inflorescence branches. A–G, Actinidiaceae. H, Roridulaceae. I–L, Sarraceniaceae. A, *Actinidia arguta* (functionally female). B, *Actinidia arguta* (functionally male). C, *Actinidia chinensis* (functionally female). D, *Actinidia arguta* (functionally male). E, *Clematoclethra scandens*. F, *Saurauia pittieri*. G, *Saurauia subspinosa*. H, *Roridula gorgonias*. I, *Sarracenia purpurea*. J, *Sarracenia leucophylla*. K, *Heliamphora nutans*. L, *Darlingtonia californica*. Scale bars, 1 cm.

Clematoclethra scandens ssp. *hemsleyi* (Baill.) Y.C.Tang & Q.Y.Xiang; SL002; cult. University of British Columbia Botanical Garden, Canada.

Saurauia pittieri Donn. Sm.; JS828; coll. A.J. Borg *s.n*., Costa Rica.

Saurauia subspinosa J.Anthony; JS898; cult. University of Vienna Botanical Garden, Austria.

Roridulaceae

Roridula gorgonias Planch.; SL028; cult. University of Vienna Botanical Garden, Austria.

Sarraceniaceae

Darlingtonia californica Torr.; SL005; cult. University of Vienna Botanical Garden, Austria.

Heliamphora nutans Benth.; SL008; cult. University of Zurich Botanic Garden, Switzerland.

Sarracenia leucophylla Raf.; JS895, SL012; cult. University of Vienna Botanical Garden, Austria.

Sarracenia purpurea L.; JS940; cult. University of Vienna Botanical Garden, Austria.

Sampling strategies and laboratory procedures

Taxa were selected to represent all genera in the sarracenioid clade and to match the taxon sampling of earlier and ongoing phylogenetic studies in Ericales (Schönenberger *et al*., 2005; Sytsma *et al*., 2009) and developmental studies in the sarracenioid clade (Shreve, 1906; Brown, 1935; van Heel, 1987; Caris, 2013).

Living floral material was fixed in formaldehyde–acetic acid–alcohol (FAA) or 70% ethanol, and subsequently stored in 70% ethanol.

For light microscopy (LM), specimens were dehydrated in an ethanol series and embedded in 2-hydroxyethylmethacrylate (Kulzer's Technovit 7100; Heraeus Kulzer, Wehrheim, Germany). Transverse sections were cut at 5–8 μm using a Microm HM rotary microtome 355 (Walldorf, Germany) and subsequently stained with ruthenium red and toluidine blue O. The methods for embedding, cutting and staining are more thoroughly described in Igersheim (1993), Weber & Igersheim (1994) and Igersheim & Cichocki (1996). Sections were permanently mounted in Histomount (National Diagnostics, Atlanta, GA, USA). Digital images of selected sections were taken with a Nikon digital sight DS-Fi1 camera (Nikon Corporation, Tokyo, Japan) on an Olympus BX50 system microscope (Olympus Optical Corporation, Tokyo, Japan). The images were edited in Adobe Photoshop CS5 (Adobe Systems Incorporated, San José,

CA, USA). Digital line drawings were made in Adobe Illustrator CS5 (Adobe Systems Incorporated).

For scanning electron microscopy (SEM), specimens were dehydrated in an ethanol series and acetone, critical point dried, mounted on SEM stubs, sputter coated with gold and studied at 5 kV in a Jeol JSM-6390 field emission scanning electron microscope. The images were edited in Adobe Photoshop CS5 (Adobe Systems Incorporated).

For X-ray tomographic studies of a *Sarracenia* gynoecium (Supporting Information Movie S1), the gynoecium was infiltrated with 1% phosphotungstate in 70% ethanol, dehydrated in an ethanol series and acetone, critical point dried, mounted on an aluminium tube and scanned in the XRadia MicroXCT-200 system (Carl Zeiss X-ray Microscopy, Inc., Oberkochen, Germany). The raw scan data were reconstructed in XMReconstructor (Carl Zeiss X-ray Microscopy, Inc.), after which Amira 3D Software for Life Sciences (FEI Visualization Group, Bordeaux, France) was used for the rendering of the file and video preparation. The methods for X-ray tomographic studies on floral material are more thoroughly described in Staedler, Masson & Schönenberger (2013).

Permanent slides of the microtome sections and SEM stubs were deposited at the Department of Botany and Biodiversity Research, University of Vienna, Austria.

RESULTS

The descriptions are based on pre-anthetic floral material (anthetic for scanning electron micrographs of *Heliamphora nutans*), closed buds or recently opened flowers, in which male meiosis had already taken place (this also applies to functionally female flowers, as the anthers normally contain sterile pollen grains). Floral structure is described in full for one taxon per genus in all families of the clade. For the additional taxa of the same genus (functionally male specimens of the same species or another species), only the characters differing from the fully described taxon are listed. The flowers are described distally to proximally (i.e. from the tip of the floral bud towards the floral base) and from the outside towards the floral centre (i.e. from the outer surface of the sepals towards the carpels). To describe individual floral organs, the terms 'dorsal' (for the side of the organ facing away from the floral centre in bud) and 'ventral' (for the side of the organ facing towards the floral centre in bud) are used. The term 'lateral' is used to describe vascular bundles flanking the dorsal vascular bundle. The course of the pollen tube-transmitting tissue (PTTT) is described in the morphological section for practical reasons. Figure 1 shows some of the gross-morphological floral diversity in the clade; Figs 2–9 detailed line drawings of histological sections; Figs 10 and 11 show androecium details; Fig. 12 shows gynoecium details; Fig. 13 shows placentation and ovules details; and Fig. 14 shows examples of histological characters (taxa not previously described in the text may be mentioned in reference to Fig. 14).

Actinidiaceae

Actinidia arguta *(functionally female flower)*

Morphology: Flowers are presented on axillary, few-flowered, cymose branches, *c*. 3 cm in diameter with an open access to the floral centre and slightly pendant (Fig. 1A); they are structurally bisexual but functionally female, pentamerous to hexamerous in the perianth (flowers with different merism occur on the same individual), actinomorphic and hypogynous (Figs 1A, 2A–M).

Sepals are proximally united for *c*. 10% and arranged in a single whorl (Fig. 2K–M); the aestivation is quincuncial in pentamerous specimens, and in hexamerous specimens it is imbricate with two sepals overlapping both of their neighbouring sepals, two being overlapped by both of their neighbours and two being intermediate. Sepals are broadly ovate and largely uniform in size, distally acute, broadly attached (Figs 1A, 2A–M) and the margin is entire (Fig. 1A). Sepal bases are massive, dorsally bulging proximally and extend downwards, beyond their region of attachment with the pedicel and therefore

Figure 2. *Actinidia* spp. (Actinidiaceae). Floral buds, transverse section series; morphological surfaces indicated by full lines; pollen tube-transmitting tissue indicated by dark grey shading; postgenital union indicated by broken lines; vasculature indicated by full lines filled with light grey shading. A–M, *Actinidia arguta* (functionally female). A–C, Asymplicate zone. A, Distal-most region of perianth. C, Transition from asymplicate to symplicate zone. C–G, Symplicate zone. E, Level of depression on top of ovary. F, Level of incomplete ovary septation. G, Proximal part of central canal. H–K, Synascidiate zone. K–M, Floral base. K–M, Level of partial synsepaly. M, Level of dorsally bulging sepals. N, *Actinidia arguta* (functionally male), level of anthers. O–R, *Actinidia chinensis* (functionally female), arrows indicate the small, inner petaloid organs. O, Symplicate zone. P, Q, Synascidiate zone. P–R, Floral base, level of synsepaly. S, *Actinidia chinensis* (functionally male), level of anthers. Scale bar, 5 mm.

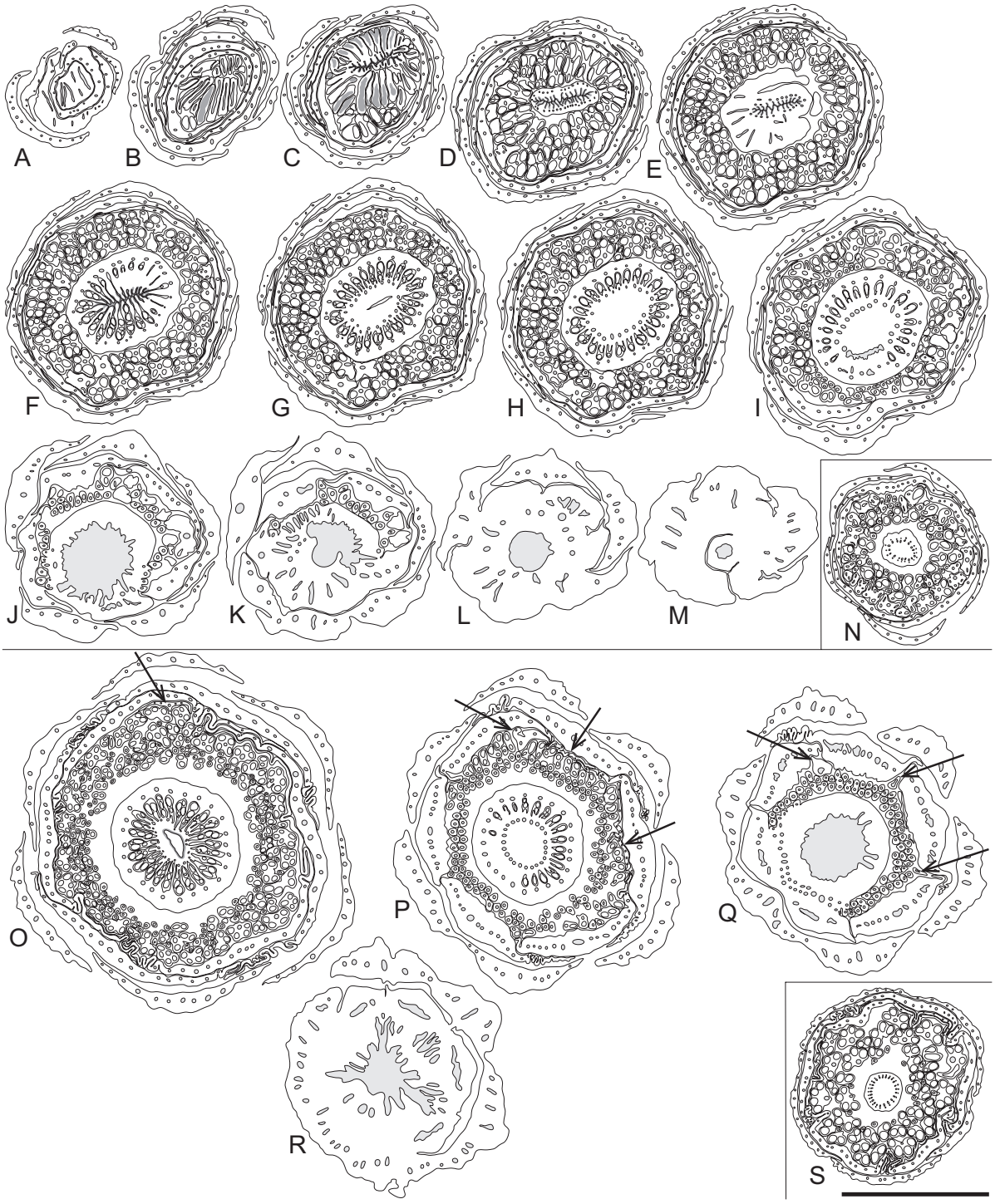


Figure 2. See caption on previous page.

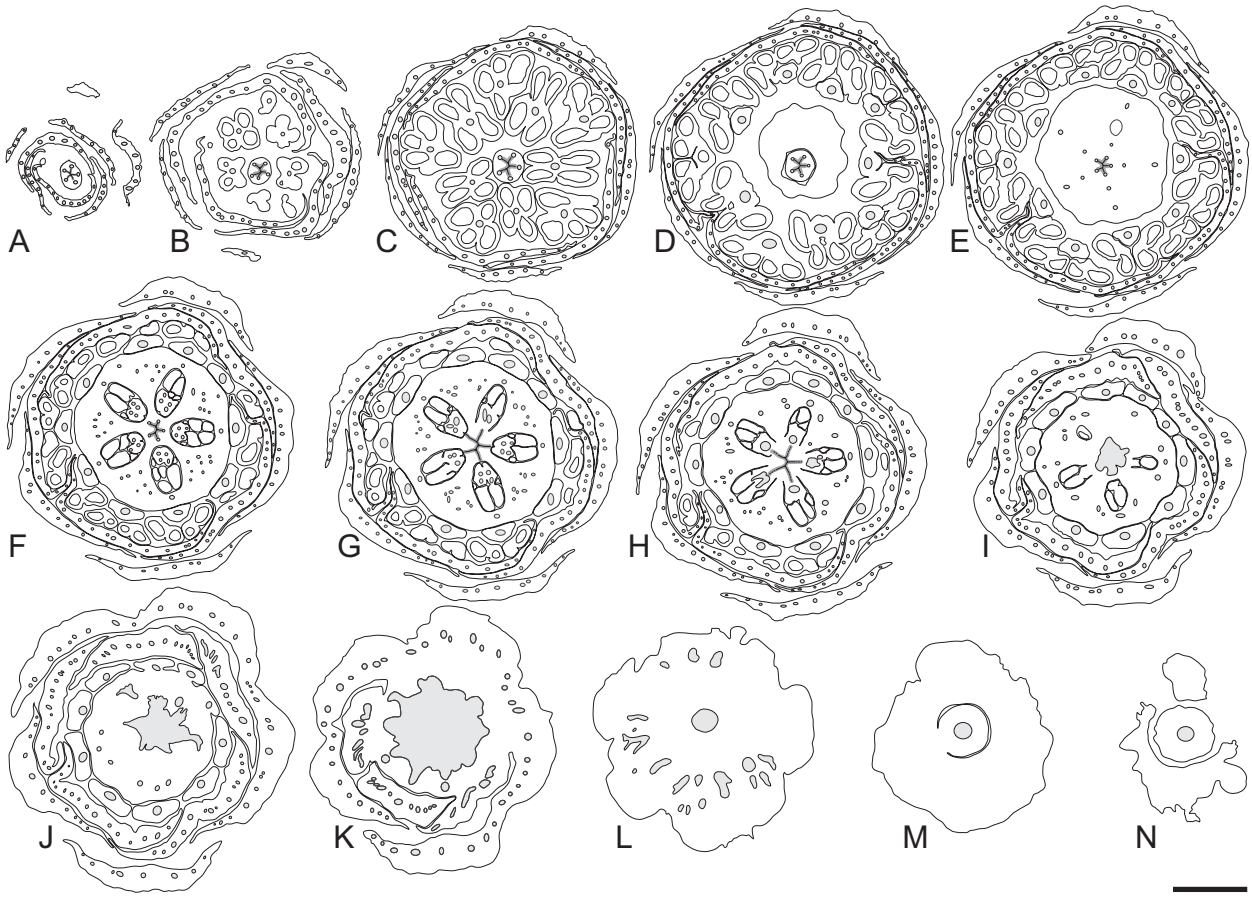


Figure 3. *Clematoclethra scandens* (Actinidiaceae). Floral bud, transverse section series; morphological surfaces indicated by full lines; pollen tube-transmitting tissue indicated by dark grey shading; postgenital union indicated by broken lines; vasculature indicated by full lines filled with light grey shading. A–H, Symplicate zone. A, Level of transition from stigma to style. D, Level of depression on top of ovary. F, G, Level of distal, free parts of placentae. I–N, Level of synsepaly. I, J, Synascidiate zone. J–M, Floral base. M, N, Level of dorsally bulging sepals. Scale bar, 1 mm.

appearing to be inserted into a shallow pit (Fig. 2M). Sepals are persistent after anthesis.

Petals are free and arranged in a single whorl (Fig. 2J–L); the aestivation is the same as sepal aestivation (Figs 1, 2). Petals are broadly obovate and largely uniform in shape and size, distally obtuse and broadly attached (Figs 1A, 2A–M); the thin (two to three cell layers thick) petal margin is minutely crenulate. Petals are proximally of more or less equal thickness to (Fig. 2J–L) or thicker than (another sectioned floral bud, not shown) the sepals.

The androecium consists of *c*. 60 staminodes (Figs 1A, 2A–M) arranged in a single series, with filaments entirely free from each other and from the petals (Fig. 2J, K). Anthers are dithecate and tetrasporangiate, sagittate and basifixed, and anther orientation is latrorse to slightly extrorse in bud (Fig. 2G–I). Anthers become inverted at the beginning of anthesis, turning the anthers upside down (to latrorse–introrse orientation and the morphological base of the thecae facing away from the floral centre). Connectives are broad on the ventral side; the joint between the filament and the anther is broad. Anther dehiscence is by longitudinal slits that extend over 80% of the length of the thecae, starting at the morphological base of the anther. The filaments are terete and approximately three times the length of the anthers at anthesis.

The gynoecium is composed of *c*. 18–24 carpels (Figs 1A, 2C–H, 12A). Carpels are arranged in a single whorl and united in the ovary and proximal part of the styles (Figs 2C–K, 12A). The area of carpel closure is flattened (compressed) as seen from above in such a way that the carpels appear to be aligned in two parallel rows (Figs 1A, 2C–G, 13A). The stigmas (as many as carpels) are elongated

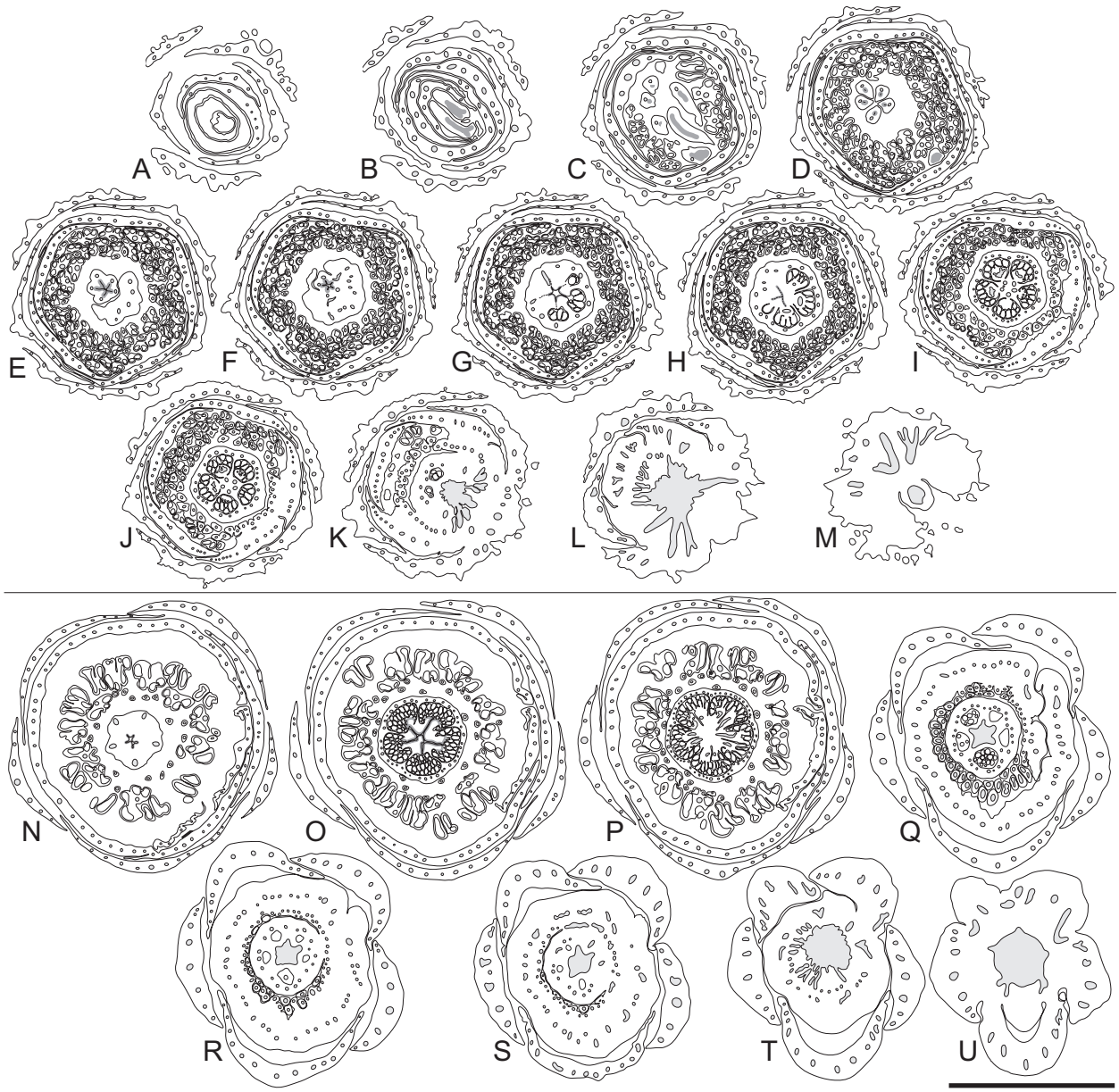


Figure 4. *Saurauia* spp. (Actinidiaceae). Floral buds, transverse section series; morphological surfaces indicated by full lines; pollen tube-transmitting tissue indicated by dark grey shading; postgenital union indicated by broken lines; vasculature indicated by full lines filled with light grey shading. A–M, *Saurauia pittieri*. A, Distal region of perianth. B–D, Asymplicate zone. E–H, Symplicate zone. E, F, Level of depression on top of ovary. G, Level of incomplete septation. H, Transition from symplicate to synascidiate zone. H–K, Synascidiate zone. I–K, Level of filament union. J, K, Level of filament–petal union. K–M, Floral base, level of synsepaly. M, Level of dorsally bulging sepals. N–U, *Saurauia subspinosa*. N, O, Symplicate zone. N, Distal-most region of locules and distal part of petal union. O, Incomplete septation of locules. P–U, synascidiate zone. Q–S, Level of filament union and filament–petal union. S, Transition from synascidiate zone to floral base. T, Stamen traces joining central vascular column (CVC). U, Secondary vasculature in sepals merging with that of the neighbouring sepal and petal vasculature joining CVC. Scale bar, 5 mm.

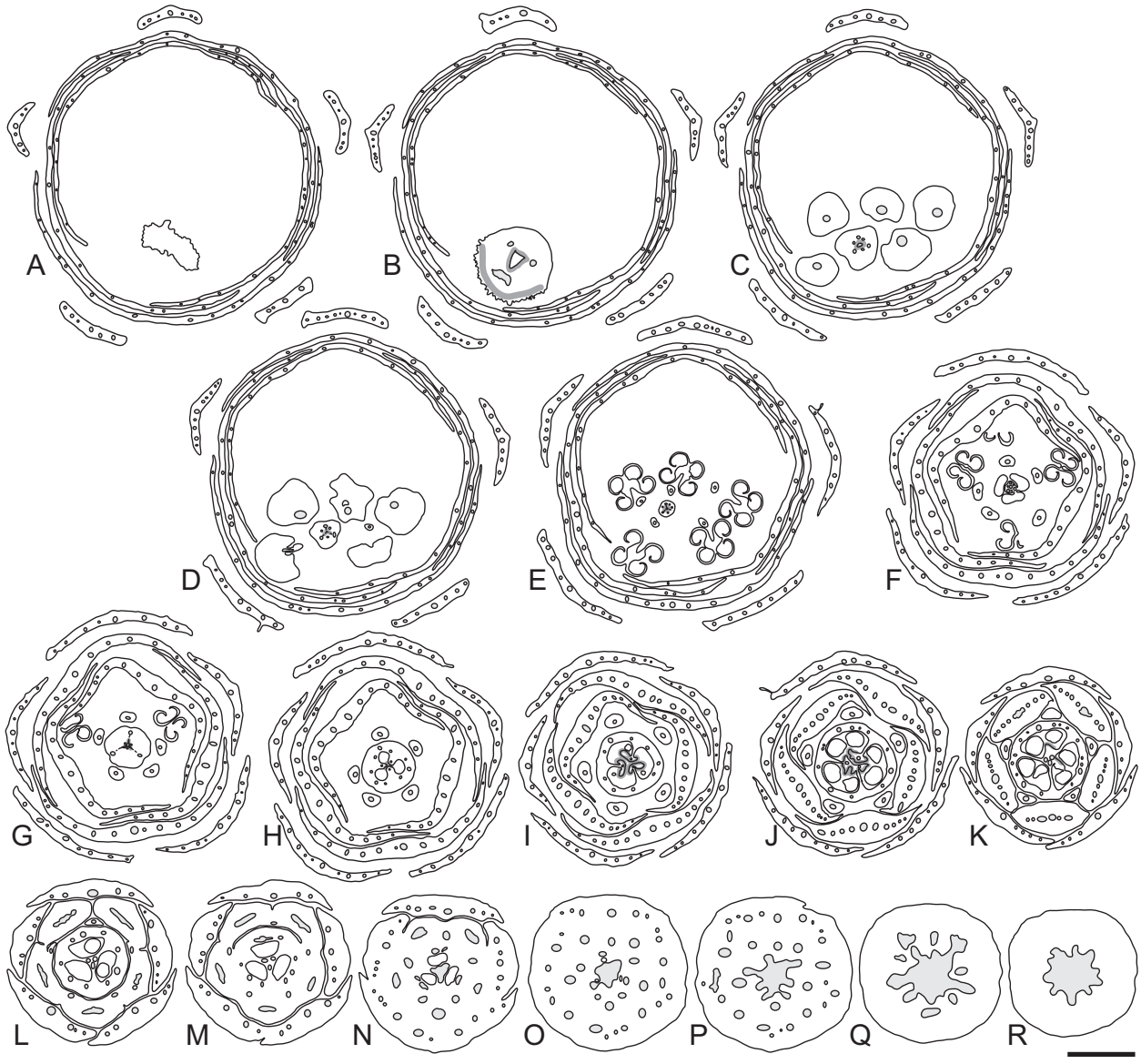


Figure 5. *Roridula gorgonias* (Roridulaceae). Floral bud (the anthers dehisced during the dehydration process), transverse section series; morphological surfaces indicated by full lines; pollen tube-transmitting tissue indicated by dark grey shading; postgenital union indicated by broken lines; vasculature indicated by full lines filled with light grey shading. A–J, Symplicate zone. A, B, Level of stigma. F, Level of depression on top of ovary. H–J, Level of incomplete septation. K–O, Synascidiate zone. L, M, Level of sympetaly and filament–petal union. M, N, Level of partial synsepaly. O, Locule base. P–R, Floral base. Scale bar, 1 mm.

(20–30% of the length of the asymplicate styles) and have reflexed apices (Fig. 12A). The stigmatic papillae are unicellular, unbranched and secretory (Fig. 12B). The styles are asymplicate for *c*. 80% of their length (Fig. 2A–C); the remaining part of the styles is symplicate (Fig. 2C–E). In the symplicate styles, the carpel margins meet in the centre, but are not postgenitally united (Fig. 2A–E); the style is inserted in a depression on top of the globose to ovoid ovary (Fig. 2E). The symplicate zone of the ovary (*c*. 50% of its total length) has a central canal and the ventral slits of the individual carpels are closed only in the proximal-most part of the ovary (Fig. 2C–F). In the distal-most part of the symplicate ovary (at the transition from style to ovary), the carpel margins meet in the centre, but are not postgenitally united (Fig. 2E); in the majority of the incompletely septate part of the symplicate ovary, the carpel margins do

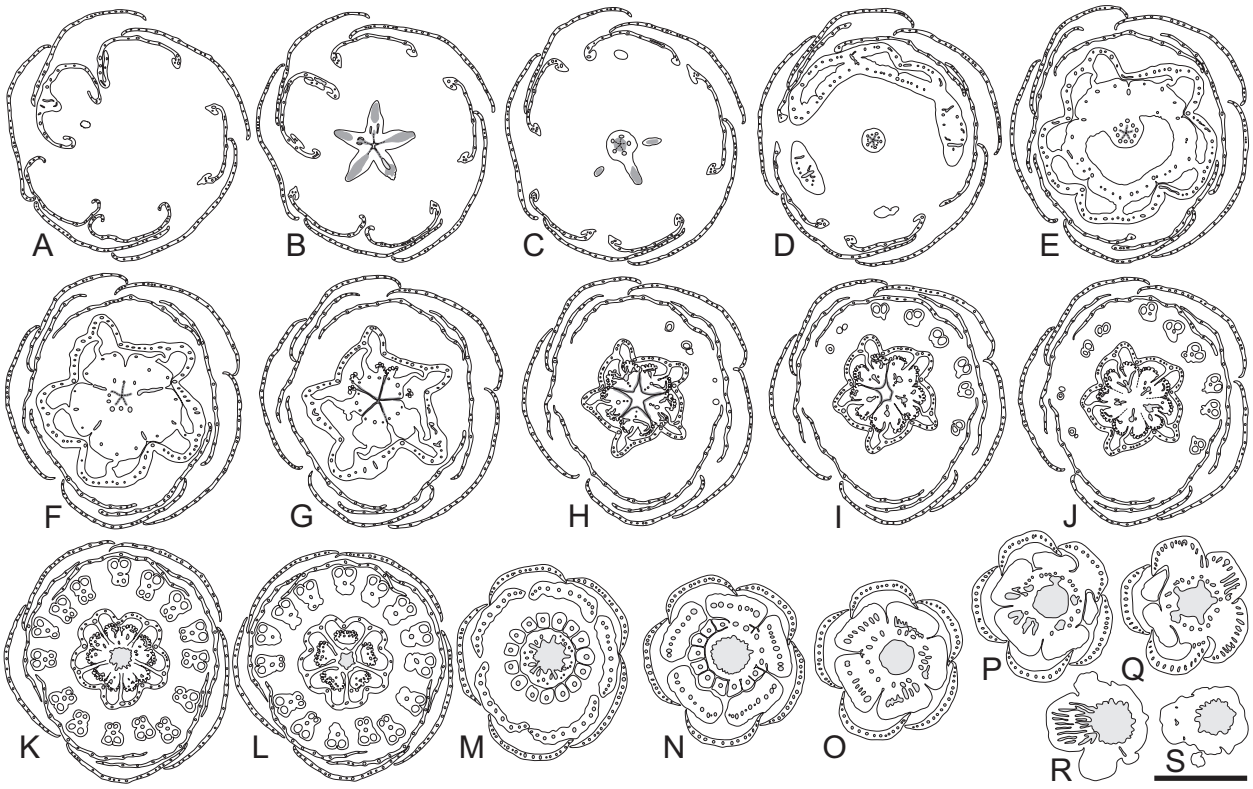


Figure 6. *Darlingtonia californica* (Sarraceniaceae). Floral bud, transverse section series; morphological surfaces indicated by full lines; pollen tube-transmitting tissue indicated by dark grey shading; postgenital union indicated by broken lines; vasculature indicated by full lines filled with light grey shading. A–C, Asymplicate zone. B Level of stigmas. C, Transition from asymplicate to symplicate zone. C–I, Symplicate zone. G–I, Level of incomplete septation. J–M, Synascidiate zone. N–S, Floral base. P, Q, Level of dorsally bulging petals. R, S, Sepal traces joining the CVC. Scale bar, 5 mm.

not meet in the centre (Fig. 2F). The central canal extends into the synascidiate zone of the ovary (Fig. 2G). In the asymplicate styles, the PTTT (Fig. 2B–F) is six to eight cell layers thick. In the symplicate style and distal part of the ovary, the PTTT (one to three cell layers thick) is continuous between the carpels, forming a compitum that lines the central canal and the ventral slits (Fig. 2D–F). Placentation is axile (Figs 2F–I, 13A). Each carpel produces eight to ten ovules arranged in one or two longitudinal rows (Figs 2F–I, 13A). The ovules are slightly pendant (Figs 2F–I, 13A) and the placentae extend over both the symplicate (Fig. 2A–F) and synascidiate (Fig. 2F–I) zones. Ovules are unitegmic (the integument is seven or eight cell layers thick), anatropous and tenuinucellar to slightly incompletely tenuinucellar (Fig. 13A, B).

Anatomy: Sepals have one primary (median) and *c.* eight secondary vascular bundles distally; the bundles merge with each other at varying levels (Fig. 2A–M) and proximally only the primary and two secondary bundles remain. In the floral base, the three remaining traces join the central vascular column (CVC) individually (Fig. 2L, M).

Petals have one primary and numerous secondary vascular bundles distally (Fig. 2B–L); the bundles merge with each other at varying levels; proximally only the primary and two secondary vascular bundles remain (Fig. 2K). In the floral base, the three remaining traces merge and the resulting, single petal vascular trace joins the CVC.

Staminodes have a single vascular bundle. In the floral base, some of the neighbouring traces merge with each other before joining the CVC (Fig. 2J, K).

In the styles and ovary, each carpel has one median (dorsal) vascular bundle supplying the stigma, the ovary wall and the locules (Fig. 2D–I). In the proximal-most part of the symplicate zone and in the synascidiate zone of the ovary, each carpel additionally has a ventral vascular bundle supplying the placenta (Fig. 2G–I). At the base of the locules,

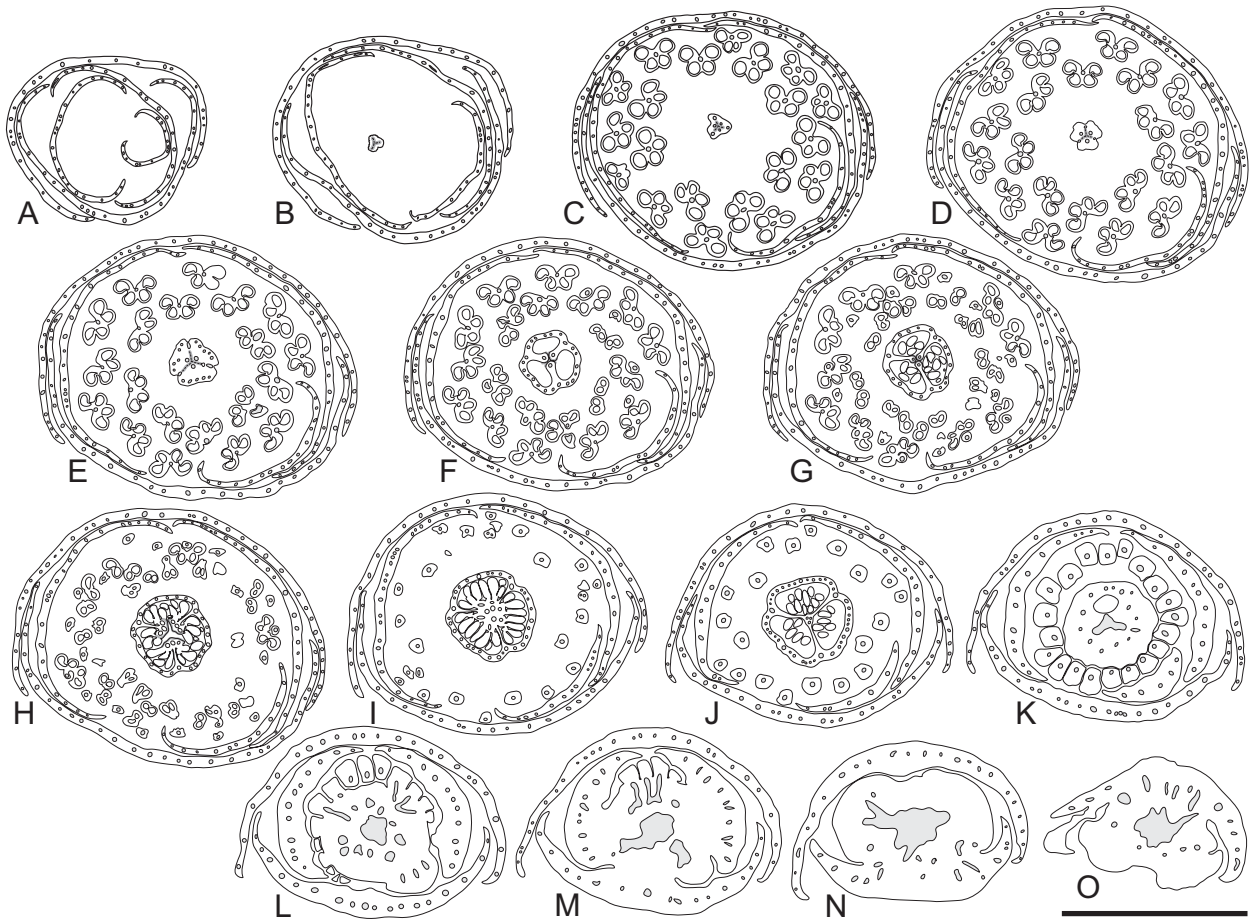


Figure 7. *Heliamphora nutans* (Sarraceniaceae). Floral bud, transverse section series; morphological surfaces indicated by full lines; pollen tube-transmitting tissue indicated by dark grey shading; postgenital union indicated by broken lines; vasculature indicated by full lines filled with light grey shading. A, Distal region of perianth. B–H, Symplicate zone. F–H, Level of incomplete septation. I–K, Synascidiate zone. K–O, Floral base. Scale bar, 5 mm.

the ventral vascular bundles merge to form a CVC. In the floral base, the dorsal vascular traces join the CVC (Fig. 2I–K). No lateral, synlateral or synventral vasculature is present (Fig. 2D–M).

Histology: Long, multicellular, uniseriate hairs cover most of the dorsal and ventral surfaces of the sepals (Fig. 14A). Uniseriate hairs also occur sparsely on the dorsal and ventral surfaces of the petals; the androecium and the gynoecium (Fig. 12A) are completely glabrous.

Stomata are present on both the dorsal and ventral surfaces of the sepals, dorsal side of the petals, anther connectives and ovary wall. Potentially nectariferous stomata (Fig. 14S) are present in the ovary walls, but no clearly differentiated nectariferous tissue is visible in the sectioned flower buds.

The dorsal and ventral sides of the sepals have rounded (Fig. 14F for *H. nutans*) to elongate (Fig. 14A), more or less smooth (Fig. 14C for *Saurauia subspinosa*) epidermal cells, whereas the epidermal cells on the dorsal surfaces of the petals are uneven. The anther epidermal cells are 'jigsaw puzzle piece'-shaped (Fig. 14P for *Sarracenia purpurea*) and those of the filaments are elongate. The epidermal cells of the styles are elongate and more or less smooth and those of the ovary are rounded and completely smooth. All epidermal cells have more or less uneven cuticles (Fig. 14P for *S. purpurea*; Fig. 14R for *Clematoclethra scandens*).

Parenchymatic cells are tightly packed in the perianth organs and no apparent palisade parenchyma is present. The parenchymatic tissue is uniform and tightly packed in the ovary.

Mucilage cells with either thickened inner tangential walls (Fig. 14H for *Actinidia chinensis*) or completely thickened (sometimes striate), cells with oxalate druses (Fig. 14I for *Roridula gorgonias*), cells

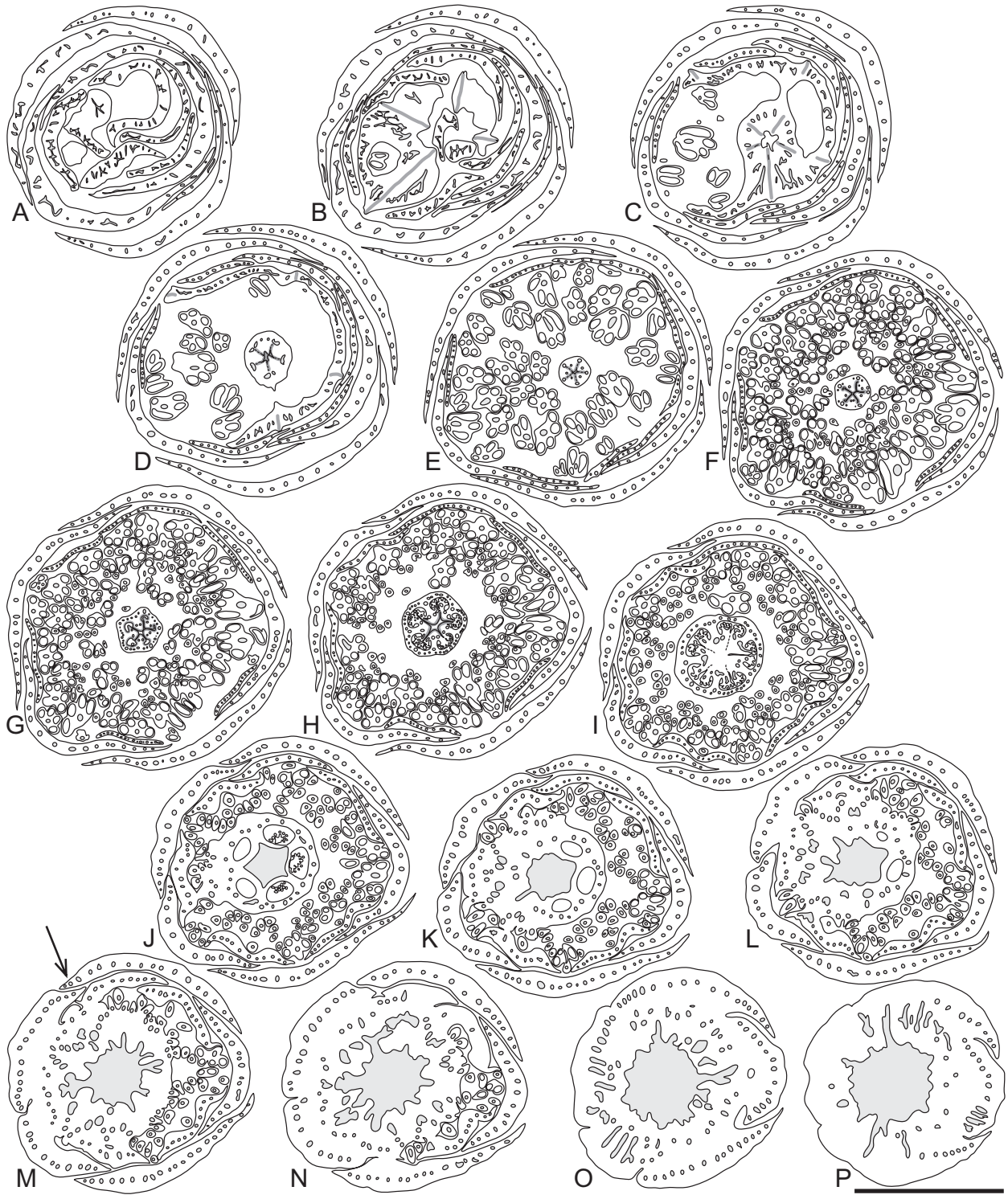


Figure 8. *Sarracenia purpurea* (Sarraceniaceae). Floral bud, transverse section series; morphological surfaces indicated by full lines; pollen tube-transmitting tissue indicated by dark grey shading; postgenital union indicated by broken lines; vasculature indicated by full lines filled with light grey shading. A–I. Symplicate zone. C–E, Asymplicate part of styles visible. F, Proximal-most part of ovary. F–H, Level of incomplete septation. I, Transition from symplicate to synascidiate zone. J–L, Synascidiate zone. M–P, Floral base. M, Arrow indicates the shared insertion position of the two smaller petals. Scale bar, 5 mm.

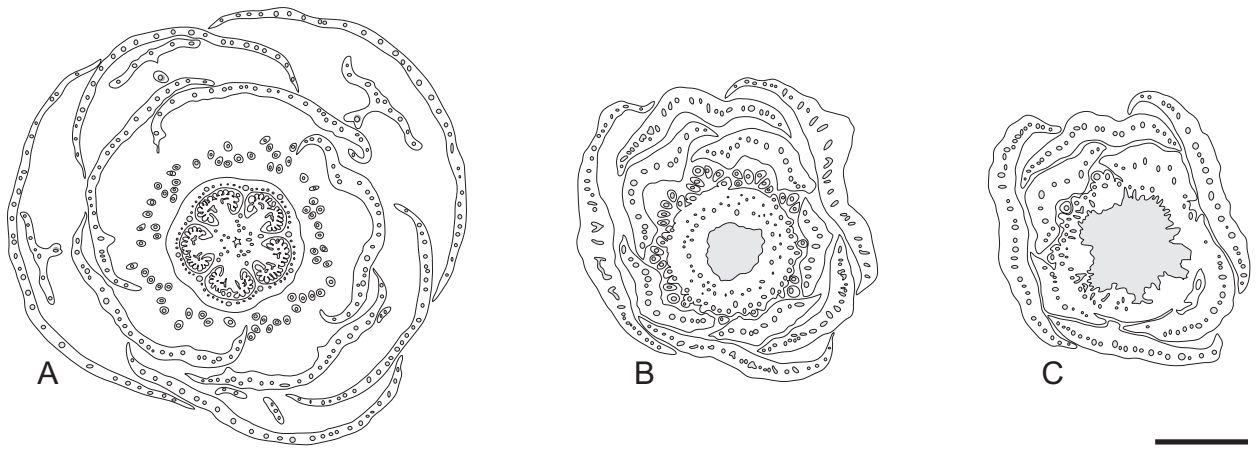


Figure 9. *Sarracenia leucophylla* (Sarraceniaceae). Floral bud, transverse section series; morphological surfaces indicated by full lines; pollen tube-transmitting tissue indicated by dark grey shading; vasculature indicated by full lines filled with light grey shading. A, Level of stigmas (asymplicate zone of styles), proximal-most part of central canal (symplicate zone of ovary). B, C, Floral base. C, Alternisepalous filament traces joining central vascular column (CVC). Scale bar, 5 mm.

Figure 10. Androecium: Actinidiaceae. Dorsal side of anthers facing towards the right side of page in all figures. A, B, *Actinidia arguta* (functionally male). A, Overview of basifixed anther, the horizontal lines and numbering correspond to the numbers in B. B, Anther cross-sections. C, D, *Actinidia chinensis* (functionally female). C, Overview of ventrifixed anther, the horizontal lines and numbering correspond to the numbers in D. D, Anther cross-sections. E, F, *Clematoclethra scandens*. E, Overview of basifixed anther, the horizontal lines and numbering correspond to the numbers in F. F, Anther cross-sections. G, H, *Saurauia pittieri*. G, Overview of ventrifixed anther, the horizontal lines and numbering correspond to the numbers in H. H, Anther cross-sections. I–K, *Saurauia subspinosa*. Note that the anthers are inverted. In earlier stages, the anthers are extrorse, but introrse in advanced buds and open flowers. I, Anther attachment; fi, filament. J, Overview of subapically ventrifixed anther, the horizontal lines and numbering correspond to the numbers in K. K, Anther cross-sections. Scale bars, 500 μm.

with calcium oxalate raphide bundles (Fig. 14 M for *C. scandens*) and tannins (Fig. 14I for *R. gorgonias*) are present in all floral organs. The mucilage cells and crystal structures are often found in combined structures in which mucilage lines a central aggregate of crystals (Fig. 14H for *A. chinensis*; Fig. 14L for *Saurauia pittieri*).

Tannin aggregates form along the internal cell walls of tanniferous cells (condensed tannins; Fig. 14I for *R. gorgonias*), and additional small vesicles that appear to contain tannins (Fig. 14K for *S. purpurea*) are scattered in the cytoplasm of cells in all organs, most abundantly in the tanniferous cells (the vesicles most closely correspond to tannin aggregates or tannosomes).

Endothecium cells with lignified wall thickenings (mainly the inner tangential cell walls) are present in the anther walls, but are lacking in the connective and the septa. The inner surface of the gynoecium (mainly the placentae) is secretory (Fig. 14D for *R. gorgonias*). The ovules contain a nucellar hypostase.

Actinidia arguta *(functionally male flower)*

Morphology: The flowers are similar to those of the functionally female *A. arguta* (Figs 1A, 2A–M) with a few clear differences: flowers are generally smaller, *c.* 2.5 cm in diameter (Figs 1B, 2N); petals are proximally markedly thicker than sepals; the androecium consists of *c.* 45 fertile stamens (Figs 2N, 10A–B); the gynoecium is strongly reduced (Figs 2N, 12C) and lacks stigmatic papillae; the styles are symplicate only in the proximal-most part and there is no depression on top of the ovary; the symplicate zone of the ovary is only weakly developed (the synascidiate zone extends almost to the top of the ovary); and PTTT, placentae and ovules are completely lacking (Fig. 13C).

Anatomy: The vascular system is similar to that of functionally female flowers, but there are no ventral vascular bundles in the ovary (Fig. 13C).

Histology: The histology is similar to that of the functionally female flowers of *A. arguta*, but stomata

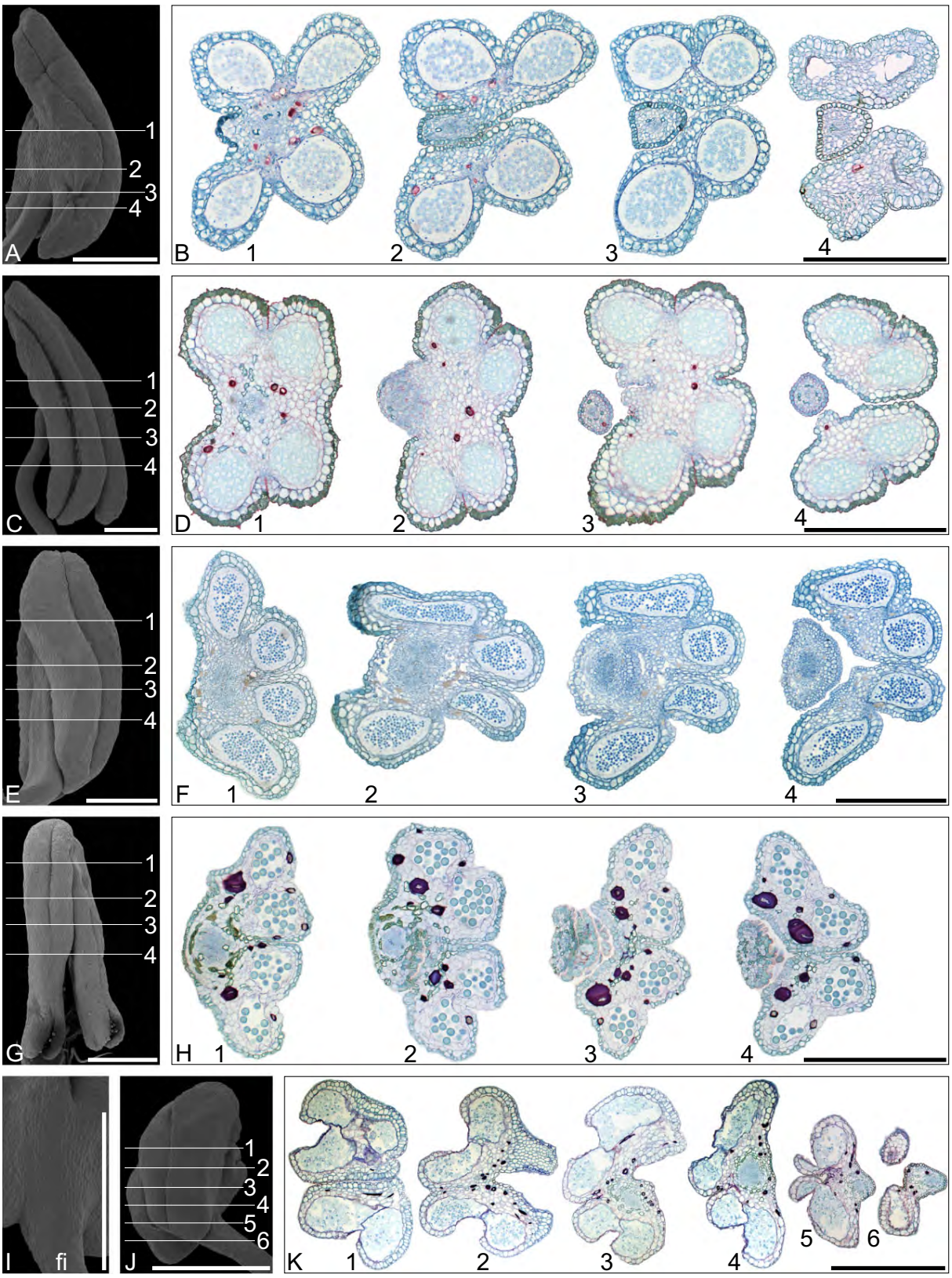


Figure 10. See caption on previous page.

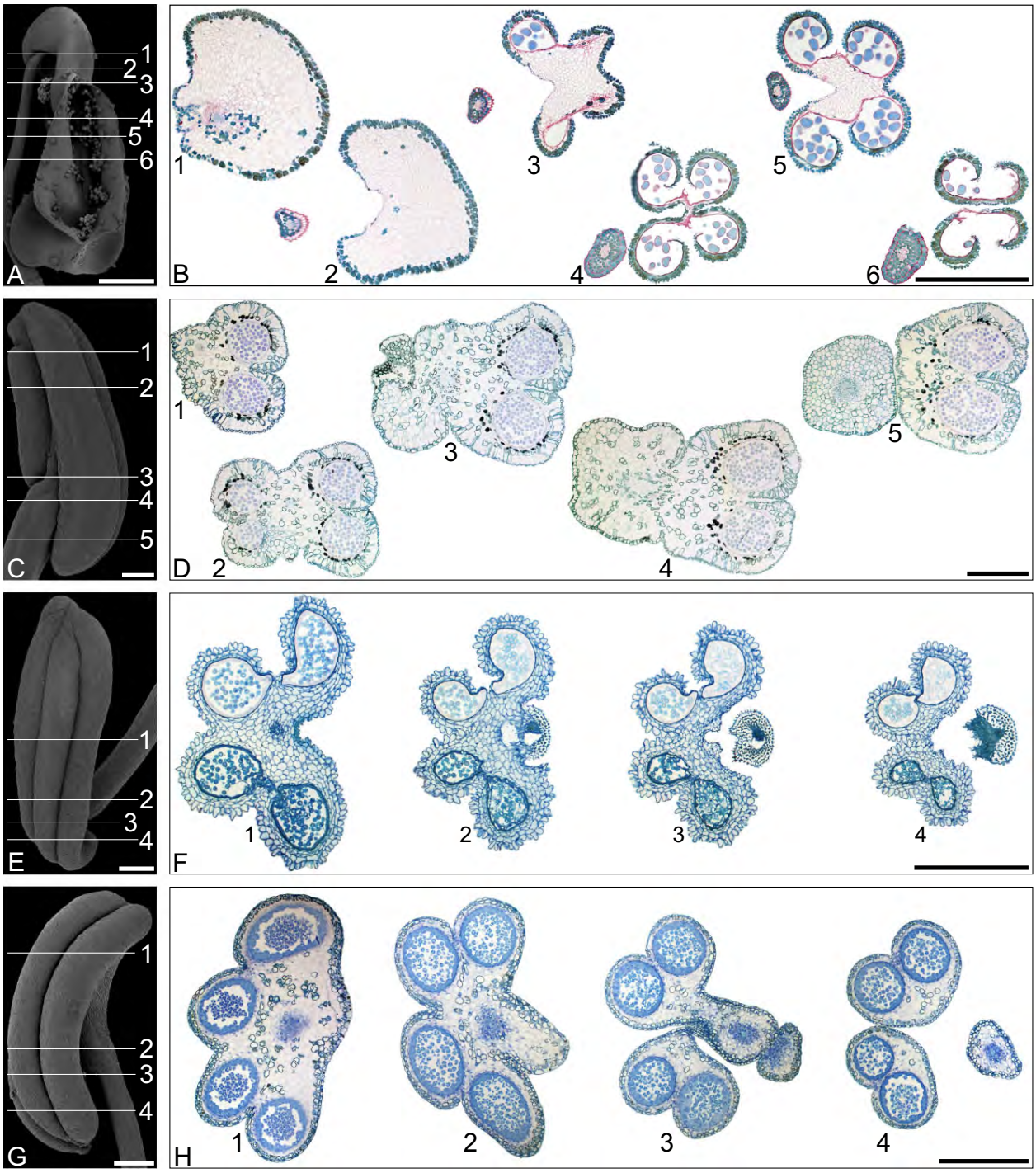


Figure 11. Androecium: Roridulaceae/Sarraceniaceae. A, B, *Roridula gorgonias*. A, Overview of subapically ventrifixed anther, the horizontal lines and numbering correspond to the numbers in B. B, Anther cross-sections. C, D, *Darlingtonia californica*. C, Overview of basifixed anther, the horizontal lines and numbering correspond to the numbers in D. D, Anther cross-sections. E, F, *Heliamphora nutans*. E, Overview of dorsifixed anther, the horizontal lines and numbering correspond to the numbers in F; note that the anther is inverted, but reflected to correspond better to the pre-anthetic position of the anthers in F. F, Anther cross-sections. G, H, *Sarracenia purpurea*. G, Overview of basifixed anther, the horizontal lines and numbering correspond to the numbers in H. H, Anther cross-sections. Scale bars, 500 μm.

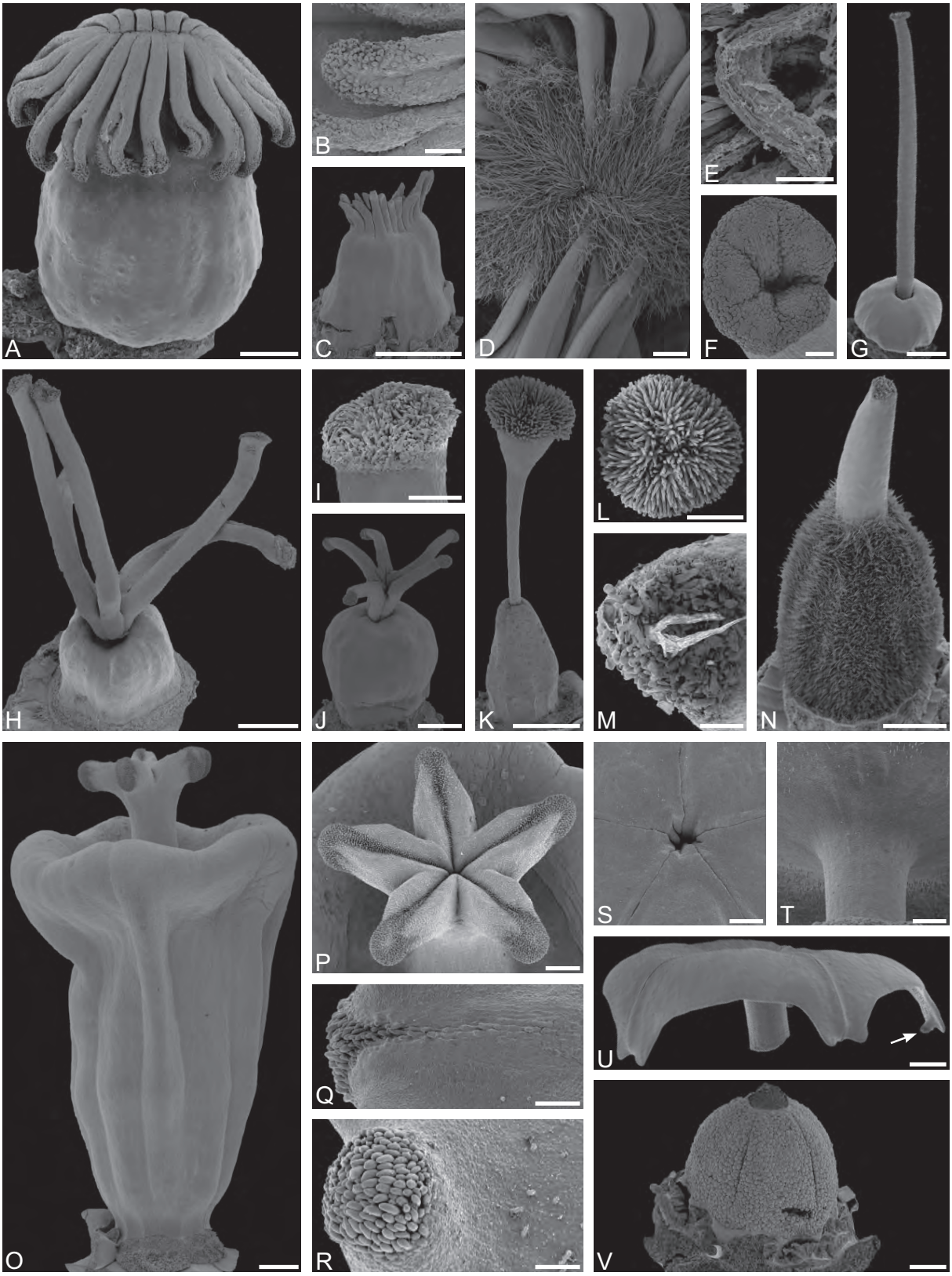


Figure 12. See caption on next page.

Figure 12. Gynoecium: Actinidiaceae/Roridulaceae/Sarraceniaceae. A, B, *Actinidia arguta* (functionally female). A, Gynoecium overview. B, Stigma. C, *Actinidia arguta* (functionally male), gynoecium overview seen from side. D, *Actinidia chinensis* (functionally female), gynoecium top view. E, *Actinidia chinensis* (functionally male), style, note the lack of stigmatic papillae. F, G, *Clematoclethra scandens*. F, Stigma. G, Gynoecium overview. H, I, *Saurauia pittieri*. H, Gynoecium overview. I, Stigma. J, *Saurauia subspinosa*, gynoecium overview. K, L, *Roridula gorgonias*. K, Gynoecium overview. L, Stigma. M, N, *Heliamphora nutans*. M, Stigma. N, Gynoecium overview. O, P, *Darlingtonia californica*. O, Gynoecium overview. P, Styles and stigmas. Q–V, *Sarracenia purpurea*. Q, Stigma, dorsal view. R, Stigma. S, Distal (ventral) centre of style. T, Distal-most part of terete style and transition zone to umbrella-like part of style. U, Umbrella-like style overview, the arrow indicates a stigma. V, Ovary overview. Scale bars: A, C, D, G, H, J, K, N, O, U, V, 1 mm; B, I, 200 μm; E, F, M, Q, R, 100 μm; L, P, S, T, 500 μm.

are not found on the petals or the ovary. In addition, the inner surface of the gynoecium is not secretory.

Actinidia chinensis *(functionally female flower)*
Morphology: The flowers are similar to the functionally female flowers of *A. arguta* (Figs 1A, 2A–M). There are, however, a few clear differences: flowers are larger, *c*. 5 cm in diameter (Fig. 1C); there are five to seven petals; petals are proximally thicker than sepals (Fig. 2Q); inside the petal whorl an incomplete whorl of weakly developed petaloid organs alternating with petals is present (Figs 1C, 2O–R); the androecium consists of *c*. 120 staminodes arranged in two loosely defined series (Fig. 2O–R); the filaments are sometimes proximally connate in sets of two or three for up to 5% of their length (Fig. 2Q); anthers are ventrifixed (Fig. 10C, D) and mostly latrorse to extrorse, with some introrse anthers (Fig. 2O) in preanthetic flowers (as a result of their inversion); anthers are, however, mostly introrse in anthetic flowers (Fig. 1C); there are *c*. 30 ovules, mostly arranged in two longitudinal rows per locule (Figs 2O, P, 13D); and the ovule integument is eight or nine cell layers thick.

Anatomy: The vascular system is similar to that of functionally female flowers of *A. arguta* with a few differences: there are more numerous secondary vascular bundles in the well-developed petals and few in the weakly developed petaloid organs of the inner whorl (Fig. 2O–Q); the vascular traces of the weakly developed petaloid organs merge with those of the filament traces in the floral base; and, in the floral base, the majority of the filament vascular traces merge in alternipetalous groups before joining the CVC (Fig. 2R).

Histology: The histology is similar to that of the functionally female flowers of *A. arguta* with a few differences: sepals and ovary (Fig. 12D) are densely covered by long, multicellular, uniseriate hairs; and no stomata are found on the dorsal side of the petals or on the ovary.

Actinidia chinensis *(functionally male flower)*
Morphology: The flowers are similar to the functionally female flowers of *A. arguta* (Figs 1A, 2A–M), but there are a few clear differences: flowers are generally larger, *c*. 4 cm in diameter (Fig. 1D); petals are proximally markedly thicker than sepals; the androecium consists of *c*. 35 fertile stamens with extrorse anthers (Figs 1D, 2N, 10A, B); the gynoecium is strongly reduced (Figs 1D, 2N); stigmatic papillae are absent (Fig. 12E); the styles are symplicate only in the proximal-most parts; the depression on top of the ovary is lacking; the symplicate zone of the ovary is only weakly developed (the synascidiate zone extends almost to the top of the ovary); and PTTT, placentae and ovules are completely lacking (Figs 2S, 13E). Compared with the functionally female flowers of *A. chinensis* (Figs 1C, 2O–R), the flowers are generally smaller (Figs 1D, 2S).

Anatomy: As in the functionally female flowers of *A. chinensis* (Fig. 2R), the filament traces merge in alternipetalous groups before joining the CVC in the floral base and, as in the functionally male flowers of *A. arguta* (Figs 1B, 2N), there are no ventral vascular bundles in the ovary (Fig. 2S).

Histology: The histology is similar to that of the flowers of functionally female *A. arguta* with a few differences. As in the functionally female flowers of *A. chinensis*, the sepals and ovary (Fig. 13E) are completely covered in multicellular, uniseriate hairs, and no stomata are found on the dorsal side of the petals or in the ovary. As in the functionally male *A. arguta*, the inner surface of the gynoecium is not secretory.

Clematoclethra scandens
Morphology: Flowers are bisexual, pentamerous, actinomorphic and hypogynous (Figs 1E, 3); they are presented on axillary, few- to many-flowered cymose branches, *c*. 0.8–1.0 cm in diameter, cup-shaped with an open access to the floral centre and slightly pendant (Fig. 1E).

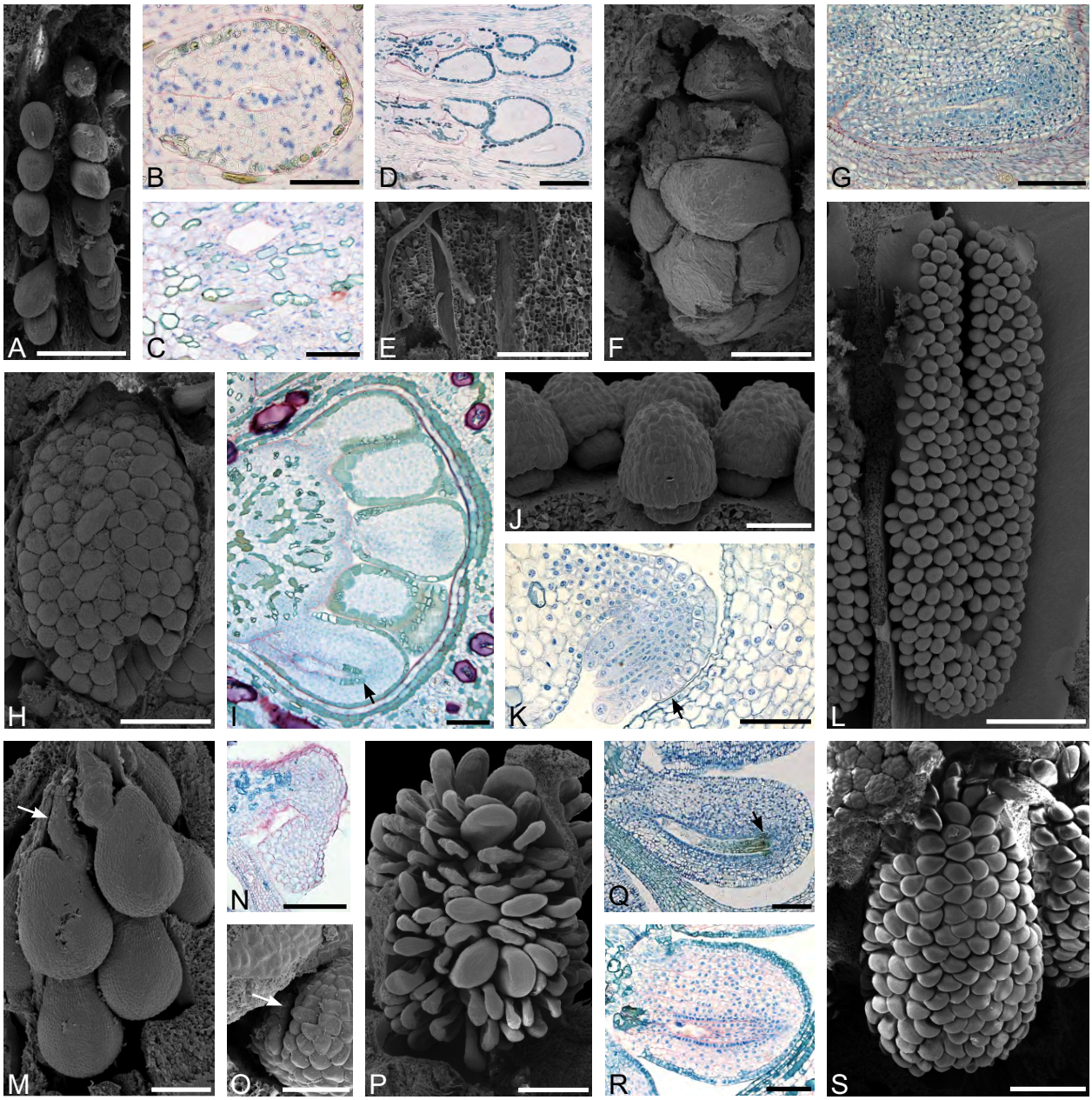


Figure 13. Placentation and ovules: Actinidiaceae/Roridulaceae/Sarraceniaceae. A, B, *Actinidia arguta* (functionally female). A, Placentation. B, Ovule. C, *Actinidia arguta* (functionally male), locules. D, *Actinidia chinensis* (functionally female), locules and ovules. E, *Actinidia chinensis* (functionally male), locules. F, G, *Clematoclethra scandens*. F, Placentation. G, Ovule. H, *Saurauia subspinosa*, placentation. I, *Saurauia pittieri*, locule and ovules. J–L, *Darlingtonia californica*. J, Ovules. K, Young ovule, the arrow indicates the outer integument. L, Placentation. M–O, *Roridula gorgonias*. M, Placentation, the arrow indicates the conspicuous funiculus. N, Ovule attachment. O, Ovule, the arrow indicates the micropyle. P, Q, *Heliamphora nutans*. P, Placentation. Q, Ovule, the arrow indicates the nucellar hypostase. R, S, *Sarracenia leucophylla*. R, Ovule. S, Placentation. Scale bars: A, F, H, P, S, 500 μm; B, C, G, I–K, N, O, Q, R, 100 μm; D, E, M, 200 μm; L, 1 mm.

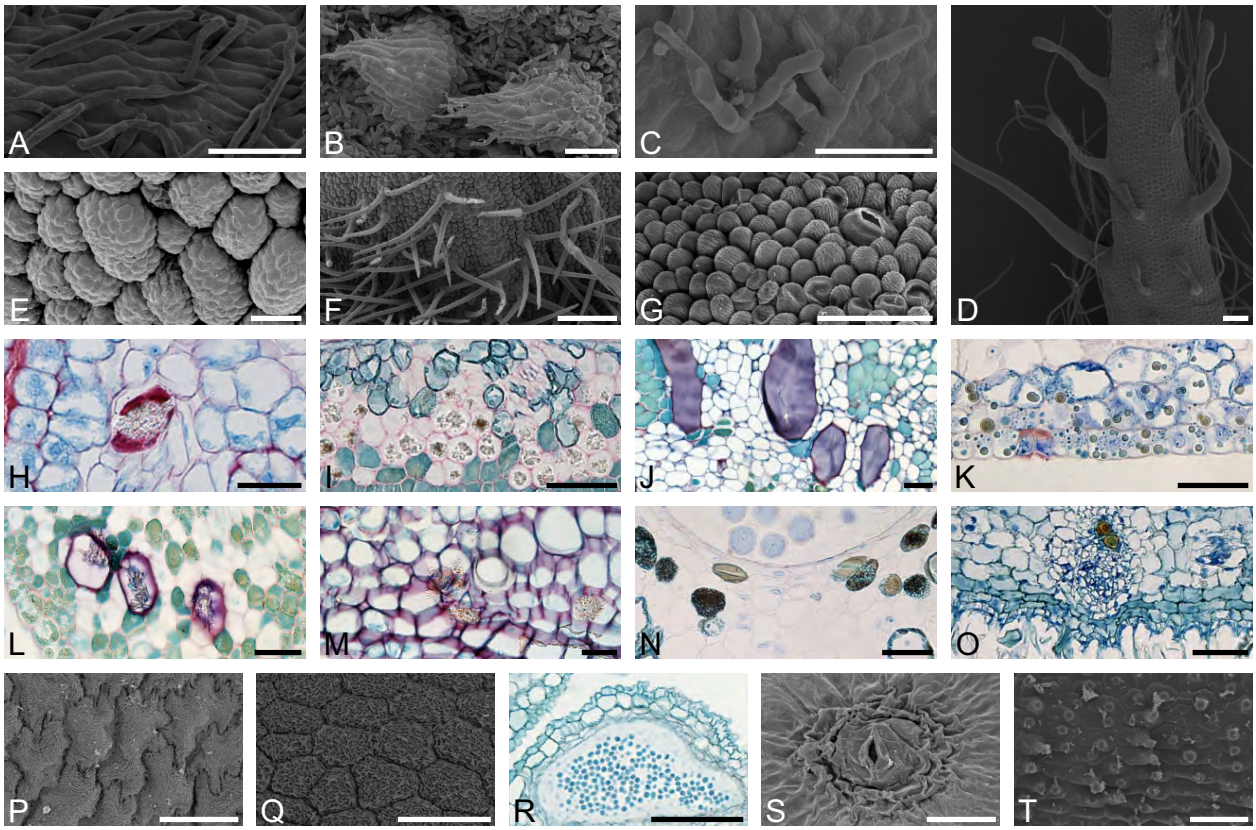


Figure 14. Anatomy and histology: Actinidiaceae/Roridulaceae/Sarraceniaceae. A, *Actinidia arguta* (functionally female), dorsal view of sepal with uniseriate hairs and elongate epidermal cells. B, *Saurauia pittieri*, dorsal view of sepal, note the uniseriate hairs and pluriseriate scale-like structures. C, *Saurauia subspinosa*, ventral view of sepal with branched hairs and otherwise a more or less smooth epidermal surface. D, *Roridula gorgonias*, dorsal view of sepal showing two kinds of hairs (uniseriate and pluriseriate glandular). E, *Sarracenia purpurea*, ovary wall, note multicellular stubby structures. F, *Heliamphora nutans*, ovary wall with bifid hairs and rounded epidermal cells. G, *Roridula gorgonias*, ovary wall, note inflated epidermal cells. H, *Actinidia chinensis* (functionally female), mucilage-lined raphide bundle in petal. I, *Roridula gorgonias*, calcium oxalate druses, tannins and condensed tannins in ovary wall. J, *Saurauia pittieri*, stone cells and tannins in sepal. K, *Sarracenia purpurea*, tannin-like droplets and stoma in petal. L, *Saurauia pittieri*, tannins and mucilage-lined calcium oxalate druses in petal. M, *Clematoclethra scandens*, raphide bundles in sepal. N, *Darlingtonia californica*, tannins in anther connective. O, *Heliamphora nutans*, calcium oxalate crystals and tannins in ovary wall. P, *Sarracenia purpurea*, 'jigsaw puzzle piece'-shaped epidermal cells with uneven cuticle structure on anther. Q, *Roridula gorgonias*, angular epidermal cells with uneven cuticle structure on anther. R, *Clematoclethra scandens*, uneven cuticle structure in anther epidermis. S, *Actinidia arguta* (functionally female), potentially nectariferous stoma in ovary wall. T, *Darlingtonia californica*, papillate epidermal cells on sepals. Scale bars: A–F, 100 μm; G–T, 50 μm.

Sepals are proximally united for *c*. 5%, arranged in a single whorl (Fig. 3I–K) and the aestivation is quincuncial (Fig. 3). Sepals are broadly ovate and the outer two sepals are slightly smaller than the inner three sepals (Fig. 3); they are distally acute (Fig. 1E), broadly attached (Fig. 2K) and the margin is entire to slightly crenulate. Sepal bases are massive, dorsally bulging and extend downwards, beyond their region of attachment with the pedicel and therefore appearing to be inserted into a shallow pit (Fig. 3M, N). Sepals are persistent after anthesis.

Petals are free and arranged in a single whorl (Fig. 3K); the aestivation is quincuncial and the margins are sometimes irregularly curled around the stamens (Fig. 3). Petals are ovate and uniform in shape and size (Figs 1E, 3), they are distally obtuse to retuse (Fig. 3E) and broadly attached (Fig. 3K). The thin (two cell layers thick) petal margin is entire to minutely crenulate.

The androecium consists of ten stamens arranged in a single series, entirely free from each other and from the petals (Fig. 3J). The alternipetalous stamens

are slightly longer than the alternisepalous ones in bud (Fig. 3B). Anthers are dithecate and tetrasporangiate (Fig. 10F); they are sagittate, basifixed and extrorse in bud and invert to introrse at anthesis (Figs 1E, 3, 10E, F). Connectives are broader on the ventral side (Fig. 10F). Anther dehiscence is by longitudinal slits that extend over 70% of the thecae, starting at the morphological base (Fig. 10E). Filaments are dorsiventrally flattened, more pronouncedly so proximally, and approximately twice the length of the anthers (Fig. 3D–J). The joint between the filament and the anther is broad (Fig. 10F).

The pentamerous gynoecium is almost completely syncarpous, except for a short asymplicate zone in the stigma (Fig. 12F, G). The stigma is small and disc-shaped (minutely five-lobed) and has a continuous stigmatic surface (Fig. 12F) of unicellular, unbranched and secretory papillae (Fig. 12F). In the style, the carpel margins meet in the centre, but the ventral slits are not postgenitally united (Fig. 3B–D). The style is inserted in a depression at the top of the flattened-globose ovary (Figs 3D, 12G). In the symplicate zone (*c*. 85% of the ovary), the carpel margins meet in the centre of the gynoecium, but are not postgenitally united (Fig. 3D–H). A short region of the symplicate ovary, just distal of the level of placenta attachment, is incompletely septate (Fig. 3G). In the style, the PTTT (Fig. 3A–H) is four or five cell layers thick and continuous between the carpels, forming a compitum that lines the ventral slits and narrow central canal. In the proximal region of the style and on the placentae, one or two cell layers of PTTT are present. Placentation is axile, the placentae are attached for *c*. 75% of their length; free placental lobes protrude upwards into the locules (Figs 3F, G, 13F). Each locule contains eight to ten ovules, arranged in two longitudinal rows, one on either side of the internal ventral slit, directed upwards to outwards in the locule (Figs 3F–I, 13F). Ovules are attached in the synascidiate and in the symplicate zone (Fig. 3F–I). Ovules are unitegmic (the integument is seven or eight cell layers thick), anatropous and tenuinucellar (Fig. 13F, G).

Anatomy: Sepals have one primary and *c*. eight secondary vascular bundles distally, the bundles merge with each other at varying levels (Fig. 3); proximally, only the primary and two secondary bundles remain. In the floral base, the three remaining traces join the CVC individually (Fig. 3L).

Petals have one primary and numerous secondary vascular bundles distally (Fig. 3); most of the bundles extend down to the proximal region, where they merge into one primary and two secondary bundles (Fig. 3K). In the floral base, the three remaining vascular traces merge into one trace before joining the CVC (Fig. 3K).

Stamens have a single vascular bundle; in the floral base, the traces join the CVC individually (Fig. 3J, K).

In the stigmatic lobes and the style, carpels have one median (dorsal) vascular bundle; in the ovary, one ventral and two lateral bundles are additionally present (Fig. 3A–J). The ventral bundles supply the placentae and the lateral bundles branch off at varying levels to supply the ovary wall and locules. In the synascidiate zone, the ventral vascular bundles merge to form a CVC. In the floral base, the lateral vascular traces merge with the dorsal traces before joining the CVC (Fig. 3I–K).

Histology: Long, multicellular, uniseriate hairs densely cover the dorsal and ventral surfaces of the sepals (Fig. 14A for *A. arguta*) and are sparsely present on the proximal region of the petals (dorsally and ventrally). The reproductive organs are completely glabrous.

No stomata were located in the studied material.

The perianth epidermal cells are rounded on both the dorsal and ventral sides. The epidermal cells of the anthers are 'jigsaw puzzle piece'-shaped (Fig. 14P for *S. purpurea*). Filament epidermal cells are elongate and more or less smooth in appearance. The epidermal cells of the styles are elongate and more or less smooth, and the cells of the ovary are rounded and more or less smooth. All epidermal cells have uneven cuticles, most pronounced in the anthers (Fig. 14R).

Parenchymatic cells are tightly packed in the perianth organs and no apparent palisade parenchyma or nectariferous tissue is present; parenchymatic tissue is uniform and tightly packed in the ovary.

Mucilage cells (Fig. 14H for *A. chinensis*), oxalate druses (Fig. 14L for *S. pittieri*) and raphides (Fig. 14M) are present in all floral organs, most abundantly in the sepals.

Tannins are present mainly in the anther walls (Fig. 14R) and stamen filaments, and additional vesicles that appear to contain tannins (Fig. 14K for *S. purpurea*) are sparsely scattered in the cytoplasm of cells in all floral organs.

Endothecium cells with lignified wall thickenings (mainly the inner tangential walls) are present in the anther walls, but are lacking in the connective and septa.

The inner surface of the gynoecium (mainly the placentae) is secretory.

The ovules potentially contain a nucellar hypostase, but they are not well defined in the sectioned ovules.

Saurauia pittieri

Morphology: Flowers are presented on axillary, many-flowered, cymose branches, *c*. 1.5–2.0 cm in diameter

with an open access to the floral centre and slightly pendant (Fig. 1F); they are bisexual, pentamerous, actinomorphic and hypogynous (Figs 1F, 4A–M).

Sepals are proximally united for *c*. 5% and arranged in a single whorl (Fig. 4J–L); the aestivation is quincuncial. Sepals are broadly ovate and uniform in size, distally obtuse (Fig. 1F) and broadly attached (Fig. 4J–L) and the margin is entire. Sepal bases are massive, dorsally bulging and extend downwards beyond their region of attachment with the pedicel therefore appearing to be inserted in a shallow pit (Fig. 4L). Sepals are persistent, also after anthesis.

Petals are free from each other and arranged in a single whorl (Fig. 4J, K); the aestivation is quincuncial. Petals are obovate and uniform in shape and size, distally obtuse to retuse (Fig. 1F), broadly attached (Fig. 4J, K), and the thin (two or three cell layers thick) margin is minutely crenulate. Petals are proximally of more or less equal thickness to the sepals (Fig. 4K, L).

The androecium consists of *c*. 45 stamens arranged in a single series (Fig. 4). Filaments are proximally connate to each other and to the petals for *c*. 5% of their length (Fig. 4I, J). Anthers are dithecate and tetrasporangiate (Fig. 10H), deeply sagittate and ventrifixed, and the joint between the filament and the anther is broad (Fig. 10G, H). Anthers are extrorse in bud (Figs 4, 10D) and become inverted to introrse orientation at anthesis (Fig. 1F). Connectives are broad on the ventral side (Fig. 10D). Anther dehiscence is by short, pore-like slits (Fig. 10G). Filaments are slightly dorsiventrally flattened in the distal region, more terete in the proximal region and approximately the same length as the anthers (Fig. 4I–K).

The pentamerous gynoecium is syncarpous in the ovary and the proximal-most part of the styles (Figs 4, 12H). The stigmas are small and discoid (Fig. 12I) and covered in unicellular, unbranched and secretory papillae (Fig. 12I). The styles are two to three times longer than the height of the ovary and distally spreading (Fig. 12H). In the symplicate style, the carpel margins meet in the centre, but are not postgenitally united. The style is inserted in a depression at the top of the flattened-globose ovary (Figs 4E, F, 12H). The ovary is symplicate for *c*. 40%; in the distal-most part, the carpel margins do not meet in the centre, whereby a central canal is formed, but the septa are postgenitally united (Fig. 4F, G). A short region, just distal of the placenta attachment, is incompletely septate (Fig. 4G). At the level of the distal placenta attachment and throughout the remainder of the symplicate ovary, the carpels are postgenitally united in the centre (Fig. 4H). In the asymplicate region, the PTTT (Fig. 4B–G) is five to seven cell layers thick. In the symplicate region of the style and the distal part of the ovary, the PTTT is one or two cell layers thick and continuous between the carpels, forming a compitum that lines the ventral slits and central canal. Placentation is axile (Figs 4G–J, 13I); the placentae are pendant (Fig. 4J) and attached for *c*. 90% of their length. Ovules (*c*. 20 per carpel) are arranged in four to six longitudinal rows on the placentae (Figs 4G–J, 13I); they are slightly pendant and present in both the symplicate and synascidiate zones of the ovary (Figs 4G–K, 13I). Ovules are unitegmic (the integument is six or seven cell layers thick), anatropous and tenuinucellar to slightly incompletely tenuinucellar (Fig. 13I).

Anatomy: Sepals have one primary and *c*. ten secondary vascular bundles distally; the bundles merge with each other at varying levels (Fig. 4); proximally, only the primary and two secondary bundles are still present. In the floral base, the remaining traces join the CVC individually (Fig. 4K–M).

Petals have one primary and *c*. ten secondary vascular bundles distally (Fig. 4); the bundles merge with each other at varying levels; proximally, only the primary and two secondary bundles remain. In the floral base, the three remaining vascular traces merge before joining the CVC (Fig. 4K, L).

Stamens have a single vascular bundle; in the floral base, the vascular traces merge in units of two to five (no distinctly alternisepalous or alternipetalous groupings), which join the CVC individually (Fig. 4K, L).

In the styles, each carpel has one median vascular bundle (Fig. 4D–F); in the ovary, each carpel additionally has one ventral and two lateral vascular bundles (Fig. 4H–J). The ventral bundles supply the placentae and the lateral bundles branch off at varying levels, supplying the ovary wall and locules. At the base of the locules, the ventral vascular bundles merge to form a CVC. In the floral base, the lateral vascular traces merge with the dorsal traces before joining the CVC (Fig. 4K).

Histology: Long, multicellular, uniseriate hairs densely cover the dorsal and ventral surfaces of the sepals (Fig. 14A for *A. arguta*) and the ventral, proximal region of the petals. Hairs also occur sparsely on the remaining surfaces of the petals. The sepals are additionally characterized by massive, multicellular, pluriseriate scale-like structures on the dorsal surfaces that are exposed in bud (Fig. 14B). The stamen filaments have long, uniseriate hairs proximally (Fig. 10G). The gynoecium is completely glabrous (Fig. 12H).

A few stomata are found on the connective, close to the anther attachment. No stomata are found on the remaining organs.

The perianth epidermal cells are smooth to slightly dome-shaped in appearance. The epidermal cells of the anthers are 'jigsaw puzzle piece'-shaped. Filament epidermal cells are elongate and more or less smooth in appearance. The epidermal cells of the styles are elongate and more or less smooth; the cells of the ovary are rounded and more or less smooth. In the ovary epidermis, a slight depression is visible along the median vascular bundle (future dehiscence line). All epidermal cells have uneven cuticles.

Parenchymatic cells are tightly packed in the perianth organs, and no obvious palisade parenchyma or nectariferous tissue is present; parenchymatic tissue is uniform and tightly packed in the ovary.

Mucilage cells (Fig. 14L), oxalate druses (Fig. 14I for *R. gorgonias*), raphides (Fig. 14H for *A. chinensis*) and stone cells (Fig. 14J) are abundant in all floral tissue. The mucilage cells, crystal structures and stone cells are often found in combination, where mucilage lines a central aggregate of stone cells and/or crystals (Fig. 14H for *A. chinensis*).

Tanniferous cells (Fig. 14J) are abundantly present in all floral tissue; condensed tannins occasionally line the internal cell walls of the tanniferous cells (Fig. 14I). Small vesicles that appear to contain tannins (Fig. 14K) are sparsely present (mainly in the tanniferous cells).

Endothecium cells with lignified wall thickenings (mainly the inner tangential cell walls) are present in the anther walls, but are lacking in the connective and the septa.

The inner surface of the gynoecium (mainly the placentae) is secretory.

The ovules contain a nucellar hypostase (Fig. 13I).

Saurauia subspinosa

Morphology: The flowers (Figs 1G, 4N–U) are, in many ways, similar to those of *S. pittieri* (Figs 1F, 4A–M) with some clear differences: they are distinctly cup-shaped (Fig. 1G); sepals are almost completely free from each other and unequal in size (the outer two are smaller than the inner three; Fig. 4N–R); there are five petals (rarely six, as in the sectioned flower), united for *c*. 30% of their length (Figs 1G, 4N–R); petals are proximally markedly thicker than the sepals (Fig. 4Q–S); there are almost invariably 50 stamens, proximally united with each other and the petals for up to 10% of their length (Fig. 4P–R); anthers are introrse in advanced buds and open flowers (Figs 4N, O, 10J, K), but extrorse in earlier stages; anthers are subapically ventrifixed (Fig. 10I–K); filaments are about twice as long as anthers; styles are shorter than the height of the ovary (Fig. 12J); the ovary has a larger portion of incomplete septation (Fig. 4N) than in *S. pittieri*; and each carpel produces numerous ovules (> 120; Fig. 13H), arranged in 12–16 longitudinal rows on each placenta (Figs 4O, 13H).

Anatomy: The vascular system is similar to that of *S. pittieri* with the following differences: sepals have numerous vascular bundles in the distal region (Fig. 4N, O); in the proximal area of the sepals, only the median dorsal and two lateral secondary bundles are present (Fig. 4S); and, in the floral base, the secondary vascular traces unite with those of the neighbouring sepal, forming synlateral vascular traces, which join the CVC in the floral base (Fig. 4T).

Histology: The histology is similar to that of the flowers of *S. pittieri* with a few differences: the multicellular, uniseriate hairs (often branched) are sparsely present on mainly the proximal, ventral surfaces of the perianth organs (Fig. 14C); anther filaments are glabrous (Fig. 10J); mucilage cells, oxalate druses, raphides, stone cells and tannins are not as abundant; stomata are present on the ventral surface of the petals.

Roridulaceae

Roridula gorgonias

Morphology: Flowers are *c*. 2.5–3.0 cm in diameter with an open access to the floral centre, outwards to upwards-facing and presented on axillary few-flowered, botryoid inflorescences (Fig. 1H); they are bisexual, pentamerous and actinomorphic and the ovary is semi-inferior (Figs 1H, 5), *c*. 15% of the total length of the locules, devoid of placentae and ovules and extends down into the floral base (Fig. 5M–O).

Sepals are free from each other or partially united in the proximal 5% and arranged in a single whorl (Fig. 5); the aestivation is quincuncial (Fig. 5). Sepals are elliptic (Figs 1H, 14D), uniform in size, distally acute (Fig. 1H), broadly attached (not dorsally bulging; Fig. 5N) and the margin is entire (Fig. 14D). Sepals are persistent after anthesis.

Petals are proximally united for 5% and arranged in a single whorl (Fig. 5L, M); the aestivation is quincuncial (Fig. 5). Petals are broadly elliptic to obovate, uniform in shape and size, distally acute, broadly attached (Figs 1H, 5) and the thin (two to three cell layers thick) margin is entire. Petal bases are proximally conspicuously massive and thicker than the sepals (Fig. 5J–M).

The androecium consists of five stamens arranged in a single whorl, completely free from each other, but proximally united with the short corolla tube for *c*. 5% of their length (Fig. 5L, M). Anthers are dithecate, tetrasporangiate (Fig. 11B), deeply sagittate, subapically ventrifixed and have a conspicuous apical

protrusion (Figs 1H, 5C, D, 11A, B). The thecae are latrorse (Fig. 5E, F), inverting 180° with the beginning of anthesis. Connectives are broad on the ventral side (Fig. 11B). Anther dehiscence is by longitudinal slits that extend from the morphological base over *c*. 90% of the length of the thecae (Figs 5E, F, 11A, B). The joint between the filament and the anther is broad (Fig. 11B). The filaments are slightly dorsiventrally flattened, more pronouncedly so in the proximal region, and are approximately twice the length of the anthers (Fig. 5C–M).

The trimerous gynoecium is fully syncarpous, except for a short asymplicate zone in the stigma (Fig. 5). The stigma is minutely three-lobed and has a continuous surface of unicellular, unbranched stigmatic papillae without obvious secretion (Figs 5, 12K, L). The distal part of the style and the stigma is conspicuously enlarged (Fig. 12K). The style has a narrow central canal, extending down into the distal part of the ovary (Fig. 5B–G). The style is inserted in a minute depression on top of the ovoid to conical ovary (Figs 5F, 12K). The symplicate zone extends through *c*. 50% of the ovary (Fig. 5F–J). Just distal of the locules, there is a short zone of postgenital union (Fig. 5J); the remainder of the symplicate zone is incompletely septate. In the distal part of the style, the PTTT is four to nine cell layers thick; in the proximal part of the style and the distal part of the ovary, the PTTT is one or two cell layers thick and continuous between the carpels, forming a compitum that lines the ventral slits and narrow central canal (Fig. 5B–J). Placentation is axile and the placentae are attached for almost their entire length, shortly pendant beyond their proximal-most point of attachment (Fig. 5K). There are four pendant ovules per locule, arranged in two longitudinal rows on the placentae, one on either side of the ventral slit (Fig. 13M). The ovules are attached in the symplicate and synascidiate zone (Figs 5I–K, 13M). Ovules have a conspicuous funiculus (Fig. 13M, N), are unitegmic (the integument is ten or eleven cell layers thick), anatropous and tenuinucellar (Fig. 13M–O).

Anatomy: Sepals have one primary and eight secondary vascular bundles distally (Fig. 5); the bundles merge with each other at varying levels; proximally, only the primary and two to four secondary bundles remain. In the floral base, the remaining traces join the CVC individually (Fig. 5Q, R).

Petals have one primary and 12–14 secondary vascular bundles distally (Fig. 5); the bundles merge with each other at varying levels; proximally, the secondary vascular bundles merge with the primary bundle (Fig. 5L). The single remaining vascular trace joins the CVC in the floral base (Fig. 5Q).

Stamens each have a single vascular bundle; in the floral base, the vascular traces join the CVC individually (Fig. 5P).

In the style, each carpel has one median (dorsal) vascular bundle (Fig. 5B–F); in the ovary, each carpel additionally has one ventral (Fig. 5J–M) and two lateral (Fig. 5H–M) bundles. The ventral bundles supply the placentae and the lateral bundles branch off at varying levels to supply the ovary wall. At the base of the locules, the ventral vascular bundles merge to form a CVC (Fig. 5N, O). In the floral base, the lateral traces merge with the dorsal traces before joining the CVC (Fig. 5M–P).

Histology: Long, multicellular, uniseriate hairs and pluriseriate glandular hairs are present on the dorsal and ventral surfaces of the sepals (Fig. 14D). The remaining organs are completely glabrous.

Stomata are present on the dorsal surface of the sepals, on the dorsal and ventral surfaces of the petals and on the ovary wall.

The epidermal cells of sepals and petals are uneven on the dorsal and ventral sides. The epidermal cells of the anthers are angular (Fig. 14Q) with a more or less smooth appearance. Filament epidermal cells are elongate and more or less smooth in appearance. The epidermal cells of the style are elongate and more or less smooth and the cells of the ovary are papillate in appearance (Fig. 14G). All epidermal cells have uneven cuticles (Fig. 14Q).

Parenchymatic cells are tightly packed in the perianth organs and no apparent palisade parenchyma or nectariferous tissue is present; parenchymatic tissue is uniform and tightly packed in the ovary, except on the ventral side of the dorsal vascular bundle (future dehiscence line) and in the septa, in which the cells are smaller.

Mucilage cells (Fig. 14H for *A. chinensis*), oxalate druses (Fig. 14I) and raphides (Fig. 14M for *C. scandens*) are present in all floral organs. The mucilage cells and crystal structures often form combined structures in which mucilage lines a central aggregate of crystals (Fig. 14L for *S. pittieri*).

Tannins (Fig. 14I) are abundant in all floral organs, except the distal part of the petals. Tannin aggregates sometimes form along the internal cell walls of tanniferous cells (condensed tannins; Fig. 14I) and additional small vesicles that appear to contain tannins (Fig. 14K for *S. purpurea*) are sparsely present in the cytoplasm of most cells.

Endothecium cells with lignified wall thickenings (mainly the inner tangential cell walls) are present in the anther walls, but are lacking in the connective and the septa.

The inner surface of the gynoecium (mainly the placentae) is secretory (Fig. 13N).

The ovules potentially contain a nucellar hypostase, but it is difficult to determine with certainty.

The anther protrusion contains carbohydrates (staining bright pink; Fig. 11B).

Sarraceniaceae

Darlingtonia californica

Morphology: Flowers are solitary and presented on tall scapes; they are pendant, *c*. 7 cm in diameter and about as long; the floral centre is concealed by the petals (Fig. 1L); they are bisexual, pentamerous, actinomorphic and hypogynous (Figs 1L, 6). Both perianth whorls are petaloid, i.e. the sepals are showy and yellow and the petals are maroon, but differentiated in shape and size (Fig. 1L).

Sepals are free, arranged in a single whorl and the aestivation is quincuncial (Fig. 6); in the distal region, the margins are induplicate (Fig. 1L); they are broadly elliptic to narrowly obovate (Fig. 1L), distally acute (Fig. 1L), broadly attached (not dorsally bulging; Fig. 6P–S) and the margin is entire (Fig. 1L). The outer two sepals are slightly larger than the inner three (Fig. 6). Sepals are persistent after anthesis.

Petals are free, arranged in a single whorl and the aestivation is quincuncial (Fig. 6). In the distal region, the petals are induplicate and more or less apert (Fig. 6A–D); they are pandurate (ovate, but constricted over the middle; Fig. 1L), distally acute (Fig. 1L), broadly attached (Fig. 6N–Q) and uniform in shape and size (Fig. 6). The thin (two to three cell layers thick) petal margin is entire. Petals are proximally conspicuously massive and thicker than the sepals (Fig. 6N–P).

The androecium consists of 15 stamens arranged in a single series, completely free from each other and the petals (Fig. 6). In the proximal-most region, the filaments are arranged in vaguely alternisepalous groups of three stamens each (Fig. 6M, N). Anthers are dithecate and tetrasporangiate (Fig. 11D); they are basifixed and the thecae are unequal in size; the two thecae are separated by a thick connective (Figs 6H–L, 11C, D). In addition, the anthers are apparently rotated 90° when compared with a 'normal' anther (Figs 6K, L, 11C, D). The result is that one theca (the larger of the two) is oriented exactly to the outside of the flower and is therefore extrorse; the smaller theca is directed towards the floral centre and is, accordingly, introrse (Fig. 6K, L). At anthesis, the anthers become inverted, causing the smaller theca to dehisce extrorsely and the larger theca introrsely. Anther dehiscence is by longitudinal slits that extend from the morphological base over almost the entire thecae. The joint between the anther and the filament is broad (Fig. 11D). The filaments are angular with rounded edges and of approximately equal length to the anthers (Fig. 6M, N).

The pentamerous gynoecium is syncarpous, except for the distal 20% of the styles (Figs 6, 12O, P). The five stigmas (one per carpel) are as long as the asymplicate styles and drop-shaped with a reflexed 'head' extending over both the dorsal and ventral side of the styles and a decurrent 'tail' reaching the central axis of the flower, in the transition zone to the symplicate styles (Fig. 12P). The stigmatic papillae are unicellular and unbranched, and no secretion is detected (Fig. 12P). The distal region of the symplicate style has a narrow central canal (open ventral slits), which becomes postgenitally united in the transition zone to the ovary. The postgenital union of the carpel margins extends down to the distal part of the ovary (and septa are thereby formed). The symplicate style is inserted in a deep depression on top of the turbinate and conspicuously ridged (along the septa) ovary (Figs 6D, E, 12O). In the distal part of the ovary, the central canal expands and forms a large cavity (Fig. 6G–I). The symplicate zone extends over *c*. 30–40% of the ovary length (Fig. 6E–I). A short region of the symplicate zone, just distal of the transition to the synascidiate zone, exhibits postgenital union of the carpel margins (Fig. 6J); the remainder of the symplicate zone is incompletely septate (Fig. 6G–I). In the distal, asymplicate part of the style, the PTTT is eight to nine cell layers thick. In the symplicate part of the style and the distal part of the ovary, the PTTT is one or two cell layers thick and continuous between the carpels, forming a compitum that lines the ventral slits and central canal (Fig. 6B–I). Placentation is axile (Figs 6, 13L) and the pendant placentae are attached for 90% of their length (Fig. 6G–L). There are *c*. 500 ovules per locule, arranged in 12 longitudinal (somewhat irregular) rows per placenta, six on either side of the ventral slit (Figs 6G–L, 13L). The ovules are slightly pendant and attached in both the symplicate and the synascidiate zone (Figs 6G–L, 13L). The ovules are anatropous, tenuinucellar and bitegmic with the four or five cell layer thick inner integument forming the micropyle (Fig. 13J, K). The outer integument is short and only three or four cell layers thick (Fig. 13K). The sectioned flower bud is rather young; therefore the integuments may not be fully developed.

Anatomy: Sepals have one primary and numerous secondary vascular bundles distally (Fig. 6); the bundles merge with each other at varying levels; proximally, only the primary and eight to ten secondary bundles remain. In the floral base, the remaining traces join the CVC individually (Fig. 6P–R).

Petals have one primary and numerous secondary vascular bundles distally (Fig. 6); the bundles merge with each other at varying levels; proximally, the primary and *c*. six secondary vascular bundles remain (Fig. 6N, O). In the floral base, the primary and remaining secondary traces merge before joining the CVC (Fig. 6P, Q).

Stamens have a single vascular bundle; in the floral base, the vascular traces merge into five alternisepalous groups of three before the units join the CVC individually (Fig. 6N, O).

In the asymplicate styles, each carpel has one median (dorsal) vascular bundle; in the symplicate styles, each carpel additionally has two ventral vascular bundles, which merge into synventral vasculature bundles prior to the transition to the ovary (Fig. 6C–E). In the ovary, each carpel additionally has synlateral, numerous lateral and two individual ventral vascular bundles (Fig. 6D–L). The ventral bundles supply the placentae and the lateral bundles branch off at varying levels to supply the ovary wall and locules. In the synascidiate zone, the individual ventral vascular bundles merge with the synventral bundles (Fig. 6I–K) before forming a CVC (Fig. 6J, K). At the level of the base of the locules, each carpel has only the dorsal, synlateral and two lateral vascular bundles (Fig. 6M). In the floral base, the dorsal, synlateral and lateral vascular traces join the CVC individually (Fig. 6M, N).

Histology: All floral organs are completely glabrous.

Stomata are present on the ventral surfaces of the sepals, the connective of the anthers and the ovary wall.

The sepal epidermal cells are slightly papillate (Fig. 14T) in appearance on both the dorsal and ventral sides, whereas the epidermis of the petals is more or less smooth. The epidermal cells of the anthers are angular and more or less smooth. Filament epidermal cells are rounded to slightly elongate and more or less smooth in appearance. The epidermal cells of the styles are rounded to slightly elongate and more or less smooth, and the cells of the ovary are rounded and more or less smooth. All epidermal cells have uneven cuticles.

Parenchymatic cells are tightly packed in the perianth organs and no apparent palisade parenchyma or nectariferous tissue is present; parenchymatic tissue is uniform and tightly packed in the ovary, except on the ventral side of the dorsal vascular bundle (future dehiscence line) and in the septa, where the cells are smaller.

No mucilage cells or raphide bundles are present in the floral tissue. In the anthers, particularly around the vascular bundles, small amounts of oxalate crystals (Fig. 14I for *R. gorgonias*) are present.

Tannins (Fig. 14I for *R. gorgonias*) are present in all floral organs, most abundantly in the sepals and anthers (Fig. 11D). Vesicles that appear to contain tannins (Fig. 14K for *S. purpurea*) are abundant in the cells of the epidermal and hypodermal layers of the perianth and sparsely present in the remaining floral tissue.

Endothecium cells with lignified wall thickenings (mainly the inner tangential cell walls) are present in the anther walls, but are lacking in the connective and the septa.

The inner surface of the gynoecium is not secretory.

No nucellar hypostase is visible in the ovules (potentially too young).

Heliamphora nutans

Morphology: Flowers are presented on axillary, scorpioid cymes, pendant and *c*. 6 cm in diameter and cup-shaped with an open access to the floral centre (Fig. 1K); they are bisexual, tetramerous to pentamerous, actinomorphic and hypogynous (Figs 1K, 7). All tepals are petaloid (showy and white to pale pink at anthesis).

The tepals appear to be inserted in two loosely defined groups of two or three with a slight offset in insertion between the two groups (Fig. 7L–O); they are completely free from each other (Fig. 7), elliptic to broadly ovate (Fig. 1K), distally acute to acuminate (Fig. 1K) and broadly attached (not dorsally bulging; Fig. 7L–O). The two outermost tepals are larger and broader than the inner ones. All tepals have thin (two or three cell layers) entire margins (Figs 1K, 7). When five tepals are present, the innermost one is clearly smaller than the other four (Fig. 7). The two outer tepals are imbricate (one outside the other) and completely enclose the inner two or three; the inner two tepals are imbricate with one outside the other (Fig. 7). When a fifth tepal is present, the innermost one is enclosed by the two other ones (Fig. 7). The inner two or three tepals are proximally thicker than the outer two (Fig. 7L, M).

The androecium consists of 20 stamens arranged in a single series and completely free from each other and the tepals (Fig. 7K–M). Anthers are dithecate and tetrasporangiate (Fig. 11F), shallowly sagittate, dorsifixed and introrse in bud (Figs 7, 11E, F). At anthesis, the anthers become inverted to an extrorse orientation (Fig. 11E, F). Anther dehiscence is by short, pore-like slits at the morphological base of the thecae. The joint between the filament and the anther is broad and the connective is dorsally broad (Fig. 11F). The filaments are angular with rounded edges and approximately twice the length of the anthers (Figs 7G–M, 11F).

The trimerous gynoecium is fully syncarpous, except for a short asymplicate zone in the stigma

(Fig. 12M, N). The stigma is punctate, minutely three-lobed and a continuous surface of unicellular, unbranched and secretory papillae (Fig. 12M). In the three-angled style, the carpels are postgenitally united in the centre (Fig. 7B–E). The ovary is narrowly ovoid to conic and has no depression at the transition from the style to the ovary (Fig. 12N). The symplicate zone extends over *c*. 60–70% of the ovary (Fig. 7D–H) and is incompletely septate (open ventral slits or central canal) for almost its entire length (Fig. 7E–H). In the distal-most part of the ovary, carpel margins meet in the centre and are postgenitally united (Fig. 7E); proximal of this region, the carpel margins meet, but are not postgenitally united (Fig. 7F, G). Just distal of the synascidiate zone, there is a short region in which the carpels do not meet in the centre (Fig. 7H). In the distal part of the style, the PTTT is eight to ten cell layers thick. In the proximal part of the style and the distal part of the ovary, the PTTT is one or two cell layers thick and continuous between the carpels, forming a compitum throughout the style and along the ventral slits (Fig. 7B–E). Placentation is axile (Fig. 7). There are *c*. 100 ovules per locule, arranged in six longitudinal (somewhat irregular) rows on each placenta, three on each side of the ventral slit (Figs 7H, I, 13P). The ovules are attached in both the symplicate and synascidiate zones (Fig. 7H, I). In the distal region of the placentae, ovules face upwards, whereas they face outwards in the middle region and are pendant in the proximal region (Figs 7G–J, 13P). Ovules are unitegmic (the integument is nine or ten cell layers thick), anatropous and incompletely tenuinucellar (Fig. 13P, Q).

Anatomy: The outer two tepals each have one primary and numerous secondary vascular bundles distally (Fig. 7); the bundles merge with each other at varying levels; proximally, the primary and eight to ten secondary bundles remain. In the floral base, the remaining traces join the CVC individually (Fig. 7M–O).

The inner tepals each have one primary and numerous secondary vascular bundles distally (Fig. 7); the bundles merge with each other at varying levels; proximally, the primary and two to ten secondary vascular bundles remain (two in the innermost tepal and ten in the other two; Fig. 7J–M). In the floral base, the remaining traces merge before joining the CVC (Fig. 7M, N).

Stamens have a single vascular bundle; in the floral base, the vascular traces merge into groups of two to four before joining the CVC (Fig. 7L, M).

In the styles, each carpel has one median (dorsal) vascular bundle and synventral vascular bundles, shared with the neighbouring carpels (Fig. 7B–D). In the symplicate part of the ovary, each carpel additionally has synlateral, numerous lateral and two ventral vascular bundles (Fig. 7E–H). The lateral vasculature supplies the ovary walls and locules and the ventral vascular bundles supply the placentae. In the proximal region of the synascidiate zone, the ventral vascular bundles merge with the synventral vascular bundles before the CVC is formed below the locules (Fig. 7J, K). In the floral base, the lateral vascular traces merge with the dorsal bundles before joining the CVC (Fig. 7K, L); the synlateral vascular bundles join the CVC individually (Fig. 7K, L).

Histology: Long, multicellular (uniseriate), bifid hairs densely cover the ovary (Figs 12N, 14F, O); the remaining organs are completely glabrous.

Stomata are present on the dorsal and ventral surfaces of the outer perianth organs.

The epidermal cells of the outer perianth organs are rounded to angular and more or less smooth in appearance on the dorsal and ventral sides, whereas the epidermal cells of the inner perianth organs are more irregular in shape. The epidermal cells of the anthers are rounded (almost inflated in appearance). Filament epidermal cells are elongate and more or less smooth in appearance. The epidermal cells of the style are elongate and more or less smooth, and the cells of the ovary are rounded. All epidermal cells of the floral organs have uneven cuticles.

Parenchymatic cells are tightly packed in the perianth organs and no apparent palisade parenchyma or nectariferous tissue is present; parenchymatic tissue is uniform and tightly packed in the ovary, except on the ventral side of the dorsal vascular bundle (future dehiscence line) and in the septa, where the cells are smaller.

Small amounts of oxalate crystals (Fig. 14L for *S. pittieri*) are found in all floral organs, particularly around the vasculature.

Tannins (Fig. 14I for *R. gorgonias*) are present in all floral organs, most abundantly in the ovary wall (Fig. 14O). Vesicles that appear to contain tannins (Fig. 14K for *S. purpurea*) are abundant in the cells of the epidermal and hypodermal layers of the perianth and sparsely present in the remaining floral tissue. Similar, larger vesicles can be found in close proximity to the vasculature of the stamens and the ovary (Fig. 14O).

Endothecium cells with lignified wall thickenings (mainly the inner tangential cell walls) are present in the anther walls, but are lacking in the connective and the septa.

The inner surface of the gynoecium is not secretory.

The ovules contain a nucellar hypostase (Fig. 13Q). No mucilage cells or raphide bundles are present in the floral tissue.

Sarracenia purpurea

Morphology: Flowers are solitary and presented on tall scapes; they are pendant, *c*. 6 cm in diameter and about as long (Fig. 1I). The floral centre is concealed by the petals (Fig. 1I). Flowers are bisexual, pentamerous (the sectioned flower shown in Figure 8 has six petals, two of which share the position of insertion at the floral base), actinomorphic and hypogynous (Figs 1I, 8). Perianth whorls are both petaloid, i.e. the sepals are showy and, like the petals, maroon at anthesis; the two whorls are differentiated in shape and size (Figs 1I, 8).

Sepals are free from each other and the aestivation is quincuncial (Fig. 8); they are broadly obovate (Fig. 1I), unequal in size (the outer three are larger than the inner two; Fig. 8), distally obtuse (Fig. 1I), broadly attached (not dorsally bulging; Fig. 8L–P) and the margin is entire. Sepals are persistent after anthesis.

Petals are free (Fig. 8) and the aestivation is quincuncial in flowers with a pentamerous corolla (irregularly imbricate in the flower shown in Fig. 8); they are pandurate (Fig. 1I), distally obtuse (Fig. 1I), broadly attached (Fig. 8K–N) and more or less uniform in shape and size (Fig. 8). The thin (two to three cell layers thick) petal margin is entire. The petals are proximally thinner than the sepals (Fig. 8J–N).

The androecium consists of *c*. 80 stamens arranged in one series (there is a slight tendency of crowding in alternipetalous and alternisepalous positions; Fig. 8J–N). The stamens are completely free from each other and from the petals (Fig. 8J–N). Anthers are dithecate and tetrasporangiate (Fig. 11H), basifixed (Fig. 11G, H) and deeply sagittate (Fig. 11H); they are mostly introrse in bud (anther orientation in bud is partly irregular; Fig. 8) and become inverted to extrorse orientation at anthesis. Anther dehiscence is by longitudinal slits that extend from the morphological base over almost the entire length of the thecae. The joint between the filament and the anther is broad, as is the connective on the dorsal side (Fig. 11G, H). The filaments are terete (to somewhat rounded-angular) and approximately 1.5 times the length of the anthers (Fig. 8F–N).

The pentamerous gynoecium is fully syncarpous, except for a short asymplicate region of the styles (Figs 1I, 8E–I, 12S–U). The style is widely expanded into an umbrella-like structure (Fig. 12U). The asymplicate zones of the styles are reflexed and face the floral axis (Fig. 12U). The small stigmas (one per carpel) are punctiform and are located on short, peg-like protrusions on the dorsal side of the carpels (i.e. on the underside of the expanded style; Fig. 12R, U). On the ventral side, a long 'tail' of stigmatic papillae extends along the ventral slit towards the centre of the style (Fig. 12Q, R). Stigmatic papillae are unicellular, unbranched and no secretion is detected (Fig. 12Q, R). The distal, ventral part of the symplicate styles corresponds to a dilated stylar canal (Figs 8A–F, 12S; Supporting Information Movie S1). The terete portion of the style has a central canal and open ventral slits (Fig. 8A–E). The ventral slits are postgenitally united only in the proximal-most region, just above the transition to the ovary (Fig. 8E). The ovary is globose to ovoid and has no depression at the transition zone from style to ovary (Fig. 12V). The symplicate zone extends over *c*. 50% the length of the ovary, and almost the entire symplicate part of the ovary is incompletely septate with an open central canal and ventral slits (Figs 8F–H, 12T). The carpel margins in the style are postgenitally united only in the transition zone to the synascidiate part of the ovary (Fig. 8I). In the asymplicate part of the styles, close to the stigmas, the PTTT (Fig. 8B–H) is nine or ten cell layers thick. In the transition zone from the umbrella-shaped part to the terete part of the style (Fig. 12T), the PTTT is five to six cell layers thick. In the remainder of the style and distal part of the ovary, the PTTT is one or two cell layers thick and forms a compitum, lining the open canal and ventral slits. In the distal part of the locules, the compitum separates and lines the placentae with one or two cell layers of PTTT. Placentation is axile (Fig. 8G–J) and the placentae are attached for almost their entire length (shortly pendant, *c*. 10%, in the proximal-most region; Fig. 8J). There are *c*. 200 ovules per locule, arranged in 8–12 rows on each placenta, four to six on each side of the ventral slit (Fig. 8H, I). Ovules are attached in both the symplicate and synascidiate zones (Fig. 8G–J). The ovules are slightly upwards facing in the locules in the distal region of the placentae, transitioning through outwards facing to slightly pendant in the proximal region (Fig. 8G–J). The ovules of the investigated floral material are too young to determine detailed characters with certainty, but they appear to be unitegmic and anatropous.

Anatomy: Sepals have one primary and numerous secondary vascular bundles in their distal region (Fig. 8); the bundles merge with each other at varying levels; proximally, the primary and eight to ten secondary bundles are still present (Fig. 8M–P). In the floral base, the remaining traces join the CVC individually (Fig. 8O, P).

Petals have a primary and *c*. 12 secondary vascular bundles in the distal region, merging at varying levels (Fig. 8); in the proximal part of the petals, the primary and six to eight secondary vascular bundles remain (Fig. 8J–M). In the floral base, the remaining vasculature merges into one to three traces before joining the CVC (Fig. 8O).

Stamens have a single vascular bundle; in the floral base, most of the androecial vascular traces merge into groups of up to ten traces in vaguely alternisepalous and alternipetalous positions before joining the CVC (Fig. 8M–O).

In the umbrella-shaped part of the style, each carpel has one median, heavily ramified vascular bundle, supplying the large stylar surface and stigmas (Fig. 8A–D). In the terete part of the style, the carpels additionally have synventral vascular bundles (Fig. 8E, F). In the ovary, the synventral bundles diverge into two ventral vascular bundles per placenta (Fig. 8F–I). In addition to the median and ventral bundles, each carpel exhibits synlateral and numerous lateral bundles in the ovary, supplying the ovary wall and locules (Fig. 8G–J). In the synascidiate region, the ventral vascular bundles merge into synventral bundles before forming a CVC at the proximal-most level of the placentae (Fig. 8H–J). In the floral base, the lateral vascular traces merge with the synlateral and median vascular traces before joining the CVC (Fig. 8J–M).

Histology: The style has short, unicellular hairs on the dorsal and ventral surfaces of the distal, umbrella-shaped part. The ovary is densely covered with multicellular (pluriseriate), stubby hairs (Fig. 14E). The remaining organs are completely glabrous.

Stomata are present on the dorsal and ventral surfaces of the sepals and petals, the anther connectives and on the dorsal and ventral surfaces of the distal, umbrella-shaped part of the style. The stomata on the perianth organs and styles exude a carbohydrate-rich liquid (visible as viscous droplets on living material), staining bright pink to red in microtome sections (Fig. 14K).

The epidermal cells of the perianth organs are rounded to slightly angular and more or less smooth in appearance on both the dorsal and ventral sides. The epidermal cells of the anthers are 'jigsaw puzzle piece'-shaped. Filament epidermal cells are elongate and more or less smooth in appearance. The epidermal cells of the styles are rounded to slightly angular and more or less smooth in the distal part, and elongate and more or less smooth in the proximal region. The epidermal cells of the ovary are uneven. All epidermal cells have uneven cuticles.

Parenchymatic cells are tightly packed in the perianth organs and no apparent palisade parenchyma or nectariferous tissue is present; parenchymatic tissue is uniform and tightly packed in the ovary, except on the ventral side of the dorsal vascular bundle (future dehiscence line) and in the septa, where the cells are smaller.

No mucilage cells or raphide bundles are present in the floral tissue. Small amounts of oxalate crystals (Fig. 14I for *R. gorgonias*) can be found in close proximity to the vasculature of all organs.

Tannins (Fig. 14L for *S. pittieri*) are present in all floral organs, most abundantly in the anthers (Fig. 11H) and the ovary. Vesicles that appear to contain tannins (Fig. 14K), larger than in the other investigated taxa, are present in all floral tissue, most abundantly in the epidermal and hypodermal layers of the perianth organs.

Endothecium cells with lignified wall thickenings (mainly the inner tangential cell walls) are present in the anther walls, but are lacking in the connective and the septa.

The inner surface of the gynoecium is not secretory.

The ovules in the investigated material are too young to determine detailed histological characters.

Sarracenia leucophylla

Morphology: The flowers (Figs 1J, 9) are similar to those of *S. purpurea* (Figs 1I, 8) with a few differences: flowers are larger (*c.* 7 × 7 cm; Fig. 1J); petals are proximally thicker than sepals (Fig. 9C); the androecium consists of *c.* 60–100 stamens (Fig. 9); the asymplicate parts of the styles are longer than in *S. purpurea* (Fig. 1J); the stigmas are attached on stalk-like structures on the dorsal side of the asymplicate styles (Fig. 9A); there are *c.* 300 ovules arranged in 14–18 rows per placenta, seven to nine on each side of the ventral slit (Figs 9, 13S); and ovules are unitegmic (the integument is six or seven cell layers thick), anatropous and incompletely tenuinucellar (Fig. 13R, S).

Anatomy: The vascular system is similar to that of *S. purpurea* with the difference that the vascular bundles of the stamens form more distinct alternipetalous and alternisepalous groups before the traces join the CVC in the floral base (Fig. 9C).

Histology: The histological characters are identical to those of *S. purpurea*, with one exception: a nucellar hypostase is visible in the ovules.

DISCUSSION

Floral structure in Actinidiaceae, Roridulaceae and Sarraceniaceae

Inflorescences

There is currently no study available directly comparing the inflorescence structure of Actinidiaceae, Roridulaceae and Sarraceniaceae, and a detailed comparative evaluation is therefore not possible. Some basic observations in this study paired with a literature review reveal that axillary solitary flowers or variations of cymose branching systems

characterize the group (this study; Macfarlane, 1908; Hunter, 1966; Soejarto, 1980; Cuong, Soejarto & Li, 2007; Li *et al*., 2007; Mellichamp, 2009). Members of Actinidiaceae have axillary single flowers or inflorescences with cymose units (Fig. 1A–G) with up to several hundred flowers in *Saurauia* (Soejarto, 1980; Cuong *et al*., 2007; Li *et al*., 2007). Hunter (1966) determined that the panicles often described in *Saurauia* are compound cymes (thyrses of scorpioid cymes), visible in young inflorescences. Members of Roridulaceae have axillary botryoid (raceme-like with a terminal flower) inflorescences (Fig. 1H; Dahlgren & van Wyk, 1988). Members of Sarraceniaceae have solitary flowers (Fig. 1I, J) on tall, axillary scapes at the growing tips of the rhizome in *Darlingtonia* and *Sarracenia* or thyrses of scorpioid cymes in *Heliamphora* (Fig. 1K; Macfarlane, 1908; Berry, Riina & Steyermark, 2005; Mellichamp, 2009). Inflorescences (scapes in *Darlingtonia* and *Sarracenia*) are supported by bracts, which are foliaceous in Actinidiaceae and Roridulaceae and scale-like in Sarraceniaceae (this study). In *Heliamphora*, *Roridula* and *Saurauia*, persistent, foliaceous bracts additionally support each flower (this study; Macfarlane, 1908; Hunter, 1966; Soejarto, 1980; Cuong *et al*., 2007; Li *et al*., 2007).

General floral organization

In all three sarracenioid families, the flowers are actinomorphic (Fig. 1) and have superior ovaries (subinferior in *Roridula*; Fig. 5). All sarracenioids have structurally bisexual flowers, but *Actinidia* and *Saurauia* are often functionally unisexual (e.g. this study; Soejarto, 1969, 1980; Cuong *et al*., 2007); flowers in all other genera are always functionally bisexual (e.g. this study; Macfarlane, 1908; Diels, 1930; Li *et al*., 2007).

The perianth is generally pentamerous, although variable, especially in *Actinidia* and *Heliamphora*, and arranged in two whorls (see below for the equivocal interpretation of the perianth in *Heliamphora* and the occasional third, incomplete, whorl of petaloid organs present in *A. chinensis*; Figs 1C, 2O–R; Li *et al*., 2007). *Actinidia* is generally pentamerous (tetramerous to hexamerous) and the number of perianth organs per whorl may vary among flowers in the same inflorescence. *Actinidia chinensis* is unusually variable with trimerous to octamerous flowers (Li *et al*., 2007). For the Central American *Saurauia conzattii* Buscal, Hunter (1966) described four to six perianth organs per whorl, also variable within the same inflorescence. Soejarto (1980) described stable tetramery in the South American *Saurauia yasicae* Loes., and commonly a few flowers with hexamery to octamery on otherwise pentamerous individuals for most South American *Saurauia* spp. The perianth in *Heliamphora* is generally interpreted as containing only sepals or tepals in variable numbers (e.g. Macfarlane, 1908; Renner, 1989; Berry *et al*., 2005). However, as shown here (Fig. 7L, M), the outer and inner organs differ considerably in several aspects: their position on the floral axis, shape, vasculature and epidermal structure, and the presence of stomata only in the outer organs. Therefore, the perianth is tentatively interpreted as two-whorled with outer (more sepaloid) and inner (more petaloid) tepals. However, to further investigate the perianth organization in *Heliamphora*, developmental studies are needed. One of the investigated flowers of *S. purpurea* has four normal petals and one pair of smaller petals (sharing one, alternisepalous, insertion point; Fig. 8N). In the literature, the perianth of *Sarracenia* is described as pentamerous, which is also the case for all other investigated flowers of both *S. purpurea* and *S. leucophylla* (e.g. Figs 1, 9; Shreve, 1906; Macfarlane, 1908; Mellichamp, 2009).

The androecia are polystemonous in all sarracenioid genera, except *Clematoclethra* (diplostemonous) and *Roridula* (haplostemonous). Dickison (1972) reported up to 30 stamens in functionally male specimens of *Clematoclethra*, but the specimens included in the study of Dickison (1972) have not been investigated to rule out potential misidentifications. A fascicled stamen arrangement was reported in *S. subspinosa* by Brown (1935), and stamen arrangement in vague fascicles in *Sarracenia* by, for example, Mellichamp (2009), although the potentially fascicled arrangement of stamens is rarely visible in advanced floral material (this study); most literature mentions solely the polystemony or stamen arrangement in a ring-like, single series (e.g. Macfarlane, 1908; Hunter, 1966; Dickison, 1972; Soejarto, 1980; Cuong *et al*., 2007). For the other polystemonous members of the clade (*Actinidia*, *Darlingtonia* and *Heliamphora*), the stamen arrangement in anthetic flowers is also described as one (ring-like in *Actinidia*) series (e.g. Macfarlane, 1908; Dickison, 1972; Berry *et al*., 2005; Li *et al*., 2007). Tracing the filament vasculature and/or ontogenetic studies are needed to assess the basic stamen arrangement in all polystemonous genera (this study; Shreve, 1906; Brown, 1935; van Heel, 1987) (see discussion below for further details).

The gynoecia in the clade range from almost completely syncarpous (only minutely lobed stigmas) in *Clematoclethra*, *Roridula* and *Heliamphora*, through largely symplicate (distally asymplicate) styles in *Darlingtonia* and *Sarracenia*, to free or only proximally united (below middle) styles in *Actinidia* and *Saurauia* (Figs 1, 12). *Clematoclethra*, *Saurauia*, *Darlingtonia* and *Sarracenia* have five carpels (some species of *Saurauia* deviate from the pentamery in the gynoecium, e.g. *Saurauia tristyla* DC; Cuong

et al., 2007), *Roridula* and *Heliamphora* have trimerous gynoecia and *Actinidia* normally has 15–30 carpels (Li *et al*., 2007). Dickison (1972) reported four or five carpels, but found ten carpels in one functionally male specimen of *Clematoclethra* (but see note above).

Sexual system

Members of the sarracenioid clade have varying sexual systems; *Clematoclethra*, some *Saurauia* spp., Roridulaceae and Sarraceniaceae are functionally bisexual (e.g. Macfarlane, 1908; Diels, 1930; Li *et al*., 2007), *Actinidia* and some *Saurauia* spp. are subdioecious (Soejarto, 1969; Li *et al*., 2007), some *Actinidia* appear to be strictly polygamous (Li *et al*., 2007), many *Saurauia* spp. are dioecious (Soejarto, 1969; Haber & Bawa, 1984; Cuong *et al*., 2007) and other *Saurauia* spp. are androdioecious (Soejarto, 1969). Although all taxa in the sarracenioid clade are structurally bisexual, functionally male flowers of *Actinidia* and some *Saurauia* spp. (e.g. *Saurauia montana* Seem.) can be distinguished by reduced and not fully developed gynoecia (e.g. this study; Haber & Bawa, 1984; Li *et al*., 2007) or even aborted pistils in *Saurauia pedunculata* Hook. (Hooker, 1941). Most dioecious *Saurauia* spp. are cryptically dioecious, with small differences in style length between the functionally female and functionally male morphs representing the only gross morphological diagnostic feature for the sex of the flowers (Soejarto, 1969; Cuong *et al*., 2007). *Actinidia* and some *Saurauia* spp. (e.g. *Saurauia excelsa* Willd. and *Saurauia putumayonis* R.E.Schult. & García-Barr.) are subdioecious (Soejarto, 1969; Li *et al*., 2007) and, for example, *Saurauia omichlophila* R.E.Schult. is androdioecious (Soejarto, 1969).

Dickison (1972), unlike other authors (e.g. Lechner, 1915; Gilg & Werdermann, 1925; Li *et al*., 2007), reported functionally male specimens of *Clematoclethra* (but see note above).

General floral shape and pollination

Flowers in the sarracenioid clade range from < 1 cm (*Clematoclethra* and *Saurauia*), through a couple of centimetres (*Actinidia*, *Saurauia*, *Roridula* and *Sarracenia*), to several centimetres (*Actinidia*, *Saurauia* and Sarraceniaceae) in diameter, and are either open to cup-shaped in Actinidiaceae, *Roridula* and *Heliamphora* or closed and synorganized with the styles (petal apices directed towards the floral axis in *Darlingtonia*; petals alternating with the asymplicate styles in *Sarracenia*; e.g. Fig. 1; Diels, 1930; Li *et al*., 2007; Mellichamp, 2009). All sarracenioid genera have pendant flowers, although not all flowers have pendant orientation in Actinidiaceae, and the flowers of *R. gorgonias* face upwards to outwards (e.g. this study; Macfarlane, 1908; Hunter, 1966; Soejarto, 1980; Anderson, Midgley & Stewart, 2003; Cuong *et al*., 2007; Li *et al*., 2007). Pollination has been studied for members of all genera in the clade, except *Clematoclethra*, although the pollination system in *Actinidia* warrants further study, as it has mainly been studied in commercial orchards (e.g. Costa, Testolin & Vizzotto, 1993; Goodwin, McBrydie & Taylor, 2013). As outlined below, there is diversity in pollination systems, although bees pollinate most groups and pollen is often the main reward (e.g. Hunter, 1966; Schmid, 1978; Renner, 1989; Ne'eman, Ne'eman & Ellison, 2006; Meindl & Mesler, 2011).

In Actinidiaceae, flowers of *Actinidia* range from just over 1 cm to > 5 cm in diameter (depending on the species and functional sex of the flower; most species fall in the lower to middle range) at anthesis, are open to cup-shaped, predominantly pendant and generally white to yellow, sometimes green, orange, pink or red (Fig. 1A–D; Li *et al*., 2007). Little is known about pollination in wild populations of *Actinidia*, but bumblebees, bees and wind are all implied, although the flowers are poorly adapted for wind pollination and it seems to play only a minor role (Schmid, 1978). Both functionally female and functionally male flowers of *A. chinensis* shed pollen in clumps (Schmid, 1978); functionally male flowers are strongly fragrant and (probably) lack nectar production, whereas functionally female flowers are faintly fragrant and lack nectar production, implying pollen as the main reward in both functionally female and male flowers (Schmid, 1978). Costa *et al*. (1993) and Goodwin *et al*. (2013) supported this assessment with the fact that wind plays a minor role in kiwifruit orchards; instead, honeybee pollination seems to be of greater importance (the only observed flower visitors). Goodwin *et al*. (2013) reported that pollinators prefer functionally female flowers, but Schmid (1978) hypothesized that functionally female flowers ought to be less attractive to pollinators with their fainter scent and non-viable pollen. The flowers of *A. arguta* may produce nectar (this study), but the pollination of the species has not been studied.

Flowers of *C. scandens* are 0.8–1.0 cm in diameter at anthesis, cup-shaped, have white to red-tinged petals, brown anthers and lack nectar production (Fig. 1E; Li *et al*., 2007). No pollination studies have been performed, but Gilg & Werdermann (1925) assumed insect pollination.

Flowers of *Saurauia* are 0.5–5.0 cm in diameter at anthesis (in most species *c*. 1 cm in diameter), cup-shaped, predominantly pendant, white to pink (sometimes cream, red or purple), anthers are yellow and flowers are often fragrant (Hunter, 1966; Soejarto, 1980; Cane, 1993; Li *et al*., 2007). *Saurauia* spp. are

often cryptically dioecious (e.g. Soejarto, 1969; Haber & Bawa, 1984; Cuong *et al*., 2007), but the single specimen of *S. subspinosa* grown in the University of Vienna Botanical Garden regularly sets fruit (hence, it is either functionally bisexual and self-fertile or parthenocarpic). Pollination has been studied or at least observed in a few species: Hunter (1966) described pollination by pollen-collecting bees in *S. montana* (the flowers do not produce nectar). Cane (1993) described buzz pollination by female bees and bumblebees in *S.* cf. *montana* on both functionally female and functionally male flowers. Brown (1935) mentioned nectar secretion and insect pollination in the protandrous, pendant stage of *S. subspinosa* flowers. Brown (1935) further noted that the stigmas are not receptive until after the nectariferous and fragrant petals are shed, after which the pedicel straightens up, so that the flower faces upwards; he hypothesized that self-pollination from younger flowers on the tree is the main pollination mechanism (pollen falling from the pendant, male-phase flowers). Roubik, Sakai & Hamid Karim (2005) described pollination by various bee species in South-East Asian *Saurauia*. Soejarto (1969) described generalist pollination by mainly hymenopterans in the scented flowers in the genus, but did not rule out or confirm nectar secretion on the petals.

Flowers of *Roridula* are protogynous, *c*. 2.5–3.0 cm in diameter at anthesis, cup-shaped with open access to the floral centre and pendant to outwards facing (*Roridula dentata*) or outwards to upwards facing (*R. gorgonias*) with pink petals and yellow anthers (Fig. 1H; Uphof, 1936; Anderson *et al*., 2003). Marloth (1903) described pollination by mutualistic hemipterans inhabiting the plants; the insects are dusted with pollen when they puncture the expanded, starch-rich, anther connective, whereupon the anther rapidly inverts. The pollination system described by Marloth (1903) has been questioned by, for example, Lloyd (1934). Vogel (1978) and Johnson (1992) noted that the flowers and anthers of *R. dentata* L. are well adapted to buzz pollination, and Vogel (1978) therefore postulated bee pollination. Anderson *et al*. (2003), however, noted that the flowering time is largely in winter, when pollinators are scarce, and additionally drew attention to the problem of the short peduncles, placing the flowers close to the insect-trapping leaves. They established that pollination is mainly self-pollination assisted by the mutualistic hemipterans, and that carpenter bees and opportunistic (petal-eating) beetles may be potential outcrossing pollinators. Conran (2004) also noted that cultivated plants are self-fertile and visited by hover flies. Removal of the petals clearly causes a reduction in seed set, indicating that pollinator attraction plays a major role, independent of the hemipterans already being present on the plants (Anderson *et al*., 2003). Another explanation for the lower seed set in artificially apetalous flowers is that the lack of petals prevents hemipterans from congregating inside the flowers, which makes the insect-aided self-pollination mechanism less likely to occur.

Flowers of *D. californica* are protandrous, 5–8 cm in diameter and about as long at anthesis, pendant and odourless; the pandurate petals of *Darlingtonia* are synorganized (distally valvate; proximally quincuncial) and form entry holes to the inner organs; the sepals are yellow (Fig. 1L; Macfarlane, 1908; Mellichamp, 2009; Meindl & Mesler, 2011). Macfarlane (1908) described nectar production on the sepals and glands in the ovary wall, but alternated between calling the glands 'honey glands' and nectaries, whilst also referring to the attracting, sugary liquid at the rim of the pitcher leaves. Neither Mellichamp (2009) nor Meindl & Mesler (2011) mentioned nectaries in the flowers of *Darlingtonia*, and the present study shows neither clear areas of nectar production, nor the glandular structure referred to by Macfarlane (1908) in the ovary wall. In a detailed pollination study, Meindl & Mesler (2011) described the flowers as pollen-limited, partly self-pollinated and partly pollinated by pollen-collecting solitary bees and one recorded visit by a honeybee. Other recorded flower visitors (not pollinators) were thrips and several species of spiders. The ovary shape and entry holes between the petals (Fig. 1L) promote stigma contact with the insect both on entry to and exit from the flowers (Meindl & Mesler, 2011).

Flowers of *Heliamphora* are protandrous, 5–8 cm in diameter and 5–7 cm long at anthesis. They are cup-shaped to open, pendant, odourless and (generally) have white to pink or magenta tepals and yellow stamens (Fig. 1K; Macfarlane, 1908; Uphof, 1936; Renner, 1989; Berry *et al*., 2005). Macfarlane (1908) described nectar glands on the bracts, tepals and ovary wall in *H. nutans*. In the present study, no apparent indication of nectar-secreting tissue, stomata or nectar glands in the flowers of *H. nutans* is present. Berry *et al*. (2005) described buzz pollination in the genus, which was also concluded by Renner (1989) in a detailed pollination study on *Heliamphora tatei* Gleason var. *neblinae* (Maguire) Steyerm.

Flowers of *Sarracenia* are protandrous, 3–10 cm in diameter and about as long at anthesis, pendant, odoriferous, green to yellow or red to maroon (pink in *Sarracenia rosea* Naczi, Case & R.B.Case) and the concealed stamens are yellow (Fig. 1I, J; Macfarlane, 1908; Uphof, 1936; Mellichamp, 2009). Macfarlane (1908) described the entire surface of the ovary as covered in nectariferous glands, whereas Ne'eman *et al*. (2006) described the nectar production as most

abundant at the base of the ovary and the ventral part of the style. In the investigated (pre-anthetic) material of *Sarracenia*, no apparent zones of nectar production are visible. The petals are synorganized with the lobes of the stylar disc to form entry and exit pathways to the inner organs, forcing stigmatic contact both on entry to and exit from the interior of the flower (Fig. 1I, J; Jones, 1908; Macfarlane, 1908; Ne'eman *et al*., 2006; Mellichamp, 2009). Various species of bees and bumblebees are usually considered to be the main pollinators (Mandossian, 1965; Burr, 1979), but Jones (1908) concluded that bumblebees are rare flower visitors in *Sarracenia flava* L., and Ne'eman *et al*. (2006) stated that they are inefficient pollinators in *S. purpurea.* Flies are potentially significant contributors to pollination as they often roost in the flowers at night (Jones, 1908; Mandossian, 1965; Ne'eman *et al*., 2006), and Jones (1908) noted that the flowers are increasingly fragrant in the evening, suggesting nocturnal insects as pollinators. Mandossian (1965) and Ne'eman *et al*. (2006) described visiting flies to be frequently covered in *Sarracenia* pollen.

Early floral development

Few ontogenetic studies of the genera in the sarracenioid clade are available, and most work has been performed in Actinidiaceae. *Actinidia chinensis* was investigated by Brundell (1975), van Heel (1987) and Caris (2013), *Actinidia kolomikta* Maxim., *Actinidia melanandra* Franch. and *Actinidia polygama* Franch. & Sav. by van Heel (1987), *S. subspinosa* by Brown (1935) and *S. purpurea* by Shreve (1906). The studies all confirmed that the perianth consists of one sepal whorl and one petal whorl. Sometimes a third, incomplete series of petaloid organs is present in *A. chinensis* (this study; Li *et al*., 2007), but, because the vascular traces of the innermost petaloid organs merge with the androecial vascular traces in the floral base, these organs may not be homologous to normal petals, but rather may be staminodial in origin (this study). The androecium of *Actinidia* basically consists of an alternipetalous whorl of stamens (van Heel, 1987), which proliferates centripetally into one series of stamens in *A. kolomikta*, *A. melanandra* and *A. polygama* (van Heel, 1987), but proliferates centrifugally into two to four series in *A. chinensis* (Brundell, 1975; van Heel, 1987; Caris, 2013). The androecium in *S. subspinosa* is arranged in two whorls; the outer (alternisepalous) whorl consists of five primordia proliferating into distinct fascicles of almost invariably nine stamens each; the inner whorl consists of single, alternipetalous stamens (Brown, 1935). According to Shreve (1906), the androecium of *S. purpurea* is arranged in one whorl of ten primary primordia arising simultaneously, one by each petal margin, secondarily proliferating into distinct fascicles. The gynoecia are arranged in single whorls as shown in all ontogenetically investigated taxa (e.g. Shreve, 1906; Brown, 1935; van Heel, 1987). More ontogenetic work is needed in the sarracenioid clade, particularly in Sarraceniaceae, in order to better understand the patterns of perianth and androecium organization.

Perianth

With the exception of *Heliamphora*, the sarracenioid clade is characterized by two isomerous perianth whorls. In *Heliamphora*, the perianth is usually interpreted as a series of petaloid sepals or tepals (e.g. Macfarlane, 1908; Berry *et al*., 2005). However, the differences in shape and size (this study; Macfarlane, 1908; Berry *et al*., 2005) and epidermal surface structure (this study) between the outer and inner perianth organs indicate that these organs may actually belong to two different whorls. This is further supported by the differing patterns of vasculature and by the fact that the outer organs are clearly separated from the inner ones along the floral axis (this study). The perianth of *Heliamphora* is therefore interpreted and discussed as consisting of separate series of sepals and petals.

In the sarracenioid clade, the sepals are petaloid (mainly white, pink, yellow or maroon) in Sarraceniaceae and sepaloid in Actinidiaceae and Roridulaceae (whitish green, green or greenish brown). Sepal aestivation is quincuncial in all pentamerous taxa and imbricate with other patterns in non-pentamerous taxa.

Sepals are proximally united in Actinidiaceae and Roridulaceae and completely free from each other in Sarraceniaceae; they are elliptic to broadly ovate (to triangular in *Actinidia* and *Saurauia*) in Actinidiaceae, Roridulaceae and *Heliamphora*, and narrowly to broadly obovate in *Darlingtonia* and *Sarracenia*. Sepals are distally acute in Actinidiaceae, *Roridula*, *Darlingtonia* and *Heliamphora* (to obtuse in *Actinidia*) and rounded in *Sarracenia*. Sepals are broadly attached (and dorsally bulging in Actinidiaceae and Roridulaceae). The sepals are of unequal size within a flower in all investigated genera; in *Actinidia*, there is no strict pattern to the size difference; in *Clematoclethra* and *S. subspinosa*, the inner three sepals are larger; and in the other investigated specimens, the outermost (*Heliamphora*) or the three outer sepals (*S. pittieri*, *Roridula*, *Darlingtonia* and *Sarracenia*) are larger. All investigated taxa have numerous vascular bundles in the sepals, with at least five vascular bundles remaining in the sepal base, joining the CVC as three or more traces in the floral base. The sepals in Actinidiaceae and Roridulaceae are variably covered by multicellular hairs and glabrous in

Sarraceniaceae. Stomata are present on the dorsal and ventral sides of the sepals in *Actinidia*, *Heliamphora* and *Sarracenia*, only the dorsal side in *Roridula*, only the ventral side in *Darlingtonia*, and completely lacking in *Clematoclethra* and *Saurauia*. The epidermal cells are more or less smooth in appearance and the parenchymatic tissue is uniform and densely packed in all genera. No obvious palisade parenchyma is present in any taxa. Although sparse in Sarraceniaceae, all genera have calcium oxalate crystal formations in and around the vasculature. In Actinidiaceae and Roridulaceae, calcium oxalate crystals, particularly in the form of distinct aggregates of raphides, are abundant. Actinidiaceae and Roridulaceae additionally have mucilage cells, often in combination with crystalline structures in their floral tissue. Massive stone cells are present in *Saurauia*. For more information on mucilage cells, raphides and stone cells, see, for example, Schönenberger *et al*. (2010) and von Balthazar & Schönenberger (2013). For more information on condensed tannins, see Lees, Hinks & Suttill (1994), Skadhauge, Thomsen & von Wettstein (1997), Bussotti *et al*. (1998), Cadot, Miñana-Castello & Chevalier (2006), Halarewicz (2011) and Brillouet *et al*. (2013). For more information on tannosomes, see Brillouet *et al*. (2013). Tanniferous cells are present in the sepals of all investigated taxa (sparsely in *C. scandens*) with increasing density of the cells in the proximal parts of the organs (only the occasional epidermal cell of *Heliamphora*). The tanniferous cells in *Actinidia*, *Saurauia* and *Roridula* occasionally have condensed tannins along the internal cells walls (Fig. 14I), and all investigated specimens have small vesicles (Fig. 14I, K, O) of what most closely corresponds to condensed tannins or tannosomes in the cytoplasm, most abundant (and comparatively larger) in Sarraceniaceae.

The petals in Actinidiaceae, *Roridula* and *Heliamphora* are generally white to cream or pink; the petals of *Darlingtonia* and *Sarracenia* are generally yellow or red to maroon. Petals are free in *Clematoclethra* and Sarraceniaceae, and free to proximally united in *Actinidia*, *Saurauia* and *Roridula*. The aestivation is quincuncial in all pentamerous taxa and imbricate with other patterns in non-pentamerous taxa. The petals are elliptic to narrowly ovate in *Heliamphora* and *Roridula*, ovate in *Clematoclethra*, broadly obovate in *Actinidia* and *Saurauia*, and pandurate in *Darlingtonia* and *Sarracenia*. Petals are acute to acuminate in *Darlingtonia*, *Heliamphora* and *Roridula* and obtuse to rounded (or shallowly indented) in Actinidiaceae and *Sarracenia*; petals are broadly attached in all investigated taxa. Petals are proximally conspicuously massive and thicker than the sepals (*S. subspinosa*, *Roridula* and *Darlingtonia*; Figs 4–6), clearly thicker than the sepals (*Actinidia*, *Heliamphora* and *S. leucophylla*; Figs 2, 7, 9), of more or less equal thickness to the sepals (functionally female *A. arguta*, *Clematoclethra* and *S. pittieri*; Figs 2–4) or somewhat thinner than the sepals (*S. purpurea*; Fig. 8). It should be noted that the sectioned flower bud of *S. purpurea* was comparably younger than the other investigated specimens and the petals may not have been fully developed. There are numerous vascular bundles in the distal region of the petals; about three vascular bundles remain in the proximal region, merging into one trace before joining the CVC as a single unit in the floral base (also in *Heliamphora*). Petals are glabrous in all three families (to sparsely hairy in Actinidiaceae). Stomata are present on both the dorsal and ventral sides of the petals in *A. arguta* (functionally female specimen), *Roridula*, *Heliamphora* and *Sarracenia*, the ventral side of the petals in *A. arguta* (functionally male specimen), *A. chinensis* (both functionally female and functionally male specimens) and *S. subspinosa*, but lacking in *Clematoclethra*, *Darlingtonia* and *S. pittieri*. Petal epidermal cells are smooth to rounded in Actinidiaceae, Roridulaceae, *Darlingtonia* and *S. purpurea* and conspicuously uneven in *Heliamphora* and *S. leucophylla*. The epidermal structure of *S. purpurea* may be similar to that of *S. leucophylla* in more advanced buds. The remaining histological characters of the petals are the same as for the sepals in all taxa.

Androecium

The stamens (staminodes in the case of functionally female flowers) of all members in the sarracenioid clade become inverted at anthesis (examples: Figs 10J, 11E). Schönenberger *et al*. (2012) described two main types of anther inversion in the sarracenioid clade: 'late anther inversion type A' (inversion from extrorse to introrse at anthesis; associated with ventrifixed anthers) in Actinidiaceae and Roridulaceae (also present in Clethraceae and early-diverging lineages in Ericaceae) and 'late anther inversion type B' (inversion from introrse to extrorse at anthesis; associated with dorsifixed anthers) present in Sarraceniaceae. The anther inversion is a result of growth processes in the distal part of the filament and autonomous in Actinidiaceae and Sarraceniaceae (e.g. this study; Schönenberger *et al*., 2012). In *Roridula*, the anther inversion is either autonomous or assisted by juvenile hemipterans feeding from the expanded connective protrusion, whereupon the anthers become inverted and dust both the insect and the stigma with pollen (Anderson *et al*., 2003). The physiological processes behind the anther inversion in Roridulaceae have not been studied in detail, but changes in turgor pressure in the connective

protrusion on puncture by the hemipterans or maturation of the anthers seem to be plausible causes for the process. In light of the present findings, the definition of both types of late anther inversion may need revision, or more types of late anther inversion may need to be described. In order to classify the anther inversion in *Actinidia* and *Roridula* as 'late anther inversion type A,' latrorse anther orientation needs to be included in the definition; additionally, the physiological process behind the anther inversion in *Roridula* warrants further investigation to either support or dispute the current classification. The conspicuous anthers of *Darlingtonia* conform to neither of the late inversion types, because of the simultaneously extrorse and introrse anther orientation on the same organ (Fig. 11D); hence, either 'late anther inversion type B' needs to be revised to include the unique case or *Darlingtonia*, or a third late anther inversion type needs to be postulated, e.g. 'late anther inversion type C'.

Clematoclethra and *Roridula* have ten and five stamens, respectively; all other investigated taxa are polystemonous. Based on stamen organization, vasculature and earlier ontogenetic studies (see above; Shreve, 1906; Brown, 1935; Brundell, 1975; van Heel, 1987; Caris, 2013), *Actinidia*, *Roridula*, *Darlingtonia* and *Heliamphora* appear to be basically haplostemonous or haplostemony-derived (Figs 2, 5–7). In *Clematoclethra*, *Saurauia* and *Sarracenia*, the stamens are apparently arranged in two weakly distinguished whorls (e.g. Figs 3, 4, 8, 9; this study; Shreve, 1906; Brown, 1935). In *Roridula*, the five stamens are inserted in an alternipetalous position (Fig. 5). In *Actinidia*, the stamens are basically inserted in alternipetalous positions (e.g. Fig. 2; van Heel, 1987). In *Darlingtonia* (15 stamens) and *Heliamphora* (20 stamens), groups of three or four stamens are apparently inserted in an alternisepalous position (Figs 6, 7), but note the uncertain perianth phyllotaxy in *Heliamphora*. In both *Clematoclethra* and *S. subspinosa*, the stamen arrangement has been described as an outer whorl of alternisepalous stamens and an inner whorl of alternipetalous stamens (Brown, 1935; Dickison, 1972), but neither author presented pictures or illustrations to support the statement. The floral material investigated here does not unequivocally support an obdiplostemonous insertion pattern and the floral ontogeny of *Clematoclethra* has not yet been investigated. In *S. leucophylla*, there is a slight crowding of the filament bases in alternipetalous and alternisepalous groups (Fig. 9) and, in *S. purpurea*, the organization is hard to assess (Fig. 8). These characters need to be further investigated by developmental studies in *Clematoclethra*, more *Saurauia* spp. and all genera of Sarraceniaceae (see also discussion above).

Stamens are free from each other in all sarracenioid genera, except *Saurauia*, where the stamens are variably free to proximally united within fascicles, but free between the fascicles; in *A. chinensis*, a small percentage of filaments are proximally united in pairs or triplets and, in *Darlingtonia*, a crowding in alternipetalous groups of three filaments can be seen at the very base (Fig. 6N).

Anthers are dithecate and tetrasporangiate in all investigated taxa. In pre-anthetic flowers, the anthers are (mainly) latrorse to extrorse in Actinidiaceae and Roridulaceae (Figs 2–5, 10, 11A, B) and introrse in *Heliamphora* and *Sarracenia* (Figs 7–8, 12E–H). *Darlingtonia* forms a special case with a strong dimorphism in size and position of the two thecae (Figs 6, 11C, D); in pre-anthetic flowers, the larger theca is extrorse and the smaller theca is introrse. Anther bases are shallowly (*Roridula*, *Darlingtonia* and *Heliamphora*) to deeply (*Actinidia*, *Clematoclethra*, *Saurauia* and *Sarracenia*) sagittate (Figs 10, 11). In *Darlingtonia*, the thecae are completely separated by the connective tissue (one extrorse and one introrse). Anther attachment is variable: basifixed in *A. arguta*, *Clematoclethra*, *Darlingtonia* and *Sarracenia*, dorsifixed in *Heliamphora* and ventrifixed (see discussion about ventrifixed anthers in Schönenberger *et al*., 2012) in *A. chinensis*, *Saurauia* and *Roridula*. Anther dehiscence is by longitudinal slits (*Actinidia*, *Clematoclethra*, *Roridula*, *Darlingtonia* and *Sarracenia*) or short, pore-like slits (*Saurauia* and *Heliamphora*). *Roridula dentata* differs from *R. gorgonias* in poricidal anther dehiscence (e.g. Anderson *et al*., 2003). The joint between the anther and the filament is broad for all investigated taxa. The filaments are terete (*Actinidia* and *Sarracenia*) to angular (*Darlingtonia* and *Heliamphora*) or dorsiventrally flattened (*Clematoclethra*, *Saurauia* and *Roridula*) and of equal length to up to nearly three times the length of the anthers. Each stamen has one vascular bundle; in *Clematoclethra* and *Roridula*, the vascular traces join the CVC individually; in *Actinidia*, *Saurauia* and Sarraceniaceae, the vascular traces merge into groups before joining the CVC in the floral base. The epidermal cells of the anthers are 'jigsaw puzzle piece'-shaped (Actinidiaceae and *Sarracenia*), rounded (*Darlingtonia* and *Heliamphora*) or angular (*Roridula*); the epidermal cells of the filaments are smooth and elongate in all genera. Stomata are present on the connectives of *Actinidia*, *Darlingtonia* and *Sarracenia*, but not found in the investigated material of *Clematoclethra*, *Saurauia*, *Roridula* or *Heliamphora*. The endothecium is restricted to the pollen locules, mainly the inner, tangential cell walls are thickened. All investigated taxa have oxalate crystals (mainly in close proximity to the vascular bundles and in the epidermal layer) and tannins (mainly in the epidermal layer) in the

anthers and filaments. Condensed tannins occasionally line the internal cell walls in *Actinidia*, *Saurauia* and *Roridula*, and all taxa have small amounts of vesicles that appear to contain tannins (most likely condensed tannins and/or tannosomes) in the cytoplasm of the epidermal and hypodermal cells. The subclade formed by Actinidiaceae and Roridulaceae is additionally characterized by the presence of mucilage cells (mainly in the connective tissue) and raphide bundles (mainly in close proximity to the vascular bundles and in the epidermal layer). Stone cells are present in *Saurauia* (mainly in the connective tissue). The expanded connectives of *Roridula* are starch-rich (Anderson *et al*., 2003).

Pollen

Comparative pollen morphology in the sarracenioids has been studied in detail by Zhang & Anderberg (2002); the pollen of Actinidiaceae by Erdtman (1952), Dickison, Nowicke & Skvarla (1982), Zhang (1987) and Kang *et al*. (1993); the pollen of Roridulaceae by Erdtman (1952) and Dahlgren & van Wyk (1988); and the pollen of Sarraceniaceae by Erdtman (1952), Thanikaimoni & Vasanthy (1972) and Oswald *et al*. (2011). The morphological pollen characters listed below are taken from the mentioned references. All sarracenioids have rather unspecialized pollen grains, shed as monads (rarely tetrads in *Saurauia*). Grains are small to medium sized (*c.* 11–50 μm in equatorial diameter, 10–40 μm long) and prolate to spherical to oblate; the tectum is thin and there is a distinct gap between the foot layer and the tectum; the exine is generally thin (sextine same thickness or thinner than nexine). The gap between the foot layer and the tectum contains few (large and fused) granulae (Actinidiaceae and Sarraceniaceae) or short, well-developed columellae (Roridulaceae). Actinidiaceae and Roridulaceae pollen grains are tricolporoidate to tricolporate (indistinct in *R. gorgonias*; sometimes tetra-aperturate in *Actinidia* and *Saurauia;* rarely polyaperturate in *Saurauia*); Sarraceniaceae pollen grains are tetracolporate to polycolporate (rarely tricolporate in *Heliamphora*). Members of Actinidiaceae have smooth to granular or ornate exine patterns; in Roridulaceae, the exine is insular or spinuliferous and perforated and, in Sarraceniaceae, the exine is scrobiculate or veruculate.

Gynoecium

The gynoecia in the sarracenioid clade are syncarpous, at least in the ovary: *Clematoclethra*, *Heliamphora* and *Roridula* are fully syncarpous (except for minute stigmatic lobes), *Darlingtonia* and *Sarracenia* have distally asymplicate styles with separate stigmas, and *Actinidia* and *Saurauia* have free to proximally united styles (up to 50% of total style length; this study; Hunter, 1966; Soejarto, 1980; Cuong *et al*., 2007; Li *et al*., 2007). Carpel number is variable in the clade; *Clematoclethra*, *Darlingtonia*, *Sarracenia* and *Saurauia* are pentamerous, *Heliamphora* and *Roridula* are trimerous and *Actinidia* is multicarpellate (normally 15–30 carpels; this study; Li *et al*., 2007; Endress, 2014), arranged in one whorl (van Heel, 1987; Caris, 2013; Endress, 2014). More than 40 carpels per gynoecium have been reported in *A. chinensis* var. *deliciosa* (A.Chev.) A.Chev. (e.g. Harvey & Fraser, 1988), and as few as five carpels have been observed in functionally male flowers of *A. kolomikta* (unpubl. data; S. D. Löfstrand; alcohol collection JS617; Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria). In *Saurauia*, carpel numbers are sometimes variable or strictly lower than the general pentamery, e.g. *Saurauia tristyla* DC. is strictly trimerous (Cuong *et al*., 2007), *Saurauia leucocarpa* Schltdl. is trimerous to pentamerous (Hunter, 1966), and *Saurauia roxburghii* Wall. is tetramerous to pentamerous (Cuong *et al*., 2007). Soejarto (1980) additionally described rare occurrences of trimerous to heptamerous gynoecia in otherwise pentamerous specimens of *Saurauia*. Dickison (1972) reported deviations from pentamery in *Clematoclethra*, which has not been reported by other authors (e.g. Lechner, 1915; Gilg & Werdermann, 1925; Li *et al*., 2007).

Clematoclethra, *Roridula* and *Heliamphora* all have a single, united, stigmatic surface, whereas all other genera have as many stigmas as carpels. The stigmas are always (except for the reduced stigmas of functionally male *Actinidia* specimens) exserted well above the anthers. In *Clematoclethra*, *Roridula* and *Heliamphora*, the stigmas are directed away from the floral base; they are directed irregularly away from the floral base or to the side in *Actinidia*, *Saurauia* and *Darlingtonia*, and are directed towards the floral base in *Sarracenia*. In *Clematoclethra*, *Saurauia* and *Heliamphora*, the stigmas are small and rounded to oval in outline, whereas they are large and decurrent in *Actinidia* and *Darlingtonia*. *Roridula* has a capitate, rounded stigmatic head, and *Sarracenia* has complex stigmatic shapes, with a dorsal part protruding from the stylar surface and a tail shape extending to the ventral side of the style (Fig. 12S–U). All sarracenioid genera are characterized by unicellular stigmatic papillae, which are conspicuously large and well developed in *Roridula*.

The asymplicate regions of the carpels in *Actinidia*, *Saurauia*, *Darlingtonia* and *Sarracenia* have a groove along the dorsal vascular bundle. In the symplicate part of the style, a central canal (or adpressed ventral slits) is present in all studied taxa, except *Heliamphora*, in which the centre of the style is postgenitally united for its entire length. In *Darlingtonia*, in the

transition zone from the asymplicate to symplicate zone, the stylar canal is postgenitally united, as is part of the stylar canal in *Roridula*.

In Actinidiaceae (except for the reduced gynoecia of functionally male *Actinidia* specimens), *Roridula* and *Darlingtonia*, the style is inserted in a depression on top of the ovary. The ovary shape ranges from flattened globose in *Clematoclethra* and *Saurauia*, through globose to ovoid in *Actinidia* and *Sarracenia*, to narrowly ovoid to conic in *Roridula* and *Heliamphora* (Fig. 12). The ovary of *Darlingtonia* is turbinate with prominent ridges and a conspicuous depression at the transition zone from style to ovary (Fig. 12O).

In the distal part of the ovary, *Darlingtonia*, *Heliamphora* and *Saurauia* have a short region of postgenital union among carpel margins, but, further down, just above the placentae, the central canal again opens up. In the symplicate zone of the ovary of *Clematoclethra*, the carpel margins meet in the centre, but are not postgenitally united. In all other genera, the ovary is at least partly incompletely septate, essentially creating a transition from proximally axile placentation to parietal placentation (in appearance only) more distally (Figs 2, 4–8). The ovaries are symplicate for *c*. 50% of their length in most investigated taxa (slightly less in *Actinidia* and *Saurauia*, more in *Clematoclethra* and *Heliamphora*). The incomplete septation (central canal in *Clematoclethra*; Fig. 3) extends through almost the entire symplicate zone; in the proximal part of the symplicate zone, a short central canal is again formed, most prominently in *Actinidia*, extending down to the synascidiate zone. The central canal in functionally female *Actinidia* specimens extends into the synascidiate zone as a result of crowding of the many carpels (Endress, 2014). In the transition zone from the symplicate to synascidiate zones, postgenital union of the carpel margins is visible, most prominently in *Darlingtonia*, *Sarracenia* and *Saurauia*.

The PTTT is four to ten cell layers thick in the distal regions of the styles, and one or two cell layers thick in the proximal region of the styles and the symplicate zone of the ovaries in all genera; throughout the symplicate zone of the gynoecia, the PTTT forms a compitum, lining the central canal or ventral slits.

The gynoecium vasculature shares some similarities in all members of the clade. Each carpel has one median (dorsal) vascular bundle extending throughout the entire gynoecium. In addition, there are ventral vascular bundle complexes and lateral vascular bundles in the ovary wall. *Actinidia* lacks lateral vasculature. In *Clematoclethra*, *Saurauia* and *Roridula*, lateral vasculature is strictly individual to the carpels (i.e. without synlateral vasculature) and, in Sarraceniaceae, both individual lateral and synlateral vasculature are present. In Actinidiaceae, the ventral vasculature extends throughout the placental region, and in Roridulaceae and Sarraceniaceae also throughout the styles. In *Sarracenia*, the ventral bundles end in the transition zone between the terete part of the style and the umbrella-shaped, distal region. In the remaining genera, vascular bundles are present in the entire symplicate part of the style. The carpels in Actinidiaceae have only individual ventral vasculature, whereas the carpels in both Roridulaceae and Sarraceniaceae have synventral vasculature. In *Roridula* and *Heliamphora*, the ventral vasculature is shared between the carpels over their entire length. In *Darlingtonia*, the ventral vascular bundles are variably individual to the carpels and synventral in the symplicate part of the styles and synventral in the placentae (additional individual vascular bundles are present in the placentae). In *Sarracenia*, the synventral vascular bundles diverge into two (individual) ventral vascular bundles in the distal part of the placentae and again merge into synventral vascular bundles in the proximal part of the placentae.

The ovaries are covered by multicellular, uniseriate trichomes (*A. chinensis*), bifid trichomes with uniseriate branches (*Heliamphora*), pluriseriate stubby hairs (*Sarracenia*) or are papillate (*Roridula*) or completely glabrous (*A. arguta*, *Clematoclethra*, *Saurauia* and *Darlingtonia*). The ovaries of some other *Saurauia* spp. are described as being covered by trichomes (Hunter, 1966; Soejarto, 1980; Li *et al*., 2007). Only *Sarracenia* has (unicellular) trichomes on the styles. Stomata are found on the ovaries of *A. arguta* (functionally female specimen), *Roridula* and *Darlingtonia*; *Sarracenia* has stomata on the distal part of the umbrella-shaped styles (dorsal and ventral sides). The parenchymatic tissue is uniform in the ovary walls, with the exception of smaller cells around the dorsal vascular bundles (future dehiscence line) and in the septa in *Saurauia*, *Roridula* and Sarraceniaceae. The grooves along the dorsal vascular bundles in *Saurauia* correspond to dehiscence lines in ripe fruits (Hunter, 1966; Soejarto, 1980; Li *et al*., 2007). Actinidiaceae and Roridulaceae have mucilage cells and raphide bundles scattered throughout the parenchymatic tissue. *Saurauia* also has evenly distributed large stone cells in the parenchyma. The gynoecia of all families contain tannins, particularly in the epidermal and hypodermal layers of the ovaries and, in *Heliamphora*, *Sarracenia* and *Saurauia*, also in and around the pericarp wall of the locules. The tanniferous tissue in *Actinidia*, *Saurauia* and *Roridula* occasionally has condensed tannins lining the internal cell walls. Small vesicles that appear to contain tannins are sparsely scattered (mainly) in the cytoplasm of the epidermal and hypodermal cells of all

investigated species. The internal surface (mainly the placentae) in the ovaries of Actinidiaceae (except functionally male *Actinidia*) and *Roridula*, unlike Sarraceniaceae, is secretory.

Placentation and ovule structure

Placentation in the sarracenioid clade is essentially axile, but the distal region (the majority of the symplicate zone) of the ovary is incompletely septate in all genera, except *Clematoclethra*, creating a transition zone from distally parietal placentation (as a result of incomplete septation) to proximally axile placentation. The placentae are attached for most of their length in all genera. However, they protrude distally into the locule in *Clematoclethra* and are pendant into the locules below their proximal-most point of attachment in *Saurauia*, *Roridula*, *Darlingtonia* and *Sarracenia*.

Ovule number is highly variable among the investigated species, ranging from four per locule (*R. gorgonias*), eight to ten (*A. arguta* and *C. scandens*), 20–30 (*A. chinensis* and *S. pittieri*) to 100 or more (*S. subspinosa*, *D. californica*, *H. nutans* and *Sarracenia*). *Roridula dentata* differs from *R. gorgonias* in having a single ovule per locule (Diels, 1930; Conran, 2004), and cultivated specimens of *A. chinensis* are reported to contain hundreds of ovules per locule (e.g. Costa *et al*., 1993). Ovules of all genera are inserted in both the symplicate and synascidiate zones and arranged in longitudinal rows: in *Actinidia*, the ovules are arranged in one or two rows on the placentae (ovules alternating when two rows); in *Clematoclethra* and *Roridula*, there are two rows per placenta, and four or more rows per placenta in *Saurauia* and Sarraceniaceae. Ovules are anatropous and, using the definition of Endress (2011), tenuinucellar to incompletely tenuinucellar. Incompletely tenuinucellar ovules are characteristic of *Heliamphora* and *Sarracenia*, and tenuinucellar (to slightly incompletely tenuinucellar) for Actinidiaceae. The exact structure of the ovules of *Darlingtonia* and *Roridula* could not be established because the ovules in the sectioned specimen of *Darlingtonia* appear to be too young. The ovules in *Roridula* are strongly pendant (no length-wise sections of ovules available) and downwards facing as compared with the other taxa. The funiculus is very short (not visible) to short in Actinidiaceae and Sarraceniaceae, and pronouncedly elongate (ovules clearly separated from the placenta by long funiculi) in *Roridula*. The ovules are unitegmic in all genera, except *Darlingtonia*, in which the inner integument forms the micropyle and a small outer integument is present. The integument epidermis is tanniferous in *Actinidia*, *Saurauia* and *Sarracenia*. *Saurauia* occasionally has stone cells in the ovules.

Endosperm formation has been described as cellular for all genera in the clade (Vijayaraghavan, 1965; Davis, 1966; Conran, 1996; Dressler & Bayer, 2004), embryo sac development conforms to the *Polygonum* type (Vijayaraghavan, 1965; Davis, 1966; An *et al*., 1983; Conran, 1996) and embryogeny corresponds to the solanad type (Crété, 1944; Vijayaraghavan, 1965; Davis, 1966; Conran, 1996).

The presence of a nucellar hypostase in the ovules has previously been reported for all sarracenioid families, and discussed as a potential synapomorphy for the sarracenioids by Anderberg *et al*. (2002). The embryological histology of *A. polygama* was investigated by Vijayaraghavan (1965), *R. gorgonias* by Vani-Hardev (1972) and *S. purpurea* by Shreve (1906); all three studies concluded that there was a nucellar hypostase in the ovules. In this study, a nucellar hypostase was located in ovules of both *Actinidia* spp., both *Saurauia* spp., *H. nutans* and *S. leucophylla*. Examples of nucellar hypostases are shown in Figure 13I (*S. pittieri*) and Figure 13Q (*H. nutans*). In *C. scandens* and *R. gorgonias*, the presence of nucellar hypostases in the ovules cannot be established with certainty. No nucellar hypostases were found in the ovules of *D. californica* or *S. purpurea*. Potential explanations for not finding the hypostases in all investigated material, assuming that they are present in all sarracenioid taxa, are that the ovules were not developed enough or were sectioned in a direction in which the hypostase is hard to distinguish.

Fruits and seeds

All sarracenioid families have fruits with persistent styles. Members of Actinidiaceae have baccate fruits (indehiscent in *Actinidia* and *Clematoclethra*; loculicidal in *Saurauia*), with seeds embedded in a mucilaginous pulp (Hunter, 1966; Soejarto, 1980; Ying, Zhang & Boufford, 1993; Cuong *et al*., 2007; Li *et al*., 2007); the mucilaginous pulp is not of arillate origin, but derived from the placentae (Schmid, 1978). The fruits of *Clematoclethra* and *Saurauia* are often described as leathery or fleshy capsules (e.g. Hunter, 1966; Soejarto, 1980; Cuong *et al*., 2007; Li *et al*., 2007), but Beentje (2010) provided narrow definitions of berries (fleshy and indehiscent) and capsules (dry and dehiscent), whereas baccate (berry-like, but can be dehiscent and/or have non-fleshy components) applies to both kinds. Roridulaceae and Sarraceniaceae have loculicidal capsules (e.g. Macfarlane, 1908; Diels, 1930; Berry *et al*., 2005; Mellichamp, 2009).

Seeds are basically small and ellipsoid–ovoid with a reticulate or warty seed coat in all sarracenioids (Gilg & Werdermann, 1925; Uphof, 1936; Hunter, 1966; Vani-Hardev, 1972). Additional seed characteristics

are a pronounced beak and exotestal hairs in *Darlingtonia* (Uphof, 1936), and winged seeds in *Heliamphora* (Uphof, 1936). All three families have exotestal, thin seed coats with thickened inner and radial cell walls of the outer epidermis (Crété, 1944; Dickison, 1972; Vani-Hardev, 1972; DeBuhr, 1975; Corner, 1976; Schmid, 1978; Huber, 1991; Takhtajan, 1991; Conran, 1996). Seed coats are tanniferous in Actinidiaceae, Roridulaceae and *Sarracenia* (this study; Vijayaraghavan, 1965; Vani-Hardev, 1972); no tannins were visible in the epidermis of the sectioned ovules of *Darlingtonia* and *Heliamphora*, but are potentially present in older stages. The endosperm is copious and oily, and the embryos are small (to large in Actinidiaceae) and linear (Gilg & Werdermann, 1925; Netolitzky, 1926; Uphof, 1936; Vani-Hardev, 1972; DeBuhr, 1975; Corner, 1976; Soejarto, 1980). Members of Roridulaceae have a mucilaginous seed coat when wet (Conran, 1996); the mucilage, as in Actinidiaceae, is potentially derived from the placentae, as both families have mucilaginous placentae in the ovaries.

Non-floral features

This section comprises a selection of non-floral features of potentially systematic importance in the sarracenioid clade.

Actinidiaceae and Roridulaceae are woody plants (trees and lianas in Actinidiaceae; shrublets in Roridulaceae), whereas members of Sarraceniaceae are herbaceous perennials with an underground rhizome (e.g. Macfarlane, 1908; Gilg & Werdermann, 1925; Diels, 1930).

Members of Actinidiaceae are autotrophic (e.g. Lechner, 1915), of Roridulaceae are proto-carnivorous with mutualistic relationships with insects (and possibly spiders; e.g. Ellis & Midgley, 1996; Anderson, 2005) and of Sarraceniaceae are carnivorous. The pathways of nutrient uptake in the carnivorous families are distinctively different: members of Sarraceniaceae attract insects by secreting a sugary liquid from stomata at the rim of the pitchers (*Darlingtonia* and *Sarracenia*) or in the hood-like structure above the mouth of the pitcher (*Heliamphora*), after which the insects are caught in the pitcher leaves and digested in the enzyme-containing liquid (e.g. Hepburn, St. John & Jones, 1920, 1927; Jaffé *et al*., 1992; Pietropalo & Pietropalo, 2005; Karagatzides, Butler & Ellison, 2009). In addition to the digestive enzymes in the pitchers, insect larvae and various microorganisms break down the trapped insects and excrete nitrogen available to the plant, and (at least) *S. purpurea* can absorb nitrogen directly from rainwater (e.g. Hepburn *et al*., 1927; Karagatzides *et al*., 2009). Members of Roridulaceae are dependent on a mutualistic relationship with hemipterans and possibly spiders to eat and digest the insects trapped on the resin-secreting, glandular hairs of the leaves, prophylls and sepals, whereupon nutrient adsorption takes place from the insect faeces (Anderson, 2005). Resin-secreting glandular hairs covering vegetative organs are also present in some members of Actinidiaceae (e.g. Dressler & Bayer, 2004; Li *et al*., 2007).

All three sarracenioid families contain iridoid compounds in the leaves (Jensen, Nielsen & Dahlgren, 1975; Albach, Soltis & Soltis, 2001); members of Sarraceniaceae additionally contain the monoterpene compound sarracenin, potentially unique to the family (Mellichamp, 2009).

Comparison with fossil taxa

Two fossil genera are tentatively placed in the sarracenioid clade with most morphological similarities shared with extant Actinidiaceae: *Glandulocalyx* Schönenberger, von Balthazar, Takahashi, Xiao, Crane & Herendeen and *Parasaurauia* Keller, Herendeen & Crane (Keller *et al*., 1996; Schönenberger *et al*., 2012). Here, the fossil flowers are compared with the extant sarracenioid families, not accounting for potentially plesiomorphic characters in Ericales or synapomorphic characters in core Ericales.

Characters linking the two fossil genera to all three sarracenioid families include quincuncial aestivation of perianth whorls; (at most) proximally united perianth organs; probable late anther inversion (late anther inversion type A is closely linked with ventrifixed anthers, see Schönenberger *et al*., 2012); styles inserted in a depression on top of the ovary in *Parasaurauia*; proximally axile to distally parietal (as a result of incomplete septation of the locules) and pendant placentae in *Glandulocalyx*; ovules arranged in longitudinal rows; reticulate epidermis structure on the ovules in *Parasaurauia*.

Some characters linking the two fossil genera to Actinidiaceae and Roridulaceae (but not Sarraceniaceae) include a sepaloid outer perianth whorl and multicellular-pluriseriate and possibly glandular trichomes present on the dorsal side of the sepals.

Characters linking the two fossil genera to Actinidiaceae include ovate petals with rounded apices; ventrifixed or basifixed, extrorse anthers; triaperturate pollen grains without exine ornamentation in *Glandulocalyx*; polystemony in *Glandulocalyx* and diplostemony in *Parasaurauia*, as well as largely asymplicate styles.

Some characters linking the two fossil genera to *Saurauia* are pluriseriate trichomes present on sepals; trimerous gynoecia; capitate stigmas with ventral grooves.

Floral structure and systematics

The taxonomic history of the three families composing the sarracenioid clade is complicated, especially with regard to suprafamiliar relationships and the taxonomic ranks of Actinidiaceae and Roridulaceae. Below, a brief historical overview is presented for each of the three families, followed by a summary of more recent hypotheses on the phylogenetic relationships of the sarracenioid families.

Members of Actinidiaceae have variably been considered as part of Dilleniaceae (e.g. Gilg, 1893; Lechner, 1915) or Clethraceae (Hallier, 1905; Hunter, 1966), or a natural group containing all three genera (e.g. van Tieghem, 1899; Gilg & Werdermann, 1925; Vijayaraghavan, 1965; Cronquist, 1968); alternatively, *Saurauia* was placed in Dilleniaceae or treated as the monogeneric family Saurauiaceae, whereas *Actinidia* and *Clematoclethra* comprised Actinidiaceae *s.s.* (e.g. Dunn, 1911; Takhtajan, 1966). A comprehensive account of the previous taxonomic alliances of Actinidiaceae can be found in Dickison (1972) and Schmid (1978).

Members of Roridulaceae have been placed in Ochnaceae (Planchon, 1848; Engler, 1907), Droseraceae (e.g. Bentham & Hooker, 1865; Netolitzky, 1926), Clethraceae (Hallier, 1912) and Byblidaceae (e.g. Domin, 1922; Cronquist, 1981), or treated as a distinct family (e.g. Marloth, 1925; Diels, 1930; Vani-Hardev, 1972; Takhtajan, 1987). A comprehensive account of the previous taxonomic alliances of Roridulaceae can be found in Vani-Hardev (1972) and Conran (1996; 2004).

Members of Sarraceniaceae have generally been considered to be a monophyletic and distinct group (e.g. Bentham, 1840; Torrey, 1853; Macfarlane, 1908; Uphof, 1936), although Chrtek, Slavíková & Studnička (1992) treated *Heliamphora* as the monogeneric family Heliamphoraceae and restricted Sarraceniaceae to only *Darlingtonia* and *Sarracenia*. The splitting of the sarraceniaceous genera into two separate families was, however, not accepted by most subsequent authors (e.g. Bayer, Hufford & Soltis, 1996; Neyland & Merchant, 2006).

In pre-molecular treatments of angiosperm diversity, the sarracenioid families and genera were considered to belong to various plant orders (e.g. Ericales, Dilleniales, Ranales, Rosales, Sarraceniales and Theales) in different subclasses (Dilleniidae and Rosidae) of angiosperms (e.g. Dickison, 1972; Vani-Hardev, 1972; DeBuhr, 1975; Schmid, 1978; Cronquist, 1981; Dahlgren, 1983; Conran, 1996, 2004).

Based on the (proto-)carnivorous nature of Roridulaceae (as a part of Byblidaceae or Droseraceae) and Sarraceniaceae, the two families were often considered to be closely related (together with, among others, Nepenthaceae) in early systematic treatments (e.g. Warming, 1878; Hallier, 1905), but nevertheless, even before the molecular systematic era, carnivory was disproven as a useful character in higher level systematics [see, for example, Uphof (1936), DeBuhr (1975) and Conran & Dowd (1993) for detailed accounts]. Based on morphology, Hunter (1966) proposed a close relationship between Actinidiaceae, Ericaceae and Clethraceae, again demonstrated by Hufford (1992) using morphological and phytochemical data. Using morphological data, Dahlgren & van Wyk (1988) first placed, albeit with expressed uncertainty, Roridulaceae in Ericales. In cladistic analyses using morphological data, Anderberg (1992, 1993) first demonstrated the close relationships of the sarracenioid families, but they did not form a monophyletic group in either study. Based on molecular data, Chase *et al*. (1993) and Soltis *et al*. (2000) found a close relationship of the sarracenioid families in their angiosperm-wide phylogenetic analyses, but, again, they did not form a monophyletic group. Finally, Anderberg *et al*. (2002) demonstrated a well-supported clade comprising Actinidiaceae, Roridulaceae and Sarraceniaceae, sister to a clade comprising Clethraceae, Cyrillaceae and Ericaceae *s.l*. These relationships were confirmed in later molecular studies (e.g. Schönenberger *et al*., 2005; Soltis *et al*., 2011).

Why was the close relationship of the sarracenioid families not recognized in the pre-molecular era? Parts of the answer lie in the vastly different ecological niches occupied by representatives of the three families and the conspicuous differences in their growth habits, but also in the diversity of their floral morphology. Great emphasis was placed on carnivory in Sarraceniaceae and Roridulaceae, linking them with, among others, Byblidaceae, Droseraceae and Nepenthaceae, whereas the flowers and growth habit of members of Actinidiaceae linked them to mainly Dilleniaceae and Theaceae (e.g. Cronquist, 1981). Even after the clade was recognized, only a few non-molecular characters, including iridoid compounds present in plant tissue (Albach *et al*., 2001) and a nucellar hypostase present in the ovules of all three families (e.g. Vijayaraghavan, 1965; DeBuhr, 1975; Conran, 1996), were proposed as potential synapomorphies (Stevens, 2001 onwards; Anderberg *et al*., 2002). Anderberg *et al*. (2002) additionally proposed branched (read 'partly asymplicate') styles as a potential synapomorphy for the sarracenioids (with a reversal to fully symplicate styles in *Roridula*).

In the following sections, the floral and non-floral features shared by the three sarracenioid families are listed, followed by features shared by the three possible family-pairs. With the help of a literature-based assessment of other ericalean families, potential

synapomorphies are identified and printed in **bold** type. Some of the features shared by all three sarracenioid families appear to be rare in Ericales and may turn out to be synapomorphic for the clade; other features appear to be common in the order and may turn out to be symplesiomorphic for Ericales or synapomorphic for core Ericales (Actinidiaceae, Roridulaceae, Sarraceniaceae, Clethraceae, Cyrillaceae and Ericaceae). The floral structure and diversity in many ericalean families are only partially known, and the suprafamiliar relationships are not completely resolved; it will therefore not be possible to assign robust synapomorphic features to the respective clades until the floral structure and systematics of Ericales have been studied more comprehensively. General information for the other ericalean families is taken from Stevens (2001 onwards), Kubitzki (2004a), Schönenberger (2009) and von Balthazar & Schönenberger (2013). References for specific families (detailed morphological studies) are: Balsaminaceae, Marcgraviaceae and Tetrameristaceae (von Balthazar & Schönenberger, 2013); Clethraceae (Kavaljian, 1952); Cyrillaceae (Copeland, 1953); Diapensiaceae (Palser, 1963); Ericaceae (Copeland, 1938a, 1941, 1947; Palser, 1952; Paterson, 1961; Leins, 1964; Palser & Murty, 1967; Jackes, 1968); Fouquieriaceae and Polemoniaceae (Schönenberger, 2009); Pentaphylacaceae and Theaceae (Keng, 1962; Corner, 1976; Sugiyama, 1997); and Styracaceae (Copeland, 1938b; Dickison, 1993).

Features shared by all three sarracenioid families

1. Solitary flowers or cymose branching in the inflorescences. Cymose patterns in the inflorescences are common in Ericales, particularly among the ericoid, primuloid and styracoid families. Members of Theaceae have solitary flowers.
2. Flowers (mainly) pendant. Note the exception in *R. gorgonias* and somewhat variable flower orientation in inflorescences of Actinidiaceae. Pendant flowers are present in many ericalean families.
3. Flowers structurally bisexual (often functionally unisexual in Actinidiaceae). Structurally bisexual flowers are plesiomorphic in Ericales.
4. Flowers polysymmetric. Most members of Ericales have polysymmetric flowers.
5. Floral tissue containing hydrolysable tannins. Data fragmentary in Ericales, but appears to be common in the balsaminoid clade, ericoid clade and Styracaceae.
6. **Floral tissue containing vesicles that appear to contain tannins (most likely condensed tannins and/or tannosomes).** Further investigations are warranted to determine the exact chemical composition of the vesicles. Condensed tannins are additionally present along the internal cell walls of tanniferous cells in *Actinidia*, *Saurauia* and *Roridula*. Data fragmentary in Ericales, but present in *Pelliciera rhizophorae* Planch. & Triana (Tetrameristaceae; J. Schönenberger, unpubl. data).
7. Floral tissue containing calcium oxalate druses. Data fragmentary, but appears to be a common trait in Ericales.
8. Largely pentamerous perianth. Note the exception of *Heliamphora*. Pentamerous perianth organization is common in core eudicots.
9. Perianth organized in two whorls. Note the potential exception of *Heliamphora*. Two-whorled perianth organization is common in core eudicots.
10. Largely free perianth organs. Note up to 50% sympetaly in some *Saurauia* spp. Union of perianth organs is variable, even within genera in Ericales.
11. Broadly attached perianth organs. Broadly attached perianth organs are common in Ericales.
12. Palisade parenchyma not present in perianth organs. Data fragmentary in Ericales, but appears to be a common trait.
13. Sepal aestivation quincuncial in pentamerous individuals. Quincuncial aestivation is a common trait in pentamerous Ericales.
14. Sepals unequal in size within a flower. Unequal size of sepals is a common trait in Ericales.
15. Sepals persistent after anthesis. Persistence of sepals after anthesis is a common trait in Ericales.
16. Stomata common on sepals. Presence of stomata on sepals is a common trait in Ericales.
17. Petal aestivation quincuncial in pentamerous individuals. Quincuncial aestivation is a common trait in pentamerous taxa in Ericales.
18. **Petals proximally thicker than sepals.** Note the exception of *S. purpurea* (potentially too young to exhibit the trait). In Ericales, petals are generally of equal thickness or (often markedly) thinner than sepals in the proximal region. Exceptions are *Schwartzia brasiliensis* (Choisy) Bedell ex Gir.-Cañas (Marcgraviaceae) and *Rhododendron hirsutum* L. (Ericaceae).
19. Petal vasculature joining the CVC as one unit (inner perianth organs in *Heliamphora*). Petal vasculature joining the CVC as a single unit is a common trait in angiosperms.
20. Stomata common on petals. Presence of stomata on petals is a common trait in Ericales.

21. Largely free stamens/staminodes. Note that the filaments of *Saurauia* are commonly united in the proximal-most region. Free androecium organs are common in Ericales.
22. Late anther inversion. Late anther inversion is restricted to the sarracenioids, Clethraceae and early-diverging lineages of Ericaceae. In contrast, most lineages of Ericaceae have early anther inversion. Anther inversion (although of three to four different types) is probably synapomorphic for core Ericales.
23. Anthers sagittate. Sagittate anthers are common in Ericales.
24. Anthers broadly attached. Broad anther attachment is a common trait in Ericales.
25. Stomata present on anther connective. Presence of stomata on the anther connectives is a common trait in Ericales.
26. Endothecium present only in anther walls. Data fragmentary, but endothecium restricted to the anther walls seems to be the most common in Ericales.
27. Pollen released as monads (rarely tetrads in *Saurauia*). Pollen released as monads is a common trait in Ericales.
28. Superior ovary. Note the subinferior ovary in *Roridula*. Hypogyny is a common trait in Ericales.
29. Distal-most part of gynoecium asymplicate. Note that only minute stigmatic lobes are asymplicate in *Clematoclethra*, *Roridula* and *Heliamphora*. Presence of asymplicate stigmatic lobes is a common trait in Ericales; the largely asymplicate styles of *Actinidia* and *Saurauia* and the partly asymplicate styles of *Sarracenia* and *Darlingtonia* are less common traits in Ericales, but present in many families.
30. Stigmas unicellular-papillate. Unicellular stigmatic papillae are a common trait in Ericales.
31. Stylar canal or open ventral slits present in symplicate zone of styles. Note that the ventral slits are postgenitally united in *Heliamphora*. An open stylar canal in the symplicate zone of the styles appears to be a common trait in Ericales.
32. PTTT forms a compitum (one or two cell layers thick) in the symplicate zone of the gynoecium. Data fragmentary, but this is probably a common trait in Ericales.
33. Styles inserted in a depression on top of the ovary. Note the exception of *Heliamphora*, *Sarracenia* and functionally male *Actinidia*. Present in Clethraceae and (at least) some Ericaceae, but is not described for most other ericalean families. May turn out to be a synapomorphic trait for core Ericales.
34. Ovary distally symplicate and proximally synascidiate. Common in Ericales.
35. Incomplete septation of the locules in the distal region. Common in Ericales.
36. Placentae extending over both symplicate and synascidiate zone. Common in Ericales.
37. Placentae not attached for the entire length. Note the exceptions of *Actinidia* and *Heliamphora*. Placentae are pendant in *Saurauia*, *Roridula*, *Darlingtonia* and *Sarracenia*; free placental lobes protrude upwards in the locules in *Clematoclethra*. Variable from fully attached to pendant in Ericales.
38. Ovules arranged in longitudinal rows. This is the most common case in Ericales.
39. Ovules attached for the entire length of the placentae. Variable, but common in Ericales.
40. Ovules anatropous. Common in Ericales.
41. Ovules tenuinucellate to incompletely tenuinucellate. Common in Ericales.
42. Stomata common in ovary wall. Data fragmentary, but probably a common trait in Ericales.
43. Unitegmy. Note the exception of *Darlingtonia*. Most core Ericales are unitegmic, as are Diapensiaceae, Polemoniaceae, Sapotaceae, Styracaceae and Symplocaceae.
44. **Nucellar hypostase present in ovules.** Data fragmentary in Ericales, but absent at least from the ericoid clade.
45. Fruits with persistent styles. Common in Ericales.
46. Loculicidal fruits. Note the exception of *Actinidia* and *Clematoclethra*. Common in Ericales, at least for genera with capsular fruits.
47. Seed coat thin and exotestal. Common in Ericales.
48. *Polygonum*-type embryo sac development. Common in Ericales.
49. Embryo straight. Common in Ericales.
50. Endosperm formation cellular. Common in Ericales.
51. Endosperm oily. Common in Ericales.
52. **Iridoid compounds present in leaves.** Absent in Clethraceae and Cyrillaceae, but reported for Ericaceae; next to core Ericales, iridoid compounds are only reported for Fouquieriaceae and Symplocaceae (Albach *et al*., 2001).

Features shared by Actinidiaceae and Roridulaceae (not present in Sarraceniaceae)

1. Woody growth habit. Common in Ericales.
2. Glandular hairs present on vegetative organs. Note that glandular hairs are not present in some Actinidiaceae. The presence or absence of glandular hairs on vegetative organs seems to be variable, but not uncommon in Ericales.

3. **Calcium oxalate raphides abundant in floral tissue.** Data fragmentary in Ericales, but absent in Sarraceniaceae and not described for the rather well-studied Diapensiaceae, ericoid families (except *Monotropa* L.; Caris, 2013), Fouquieriaceae and Polemoniaceae or Styracaceae. Present in the balsaminoid families.
4. **Mucilage cells present in floral tissue.** Data fragmentary in Ericales, but absent in Sarraceniaceae and not described for the rather well-studied Diapensiaceae, ericoid families, Fouquieriaceae and Polemoniaceae or Styracaceae. Present in the balsaminoid families.
5. Outer perianth whorl sepaloid. Petaloid sepals are uncommon in Ericales and appear to be apomorphic for Sarraceniaceae.
6. Sepals proximally united. Proximally united sepals are common in Ericales.
7. Multicellular hairs (generally) present on dorsal side of sepals. Both uniseriate and pluriseriate glandular hairs present in *Roridula*. Common in Ericales.
8. Anthers ventrifixed or basifixed (deeply sagittate and latrorse–extrorse). The anthers of Sarraceniaceae are basifixed or dorsifixed; ventrifixed anthers (or deeply sagittate basifixed and extrorse anthers) may turn out to be a synapomorphy for core Ericales. Also present in Polemoniaceae.
9. Late anther inversion type A. Note that the definitions of all late anther inversion types in Ericales may need to be revised. Also present in Clethraceae and early-diverging lineages of Ericaceae. May turn out to be symplesiomorphic in core Ericales.
10. Tricolporoidate to tricolporate pollen with little exine ornamentation (a few exceptions in *Saurauia*). Common in Ericales.
11. **Inner surface of gynoecium secretory.** Data fragmentary in Ericales, but feature absent in Sarraceniaceae and not described for the rather well-studied Diapensiaceae, ericoid families, Fouquieriaceae and Polemoniaceae or Styracaceae. Present in the balsaminoid families.
12. **Synlateral vasculature lacking in ovary.** Synlateral vasculature is present in the ovaries of Sarraceniaceae, the balsaminoid clade, Diapensiaceae, most ericoid taxa, Fouquieriaceae and Polemoniaceae, Pentaphylacaceae, Styracaceae and Theaceae.

Features shared by Actinidiaceae and Sarraceniaceae (not present in Roridulaceae)

1. Polystemony. Note the exception of *Clematoclethra*. In *Actinidia*, *Darlingtonia* and *Heliamphora*, the stamens are arranged in one whorl; in *Saurauia*, the stamens are arranged in two whorls; in *Sarracenia*, the number of whorls is currently hard to assess, but two whorls are likely. In core Ericales, polystemony is restricted to the sarracenioid clade; outside core Ericales, various kinds of polystemony are common in Lecythidaceae, Marcgraviaceae, Mitrastemonaceae, Freziereae and Ternstroemieae of Pentaphylacaceae, Isonandrae and Omphalocarpeae of Sapotaceae, Symplocaceae and Theaceae; hence, the trait has probably evolved on numerous occasions during the history of the order. Polystemony may have been present in the most recent common ancestor of the sarracenioid clade, with either plasticity in stamen numbers in the ancestral lineage or secondary loss of polystemony in *Clematoclethra* and *Roridula*. The systematic importance of the widespread polystemony in the sarracenioid clade cannot be properly addressed until further developmental studies are performed in the clade, and the polytomies in the backbone of the ericalean phylogeny are resolved; of particular interest is the position of the polystemonous Theaceae.
2. Weakly developed funiculus. Common in Ericales. The large conspicuous funiculi of *Roridula* are potentially apomorphic for Roridulaceae.

Features shared by Roridulaceae and Sarraceniaceae (not present in Actinidiaceae)

1. Insectivory. The systems of insectivory are different and most likely evolved independently (see discussion above). The glandular hairs of Roridulaceae are potentially homologous with the glandular hairs sometimes present on vegetative organs in many families in Ericales.
2. Entire petal margin. Entire petal margins are common in Ericales.
3. Loculicidal capsular fruits. Common in Ericales.

CONCLUSIONS

The present comparative study of floral structure identifies a few potential floral synapomorphies (presence of vesicles that appear to contain tannins in floral tissue, petals proximally thicker than sepals and nucellar hypostase present in ovules) and one potential non-floral synapomorphy (presence of iridoids in leaves) for the sarracenioid families. The subclade formed by Actinidiaceae and Roridulaceae is more easily distinguished using floral characters (presence of raphides and mucilage cells in floral tissue; inner surface of gynoecium secretory; synlateral vascular bundles lacking in ovary), perhaps not surprisingly because of their sister group

relationship and a more recent last common ancestor than that of the entire sarracenioid clade.

The identification of synapomorphic characters is particularly important in cases such as the sarracenioid clade, for which the circumscription has been based purely on molecular data and the families were rarely affiliated before the rise of molecular systematics. This study further reinforces the notion that floral characters previously considered to be of high taxonomic value (e.g. number of stamens, number of carpels, union of organs and integument number) are rather homoplasious when considered in a sound phylogenetic framework, whereas anatomical, histological and phytochemical characters may be of considerable use for the circumscription of higher taxa.

We would finally like to point out that detailed higher level comparative structural studies, such as this, may help to refine the hypotheses of floral evolution in higher taxa and provide a basis for fossil placement analyses. This, in turn, may be of use in neighbouring research fields, such as the determination of the age and biogeography of a given taxon, the evo–devo study of floral development or pollination biology.

ACKNOWLEDGEMENTS

We would like to thank the UZH Botanic Garden, UniVie Botanical Garden, Eric La Fountaine at UBC Botanical Garden, Heidemarie Halbritter and Agneta Julia Borg for providing floral material for the study; Perica Brodaric, Susanne Pamperl, Susanne Sontag and Yannick Städler for technical assistance; Maria von Balthazar and Ursula Schachner for proofreading the text prior to submission; and two anonymous reviewers for suggestions on how to improve the text.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Movie S1. X-Ray tomography of *Sarracenia purpurea* gynoecium. MPEG video file of three-dimensional gynoecium reconstruction, digital longitudinal section and digital transverse section series.

CHAPTER III

EARLY FLORAL DEVELOPMENT AND ANDROECIUM ORGANISATION IN THE SARRACENIOID CLADE (ACTINIDIACEAE, RORIDULACEAE AND SARRACENIACEAE) OF ERICALES

Submitted to Botanical Journal of the Linnean Society (6 July 2015).

Authors' contributions: conceptualisation, laboratory work, writing and correspondence by Stefan D. Löfstrand; conceptualisation and comments on writing Jürg Schönenberger; comments on writing by Maria von Balthazar.

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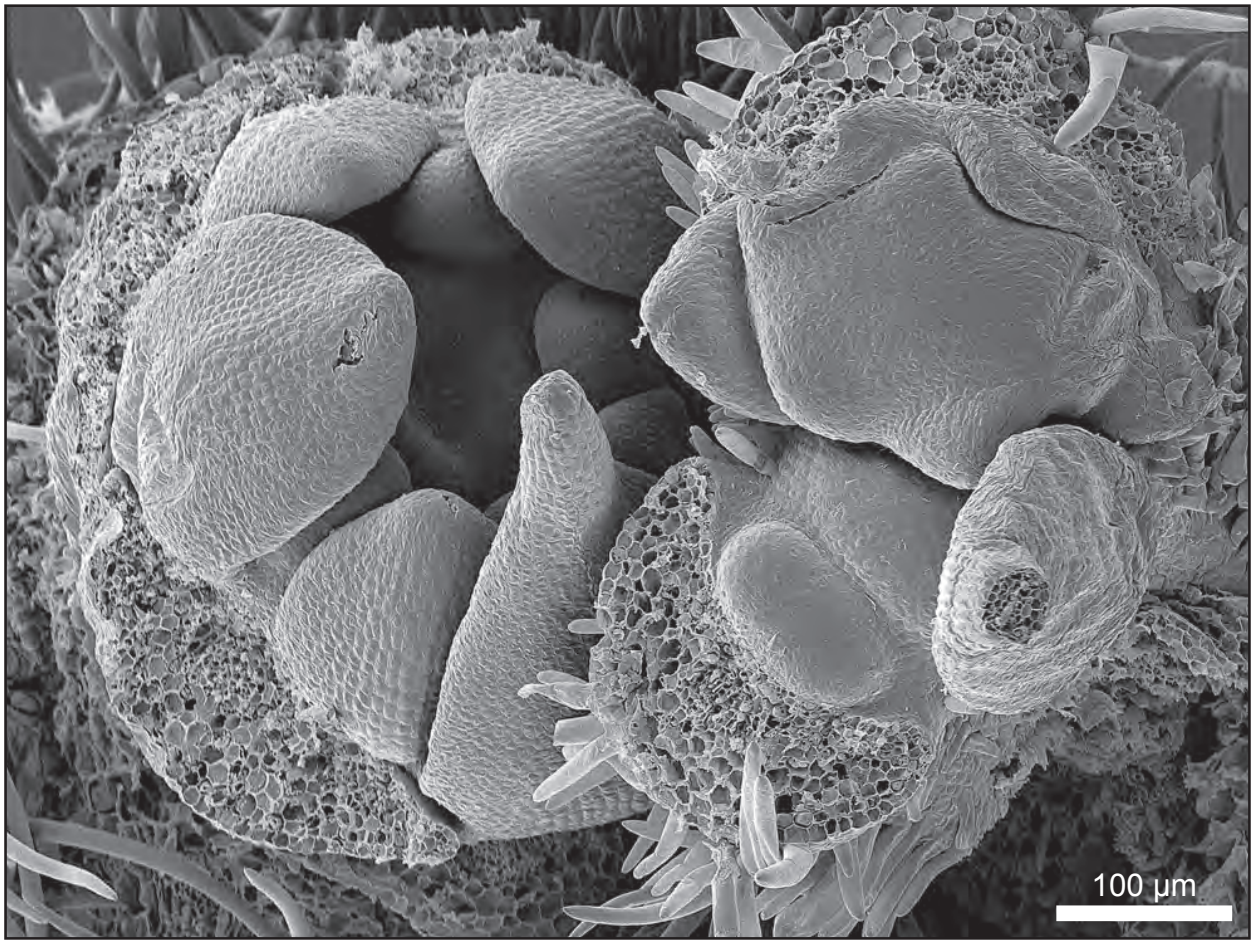

Scanning electron micrograph of young *Roridula gorgonias* infloresence.

ABSTRACT

Early floral development of *Actinidia (A. arguta*, *A. callosa*, *A. chinensis* and *A. kolomikta*; Actinidiaceae), two Asian and two Neotropical species of *Saurauia* (*S. montana*, *S. oldhamii*, *S. pittieri* and *S. subspinosa*; Actinidiaceae), *Roridula gorgonias* (Roridulaceae) and *Heliamphora nutans* (Sarraceniaceae) was comparatively studied using scanning electron microscopy. The late stages of androecium development are additionally presented for *Clematoclethra scandens* (Actinidiaceae), *Darlingtonia californica* (Sarraceniaceae) and *Sarracenia leucophylla* (Sarraceniaceae). The usually pentamerous flowers of these taxa share a number of developmental features: the perianth organs emerge in a clockwise or anticlockwise spiral on the floral apex with relatively long plastochrons between successive organs, resulting in conspicuous size differences among perianth organs during early developmental stages; the perianth always consists of two differentiated whorls (unlike earlier interpretations of the perianth in *Heliamphora*); the usually polystemonous androecium is initiated on a ring primordium with leading secondary stamen primordia in alternipetalous positions; successive stamen primordia appear in a lateral sequence until a whorl-like structure is formed on the ring primordium; and the anthers invert shortly before anthesis. Later androecial development differs conspicuously between taxa and primordia may in addition proliferate centrifugally, centripetally and/or laterally. For Ericales unusual features of floral development include: spirally initiated petals (but later organised in a whorl) with comparatively long plastochrons between individual petals (except *Saurauia*), common occurrence of perianth organs in double position in Actinidiaceae and anther inversion close to anthesis. In addition, floral development in the sarracenioid families is further compared to other families and clades in Ericales, further emphasising the highly variable patterns of androecium development in the order.

ADDITIONAL KEYWORDS: *Actinidia* – anther inversion – asterids – *Heliamphora* – floral ontogeny – perianth – *Roridula* – *Saurauia* – scanning electron microscopy

INTRODUCTION

The sarracenioid clade is comprised of three families (Actinidiaceae, Roridulaceae and Sarraceniaceae) and is sister to the ericoid clade (Clethraceae, Cyrillaceae and Ericaceae). The sarracenioid and ericoid clades together form the so-called core Ericales (Schönenberger, Anderberg & Sytsma, 2005). Actinidiaceae is sister to Roridulaceae and the Actinidiaceae–Roridulaceae clade is sister to Sarraceniaceae (Schönenberger *et al*., 2005). All core ericalean taxa, apart from the two monotypic genera of Cyrillaceae, are characterised by anther inversion at some point during floral development (Schönenberger *et al*. 2012). Another interesting feature that is present in most families of core Ericales are truly ventrifixed anthers or seemingly ventrifixed anthers, which are basifixed, sagittate, extrorse, and have a filament joining from the ventral side. This feature is apparently closely linked with anther inversion from extrorse to introrse anther orientation (Schönenberger *et al*., 2012; Chapter IV.). While most taxa in the sarracenioid clade are polystemonous (all except *Clematoclethra* and *Roridula*; Löfstrand & Schönenberger, 2015), the ericoid clade is largely characterised by diplostemonous flowers.

Actinidiaceae are classified in three genera: *Actinidia* Lindl. with 52 species, the monotypic *Clematoclethra* (Franch.) Maxim. and *Saurauia* Willd. with approximately 300 species (Li, Li & Soejarto, 2007). Roridulaceae are monogeneric with the genus *Roridula* Burm ex. L. containing two species (Conran, 2004). Sarraceniaceae are classified in three genera, the monotypic *Darlingtonia* Torr., *Heliamphora* Benth. with 23 species and *Sarracenia* L. with 11 species (Mellichamp, 2009; Berry, Riina & Steyermark, 2005). The lianescent genera *Actinidia* and *Clematoclethra* are native to East Asia, whereas the arborescent *Saurauia* is present in the Neotropics, South Asia, Southeast Asia and tropical Oceania (Dressler & Bayer, 2004). The small, protocarnivorous shrubs of *Roridula* are endemic to the Cape region of South Africa

(Conran, 2004). The rosettiform, carnivorous herbs of Sarraceniaceae are native to North America (*Darlingtonia* Torr. and *Sarracenia* L.) and the Guiana Highlands of South America (*Heliamphora* Benth.; Mellichamp, 2009; Berry *et al*., 2005). All flowers in the sarracenioid clade are actinomorphic and either bisexual (*Clematoclethra, Saurauia* p.p., *Actinidia* p.p., *Roridula* and Sarraceniaceae) or unisexual (*Actinidia* p.p. and *Saurauia* p.p.; Löfstrand & Schönenberger, 2015). The perianth is most often pentamerous (although with variable merism in *Actinidia, Saurauia* and *Heliamphora*) and rarely more than proximally united in the respective organ whorl (Löfstrand & Schönenberger, 2015). The androecial organs are mostly free from each other and the corolla. Stamen number ranges from five in *Roridula*, through 10 in *Clematoclethra*, 15 in *Darlingtonia*, 20–50 in most *Actinidia, Saurauia* and *Heliamphora* species, to well over a hundred in some *Sarracenia* and large-flowered representatives of *Actinidia* and *Saurauia* (Li *et al*., 2007; Löfstrand & Schönenberger, 2015). The superior gynoecium is partially (styles are partially or entirely free in *Actinidia*, *Saurauia*, *Darlingtonia* and *Sarracenia*) to fully syncarpous (*Clematoclethra*, *Roridula* and *Heliamphora*) and consists of three (*Clematoclethra*, *Saurauia* p.p., *Roridula* and *Heliamphora*), typically five (*Saurauia* p.p., *Darlingtonia* and *Sarracenia*) or typically more than 15 (*Actinidia*) carpels (Soejarto, 1980; Li *et al*., 2007; Löfstrand & Schönenberger, 2015).

Studies of floral development have helped to clarify many controversial interpretations of floral structures (e.g. the calyptra of Eupomatiaceae, Endress 2003; the perianth of Penaeaceae, Schönenberger & Conti 2003; the androecium of Malvaceae, von Balthazar *et al*. 2004, 2006). In polystemonous flowers, as present in the sarracenioid clade, a developmental study is the only way to unequivocally determine the organisation of the androecium. The androecium organisation in Ericales has been investigated through flower developmental studies in many taxa (e.g. Tsou, 1998; Zhang, Ma & Wang, 2007, 2008; Wang *et al*., 2010; Caris, 2013; Zhang & Schönenberger, 2014). Androecia may proliferate centrifugally, centripetally and/or laterally (e.g. Caris, 2013) giving rise to a broad diversity of polystemonous flowers. In addition, reconstructions of character evolution indicate that a haplostemonous androecium organisation is most likely plesiomorphic in Ericales, with several apomorphic changes to a diplostemonous androecium organisation or various types of polystemony (Schönenberger *et al*., 2005). At the level of asterids, polystemonous flowers are relatively rare, while in the two early diverging asterid plant orders Cornales and Ericales, several families display polystemony of various patterns (Endress, 2003; Kubitzki, 2004). While some detailed developmental studies are at hand for *Actinidia* (Brundell, 1975; van Heel, 1987; Caris, 2013) and, in part, one *Saurauia* species (Brown, 1935) and one *Sarracenia* species (Shreve, 1906), information is largely lacking in all remaining genera of the sarracenioid clade.

Here, we complement and test earlier interpretations of floral development and organisation in sarracenioid families with special attention to androecium development and organisation. In addition, we also take a closer look at the perianth of *Heliamphora*, which has traditionally been interpreted as being apetalous (e.g. Macfarlane, 1908; Berry *et al*., 2005). This view has recently been challenged based on a comparative analyses of mature flowers in the sarracenioid clade (Löfstrand & Schönenberger 2015), but needs to be tested based on a study of the earliest stages of the floral development.

MATERIAL AND METHODS

MATERIAL

Taxa were sampled to represent all genera in the sarracenioid clade, as well as a few morphologically different species of *Actinidia* and both Neotropical and Asian species of *Saurauia*.

Actinidiaceae

Actinidia arguta Miq. (functionally female specimen); JS616 and JS714, cult. Botanical Garden of the University of Zurich, Switzerland.

Actinidia callosa Lindl. (functionally male specimen); SL1, cult. Botanical Garden of the University of Vienna, Austria.

Actinidia chinensis Planch. (parthenocarpic specimen); SL34; cult. private collection of S.L., Vienna, Austria.

Actinidia kolomikta Maxim. (functionally male specimen); JS617, cult. Botanical Garden of the University of Zurich, Switzerland.

Clematoclethra scandens Maxim. (subsp. *hemsleyi* Baill.) Y.C.Tang and Q.Y.Xiang); SL2, cult. University of British Columbia Botanical Garden, Canada.

Saurauia montana Seem.; JS908, coll. Schönenberger *s.n*., Costa Rica.

Saurauia oldhamii Hemsl. ex F.B.Forbes & Hemsl.; JS 919, coll. Wu *s.n*., Taiwan, People's Republic of China.

Saurauia pittieri Donn.Sm.; JS 828, coll. Borg 17, Costa Rica.

Saurauia subspinosa J.Anthony; SL4; cult. Botanical Garden of the University of Vienna, Austria.

Roridulaceae

Roridula gorgonias Planch.; SL27–29, cult. Botanical Garden of the University of Vienna, Austria.

Sarraceniaceae

Darlingtonia californica Torr.; SL5 and SL7, cult. Botanical Garden of the University of Vienna, Austria.

Heliamphora nutans Benth.; SL8, cult. Botanical Garden of the University of Zurich, Switzerland; SL30, cult. Botanical Garden of the University of Vienna, Austria; SL33, cult. Bergius Botanic Garden, Sweden; and SL41, cult. Austrian National Botanical Gardens – Castle Garden Schönbrunn, Austria.

Sarracenia leucophylla Raf.; JS915 and SL12, cult. Austrian National Botanical Gardens – Castle Garden Schönbrunn, Austria.

METHODS

Inflorescences or flower buds of various developmental stages were fixed in formaldehyde-acetic acid-alcohol (FAA) and stored in 70% ethanol. Dissected flowers and floral buds were dehydrated in an ethanol series and acetone, critical point dried, mounted on stubs and sputter coated with gold, and thereafter studied at 10 kV in a Jeol JSM-IT300 field emission scanning electron microscope (JEOL Germany GmbH, Munich, Germany). Permanent SEM stubs are deposited at the Department of Botany and Biodiversity Research, University of Vienna, Austria. The line drawings of *Darlingtonia californica* and *Sarracenia leucophylla* are based on light micrographs; see Löfstrand & Schönenberger (2015) for methods.

GLOSSARY

Alterni- (prefix): alternating with.

Ante- (prefix): in the same radius as.

Apical: the distal-most point of an entire morphological unit, e.g. the entire gynoecium (not to be confused with distal).

Basal: the proximal-most point of an entire morphological unit, e.g. the entire gynoecium (not to be confused with proximal).

Basifixed anther: the anther attachment is positioned in the proximal-most region of the anther connective (no connective tissue joins the thecae proximal of the anther attachment).

Centrifugal: away from the floral centre, towards the periphery of the flower

Centripetal: towards the floral centre, away from the periphery of the flower

Dorsifixed anther: the anther attachment is positioned on the dorsal side of the anther with connective tissue joining the thecae both distally and proximally of the point of attachment.

Fibonacci spiral: an approximation of the golden spiral, composed of quarter circle arcs with radii of integer Fibonacci number. Hence, the divergence angle between the first two organs is *c*. 180°, between the second and third *c*. 120°, between the third and fourth *c*. 144°, and thereafter *c*. 137.5°.

Hofmeister's rule: primordia emerge in the largest available space (e.g. the divergence angles in a spiral phyllotaxis can become somewhat irregular as a result of the spatial displacements and growth processes of preceding organs; Hofmeister, 1868).

Irregular phyllotaxis: a set of primordia emerging in an unordered sequence and/or irregular plastochrons, particularly in flowers with many organs and/or comparatively small primordia in relation to the size of the floral apex. Commonly occurs in polystemonous androecia (e.g. *Actinidia*).

Lateral: directed towards the sides (i.e. on the same radius of actinomorphic flower, neither closer to nor further away from the floral centre).

Leading stamen primordium: the first emerging (and/or larger) secondary primordium on a ring primordium.

Plastochron: the time span between the emergences of two successive organ primordia on the floral apex.

Proximal: relatively close to the base (not to be confused with basal).

Ring primordium: a ring-like meristematic mound, giving rise to numerous individual secondary primordia.

Secondary primordium: a primordium arising on a ring-primordium and development either directly into an individual floral organ or undergoing secondary proliferation by division.

Spiral initiation of organs in whorled flowers: the insertion of organs follows that of a spiral phyllotaxis, whereas the phyllotaxis in mature flowers is distinctly whorled (as a result of growth processes and shifted organ positions during floral development). In core eudicots, this process is common in the calyx, but less common in whorls closer to the floral centre.

Spiral phyllotaxis (also in mature flowers): a series of organs separated by equal plastochrons and divergence angles between successive organs approaching 137.5° (i.e. a Fibonacci spiral). Intermediate forms of organ classes are commonly presented (e.g. the prophylls and perianth organs in *Camellia* L., see Tsou, 1998).

Ventrifixed anther: the anther attachment is positioned on the ventral side of the anther with connective tissue joining the thecae both distally and proximally of the point of attachment.

Whorled phyllotaxis: a set of organs emerging simultaneously or in a rapid spiral, with comparatively long plastochrons separating a given whorl from neighbouring whorls; organs within the whorl are equidistant, but the divergence angle between the last organ of the preceding whorl and the first organ of the successive whorl are different from within the respective whorls (i.e. the plastochrons between successive primordia in the whorl are exceedingly short (approaching zero), whereas plastochrons separating the whorl from surrounding whorls are distinct; and in e.g. a trimerous perianth with alternating whorls, the within-whorl divergence angles are *c*. 120°, whereas the divergence angle between the third tepal in the first whorl and the first tepal in the successive whorl is *c*. 180°). Intermediate forms of organ classes are uncommon.

RESULTS

The androecial primordia and androecial organs are referred to as ‘stamens’ regardless of the functional sex of the investigated flowers. The androecial organs in functionally female specimens of Actinidiaceae are largely identical to the stamens of functionally male and bisexual flowers (the main difference is sterile pollen in functionally female specimens; Soejarto, 1969; van Heel, 1987; Löfstrand & Schönenberger, 2015).

ACTINIDIA ARGUTA (ACTINIDIACEAE)

The investigated floral buds are functionally female with a pentamerous, hexamerous or rarely heptamerous perianth. Each flower is preceded by two, almost oppositely, arranged bracts, in the axils of which axillary buds are formed (Fig. 1A, B). No prophylls are formed and the next organ to develop is the first sepal that emerges at a divergence angle of *c.* 130° relative to the youngest bract (Fig. 1A, B). Both clockwise and anticlockwise spiral sequences are common (Fig. 1A–I). The second and third sepal, respectively, emerge with divergence angles of *c*. 135–140° from the previous sepal in buds with a future pentamerous perianth (Fig. 1C, E). The divergence angle between the third and the fourth sepal is *c*. 145° and between the fourth and the fifth sepal *c*. 140° (Fig. 1C, E). In flowers with a hexamerous perianth, the divergence angles between the first and second sepals and second and third sepals, respectively, are *c*. 120° (Fig. 1D). The divergence angle between the third and fourth sepals is *c*. 180° and the divergence angles between the fourth and fifth sepals and fifth and sixth sepals are, respectively, *c*. 120° (Fig. 1D, E). In some hexamerous flowers, a pair of sepals emerges in the position that would be occupied by the fifth sepal in a pentamerous flower (Fig. 1G). Plastochrons between sepals are relatively long, resulting in large size differences among sepals during early developmental stages (Fig. 1B–E). Sepals have a broad base and the shape changes from semi-circular in early developmental stages (Fig. 1B–D) to broadly ovate in later stages. They are bent towards the floral centre, covering the younger floral organs (Fig. 1F). Sepal aestivation is quincuncial in pentamerous flowers and imbricate with other patterns in hexamerous flowers. The exact sequence of sepal development and, equally, aestivation pattern could not be established in the

heptamerous flower. At anthesis, calyx phyllotaxis is more or less distinctly whorled and the neighbouring sepals are arranged equidistantly from each other.

Petals emerge as distinct organs in alternisepalous positions on the floral apex (Fig. 1D–H). The plastochron between the last sepal and the first petal is close to those between sepals (estimated based on relative organ size; Fig. 1E, F). The divergence angle between the last sepal and the first petal is *c.* 115° in flowers with a pentamerous perianth (emerging between the third and first sepal; Fig. 1E). The divergence angle between successive petals is *c.* 135–145° (narrower in hexamerous flowers; Fig. 1G–I). In the hexamerous flowers where paired petals occupy the position that would house solely the fifth petal in a pentamerous flower (Fig. 1G, I). Similarly to the sequence of sepal development, the sequence of petal emergence on the floral apex is difficult to interpret in the heptamerous flower (Fig. 1F). Plastochrons between successive petals are somewhat shorter than between successive sepals, resulting in more equally sized petals, but a spiral sequence of primordium emergence can be observed (Fig. 1E–I). The floral apex is slightly dome-shaped and unevenly pentagonal (or hexagonal, rarely heptagonal) after the initiation of the petals (Fig. 1G–I). Petals have a broad base (although narrower than the sepal bases in the youngest stages) and the shape changes from ovate in early developmental stages (Fig. 1H, I) to broadly ovate with obtuse or retuse apices in later stages. They are bent towards the floral centre, covering the younger floral organs (Fig. 1G–I). Petal aestivation is the same as the sepal aestivation. At anthesis, corolla phyllotaxis is more or less distinctly whorled and the neighbouring petals are arranged equidistantly from each other.

The androecium development starts with an indistinct ring primordium with leading stamen primordia emerging in alternipetalous positions shortly after the early differentiation of the petals (Fig. 1G). The plastochrons between the leading stamen primordia are exceedingly short (as compared to the plastochrons between perianth organs), thus the leading stamen primordia emerge almost simultaneously on the ring primordium (Fig. 1F, G). Successive secondary stamen primordia emerge in a lateral sequence to the leading primordia, soon filling the spaces between leading primordia and forming a whorl-like arrangement (whorl-like arrangements on a ring primordium are henceforth referred to as ‘whorl’; Fig. 1H–J). The plastochrons between successive secondary stamen primordia are short, but the older primordia are in more alternipetalous positions and younger in more antepetalous positions (based on size differences; Fig. 1G–I). Some of the stamen primordia (apparently never the leading primordia) secondarily proliferate laterally (Fig. 1J, K). The proliferation of stamen primordia continues until the onset of gynoecium formation (increasingly convex floral apex, clearly separated from the androecium), at which point size differences between stamen primordia are difficult to discern (Fig. 1I). The final number of stamen primordia varies among individual flowers, but is most commonly 40–60 (Figs. 1J, 2A, B). As the stamen primordia start to enlarge and differentiate, approximately every other young stamen is pushed towards the floral centre and every other towards the periphery (the result is visible as two more or less regular whorls of stamens in an apical view; Fig. 1L). Stamen arrangement becomes increasingly irregular and the anthers are tightly packed as the flower approaches anthesis (Fig. 2A–C). The filament bases, however, remain in one (more or less) regular whorl (not shown). The fully differentiated anthers are extrorse-latrorse, basifixed, sagittate, dithecate and tetrasporangiate (Fig. 2B, C). The anthers invert from their extrorse–latrorse orientation to an introrse–latrorse orientation at the onset of anthesis (Fig. 2C).

The *c.* 15–30 carpel primordia emerge simultaneously in a whorl just to the inside (towards the floral centre) of the androecium (Fig. 1J, K). The carpels form a syncarpous ovary (Figs. 1L; 2A–C). The remaining, central floral apex is not involved in carpel formation and remains undifferentiated (Fig. 1L). When the carpels begin to close, the distal part of the gynoecium often becomes flattened (compressed), with the carpels appearing to be arranged in two parallel rows (Fig. 2A). The remaining, slit-like opening of the syncarpous ovary is closed by postgenital fusion (Fig. 2B,C). The styles are free for almost their entire length (Fig. 2B, C).

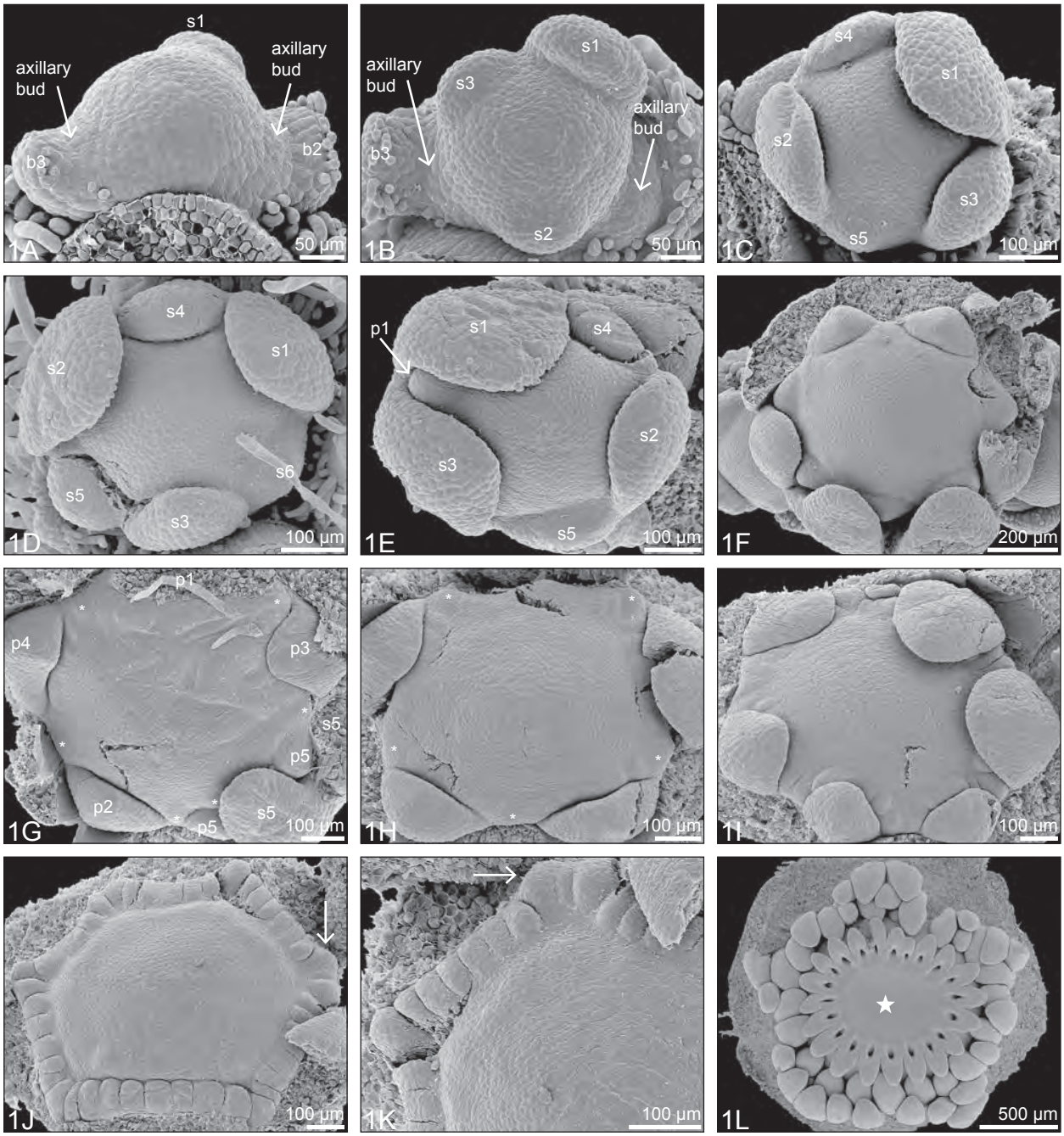

Fig. 1. *Actinidia arguta* floral development. Abbreviations used: b = bract; p = petal; s = sepal; asterisk (*) = leading stamen primordium; star (★) = remaining, undifferentiated floral apex; numbers after letters indicate the ontogenetic, spiral sequence of organ initiation. A, bracts and first sepal primordium; arrows indicate axially floral buds. B, bracts and first three sepal primordia (future hexamerous perianth); arrows indicate axillary meristems of bracts. C, five sepal primordia (pentamerous perianth) and axillary floral bud. D, six sepal primordia (note the three peripheral and three central sepals). E, emerging petal primordium in pentamerous flower bud. F, early petal differentiation on heptamerous floral bud. G–I, petal differentiation; stamen primordia emerging in a lateral sequence to the leading primordia and early androecium differentiation; note the alternipetalous, leading stamen primordia. J, K, laterally proliferating stamen primordia and emerging carpels. L, anther displacement and early gynoecium differentiation; note the undifferentiated central floral apex.

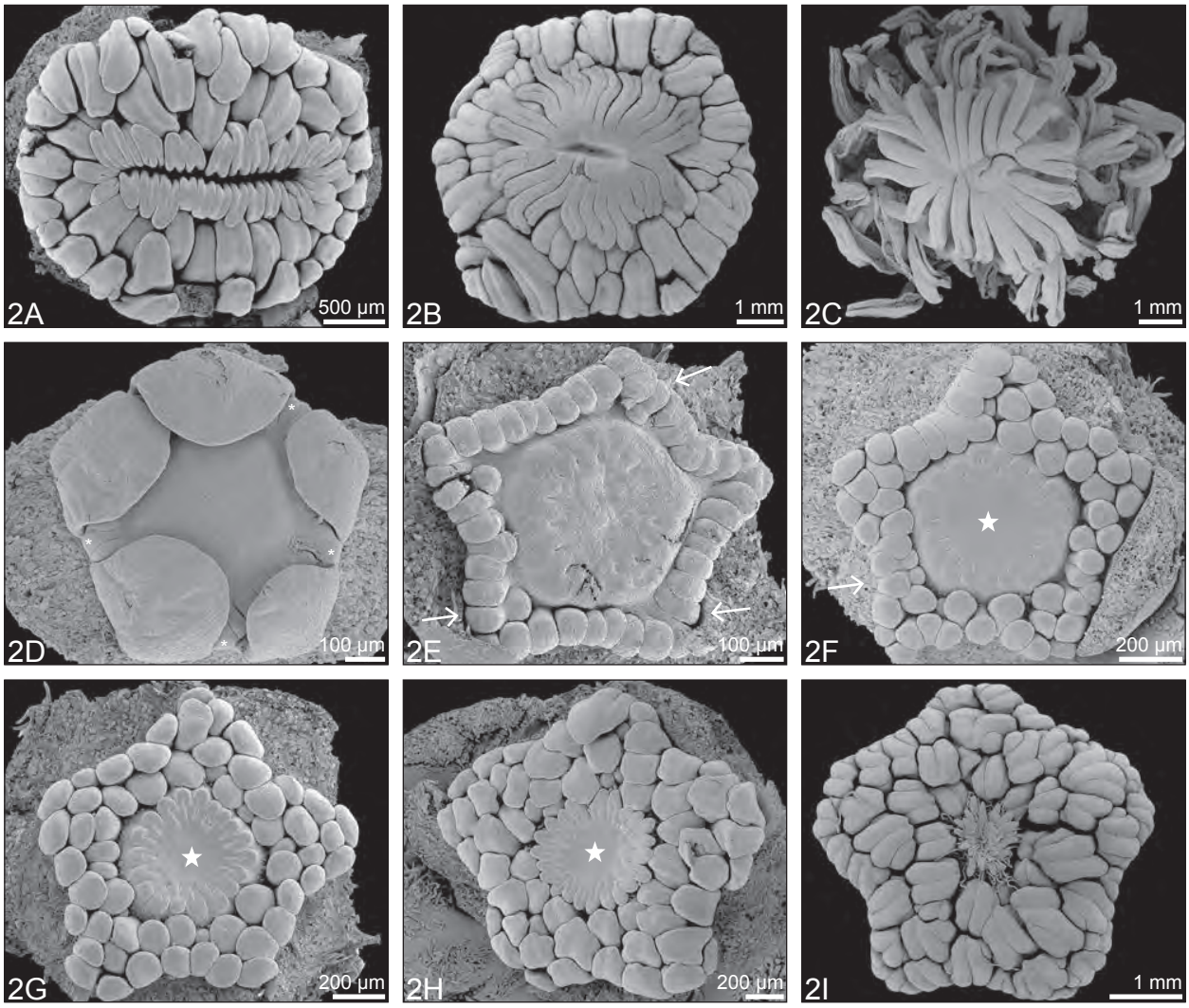

Fig. 2. *Actinidia arguta* and *A. callosa* flower development. asterisk (*) = leading stamen primordium; star (★) = remaining, undifferentiated floral apex. A–C , *A. arguta.* A, closing carpels and androecium differentiation; note the parallel carpels. B, fully formed, pre-anthetic androecium and gynoecium. C, anthetic androecium and gynoecium; note the inverted anthers. D–I, *A. callosa*. D–F, early androecium differentiation. D, note the alternipetalous, leading stamen primordia. E, F, arrows indicate centripetally proliferating stamen primordia; note the remaining, undifferentiated floral apex. G, all androecial organs formed, early anther differentiation; note the remaining, undifferentiated floral apex. H, carpel closure; note the remaining, undifferentiated floral apex. I, androecium and gynoecium shortly before anthesis.

ACTINIDIA CALLOSA (ACTINIDIACEAE)

The investigated floral buds are functionally male. Floral development and organisation in *Actinidia callosa* (Fig. 2D–I) are similar to that of *A. arguta* (Figs. 1, 2A–C) with the following differences: the perianth is pentamerous in all investigated flower buds (Fig. 2D–I). Stamen primordia secondarily proliferate centripetally after the initial whorl of organs has formed (Fig. 2D–F). After all stamen primordia are formed, the stamens appear to be arranged in two to three indistinct whorls, as seen in an apical view (Fig. 2F, G). The final number of stamens is 60–70 and the fully formed anthers are almost exclusively extrorse in pre-anthetic stages (Fig. 2I). Gynoecium development stops shortly after the closure of the carpel margins (Fig. 2I; functionally male). The distal part of the gynoecium becomes less pronouncedly flattened (Fig. 2I) as in *A. arguta* and the styles become almost completely concealed by the anthers in later stages of floral development (Fig. 2I).

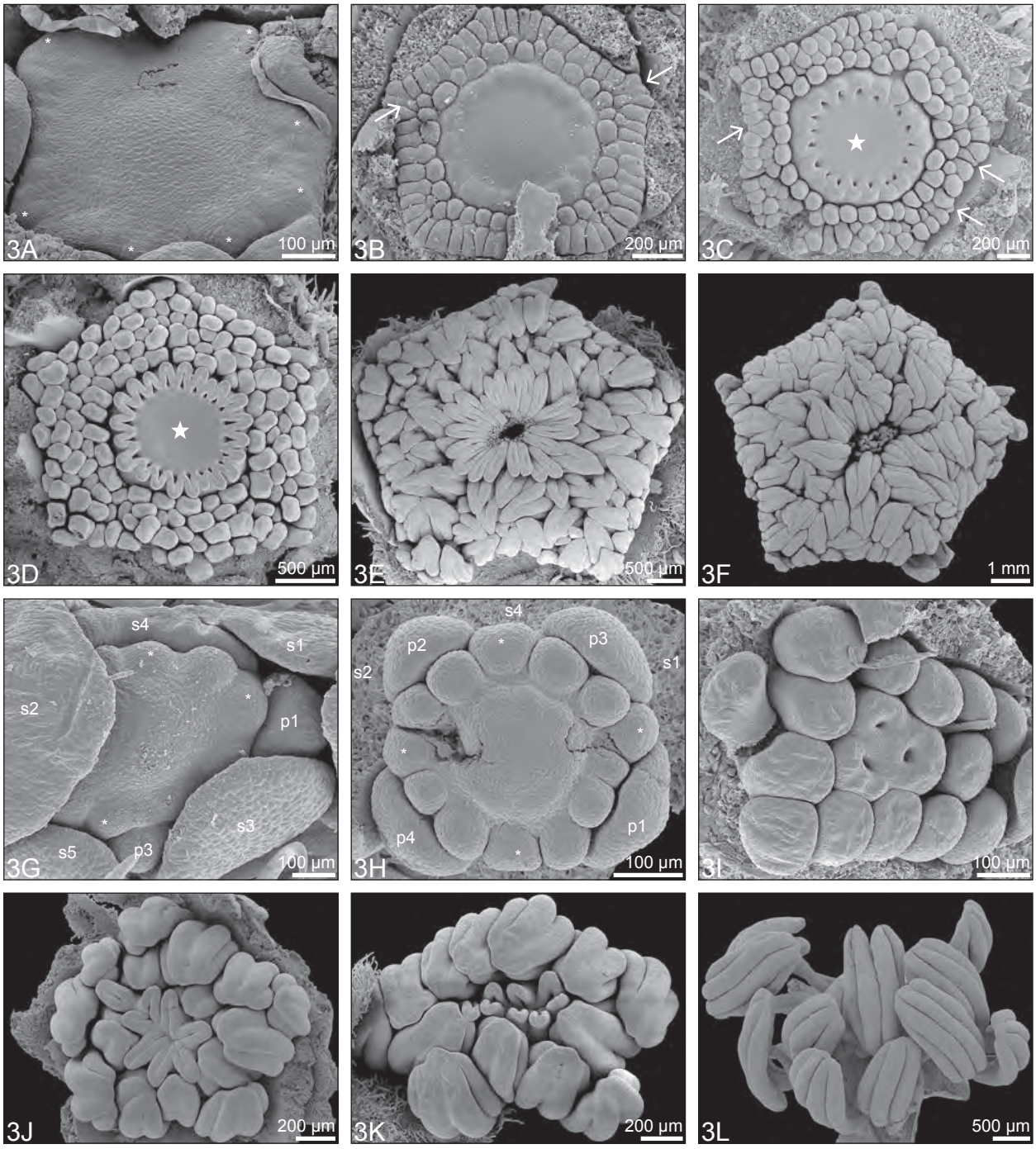

Fig. 3. *Actinidia chinensis* and *A. kolomikta* flower development. Abbreviations used: p = petal; s = sepal; asterisk (*) = leading stamen primordium; star (★) = remaining, undifferentiated floral apex. A–F, *A. chinensis.* A, emerging stamen primordia; note the alternipetalous, leading stamen primordia. B, early androecium proliferation and emerging carpels, arrows indicate centrifugally and laterally proliferating primordia. C, continued centripetal and lateral proliferation of stamen primordia (centrifugal proliferation indicated by arrows) and early gynoecium differentiation; note the remaining, undifferentiated floral apex. D, all stamens formed, early anther differentiation; note the remaining, undifferentiated floral apex. E, anthers differentiated (note variably extrorse, introrse and latrorse orientation) and carpel closure. F, androecium and gynoecium shortly before anthesis. G–L, *A. kolomikta*. G, early petal differentiation and emerging stamen primordia. H, all stamen primordia formed, onset of carpel emergence. I, early stamen differentiation and early gynoecium differentiation (note the displacement of the androecial organs and the flattened nature of the floral bud). J, carpels closure. K, L, androecium shortly before anthesis.

ACTINIDIA CHINENSIS (ACTINIDIACEAE)

The investigated floral buds are parthenocarpic (potentially asexual). Floral development and organisation in *Actinidia chinensis* (Fig. 3A–F) are similar to that of *A. arguta* (Figs. 1, 2A–C) with the following differences: the initial stamen primordia emerge almost simultaneously on an indistinct ring primordium and display minor size differences (i.e. no obvious leading stamen primordia; Fig. 3A). During slightly older stages (Fig. 3B), there is a distinct central whorl of semi-globose secondary primordia, most of which will give rise to individual stamens. Occasionally, these primordia proliferate laterally (Fig. 3B), giving rise to two individual stamens. Peripherally to the central whorl of secondary stamen primordia, there is a whorl of radially elongate secondary primordia. During further development, these elongate primordia mainly proliferate laterally and centripetally (occasionally also centrifugally), each giving rise to two to four individual stamens (Fig. 3B, C). The final stamen number is most commonly 150–170 arranged in three to four indistinct whorls (Fig. 3D); the central-most anthers are introrse–latrorse during later floral development (Fig. 3E, F) and occasionally do not invert at the onset of anthesis. The anthers are mainly ventrifixed (similar in appearance to those of *A. kolomikta*, Fig. 3L), but the stamens in the central-most whorl are dorsifixed. The multicarpellate gynoecium is less pronouncedly flattened (Fig. 3E, F) than in *A. arguta* and the styles are almost completely concealed by the anthers in the latest stages before anthesis (Fig. 3F).

ACTINIDIA KOLOMIKTA (ACTINIDIACEAE)

The investigated floral buds are functionally male. The floral development and organisation in *Actinidia kolomikta* (Fig. 3G–L) is similar to that of *A. arguta* (Figs. 1, 2A–C) with the following differences: the perianth is tetramerous or pentamerous (Fig. 3G–L). In tetramerous flowers, the second sepal primordium emerges nearly opposite of the first primordium (c. 170°), the third at a *c*. 90° angle to the second and the fourth nearly opposite the third; the first petal primordium in tetramerous flowers appears at a divergence angle of *c*. 150–160° from the fourth sepal, thereafter the sequence is similar to that of the sepals (Fig. 3H). Flower buds are often asymmetrically (flattened) tetragonal or pentagonal (as a result of uneven divergence angles and size differences among sepals; Fig. 3G, I, K). Four or five leading stamen primordia emerge in alternipetalous positions on the indistinct ring primordium, thereafter two or three secondary primordia emerge in antepetalous positions (Fig. 3H). There is no secondary proliferation of stamen primordia (Fig. 3G, H). The final stamen number is 12–20 (Fig. 3I–L) and the anthers are ventrifixed (Fig. 3L). The gynoecium consists of 3–8 carpels (Fig. 3I–L). The gynoecium stops developing shortly after the closure of the carpel margins (Fig. 3K) and the styles are almost completely concealed by the anthers in later stages of floral development (Fig. 3K, L).

CLEMATOCLETHRA SCANDENS (ACTINIDIACEAE)

Each flower is borne in the axil of a subtending bract and similarly to *Actinidia* there are no prophylls (not shown). The perianth is pentamerous and the respective whorl has a quincuncial aestivation (not shown). The sepals are united in the basalmost region (*c*. 5%) and petals are completely free from each other (not shown). Early floral development cannot be assessed with the investigated material, but during later developmental stages, the androecium consists of five alternipetalous stamens in a more peripheral position and five antepetalous stamens in a more central position (Fig. 4A, B). The fully differentiated anthers are extrorse, ventrifixed, sagittate, dithecate and tetrasporangiate (Fig. 4). The anthers invert from an extrorse orientation to an introrse orientation at the onset of anthesis (Fig. 4C, D). The gynoecium is entirely syncarpous (only minute lobes remain on the stigma; Fig. 4A-C).

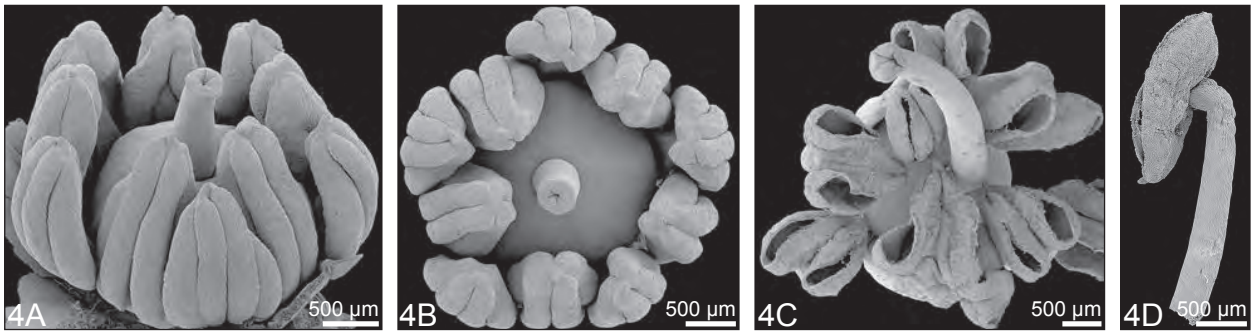

Fig. 4. *Clematoclethra scandens* androecium organisation and anther inversion. A, B, androecium and gynoecium shortly before anthesis. C, anthetic androecium and gynoecium. D, inverted anther.

SAURAUIA MONTANA (ACTINIDIACEAE)

Each flower is borne in the axil of a subtending bract (not shown). No prophylls precede the flower bud. The first sepal emerges at a divergence angle of *c.* 140° to the bract (Fig. 5A). Both clockwise and anticlockwise spiral sequences are common (Fig. 5A–D). The second sepal emerges almost opposite to the first one (c. 170°) and the third sepal emerges with a divergence angle of *c*. 135–140° from the second sepal (Fig. 5A, B). The divergence angle between the third and the fourth sepals is *c*. 145° and that between the fourth and the fifth sepal *c*. 155° (Fig. 5B). Plastochrons between sepals are relatively long, resulting in large size differences among sepals during early developmental stages (Fig. 5B). Sepals have a broad base and the shape changes from semi-circular in early developmental stages (Fig. 5B, C) to broadly ovate with obtuse apices in later stages. They are bent towards the floral centre, covering the younger floral organs (Fig. 5B, C). Sepal aestivation is quincuncial. At anthesis, calyx phyllotaxis is more or less distinctly whorled and the neighbouring sepals are arranged equidistantly from each other.

Petals emerge as distinct organs in alternisepalous positions on the floral apex (Fig. 5C–F). The plastochron between the last sepal and the first petal is longer than between sepals (based on relative organ sizes; Fig. 5C). Plastochrons between petals are exceedingly short and all five organs appear to emerge almost simultaneously (Fig. 5C–D). The floral apex is more or less flat and evenly pentagonal after the initiation of the petals (Fig. 5C–F). Petals have a broad base and change from semi-circular in early developmental stages to broadly ovate with obtuse apices in later stages. They are bent towards the floral centre, covering the younger floral organs. Petal aestivation is quincuncial. At anthesis, the petals are united with each other in their basalmost region (less than 5% of their total length; most likely as a result of late growth in the floral base).

Androecium development starts with a shallow ring primordium with five leading stamen primordia emerging almost simultaneously in alternipetalous position (Fig. 5D). Successive secondary stamen primordia emerge in a lateral sequence from the leading stamen primordia towards the antepetalous radii, soon forming a whorl of stamen primordia (Fig. 5D–G). By the developmental stage when the syncarpous ovary is clearly visible on the floral apex, size differences between the leading and successive stamen primordia are difficult to discern (Fig. 5G). There is no secondary proliferation of stamen primordia (Fig. 5D–G). The total number of stamen primordia is almost invariably 35 (Fig. 5G, H). As the stamen primordia start to enlarge and differentiate, approximately every other young stamen is pushed towards the floral centre and every other towards the periphery (the result is visible as two more or less regular whorls of stamens in an apical view; Fig. 5G–I). Anthers arrangement attains an increasingly irregular pattern as the flower approaches anthesis (Fig. 5I–K), but the filament bases remain in one whorl (Fig. 5L). The fully differentiated anthers are extrorse, basifixed, deeply sagittate, dithecate and tetrasporangiate (Fig. 5K, L). The anthers invert from their extrorse orientation to an introrse orientation at the onset of anthesis (Fig. 5K, L).

At anthesis, the stamen filaments are united with each other in their basalmost region (less than 5% of their total length) and are also united with basalmost part of the petals (most likely as a result of late growth in the floral base; Fig. 5L).

The five or six carpels emerge simultaneously on the slightly raised floral apex (Fig. 5D–G). The carpels form a syncarpous ovary, which is slightly compressed when the carpel margins begin to close (Figs. 5G–J). The ovary shape changes to a rounded/globose shape and the long, free styles are formed as the flower matures (Fig. 5J, K). The free styles bent to one side until anthesis (Fig. 5K), at which point they attain a radial symmetry.

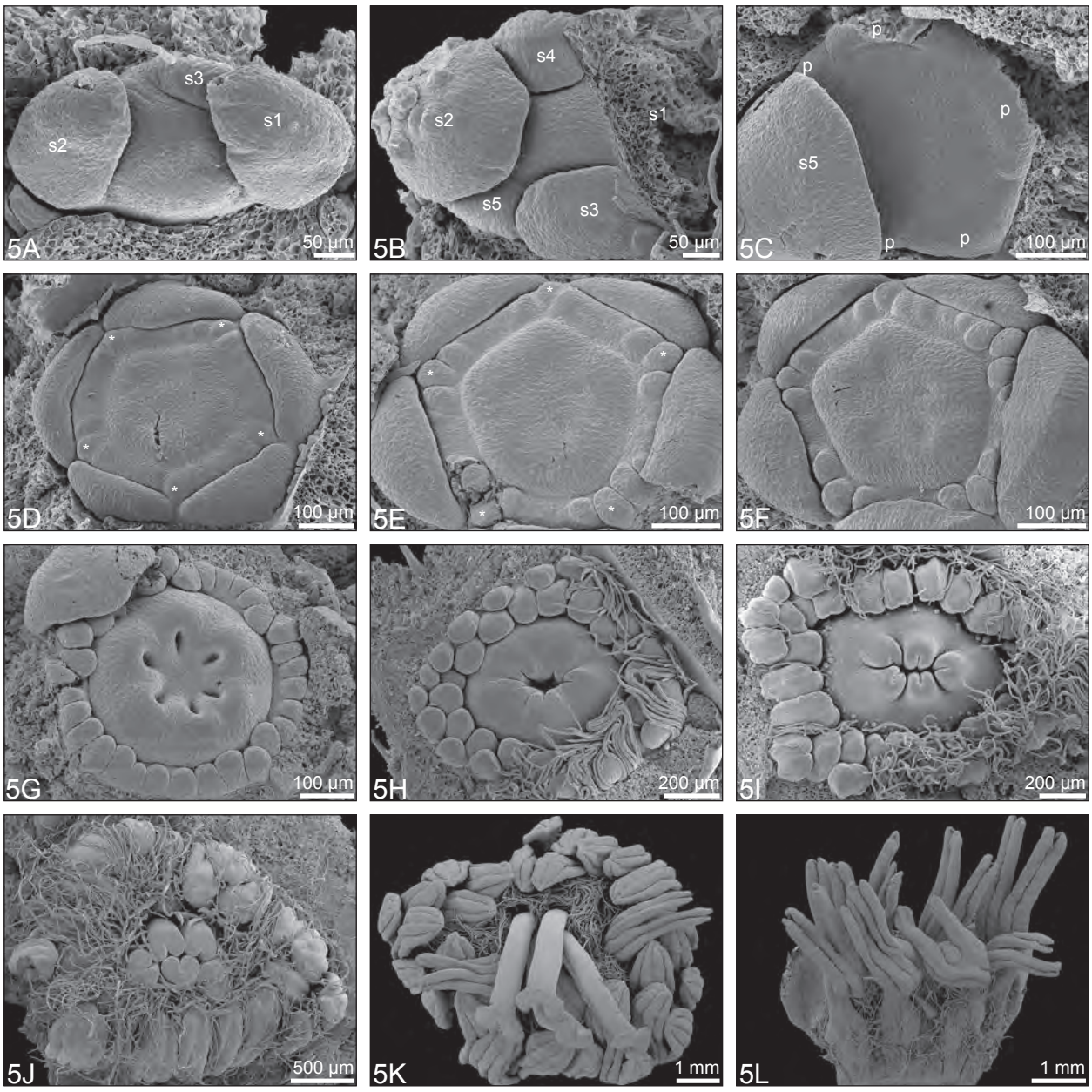

Fig. 5. *Saurauia montana* flower development. Abbreviations used: p = petal; s = sepal; asterisk (*) = leading stamen primordium. A, B, sepal primordia and young sepals. C, fifth sepal and all petal primordia formed. D–F, stamen primordia formed and initiation of gynoecium formation. G, early androecium and gynoecium differentiation. H–J, continued androecium and gynoecium differentiation; note the hairs originating on the floral base and filament bases. K, androecium and gynoecium shortly before anthesis. L, inverted anthers and proximally united filaments.

SAURAUIA OLDHAMII (ACTINIDIACEAE)

The floral development and organisation in *Saurauia oldhamii* (Fig. 6A–I) is similar to that of *S. montana* (Fig. 5) with the following differences: initially, the indistinct androecial ring primordium (Fig. 6A) gives rise to a whorl of 12-13 primordia, each of which develops into a single stamen (Fig. 6B,C). A secondary whorl of primordia develops by centrifugal proliferation, with primordia emerging on the peripheral rim of the ring primordium (Fig. 6B, C). Most secondary primordia of this peripheral whorl develop into individual stamens but a small proportion further proliferates laterally and gives rise to two stamens per primordium (Fig. 6E). In total, 40–50 stamens are formed and due to shifts in anther position caused by their increase in size, stamen arrangement appears irregular at later developmental stages, but the filaments remain in two indistinct whorls (Fig. 6F, I). Anthers are ventrifixed and shallowly sagittate (Fig. 6I). Anthers partially invert relatively early during further development of the flower (Fig. 6E, F). The inversion of the anthers is completed upon anthesis (Fig. 6I). At anthesis, the stamen filaments are united with each other (both whorls) and with the corolla tube for *c*. 5% of their total length (Fig. 6H). The corolla is clearly sympetalous (*c*. 60% of its total length at anthesis; Fig. 6G). The gynoecium consists of 3–5 (most commonly three) carpels (Fig. 6A–F, I); and the styles are united for *c*. 60% of their length in anthetic flowers (Fig. 6I)

SAURAUIA PITTIERI (ACTINIDIACEAE)

The floral development and organisation in *Saurauia pittieri* (Fig. 6J–L) is essentially identical to that of *S. montana* (Fig. 5). Note that the available material was limited for this species; often only one floral bud was available for each key developmental stage. A couple minor differences were observed: the fully formed flowers have 40–50 stamens arranged in two to three indistinct whorls in an apical view, but as in *S. montana,* the filaments are arranged in a single whorl towards the floral base; Fig. 6K, L).

SAURAUIA SUBSPINOSA (ACTINIDIACEAE)

The floral development and organisation in *Saurauia subspinosa* (Fig. 7) is similar to that of *S. montana* and *S. oldhamii* (Figs. 5, 6A-I) with the following differences: the perianth is pentamerous to hexamerous (Fig. 7A–F); when six sepals are present, a pair of sepals emerge in the position that would be occupied by one sepal in pentamerous flowers (Fig. 7B). The plastochrons between petals are longer than in other studies *Saurauia* species (but shorter than in *Actinidia* species; Fig. 7A) and a spiral sequence can be observed. When six petals are present, two are, similarly to the sepals, paired (Fig. 7A). Androecium development is very similar to that of *S. oldhamii* with a central whorl of secondary primordia that give rise to individual stamens and a secondary, peripheral whorl of primordia on the ring primordium, which further proliferates laterally (Fig. 7D, E). In fully formed flowers, the androecium consists of 50–55 stamens (most commonly 50 in pentamerous flowers) appearing to be arranged in four or more whorls in an apical view, but the filament remain in two indistinct whorls (Fig. 7F). Anthers are ventrifixed and only shallowly sagittate (Fig. 7F–H). Anthers partially invert relatively early during further development of the flower (Fig. 7F, G). Anther inversion is completed upon anthesis (Fig. 7H). At anthesis, the petals are united for up to *c*. 40% of their total length (Fig. 7I). The gynoecium consists of five or six carpels (Fig. 7D, F) and the styles are united for *c*. 40% of their length in anthetic flowers (Fig. 7H).

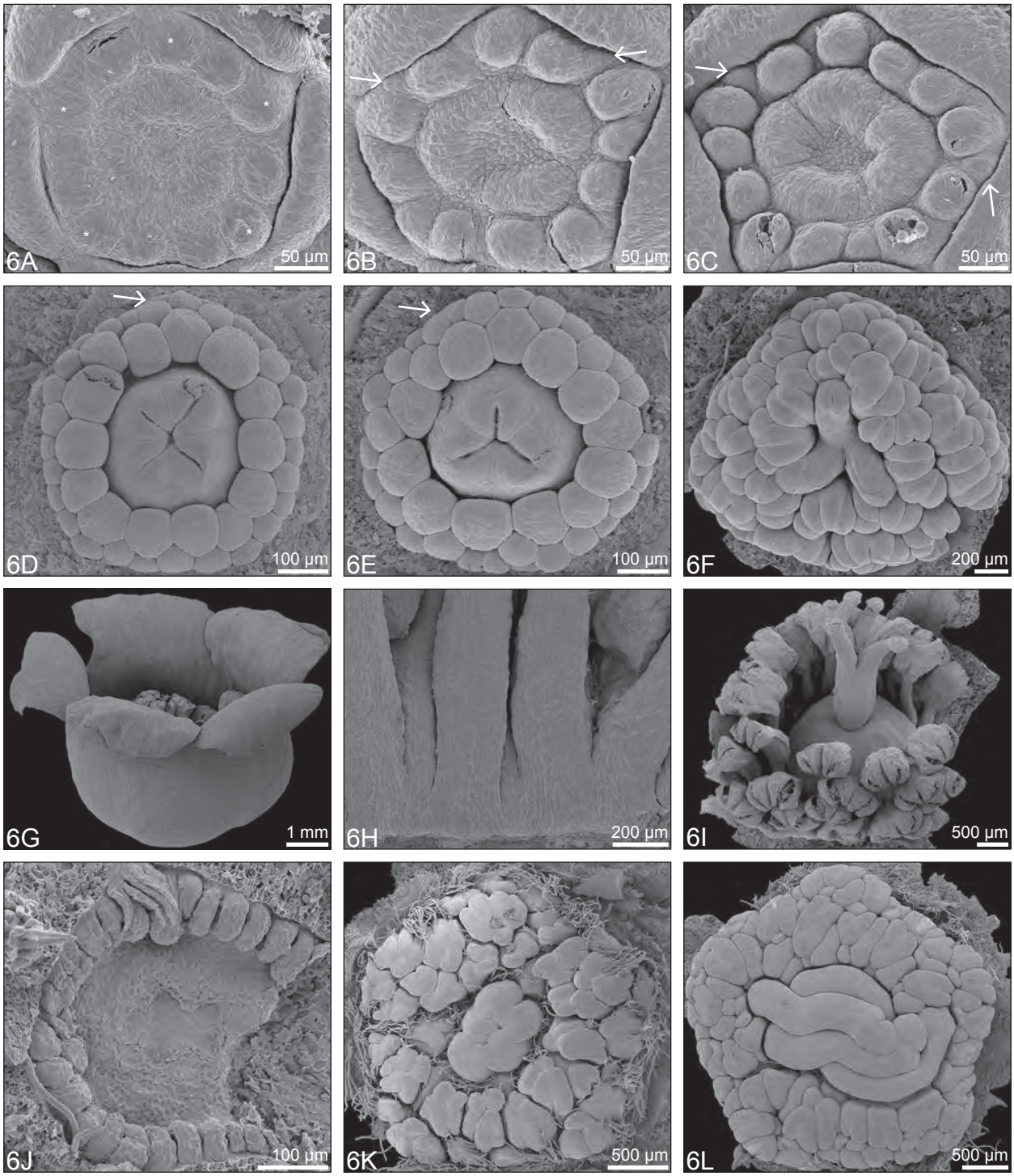

Fig. 6. *Saurauia oldhamii* and *S. pittieri* flower development. Asterisk (*) = leading stamen primordium A–I, *S. oldhamii*. A–D, early androecium and gynoecium differentiation; note the alternipetalous, leading stamen primordia, arrows indicate centrifugally proliferating stamen primordia. E, continued androecium proliferation and carpel closure, arrows indicate laterally proliferating stamen primordium. F, young floral bud with all organs formed; note the partially inverted anthers. G, petal union. H, filament union. I, anthetic androecium and gynoecium; note the completed anther inversion. J–L, *S. pittieri*. J, all stamen primordia formed and carpels emerging. K, androecium and gynoecium differentiation; note the carpel closure. L, fully differentiated androecium and gynoecium, shortly before anthesis.

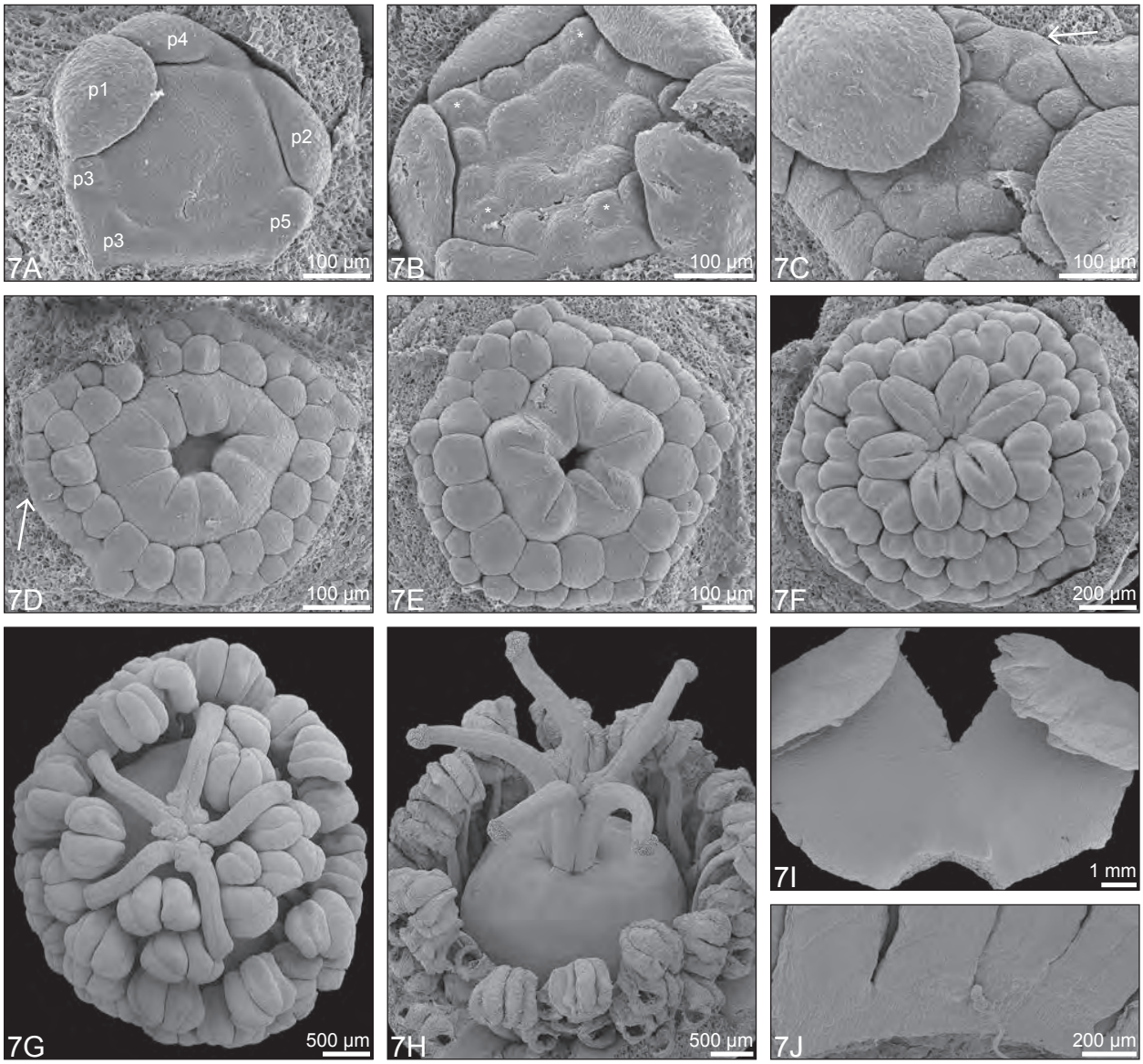

Fig. 7. *Saurauia subspinosa* flower development. Abbreviations used: p = petal; asterisk (*) = leading stamen primordium. A, young floral bud; note the paired petals in position three. B–D, early androecium and gynoecium differentiation. B, note the alternipetalous, leading stamen primordia. C, D, arrows indicate centrifugally proliferating stamen primordia. E, all stamen primordia formed and initiated carpel closure. F, all organs formed; note the partially inverted anthers and hexamerous gynoecium. G, androecium and gynoecium shortly before anthesis. H, anthetic androecium and gynoecium; note the finalised anther inversion. I, petal union (dorsal side). J, filaments union.

RORIDULA GORGONIAS (RORIDULACEAE)

Each flower is borne in the axil of a subtending bract and followed by two prophylls (Fig. 8A–C). The divergence angle between the bract and the first prophyll is *c*. 130° and the angle between the two prophylls is *c*. 150° (Fig. 8A–C). Both clockwise and anticlockwise spiral initiation patterns are common (Fig. 8A–E).

The divergence angle between the second prophyll and the first sepal, as well as between the first two sepals is *c*. 130° (Fig. 8A). The divergence angle between the second and third sepal is *c*. 140° (Fig. 8B, C), whereas the angle is larger (*c*. 150°) between the third and fourth sepal (Fig. 8B, C). The divergence angle between the fourth and fifth (last) sepals is *c*. 140° (Fig. 8C). Plastochrons between sepals are relatively long, resulting in large size differences among sepals during early developmental stages (Fig. 8B–E). Sepals have a broad base and the shape changes from semi-circular in the earliest developmental stages (Fig. 5B, C) to narrowly ovate to broadly lanceolate with acute to acuminate apices in later stages. They are slightly bent towards the floral centre and partially conceal the younger organs (Fig. 8D, E) in intermediate stages, whereas they closely envelop all younger organs in more mature stages. Sepal aestivation is quincuncial (Fig. 8D, E). At anthesis, calyx phyllotaxis is more or less distinctly whorled and the neighbouring sepals are arranged equidistantly from each other.

Petals emerge as distinct organs in alternisepalous positions on the floral apex in a spiral series continued from the sepals (Fig. 8C, D). The plastochron length between the last sepal and the first petal is similar to those between sepals (based on relative organ size; Fig. 8A–E). The divergence angle between the fifth sepal and the first petal is *c*. 130–140° (emerging between the third and first sepals; Fig. 8C). The divergence angle between successive petals is *c.* 130–140° (Fig. 8D). Plastochrons between petals are shorter than between sepals, resulting in more similarly sized organs (Fig. 8D, E). The floral apex is more or less flat and evenly pentagonal after the emergence of the petal primordia (Fig. 5C–F). Petals have a broad base (narrower than sepals) and are broadly ovate with obtuse apices in early developmental stages, changing to narrowly ovate to broadly lanceolate with acute apices in later stages. They are slightly bent towards the floral centre and partially conceal the younger organs (Fig. 8E) in intermediate stages, whereas they closely envelop all younger organs in more mature stages. Petals unite in the basalmost region close to anthesis (less than 5%, most likely as a result of late growth in the floral base). Petal aestivation is quincuncial. At anthesis, corolla phyllotaxis is more or less distinctly whorled and the neighbouring petals are arranged equidistantly from each other.

The five stamen primordia emerge almost simultaneously with the fifth petal (Fig. 8D). The plastochrons between the androecial organs are exceedingly short (as compared to the plastochrons between perianth organs; Fig. 8D). The fully differentiated anthers are extrorse–latrorse, subapically ventrifixed (between the thecae and the massive connective protrusion), deeply sagittate, dithecate and tetrasporangiate (Fig. 8F–J). The anthers invert from their extrorse to an introrse orientation close to anthesis, either from irritation by pollinators or autonomously (Fig. 8I, J). The filaments remain free from each other but are united with the short sympetalous zone of the corolla in the basalmost region (less than 5%, most likely as a result of late growth in the floral base) at anthesis.

The three carpels emerge simultaneously on the remaining floral apex (Fig. 8D, E). The carpel margins unite to form a fully syncarpous gynoecium (only minute lobes remain on the stigma; Figs. 8F–H). The ovary becomes narrowly ovoid as the flower matures and the stigma enlarges into a massive stylar head (Fig. 8G, H).

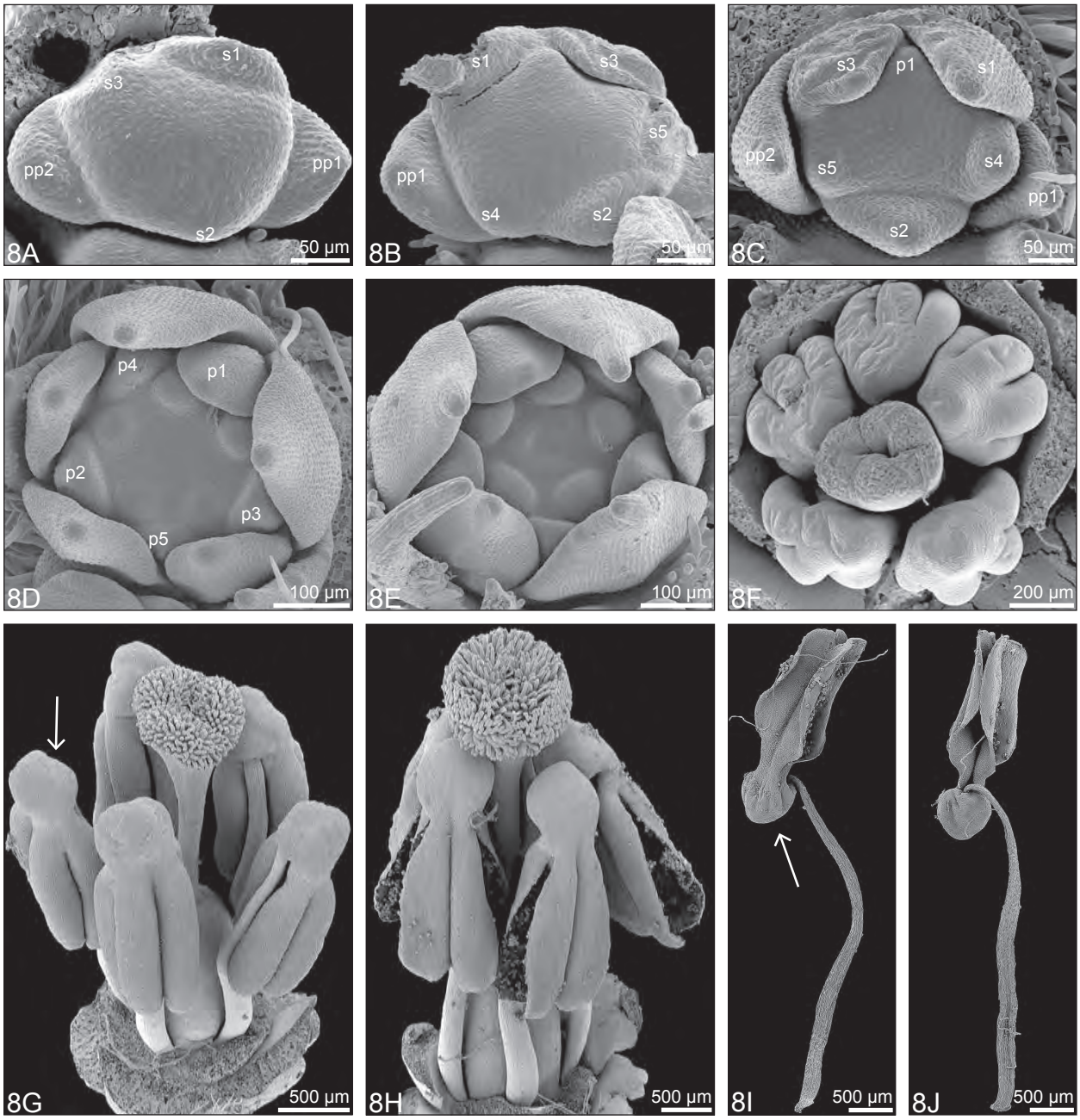

Fig. 8. *Roridula gorgonias* flower development. Abbreviations used: p = petal; pp = prophyll; s = sepal. A, early prophyll differentiation and emerging sepal primordia. B, all sepal primordia formed. C, early sepal differentiation and first petal primordium. D, early petal differentiation and emerging stamen primordia. E, emerging carpel primordia. F, carpel closure. G, fully differentiated androecium and gynoecium; the arrow indicates the apical protrusion on the anther connective. H, androecium and gynoecium shortly before anthesis; note that the anthers dehisced during the critical point drying process. I, J, anthetic, inverted anthers; the arrow indicates the apical protrusion on the anther connective.

HELIAMPHORA NUTANS (SARRACENIACEAE)

Each flower is borne in the axil of a very broadly attached subtending bract followed by two prophylls (Fig. 9A, B, F). The young floral apex is elliptic in outline and the first sepal emerges at a divergence angle of *c.* 130° from the second prophyll (Fig. 9B). Both clockwise and anticlockwise spiral sequences are common (Fig. 9B–F). The second sepal emerges shortly after the first with a divergence angle of *c*. 130° (Fig. 9B). The sepals attain a nearly opposite position before the first petal primordium is initiated on the floral apex (Fig. 9C). Sepals have a conspicuously broad base and the shape changes from semi-circular in earliest developmental stages (Fig. 9B, C) to ovate or broadly lanceolate with acute to acuminate apices in later stages (Fig. 9L). The two sepals become more similar in size after the androecial organ primordia have become visible on the floral apex. They are tightly imbricate (one outside the other) and bent towards the floral centre, covering the younger floral organs (Fig. 9C). At anthesis, calyx phyllotaxis is more or less distinctly whorled and the neighbouring sepals are arranged equidistantly from each other.

Petals emerge as distinct organs in alternisepalous positions on the floral apex (Fig. 9C–E). The plastochron between the last sepal and the first petal is longer than between sepals (Fig. 9C). The divergence angle between the last sepal and the first petal is *c.* 110° (as a resulted of the shifted positions of the sepals; Fig. 9C). The divergence angle between first and second petal is *c.* 170°, i.e. they are positioned approximately opposite to each other (Fig. 9D–G). The plastochron between the petals is shorter than between sepals, resulting in more similarly sized organs (Fig. 9C–G). When a third petal is present, the divergence angle from the second petal is *c*. 130° and the plastochron is longer than between the first two petals (based on relative size; Fig. 9D). The two petals remain similar to each other in size throughout flower development (when a third petal is present it is markedly smaller). The floral apex is flattened to slightly concave and unevenly rounded–tetragonal to rounded–pentagonal after the emergence of the petals (Fig. 9D). Petals have a broad base (narrower than the sepals) and are semi-circular to broadly ovate with retuse apices in young developmental stages and ovate to broadly lanceolate with acute apices in mature flowers (Fig. 9D–G, M). They are tightly imbricate (one outside the other, the peripheral two enclosing the third in trimerous corollas) and bent towards the floral centre, covering the younger floral organs (Fig. 9C). At anthesis, corolla phyllotaxis is more or less distinctly whorled and the neighbouring petals are arranged equidistantly from each other (in dimerous corollas).

Four to five leading stamen primordia emerge almost simultaneously on a shallow ring primordium after the early differentiation of the petals (Fig. 9D). Thereafter, secondary stamen primordia emerge in a lateral sequence to the leading primordia, soon forming a whorl of stamens (Fig. 9E–G). There is no secondary proliferation of the stamen primordia (Fig. 9E–H). The plastochrons between the stamen primordia are short, but youngest primordia are positioned between the leading primordia (Fig. 9E, F). At later developmental stages, size differences between stamen primordia are difficult to discern (Fig. 9G). There is typically a total of 12–20 primordia (Fig. 9E–J). As the stamen primordia start to enlarge and differentiate, approximately every other young stamen is pushed towards the floral centre and every other towards the periphery (the result is visible as two more or less regular whorls of stamens in an apical view; Fig. 9H–J). The filament bases, however, remain in a single whorl (Fig. 9J). The fully differentiated anthers are introrse, dorsifixed, shallowly sagittate, dithecate and tetrasporangiate (Fig. 9I, J). The anthers invert from their introrse orientation to an extrorse orientation at the onset of anthesis (Fig. 9K).

The three carpels emerge simultaneously on the remaining floral apex (Fig. 9F, G). The carpel margins unite to form a fully syncarpous gynoecium (only minute lobes remain on the stigma; Figs. 9H–J). The ovary becomes narrowly ovoid to conical as the flower matures.

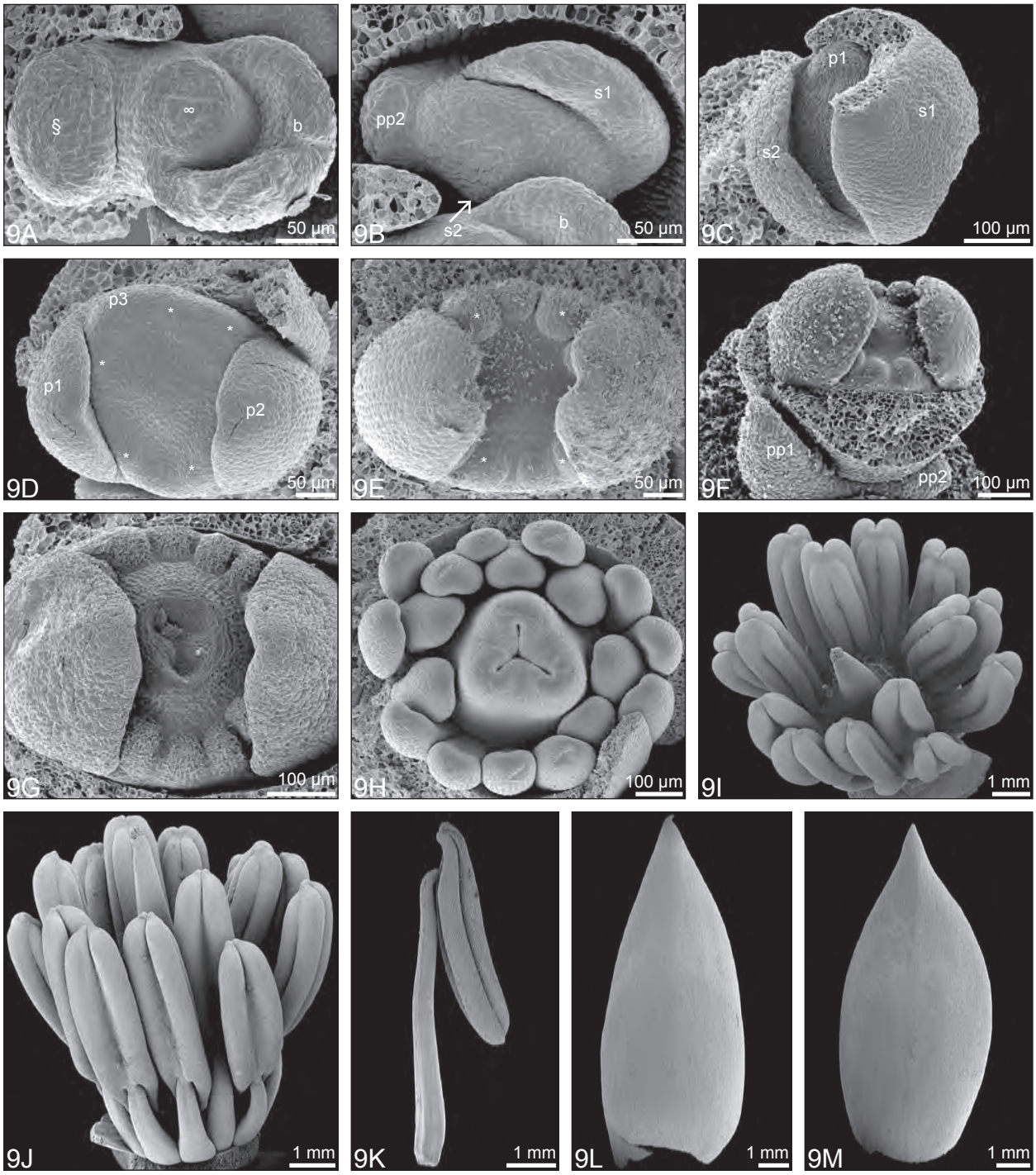

Fig. 9. *Heliamphora nutans* flower development. Abbreviations used: b = bract; p = petal; pp = prophyll; s = sepal; asterisk (*) = leading stamen primordium; *signum sectiōnis* (§) = undifferentiated floral apex; infinity symbol (∞) = inflorescence tip. A, inflorescence tip, bracts and undifferentiated floral apex. B, second prophyll and sepal primordia. C, early sepal differentiation and petal primordia. D, third petal primordium; note the emerging (leading) stamen primordia. E, all stamen primordia formed; note the size difference between leading and successive stamen primordia and retuse petal apices. F, young bud and prophylls. G, emerging carpel primordia. H, androecium differentiation and carpel closure. I, J, androecium and gynoecium shortly before anthesis. K, inverted anther. L, sepal; note that the sepal is broader than it seems, due to curvature (tightly imbricate). M, petal.

DARLINGTONIA CALIFORNICA (SARRACENIACEAE)

The solitary flower is borne in the axil of a subtending bract, followed by several spirally inserted prophylls on the scape (not shown). The perianth is pentamerous and the aestivation is quincuncial in the calyx and in the corolla. All sepals and petals are completely free from each other. Early floral development could not be assessed with the available material, but the androecium invariably consists of 15 stamens apparently arranged in a single whorl (Fig. 10A). In transverse sections, the stamens appear to be arranged in five weakly defined antepetalous groups of three (Fig. 10B, C). The filament bases in the respective groups are united to each other and the petals for *c*. 5% of their length (most likely as a result of late growth in the floral base; Fig. 10B). The vascular traces in the respective antepetalous groups merge into one massive trace before joining the central vascular bundle together with the petal vasculature (Fig. 10C). The anthers are basifixed, dithecate and tetrasporangiate; anthers have a larger, extrorse theca and a smaller, introrse theca (Fig. 10A). The anthers invert at the onset of anthesis so that the larger (previously extrorse) thecae attain an introrse orientation, whereas the smaller thecae (previously introrse) attain an extrorse orientation (not shown).

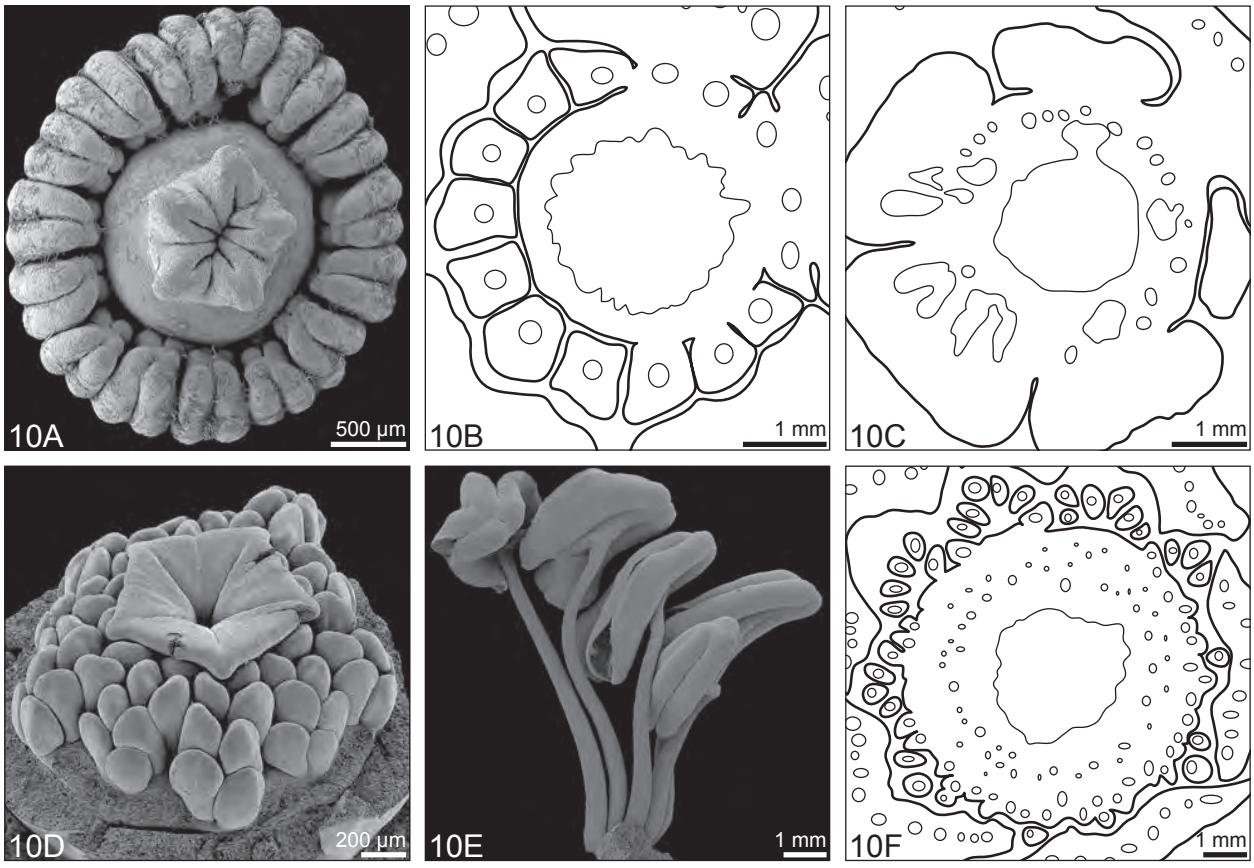

Fig. 10. *Darlingtonia californica* and *Sarracenia leucophylla* androecium organisation and vascular pattern. A–C, *D. californica*. A, all stamens differentiated and carpel closure. B, antepetalous groups of stamens. C, androecium and corolla vascular traces in floral base. D–F, *S. leucophylla*. D, all stamens differentiated and carpel closure; note the alternipetalous and antepetalous groupings. E, partial groups of stamens from mature flower. F, vaguely defined groups of stamens at floral base.

SARRACENIA LEUCOPHYLLA (SARRACENIACEAE)

The solitary flower is borne in the axil of a subtending bract, followed by three spirally inserted prophylls situated just proximal of the sepals. The perianth is pentamerous, sepals and petals are completely free from each other, and aestivation is quincuncial in both whorls. Early floral development could not be assessed with the investigated material, but the androecium consists of five alternipetalous (more peripheral) and five antepetalous (more central) groups of stamens (Fig. 10D–F). Each group is composed of 6–10 stamens (a total of 60–100 stamens per flower) that are arranged in two more or less regular, radial rows. During later developmental stages, the proximal parts of the stamen filaments are arranged in ten loosely defined groups Fig. 10E, F). Anthers are dorsifixed, dithecate and tetrasporangiate (Fig. 10E). The anthers invert from an introrse orientation to an extrorse orientation at the onset of anthesis (not shown).

DISCUSSION

Previous floral developmental studies in the sarracenioid clade have been performed for a few species of *Actinidia* (Actinidiaceae, van Heel, 1975; Brundell, 1987; Caris, 2013), for *Saurauia subspinosa* (Actinidiaceae; Brown, 1935) and for *Sarracenia purpurea* L. (Sarraceniaceae; Shreve, 1906). The two latter studies were, however, limited by the lack of modern technical equipment and to some extent also by the lack of suitable floral material. The focus on *Actinidia* in earlier ontogenetic work may be explained by its economic importance both as a crop and ornamental plant as well as by the fact that plants produce many flowers. Sarraceniaceae are equally common in botanical gardens, but especially *Darlingtonia* and *Heliamphora* are often difficult to cultivate and rarely flower in greenhouse conditions (personal observation, SL). *Darlingtonia* and *Sarracenia* (Sarraceniaceae) additionally form their single flowers on their rhizome tips during the previous vegetative season, making collection of the young developmental stages particularly difficult (personal observation, SL). *Clematoclethra*, *Saurauia* and *Roridula* are more rarely cultivated, which reduces the availability of material to the scientific community (personal observation, SL). While the floral developments of members of Actinidiaceae (*Saurauia subpinosa* and several *Actinidia* species) and Sarraceniaceae (*Sarracenia purpurea*) have, at least in part been investigated before (Shreve, 1906; Brundell, 1975; van Heel, 1987; Caris, 2013), this is the first study to comparatively investigate the floral developmental patterns (but see Caris, 2013) in the three families. Part of the reason may lie in the fact that before the rise of molecular phylogenetics, the families were not considered closely related (e.g. Cronquist, 1981).

PERIANTH

At anthesis, the perianth is generally organised in a pentamerous sepal whorl and a pentamerous petal whorl in all members of the sarracenioid clade (Figs. 1–10; Löfstrand & Schönenberger, 2015). However, perianth merism is rather variable in *Actinidia* and *Saurauia* (mostly ranging from tetramery to hexamery; Hunter, 1966; Soejarto, 1980; Cuong, Soejarto & Li, 2007; Li *et al*., 2007). Perianth merism may vary even within inflorescences (e.g. *Actinidia arguta*; Fig. 1C–J) and some *Saurauia* species rarely display pentamerous flowers (Soejarto, 1980). A sixth petal may also occur in *Sarracenia*, as a result of paired organs (Löfstrand & Schönenberger, 2015), similar to those of *Actinidia arguta* (Fig. 1) and *Saurauia subspinosa* (Fig. 7). The perianth of *Heliamphora* has traditionally been considered to consist of one tetramerous to hexamerous petaloid whorl of sepals or tepals (e.g. Macfarlane, 1908; Berry *et al*., 2005), but Löfstrand & Schönenberger (2015) hypothesised a two-whorled dimerous to trimerous perianth in *Heliamphora*. This hypothesis was based on organ shape and position, as well as on vascular patterns in the floral base and histological features of the perianth organs (see below for further discussion).

The perianth has a similar developmental pattern in all sarracenioid genera (except for the corolla of *Saurauia*): a clockwise or anticlockwise spiral initiation sequence with distinct

plastochrons between successive organs (indicated by size differences between successive young organs; Fig. 1–9). A spiral initiation with long plastochrons between the successive sepals in the calyx is common in eudicots, but less common between the successive petals in the corolla (Endress, 2011). The divergence angles between successive perianth organs approaches a Fibonacci spiral, albeit with adjusted divergence angles as a result of growth processes and displacements of previously emerging organs (Hofmeister's rule; Figs. 1–9). As it is the case in almost all eudicot flowers, the arrangement of the perianth organs in fully developed (anthetic) flowers – irrespective of their distinctly spiral initiation – conforms to a whorled phyllotaxis also in the sarracenioid clade (Figs. 1–9; Endress, 1994, 2010, 2011). Any early differences in organ size and in divergence angles among the organs of a given whorl are levelled out during later floral development leading to a typical eudicot perianth with a whorl of sepals alternating with a whorl of petals. Solely, the quincuncial aestivation (in pentamerous flowers) still reflects the initial spiral phyllotaxis of the perianth organs (Endress, 1994, 2010, 2011).

The ontogenetic spiral of the sepals is easily distinguishable in *Actinidia*, *Saurauia*, *Roridula* and *Heliamphora* (Figs. 1, 5, 8, 9; Caris, 2013). A partial exception is the prolonged plastochron between the third and fourth sepal in some hexamerous flowers of *Actinidia chinensis* (Caris, 2013), which leads to a calyx that appears to consist of two trimerous whorls (similar to Fig. 1D). Spirally inserted sepals in variably clockwise or anticlockwise sequences appear to be the most common state in Ericales (Tsou, 1998; Schönenberger & Grenhagen, 2005; Zhang *et al*., 2007, 2008; Caris, 2013; Zhang & Schönenberger, 2014). A plastochron of similar length to those between sepals separates the last sepal and the first petal in *Actinidia* and *Roridula* (Fig. 1E–I, 3G, H; 8C, D), thus there is no clear chronological interruption between the respective perianth whorls. A similar pattern has been described for Fouquieriaceae (Schönenberger and Grenhagen 2005), Pentaphylacaceae (Zhang *et al*., 2007, 2008; Zhang & Schönenberger, 2014) and Theaceae p.p. (Erbar, 1986; Tsou, 1998). In *Heliamphora* and *Saurauia* the plastochron separating the sepal whorl from the petal whorl appears to be longer than between the sepals (Figs. 5C, 7A, 9C, D). However, the ontogenetic spiral of the sepals is continued in the petals in *Heliamphora* (Fig. 9A–D) and to some extent in *Saurauia subspinosa* (Fig. 7A).

Early patterns of corolla development are more variable in the sarracenioid clade: in *Actinidia*, *Roridula* and *Heliamphora* a distinctly spiral insertion can be observed, even though the plastochrons are shorter than between sepals (Figs. 1E–I, 8C–E, 9C, D). In *Saurauia*, neither distinct plastochrons nor any conspicuous size differences are present among young petals (Figs. 5C–F, 6A–C, 7A–C). Another important difference between *Saurauia* and the former three genera is that the petal primordia in *Saurauia* are wide from the start, enclosing the entire floral centre as they emerge, whereas they are much narrower during early developmental stages in *Actinidia*, *Roridula* and *Heliamphora* (Figs. 1–9). The whorled initiation and broad attachment of the petals of *Saurauia* are linked with the distinct sympetaly that is present in this genus (see also below).

Whorled corollas with spiral petal insertion and comparatively long plastochrons between the consecutive organs are, while uncommon in eudicots, are present in various groups in Ericales (Fouquieriaceae, Pentaphylacaceae and Theaceae; Erbar, 1986; Tsou, 1998; Schönenberger & Grenhagen 2005; Zhang *et al*., 2007, 2008; Endress, 2011; Caris, 2013; Zhang & Schönenberger, 2014). Ericalean taxa with spiral perianth phyllotaxis also at anthesis are *Camellia*, *Polyspora* Sweet ex G.Don and *Pyrenaria* Blume (Theaceae), where the divergence angles between perianth organs (including prophylls) follow a more or less strict Fibonacci spiral throughout the flower development, the differentiation between prophylls, sepaloid organs and petaloid organs take place comparatively late in the flower development and intermediate forms between the organ classes are generally present (Sugiyama, 1991; Tsou, 1998). An interesting difference between the spiral phyllotaxis in e.g. *Camellia* and the spirally inserted, but later whorled perianths in other Ericales is the shape of the floral apex during early development: in the spiral flowers, the floral apex is raised (distinctly dome shaped) and strictly following the Fibonacci

spiral in the emergence of perianth organs (Sugiama, 1991; Tsou, 1998). In the ericalean taxa with spirally initiated, but later whorled corollas (Fouquieriaceae, Pentaphylacaceae and Theaceae p.p.), the floral apex remains relatively flat during early floral development and the organ positions are often distorted from their insertion point when the petals differentiate (hence, they become equidistant to each other; Figs. 1–3, 8, 9; Erbar, 1986; Tsou, 1998; Schönenberger & Grenhagen 2005; Zhang *et al*., 2007, 2008; Caris, 2013; Zhang & Schönenberger, 2014).

Perianth organisation in Heliamphora

As mentioned above, the perianth of *Heliamphora* is generally referred to as a single whorl of petaloid sepals or tepals (Macfarlane, 1908; Berry *et al.*, 2005). However, there are conspicuous differences in overall shape and insertion on the floral base as well as differences in anatomy and histology among perianth organs (Löfstrand & Schönenberger 2015). Here, we demonstrate that the peripheral two and the central two to three perianth organs show clear differences during early floral development (Fig. 9B–D). The sepals and petals are separated by their positions on the floral apex, by their shapes and by a comparatively long plastochron between the second sepal and the first petal (Fig. 9). Among the sarracenioid taxa investigated here, the plastochron between last sepal and first petal represents by far the longest chronological gap between two successive perianth organs while still retaining a spiral pattern of insertion (Figs. 1, 5, 7–9). In *Heliamphora*, the two-whorled nature of the perianth, in connection with the four or five leading stamen primordia on the androecial ring primordium, indicates an ancestral tetramerous to pentamerous perianth organisation (Fig. 9B–D). The reduction of perianth merism in *Heliamphora* is further indicated by the sister group relationship between *Heliamphora* and *Sarracenia* (*Darlingtonia* sister to the *Heliamphora–Sarracenia* clade; Ellison *et al*., 2012); both *Darlingtonia* and *Sarracenia* (and, equally, Roridulaceae and most Actinidiaceae) have pentamerous perianths (Löfstrand & Schönenberger, 2015). The floral architecture of *Heliamphora* differs substantially from those of *Darlingtonia* and *Sarracenia*, probably due to the different pollination systems; *Heliamphora* has open flowers, whereas *Darlingtonia* and *Sarracenia* have complex, highly synorganised perianths and gynoecia to facilitate pollination (Löfstrand & Schönenberger, 2015); and *Heliamphora*, unlike *Darlingtonia* and *Sarracenia*, is buzz pollinated (Mandossian, 1965; Renner, 1989; Ne'eman, Ne'eman & Ellison, 2006; Meindl & Mesler, 2011).

ANDROECIUM

Androecial development and organisation is diverse in the sarracenioid clade. Particularly interesting is the development of polystemonous androecia in all genera except *Clematoclethra* and *Roridula* (Kubitzki, 2004; Löfstrand & Schönenberger, 2015). *Roridula* is haplostemonous and *Clematoclethra* has ten stamens (organisation as of yet undetermined; Figs. 4, 8). So far, development has neither been studied in *Clematoclethra* nor in *Darlingtonia* and only partially in *Sarracenia* (Shreve, 1906).

Based on our study and earlier developmental investigations (Brundell, 1975; van Heel, 1987; Caris, 2013), it becomes clear that, in the sarracenioid clade, polystemony is achieved through developmental processes that are similar at the onset of androecium development but may diverge during later stages of floral development. In all polystemonous species that have been studied in detail so far, the androecial development starts with a more or less distinct ring primordium, on which leading stamen primordia emerge in alternipetalous positions on flat to marginally convex floral apex (unclear in *Sarracenia*; Shreve, 1906). These leading primordia are followed by a lateral succession of additional primordia, forming a continuous whorl with the youngest primordia in antepetalous positions (Figs. 1–3, 5–9; van Heel, 1987; Caris, 2013). In *Actinidia*, the ring primordium is rather distinct and there are only minor size differences between the leading and successive stamen primordia (Fig. 1–3; van Heel, 1987; Caris, 2013). In *Saurauia* and *Heliamphora*, the ring primordium is shallow and the leading stamen primordia are

markedly larger than the successive stamen primordia (Figs. 5–7, 9). Brown's (1935) interpretation of the androecial development in *Saurauia subspinosa* differs from our findings; Brown (1935) interpreted the androecium as basically two-whorled, with centrifugal proliferation of the primordia in the more central (antepetalous) whorl. Contrastingly, our study of *S. subspinosa* indicates an essentially identical early androecium development to that of *Actinidia*: a ring primordium and leading stamens in alternipetalous positions (Figs. 1–3, 5), also demonstrated by van Heel, (1975). The androecial development in *Sarracenia* has, so far, not been completely established (Fig 10C–F; Shreve, 1906). While the later stages in the androecial development points to a two-whorled, fascicled androecium (Fig. 10D, Macfarlane, 1908; Mellichamp, 2009; Löfstrand & Schönenberger, 2015), Shreve's (1906) study of *S. purpurea* indicates a one-whorled androecium with ten groups of primordia (two groups of stamen primordia emerging in every alternipetalous position), which would fit the general developmental pattern for other sarracenioid taxa described here and elsewhere. Mellichamp (2009) states 10–17 groups of stamens in mature flowers of *Sarracenia*, but does not mention the position of the stamen groups; neither the material investigated here (Fig. 10D–F), nor that of Löfstrand & Schönenberger (2015) identifies more than ten groups of stamens.

After the initial whorl of secondary stamen primordia has formed on the ring primordium, no further androecial proliferation occurs in *Actinidia kolomikta*, *Actinidia melanandra* Franch., *Actinidia polygama* Franch. & Sav., *Saurauia montana*, *Saurauia pittieri* and *Heliamphora nutans* (Figs. 3G, H, 5F–H, 6J, 9E–H, van Heel, 1987). A slightly more complicated pattern is found in *Actinidia arguta*, where some of the primordia proliferate by lateral division (Fig. 1I, J). In *Actinidia callosa*, the primordia proliferate centripetally (Figs. 2D–F). A similar pattern is found in *Saurauia oldhamii* and *S. subspinosa*, where primordia proliferate mainly centrifugally, but to a smaller extent also laterally (Figs. 6A–F, 7A–F). In *Actinidia chinensis*, the first radial proliferation of secondary primordia is already underway when they emerge on the ring primordium (Fig. 3A–C). After the division, the primordia in the more central whorl are dominant and the primordia in a peripheral whorl are less differentiated and continuously proliferating, indicating that the proliferation pattern was centrifugal (Fig. 3A–C; van Heel, 1987; Caris, 2013). Subsequent proliferation of stamen primordia in *A. chinensis* is centripetal and lateral (Fig. 3B–D; van Heel, 1987; Caris, 2013). As the flower buds mature (all sarracenioids), the stamens and anthers attain an increasingly disorganised organisation ('stuffing') or changed, yet organised organisation ('stacking'), common in all eudicots, particularly those with high stamen numbers (Figs. 1–10; Endress, 1994).

In Actinidiaceae and Roridulaceae, the anthers are ventrifixed or basifixed and extrorse–latrorse, similar to the anthers in Clethraceae and Ericaceae (Figs. 1–7; Kubitzki, 2004; Caris, 2013; Löfstrand & Schönenberger, 2015). In Sarraceniaceae, the anthers are dorsifixed or basifixed and introrse (*Heliamphora* and *Sarracenia*; Fig. 9J, K, 10D), whereas *Darlingtonia* has basifixed, simultaneously introrse and extrorse anthers (Fig. 10A; Löfstrand & Schönenberger, 2015). The ventrifixed or basifixed, sagittate and morphologically extrorse anthers (i.e. the anther attachment is positioned on the ventral side of the anther) of Actinidiaceae, Roridulaceae, Clethraceae and Ericaceae are closely linked to anther inversion from extrorse to introrse anthers occurring during floral development (Schönenberger *et al*., 2012; Löfstrand & Schönenberger, 2015; Chapter IV).

Anther inversion

All sarracenioid taxa have anthers that invert during the later stages of androecium development or at the onset of anthesis (Löfstrand & Schönenberger, 2015). In Ericales, anther inversion is restricted to the sarracenioid families, Ericaceae and Clethraceae and has been suggested to be a potential synapomorphy for core Ericales with a secondary loss of the trait in Cyrillaceae (Schönenberger *et al*., 2012). Actinidiaceae, Roridulaceae, Clethraceae and the early diverging lineages of Ericaceae (subfamilies Arbutoideae, Enkianthoideae and Monotropoideae)

all have anthers that invert comparatively late from an extrorse anther orientation to an introrse anther orientation, 'Late anther inversion type A' (Matthews & Knox, 1926; Leins, 1964; Hermann & Palser, 2000; Schönenberger *et al*., 2012; Caris, 2013; Löfstrand & Schönenberger, 2015). In Sarraceniaceae, *Heliamphora* and *Sarracenia,* contrastingly, have anthers that invert in the opposite direction at anthesis, from introrse to extrorse, 'Late anther inversion type B' (Figs. 9J, K, 10E; Schönenberger *et al*., 2012; Löfstrand & Schönenberger, 2015), whereas *Darlingtonia* has a form of anther inversion where the anthers invert at anthesis, but the direction cannot be assigned, due to the peculiar anther shape, 'Late anther inversion type C' (Fig. 10A; Löfstrand & Schönenberger, 2015). The unique anther morphology and main direction of dehiscence may play an important role in the pollination of *Darlingtonia* (Meindl & Mesler, 2011). Crown group Ericaceae (subfamilies Cassiopoideae, Ericoideae, Harrimanelloideae, Styphelioideae and Vaccinioideae) are all characterised by anthers that invert from an extrorse orientation to an introrse orientation, but occurring early during floral development, referred to as 'Early anther inversion' (Matthews & Knox, 1926; Leins, 1964; Hermann & Palser, 2000; Schönenberger, 2012; Caris, 2013). Some variations are present within the main types of late anther inversion: anthers in the flowers of *Saurauia oldhamii* and *S. subspinosa* partially invert clearly before anthesis (Figs. 6F, I, 7F–H; Löfstrand & Schönenberger, 2015). In *Roridula*, anther inversion can be triggered by irritation/puncturing of the enlarged connective apex (during pollination), upon which the anthers rapidly invert in a catapult-like mode, whereby a cloud of pollen is expelled (Anderson, Midgley & Stewart, 2003). In Cassiopoideae (Ericaceae) anther inversion is initiated early in the floral development, but only completed at the beginning of anthesis (Palser, 1951).

GYNOECIUM

The gynoecium of all sarracenioid taxa is characterised by three or more carpels emerging simultaneously in a single whorl on the floral apex, shortly after the emergence of the first stamen primordia (Figs. 1–3, 5–9; van Heel, 1987; Caris, 2013). The carpels are in alternipetalous position in pentamerous-isomerous taxa (Figs. 5–7, 10; Löfstrand & Schönenberger, 2015). The gynoecia are trimerous in *Roridula* and *Heliamphora*, pentamerous in *Clematoclethra*, *Darlingtonia* and *Sarracenia*, generally tri- or pentamerous in *Saurauia* and generally multicarpellate in *Actinidia* (Figs. 1–3, 5–10; Hunter, 1966; Soejarto, 1980; Macfarlane, 1908; Li *et al*., 2007; Löfstrand & Schönenberger, 2015). For a review on the occurrence, development, organisation and architectural constraints of multicarpellate-syncarpous gynoecia in angiosperms, see Endress (2014). *Clematoclethra*, *Roridula* and *Heliamphora* have fully syncarpous styles (only short stigmatic lobes are present), whereas all other sarracenioid taxa have partly or fully free styles (Figs. 2–10; Löfstrand & Schönenberger, 2015). *Roridula* differs from the other members of the sarracenioid clade by having a semi-inferior ovary (Löfstrand & Schönenberger, 2015).

FLORAL DEVELOPMENT AND SYSTEMATICS

Taxonomic history

The taxonomic history of the sarracenioid families is complicated, especially concerning the suprafamiliar affiliations and the taxonomic ranks of Actinidiaceae and Roridulaceae. In earlier classifications, much weight has been put on superficial floral structure, absence or presence of a carnivorous habit and vegetative structures to determine their systematic position (e.g. Netolitzky, 1926; Melchior, 1964; Cronquist, 1981). In Cronquist's (1981) classification, Actinidiaceae were placed in Theales (Dilleniidae), Roridulaceae in Rosales (Rosidae) and Sarraceniaceae in Nepenthales (Dilleniidae). Members of Actinidiaceae have been treated as part of Dilleniaceae, Clethraceae or Actinidiaceae (e.g. Lechner, 1915; Hunter, 1966; Cronquist, 1968). Alternatively, *Saurauia* was treated as the monogeneric family Saurauiaceae, and thus Actinidiaceae was restricted to contain only *Actinidia* and *Clematoclethra* (e.g. Takhtajan,

1966). Roridulaceae have previously been placed in Byblidaceae, Clethraceae, Droseraceae and Ochnaceae, or treated as the distinct family Roridulaceae (e.g. Engler, 1907; Hallier, 1912; Netolitzky, 1926; Cronquist, 1981; Takhtajan; 1987). Sarraceniaceae have generally been undisputed as a distinct family (e.g. Uphof, 1936). *Heliamphora* was, however, at one point raised to the monogeneric family Heliamphoraceae (Chrtek, Slavíková & Studnička, 1992), but treated as a part of Sarraceniaceae by most subsequent authors (e.g. Bayer, Hufford & Soltis, 1996; Neyland & Merchant, 2006). For a comprehensive account on earlier taxonomic ranks and systematic placements of the sarracenioid genera and families, see e.g. Dickison, (1972), Vani-Hardev, (1972), DeBuhr (1975), Schmid (1978) and Conran (1996).

Since the rise of molecular phylogenetics, the sarracenioid clade has been consistently recovered (Sarraceniaceae sister to a clade formed by Actinidiaceae and Roridulaceae; Schönenberger *et al*. 2005; Soltis *et al*., 2011; Magallón *et al*., 2015). The sister relationship between the sarracenioid clade and the ericoid clade (Clethraceae, Cyrillaceae and Ericaceae) is also well established (e.g. Schönenberger *et al*., 2005; Soltis *et al*., 2011). The phylogenetic relationships between core Ericales (comprised of the ericoid and sarracenioid clades) and other ericalean families is to this date not well established, but the respective studies by Soltis *et al*. (2011) and Magallón *et al*. (2015) both indicate the styracoid clade (Diapensiaceae, Styracaceae and Symplocaceae) as the sister group. Within Actinidiaceae, *Saurauia* is sister to a clade formed by *Clematoclethra* and *Actinidia* (Chapter IV). Furthermore, *Saurauia* contains an Asian–Oceanian clade and a Neotropical clade (Chapter IV). Within Sarraceniaceae, *Darlingtonia* is sister to a clade formed by *Heliamphora* and *Sarracenia* (Ellison *et al*., 2012).

General patterns of floral development in the sarracenioids

The patterns of floral development and organisation revealed in this and earlier developmental studies (Shreve, 1906; Brown, 1935; Brundell, 1975; van Heel, 1987; Caris, 2013) indicate some common patterns in the sarracenioid clade: the perianth is inserted in a clockwise or anticlockwise spiral pattern, with sepals markedly separated by plastochrons; the plastochron between the last sepal and the first petal is no longer than between successive sepals (except *Heliamphora* and *Saurauia*); petals emerge in a continued spiral (from the sepals) with comparatively long plastochrons between successive organs (except *Saurauia*); the plastochron between the petal primordia and the stamen primordia is, comparatively, extended; polystemonous taxa have an androecial ring primordium, typically with leading stamen primordia in alternipetalous positions (uncertain in *Clematoclethra, Darlingtonia* and *Sarracenia*); plastochrons between leading stamen primordia are exceedingly short (between most primary primordia in *Actinidia*); and carpel primordia emerge simultaneously on the floral apex, shortly after the first stamen primordia become clearly distinguishable.

One developmental character that among the sarracenioids is common in Actinidiaceae, but not the other families, is the commonly occurring irregular placement of the sixth and successive perianth organs in flowers with higher merism than five (Figs. 1, 3, 7). In many cases, the higher perianth merism is the result of doubling (‘dédoublement’) of organs (Figs. 1G, 7A, B; Endress, 1994), also present in one investigated flower of *Sarracenia purpurea* (Löfstrand & Schönenberger, 2015). It should, however, be noted that among the sarracenioids only *Actinidia* and *Saurauia* commonly have higher merism than pentamery (Figs. 1–10; Soejarto, 1980; Kubitzki, 2004; Li *et al*., 2007). *Saurauia* is the only genus among the sarracenioids that has a whorled corolla without discernible plastochrons between individual petals (a spiral pattern is hinted at in *S. subspinosa*; Figs. 1–3, 5–9). *Saurauia* (*S. oldhamii* and *S. subspinosa*; Figs. 6G, 7I) is additionally the only genus in the sarracenioid clade with distinct corolla tubes, suggesting that a whorled inception of the petals as well as their broad attachment are a prerequisite of a sympetalous corolla. All other ericalean species with a sympetalous corolla where the early floral development is known have a whorled corolla inception with exceedingly short plastochrons between the organs; see Caris (2013) for an overview.

Actinidiaceae also include the only taxa with established proliferation of stamen primordia beyond the initial whorl of primordia (although this is likely the case also in *Sarracenia*; Figs. 1–10; Shreve, 1906; van Heel, 1986; Caris, 2013). *Actinidia* is the only genus among the sarracenioids that has centripetal proliferation of stamen primordia (*A. callosa* and *A. chinensis*; Figs. 2D–F, 3A–D; Brundell, 1975; van Heel, 1987; Caris, 2013). Within *Saurauia*, the Asian species (*S. oldhamii* and *S. subspinosa*) have laterally and centrifugally proliferating stamen primordia, an often sympetalous corolla and a comparatively large degree of style union, whereas the Neotropical species (*S. montana* and *S. pittieri*) have no secondary proliferation of stamen primordia and largely distinct petals and free styles (Figs. 5–7; Hunter, 1966; Soejarto, 1980; Cuong *et al*., 2007; Li *et al*., 2007). Roridulaceae are the only haplostemonous members of the sarracenioids (Figs. 1–10). Sarraceniaceae contain the only sarracenioid taxa with apparently grouped stamens (*Darlingtonia* and *Sarracenia*, the developmental origin of the groups is unclear in both genera; Fig. 10; Macfarlane, 1908; Mellichamp, 2009; Löfstrand & Schönenberger, 2015).

The ancestral state of the androecia in the sarracenioid clade is reconstructed as one-whorled polystemonous (considering the ring-primordia in this clade to be a single whorl; Chapter IV). Theoretically, the ring primordium could consist of two merged whorls (from an evolutionary point of view; cf. Malvaceae; von Balthazar et al., 2004, 2006), but the leading stamens in alternipetalous positions paired with the lateral sequence of primordium emergence makes this scenario improbable (Figs. 1–3; 5–9; Caris, 2013). Hence, according to this reconstruction, the five stamens in *Roridula* and ten stamens in *Clematoclethra* are derived states within the clade (loss of polystemony). With the phylogenetic context and the reconstructed ancestral state in mind, it seems unlikely that *Clematoclethra* is truly diplostemonous as is often assumed (e.g. Gilg & Werdermann, 1925; Keller, Herendeen & Crane, 1996). Based on our present knowledge of patterns of early androecium development and phylogenetic relationships among sarracenioid taxa, the most likely interpretation of the androecium of *Clematoclethra* is that the ten stamens are initiated on a indistinct ring primordium in a single whorl and that the seemingly diplostemonous arrangement of the anthers is the result of space constraints and unequal growth processes during later floral development. According to Hofmeister's rule, a decamerous androecium paired with a pentamerous corolla would typically result in five alternipetalous and five antepetalous stamens (similar in appearance to a diplostemonous androecium; Hofmeister, 1868). Similarly, we hypothesise that the early androecium development of *Clematoclethra, Darlingtonia,* and *Sarracenia* is also characterised by an initial ring primordium with leading stamens in alternipetalous position and that the seemingly diplostemonous androecium organisation of *Clematoclethra* and the seemingly fascicled androecium of *Sarracenia* are the results of relatively late developmental processes. However, this hypothesis remains to be tested in future developmental studies. Alternatively, *Clematoclethra* and *Sarracenia* independently acquired a second whorl of stamens; hence *Clematoclethra* may be interpreted as diplostemonous and *Sarracenia* as two-whorled polystemonous. Assuming that these two genera have two androecial whorls, they would be similar to most species in the ericoid clade, Diapensiaceae, Styracaceae, most species in the primuloid clade (Ebenaceae, Primulaceae s.l. and Sapotaceae; Kubitzki, 2004; Schönenberger *et al*., 2005; Caris, 2013). However, Schönenberger *et al*.'s (2005) study did not resolve the ancestral state of androecium organisation throughout the phylogeny and Chapter IV has a limited sampling outside core Ericales. Therefore, additional ontogenetic studies and reconstructions of character evolution on a large scale in Ericales are needed to unequivocally determine the origin of the second whorl of stamens in two-whorled ericalean taxa. Ronse Decraene & Smets (1995, 1998) presents a compelling argument that two-whorled androecia evolved from polystemonous androecia. If the ancestral state in all (or part of) Ericales indeed is polystemonous androecia, this implies that the various supra- and infrafamilial groups of Ericales with two-whorled androecia evolved independently.

Comparison with other groups in Ericales

Floral development has been investigated in relatively few ericalean taxa, but at least one or few representative of each of the major suprafamilial clades have been studied (Tsou, 1998; Caris, 2013; Zhang & Schönenberger, 2014). In the ericoid clade – the sister group of the sarracenioid clade – floral developmental studies include members of all three families (Clethraceae, Cyrillaceae and all subfamilies of Ericaceae; Caris, 2013). The calyx development in the ericoid clade is similar to that of the sarracenioids, but unlike the sarracenioids, the ericoids all have a distinctly whorled (and usually sympetalous) corolla without an obviously spiral initiation of petals, i.e. the corolla is clearly separated from the calyx by a long plastochron and all petal primordia emerge almost simultaneously (Caris, 2013). Additionally, almost all ericoids, unlike the sarracenioids, have either haplostemonous or distinctly diplostemonous (with the stamens initiated in two distinct whorls) androecia (Leins, 1964; Kubitzki, 2004; Caris, 2013).

Closely related to core Ericales (formed by the ericoid and sarracenioid clades) are the styracoids (Diapensiaceae, Styracaceae and Symplocaceae) and Theaceae (Schönenberger, 2005; Soltis *et al*., 2011). In Theaceae, there are two main types of perianth development: spiral (e.g. *Camellia;* Sugiyama, 1991; Tsou, 1998) or, similarly to the sarracenioids, spirally initiated perianth organs that become whorled during later floral development (e.g. *Stewartia*; Erbar, 1986; Tsou, 1998). The androecia in Theaceae are also, like in the sarracenioids, polystemonous, but the developmental patterns differ. There are three main types of polystemonous patterns in Theaceae: a ring primordium with centrifugally proliferating secondary primordia (e.g. *Camellia*; Sugiyama, 1991; Tsou, 1998), spirally initiated, antepetalous stamen fascicles with centripetally proliferating secondary primordia (e.g. *Stewartia*; Erbar, 1986; Tsou, 1998) and a ring primordium with centrifugally proliferating secondary primordia forming antepetalous fascicles that unite in later stages of flower development (e.g. *Schima* Aucl. ex Steud.; Tsou, 1998). None of the investigated species of Theaceae have leading stamen primordia (Erbar, 1986; Sugiyama, 1991; Tsou, 1998). Additionally, the stamens are primarily arranged in antepetalous positions and they do not invert during development (Erbar, 1986; Sugiyama, 1991; Tsou, 1998). None of the investigated species of the styracoid families (Diapensiaceae, Styracaceae and Symplocaceae) have spirally initiated petals (Caris *et al*., 2002; Wang *et al*., 2010; Caris, 2013). The androecia are either diplostemonous (Diapensiaceae and Styracaceae) or arranged in one-whorled fascicles without leading stamen primordia (Symplocaceae; Caris *et al*., 2002; Wang *et al*., 2010; Caris, 2013). Additionally, none of the styracoid taxa have anthers that invert during the floral development (Schönenberger *et al*., 2012).

Pentaphylacaceae are sister to the clade comprised of core Ericales, the styracoid clade and Theaceae (not strongly supported; Soltis *et al*., 2011; Magallón *et al*., 2015). Pentaphylacaceae, similarly to most sarracenioids, have spirally initiated perianth organs, but unlike the sarracenioids, some Pentaphylacaceae have antesepalous petals (Payer, 1857; Zhang *et al*., 2007, 2008; Zhang & Schönenberger, 2014). Androecium development in polystemonous Pentaphylacaceae conforms to two main types: formation of a ring primordium with leading primordia in alternipetalous positions (e.g. *Cleyera* Adans; Zhang *et al*., 2007, 2008; Zhang & Schönenberger, 2014) and formation of a ring primordium with leading primordia in antepetalous positions (e.g. *Ternstroemia* Mutis ex L.*f*; Zhang & Schönenberger, 2014). However, unlike most sarracenioids, the stamen primordia develop into groups during later floral development and the leading stamen primordia are more prominently differentiated (by size) from successive stamen primordia (Zhang & Schönenberger, 2014). Hence, the floral development in Pentaphylacaceae shows considerable similarity to that of the sarracenioids, but as the families are not closely related (Schönenberger *et al*., 2005; Soltis *et al*., 2011; Zhang & Schönenberger, 2014; Magallón *et al*., 2015), the pattern most likely arose independently in the two clades. One important difference between the sarracenioids and Pentaphylacaceae is that the

anthers do not invert during the floral development in the latter family (Zhang *et al*., 2007, 2008; Zhang & Schönenberger, 2014).

Other, more distantly related ericalean families, in which floral development has been investigated for at least some species, include the primuloid families (Ebenaceae, Primulaceae s.l. and Sapotaceae), the polemonioid families (Fouquieriaceae and Polemoniaceae), Lecythidaceae and two of the balsaminoid families (Balsaminaceae and Marcgraviaceae; Schönenberger *et al*., 2005). Of these families, only Fouquieriaceae have distinctly spirally initiated petals, but the androecium is clearly two-whorled and rarely polystemonous (Schönenberger & Grenhagen, 2005; Caris, 2013). Ebenaceae, Lecythidaceae and Marcgraviaceae all have androecial ring-primordia, often with leading alternipetalous stamen primordia, but as mentioned above, they are not closely related and the general floral architecture is very different from the sarracenioid families (Endress, 1994; Kubitzki, 2004; Schönenberger *et al*., 2005; Caris, 2013).

CONCLUDING REMARKS

In sum, the key findings of this study are: *Heliamphora* has two (di- to trimerous) perianth whorls; *Actinidia*, *Roridula* and *Heliamphora* have spirally inserted petals, not distinctly separated from the sepals by plastochron length, whereas the petals in *Saurauia* emerge in whorls without discernible plastochrons between successive petals; polystemonous taxa have androecial ring-primordia, hence *Saurauia* does not, as previously thought (Brown, 1935), have a two-whorled androecium (uncertain in *Darlingtonia* and *Sarracenia*); centripetal proliferation of stamen primordia is restricted to *Actinidia*; centrifugal proliferation of stamen primordia is restricted to *Actinidia*, Asian *Saurauia* species and (most likely) *Sarracenia*; the stamen primordia in the Neotropical *Saurauia* species do not proliferate beyond the initial whorl, whereas the stamen primordia in the Asian *Saurauia* species proliferate both centrifugally and laterally; and the anthers in the Asian *Saurauia* species, unlike other sarracenioids, partially invert before anthesis.

More sarracenioid species need to be studied to solidify the taxonomic patterns of floral development in the clade, as well as to find potential infrageneric patterns. Of particular interest for further floral ontogenetic studies are *Darlingtonia*, *Sarracenia*, *Clematoclethra* and Oceanian *Saurauia* species.

ACKNOWLEDGEMENTS

We thank the Austrian National Botanical Gardens – Castle Garden Schönbrunn, the Bergius Botanic Garden, the Botanical Garden of the University of Zurich, the University of British Columbia Botanical Garden and the University of Vienna Botanical Garden for providing material for the study; Eric La Fountaine, Peter Endress, Åsa Krüger, Agneta Julia Borg and Shu-Hui Wu for preparing alcohol collections; and Susanne Sontag for assistance with critical point drying and gold sputtering.

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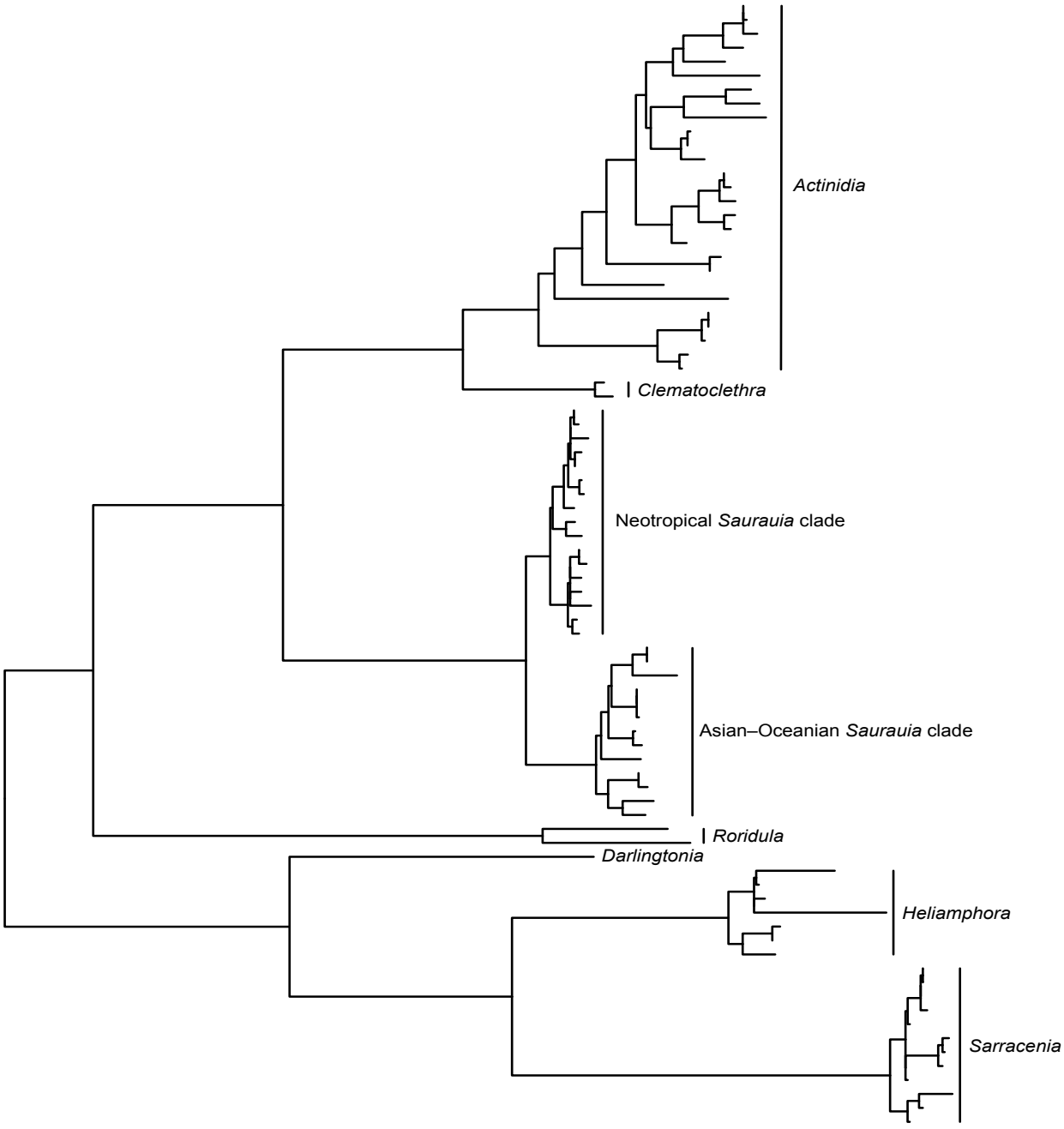
CHAPTER IV

MOLECULAR SYSTEMATICS AND FLORAL EVOLUTION IN THE SARRACENIOID CLADE (ACTINIDIACEAE, RORIDULACEAE AND SARRACENIACEAE) OF ERICALES

Accepted in TAXON with minor revision (6 July 2015, revised version submitted 13 July 2015).

Authors' contributions: conceptualisation, laboratory work, analyses, writing and correspondence by Stefan D. Löfstrand; conceptualisation and comments on writing by Jürg Schönenberger.



Phylogram of the sarracenioid genera

ABSTRACT

The sarracenioid families (Actinidiaceae, Roridulaceae and Sarraceniaceae) were rarely affiliated with other ericalean taxa in pre-molecular classifications and have seldom been considered closely related to each other. In molecular phylogenetic studies, the sarracenioids form a strongly supported clade and is sister to the ericoid clade (Clethraceae, Cyrillaceae and Ericaceae); the sarracenioids and ericoids together make up core Ericales. To date, no phylogenetic study has included all sarracenioid genera (*Actinidia*, *Clematoclethra* and *Saurauia* in Actinidiaceae; *Roridula* in Roridulaceae; *Darlingtonia*, *Heliamphora* and *Sarracenia* in Sarraceniaceae). In particular, the monophyly of *Saurauia* has not previously been tested using molecular characters. We shed light on the phylogenetic relationships within the sarracenioid clade and, based on ancestral state reconstructions, test floral characters previously suggested as potential synapomorphies for the sarracenioids and ericoids. Phylogenetic analysis was performed for the DNA regions ITS, *rbcL*, *rpl32–trnL, trnK* and *trnL–F* using RAxML, MrBayes and PAUP*. Our results support the monophyly of the sarracenioid clade as well as of all its families and non-monotypic genera. Two distinct geographical lineages are identified in *Saurauia*; the two lineages are characterised by differences in petal union (choripetaly versus sympetaly), style union (free versus partially united), gynoecium merism and basic chromosome numbers. Our analyses identify the following floral characters as synapomorphic for core Ericales: adaxial anther attachment, anther inversion and a depression at the ovary to style transition. Proximally thick to massive petals, the presence of a nucellar hypostase in ovules and polystemony are synapomorphies of the sarracenioid clade. The presence of calcium oxalate raphides, mucilage cells, a secretory inner gynoecium surface and the absence of synlateral vasculature in the ovary are synapomorphies of the Actinidiaceae–Roridulaceae clade. A two-whorled androecium is a synapomorphy of the ericoid clade.

ADDITIONAL KEYWORDS: ancestral state reconstruction – Ericales – ericoid clade – floral evolution – phylogenetic reconstruction – sarracenioid clade

INTRODUCTION

Since the rise of molecular systematics, Ericales have been subject to major systematic changes. The order, as recognised by the APGIII system, comprises 22 families and more than 11,500 species (Angiosperm Phylogeny Group, 2009). Several molecular phylogenetic studies have provided a framework of the suprafamilial relationships in Ericales but several deeper nodes in the phylogeny remain unresolved (*e.g*. Geuten & al., 2004; Schönenberger & al., 2005; Soltis & al., 2011). In pre-molecular classifications (*e.g*. Cronquist, 1981; Dahlgren, 1983), the ericalean families were placed in up to 12 different orders in three different subclasses of angiosperms. The sarracenioid families were placed in three orders in two subclasses of angiosperms: Actinidiaceae in Theales (Dilleniidae), Roridulaceae in Rosales (Rosidae) and Sarraceniaceae in Nepenthales (Dilleniidae; Cronquist, 1981).

The monophyly, suprafamilial relationships (Sarraceniaceae sister Actinidiaceae and Roridulaceae) and systematic position of the sarracenioid clade within Ericales (sister to the ericoid clade comprising Ericaceae, Clethraceae and Cyrillaceae) are well supported in molecular phylogenetic analyses (*e.g*. Anderberg & al., 2002; Schönenberger & al., 2005; Soltis & al., 2011). The clade comprises seven genera (*c.* 400 species): Actinidiaceae with around 360 species in three genera (*Actinidia* Lindl., *Clematoclethra* (Franch.) Maxim. and *Saurauia* Willd.; Li & al*.,* 2007), Roridulaceae with two species in a single genus (*Roridula* Burm. ex L.; Conran, 2004) and Sarraceniaceae with 35 species in three genera (*Darlingtonia* Torr., *Heliamphora* Benth. and *Sarracenia* L.; McPherson & Schnell, 2011; McPherson & al., 2011). To date, no study has included all genera in a single analysis and neither the monophyly and intergeneric relationships in Actinidiaceae, nor the infrageneric relationships in *Saurauia* have been tested. Previous molecular phylogenetic studies in Actinidiaceae have focused on the infrageneric classification of *Actinidia*, utilising *Clematoclethra* and *Saurauia* as outgroups (Li & al., 2002;

Chat & al., 2004). Ellison & al. (2012) investigated the phylogenetic relationships of Sarraceniaceae and showed the intergeneric relationships to be well supported, but infrageneric relationships remained largely unresolved. More recently, Stephens & al. (2015) largely resolved the infrageneric relationships in *Sarracenia* using target enrichment.

The geographical distribution in the sarracenioid clade is disjunct: Actinidiaceae are present in the Neotropics (*Saurauia*), temperate to tropical Asia (*Actinidia*, *Clematoclethra* and *Saurauia*) and tropical Oceania (*Saurauia*); Roridulaceae are endemic to the Cape region of South Africa; and Sarraceniaceae are restricted to temperate North America (*Darlingtonia* and *Sarracenia*) and the Neotropics (*Heliamphora*; Tropicos, 2015).

The sarracenioids are diverse and differ conspicuously in regard to reproductive and vegetative morphology, habit and ecology: Sarraceniaceae are herbaceous perennials carrying insect trapping pitcher leaves, Roridulaceae are shrublets, densely covered in glandular hairs and Actinidiaceae are several metres tall lianas and trees (Kubitzki, 2004). Flowers range in size from a few millimetres to several centimetres at anthesis and breeding systems include dioecy and hermaphroditism (Kubitzki, 2004). The families also exhibit great diversity in habit and nutrient uptake: Actinidiaceae are autotrophous, Roridulaceae are protocarnivorous and Sarraceniaceae are carnivorous (Kubitzki, 2004). For a more comprehensive account on morphological, anatomical and histological characters in the sarracenioid clade, see Löfstrand & Schönenberger (2015).

An interesting floral feature that, in Ericales, is restricted to the sarracenioid and ericoid clades (except for Cyrillaceae) is anther inversion during floral development (*e.g.* Schönenberger & al, 2012; Löfstrand & Schönenberger, 2015). Schönenberger & al. (2012) postulated three main types of anther inversion in Ericales: 'Late anther inversion type A' (anthers invert from extrorse to introrse at the onset of anthesis); 'Late anther inversion type B' (anthers invert from introrse to extrorse at the onset of anthesis; and 'Early anther inversion' (anthers invert from extrorse to introrse early in the floral development). Löfstrand and Schönenberger (2015) found that these definitions do not sufficiently encompass the anther inversion in *Darlingtonia*. Hence, they suggested a fourth anther inversion type: 'Late anther inversion type C' (anthers invert at the onset of anthesis, but a direction cannot be unequivocally assigned because of anther morphology).

In this study, we test phylogenetic relationships in the sarracenioid clade based on analysis of DNA sequence data (ITS, *rbcL*, *rpl32–trnL* intergenic spacer, *trnK–matK–trnK* intron and *trnL–trnF* intergenic spacer) from a broad sample of taxa representing all genera in the clade. Of particular interest is *Saurauia* (Actinidiaceae), for which infrageneric relationships and monophyly have not yet been tested with a molecular phylogenetic approach. Using the new phylogenetic hypotheses, we analyse the phylogenetic pattern of several, potentially synapomorphic floral characters for the sarracenioids and its subclades, as well as other floral features of potentially systematic importance, suggested by Löfstrand & Schönenberger (2015). This study, together with our earlier study on comparative floral structure (Löfstrand & Schönenberger, 2015), provides a solid basis for future work to incorporate Cretaceous floral mesofossils (Keller & al. 1996, Schönenberger & al. 2012) into phylogenetic, dating and biogeographical analyses.

MATERIAL AND METHODS

SAMPLING

Our analyses include representatives from all seven extant sarracenioid genera: 27 species of *Actinidia*, two subspecies of *Clematoclethra*, 30 species of *Saurauia*, both species of *Roridula*, the monotypic *Darlingtonia*, seven species of *Heliamphora* and 12 representatives of *Sarracenia* (including two subspecies of *Sarracenia purpurea* L.). Analyses also include ten representatives

from the ericoid clade: one species of Clethraceae, one species of Cyrillaceae and one species from each subfamily of Ericaceae (Arbutoideae, Enkianthoideae, Ericoideae, Cassiopoideae, Harrimanelloideae, Monotropoideae, Styphelioideae and Vaccinioideae). *Camellia* L. (Theaceae) was used as the outgroup (Schönenberger & al., 2005). In sum, the sampling includes 59 Actinidiaceae taxa, two Roridulaceae species, 20 Sarraceniaceae taxa, one Clethraceae species, one Cyrillaceae species, eight Ericaceae species and one Theaceae species; the full taxon sampling is presented in Appendix 1.

Molecular markers included in the analyses are the nuclear rDNA region ITS (ITS1–5.8s–ITS2) and the plastid DNA regions *rbcL, rpl32–trnL* (*rpl32–trnL*^{UAG} intergenic spacer), *trnK* (*5'trnK–matK–3'trnK*) and *trnL–F* (*trnL*^{UAA} intron and *trnL*^{UAA}*–trnF*^{GAA} intergenic spacer).

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total genomic DNA extractions were performed with QIAGEN DNeasy® Plant Mini Kit (QIAGEN GmbH, Hilden, Germany), using to the manufacturer's instructions.

The following mix was used for all polymerase chain reactions (PCR): 7.5 µl Thermo Scientific 2X Reddy Mix PCR Master Mix (Fisher Scientific Austria GmbH, Vienna, Austria); 0.15 µl (32 µM) forward primer; 0.15 µl (32 µM) reverse primer; 0.2 µl (20mg/ml) bovine serum albumin (BSA; Fisher Scientific Austria GmbH, Vienna, Austria); 6.7–6.9 µl PCR grade water; and 0.1–0.3 µl DNA template (15 µl total volume). The following PCR program was utilised for the DNA amplification: 1 × [94°C for 2 min], 35 × [94°C for 30 s; 48–55°C for 30 s; 72°C for 60–90 s], 1 × [72°C for 7 min] and 1 × [4°C ∞]. Primers, primer sequences and annealing temperatures are presented in Appendix 2. Elongation time was dependent on fragment length (<1,000 bp = 60 s; 1,000< bp = 90 s). PCR products were purified with exonuclease I (Exo I; Fisher Scientific Austria GmbH, Vienna, Austria) and thermo sensitive alkaline phosphatase (FastAP; Fisher Scientific Austria GmbH, Vienna, Austria), using the manufacturer's instructions.

Cycle sequencing reactions were performed using the ABI PRISM BigDye Terminator Cycle Sequencing kit (Applied Biosystems, Vienna, Austria) according to the manufacturer's instructions. Sequences were produced on a capillary sequencer (3730 DNA Analyzer; AB, Life Technologies). Sequence reads were assembled using CodonCode Aligner v.5.1.4 (CodonCode Corporation, Centerville, MA, USA). Sequences typically displayed few, if any, ambiguous or polymorphic base-pair readings; these were treated as missing data. DNA sequences generated for this study (261 sequences) were deposited in GenBank Additional sequences (100 sequences) were obtained from GenBank. See Appendix 1 for a complete list of accession numbers.

ANALYSES

Sequences were aligned in MUSCLE v.3.8.31 (Edgar, 2004).

Nucleotide substitution models were selected under the corrected Akaike information criterion (AICc) as implemented in jModelTest v. 2.1.7 (Darriba & al., 2012; Guindon & Gascuel, 2003); GTR + Γ was selected for *rpl32–trnL*, *trnK*, and *trnL–F*; GTR + I + Γ was selected for ITS and *rbcL*.

Phylogenetic reconstructions were performed on all single region datasets and the combined [ITS/*rbcL*/*rpl32–trnL*/*trnK*/*trnL–F*] dataset (henceforth referred to as 'combined dataset') under the maximum likelihood optimality criterion as implemented in RAxML-VI-HPC on the T-REX web server (Stamatakis, 2006; Boc & al., 2012). Node support was assessed with 1,000 bootstrap replicates. The ITS and *rbcL* datasets were analysed with the GTR + Γ nucleotide substitution model (second best option; GTR + I + Γ is discouraged in RAxML; Stamatakis, 2006). The combined dataset was analysed partitioned under the GTR + Γ nucleotide substitution model.

Phylogenetic reconstructions were additionally performed on the combined dataset with Bayesian Markov chain Monte Carlo (MCMC) inference as implemented in MrBayes v.3.2 (Ronquist & al., 2011) and under the parsimony optimality criterion as implemented in PAUP* v.4.0b10 (Swofford, 2002). The Bayesian analysis comprised two runs of four MCMC chains, each of which was run for ten million generations (25% burnin), sampled every 1,000 generations. Convergence of the MCMC chains was confirmed (standard deviation of split frequencies for the parallel runs ≤ 0.01) in the post-burnin generations. These samples were used to calculate Bayesian posterior probabilities. The dataset was analysed as partitioned (unlinked). The parsimony analysis was performed with a heuristic search, the tree-bisection-reconnecting (TBR) branch swapping algorithm and with Multrees on (maximum ten trees saved per replicate). Node support was calculated with 1,000 bootstrap replicates.

ASSESSMENT OF TREES

We applied the following support value thresholds: maximum likelihood bootstrap and parsimony bootstrap supports < 70 were considered unsupported, 70–94 moderately supported (Alfaro & al., 2003; Erixon & al., 2003) and ≥ 95 strongly supported (Erixon & al., 2003; Simmons & Norton, 2014). A Bayesian posterior probability < 0.95 was considered unsupported and ≥ 0.95 supported without distinction between moderate and strong support (Alfaro & al., 2003; Erixon & al., 2003; Alfaro & Holder, 2006; Simmons & Norton, 2014). Following the instructions of Pirie (2015), sequences resulting in conflicting topologies (*i.e.* maximum likelihood bootstrap support ≥ 70) were removed the analyses repeated before concatenating the data.

ANCESTRAL STATE RECONSTRUCTIONS

Ancestral states for floral characters considered to be of systematic value for the sarracenioids by Löfstrand & Schönenberger (2015), earlier proposed synapomorphies for the sarracenioids (Anderberg & al., 2002), as well as anther attachment and inversion characters (see Schönenberger & al., 2012) were reconstructed in Mesquite ver. 3.02 (Maddison & Maddison, 2015). Reconstructions were performed using likelihood on a pruned topology of the best scoring maximum likelihood tree (combined dataset) with manually inserted sister group and outgroup taxa. The sister group of the sarracenioid clade was sampled and added to the tree following the phylogenetic study by Kron & al. (2002). Outgroups were sampled and inserted following the study by Magallón & al. (2015). Only species where detailed morphological, anatomical, histological and/or developmental studies have been performed were included in the sampling. Taxa included in the ancestral state reconstructions were: *Actinidia arguta* Franch. & Sav., *Actinidia chinensis* Planch, *Clematoclethra scandens* Maxim., *Saurauia pittieri* Donn.Sm. and *Saurauia subspinosa* J.Anthony (Actinidiaceae); *Roridula gorgonias* Planch. (Roridulaceae); *Darlingtonia californica* Torr., *Heliamphora nutans* Benth., *Sarracenia leucophylla* Raf. and *Sarracenia purpurea* L. (Sarraceniaceae); *Clethra alnifolia* L. (Clethraceae); *Cyrilla racemiflora* L. (Cyrillaceae); *Arbutus unedo* L. (Arbutoideae, Ericaceae); *Cassiope mertensiana* (Bong.) D.Don (Cassiopoideae, Ericaceae); *Enkianthus campanulatus* G.Nicholson (Enkianthoideae, Ericaceae); *Erica carnea* L. (Ericoideae, Ericaceae); *Harrimanella stellariana* Coville (Harrimanelloideae, Ericaceae); *Monotropa hypopitys* L. (Monotropoideae, Ericaceae); *Leucopogon amplexicaulis* R.Br. (Styphelioideae, Ericaceae); *Vaccinium vitis-idaea* L. (Vaccinioideae, Ericaceae); *Galax urceolata* (Poir) Brummitt (Diapensiaceae); *Styrax japonicus* Siebold & Zucc. (Styracaceae); *Symplocos paniculata* Miq. (Symplocaceae); *Camellia japonica* L. (Theaceae); and *Pentaphylax euryoides* Gardner & Champ (Pentaphylacaceae).

When a detailed floral morphological study (including anatomy and histology) of the species was available, calcium oxalate raphide bundles, mucilage cells and secretory inner gynoecium surface were assumed to be absent unless explicitly mentioned (see discussion). Similarly, when the study described the ovules in detail and no nucellar hypostase was mentioned, absence was

assumed. Monotropoideae was coded as 'missing data' for proximal petal thickness (*Monotropa hypopitys* is asepalous; Copeland, 1941). For genera with well-described ovule histology, but where the species differs from the one included here, the presence or absence of a nucellar hypostase in ovules was assumed to be constant within genera; see Johri & al. (1992) for an overview. The character matrix is available in Appendix 3. References for the remaining morphological characters are: Sarracenioid clade (Löfstrand & Schönenberger, 2015; Chapter III); Clethraceae (Kavaljian, 1952; Johri & al., 1992; Caris, 2013); Cyrillaceae (Copeland, 1953; Anderberg & Zhang, 2002; Caris, 2013); Diapensiaceae (Palser, 1963; Rönblom & Anderberg, 2002; Caris, 2013); Ericaceae (Copeland, 1941; Palser, 1951, 1952, 1954, 1961; Paterson 1961; Palser & Murty, 1967; Johri & al., 1992; Hermann & Palser, 2000; Caris, 2013); Pentaphylacaceae (Mauritzon, 1936; Min & Bartholemew, 2007a); Styracaceae (Dickison, 1993; Caris, 2013); Symplocaceae (Caris & al., 2002; Fritsch & al., 2008); and Theaceae (Sugiyama, 1991, 1997; Min & Bartholemew, 2007b).

RESULTS

MOLECULAR PHYLOGENETIC ANALYSES

The combined analyses comprised 92 taxa and a total alignment length of 7,046 base pairs (2,254 distinct alignment positions; 32% gaps and missing data). The different methods of phylogenetic inference resulted in trees with similar resolution. The Bayesian analysis produced a slightly higher proportion of supported nodes than the maximum likelihood analysis. The parsimony analysis generally produced lower bootstrap support values than the maximum likelihood analysis (Appendix 4). Support for intergeneric relationships and the two major infrageneric lineages within *Saurauia* is presented in Figure 1 and Appendix 4; support for the remaining infrageneric relationships are presented solely in Appendix 4. Support values are henceforth presented as follows: (maximum likelihood bootstrap / Bayesian posterior probability / parsimony bootstrap).

According to our results, the sarracenioid families form a clade (80 / 1.00 / 51); this sarracenioid clade is sister to the ericoid clade (89 / 0.99 / 81). Sarraceniaceae are sister to a clade comprising Actinidiaceae and Roridulaceae (100 / 1.00 / 91). In the ericoid clade, Clethraceae are sister to a clade comprising Cyrillaceae and Ericaceae (89 / 1.00 / 88). Phylogenetic relationships in the ericoid clade (Fig. 1; Appendix 4) will not be further presented here. All sarracenioid families, the previously recognised clade formed by *Heliamphora* and *Sarracenia* (Sarraceniaceae), a clade formed by *Actinidia* and *Clematoclethra* (Actinidiaceae) and all genera in the sarracenioid clade are monophyletic. Each of these clades is strongly supported (100 / 1.00 / 100; note that *Clematoclethra* and *Darlingtonia* are monotypic). In *Saurauia*, two major lineages with distinct phytogeographic distributions are present: a Neotropical clade (96 / 1.00 / 98) and an Asian–Oceanian clade (100 / 1.00 / 100).

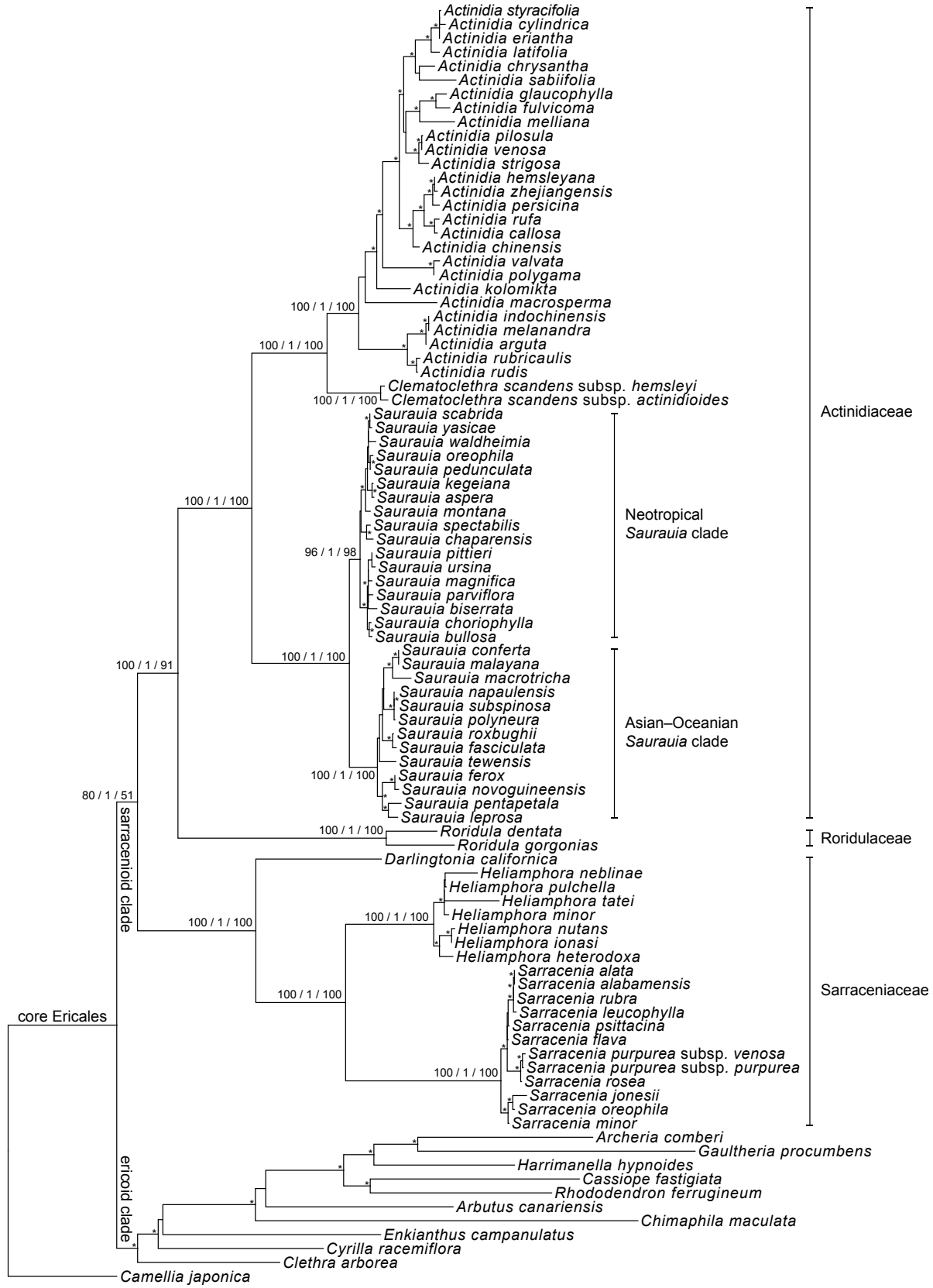


Figure 1. Best scoring maximum likelihood tree (phylogram), rooted with *Camellia*. Branch support (maximum likelihood bootstrap / bayesian posterior probability / parsimony bootstrap) is presented next to nodes for clades explicitly treated in the text. Asterisks (*) indicate other supported nodes. See Appendix 4 for a cladogram with all support values presented.

ANCESTRAL STATE RECONSTRUCTIONS

The suprafamilial clades discussed below are presented in figure 2. The character matrix and support values for the inferred states are presented in Appendix 3. Changes from the ancestral states in Ericaceae will not be presented in detail (but see Figs. 3, 4).

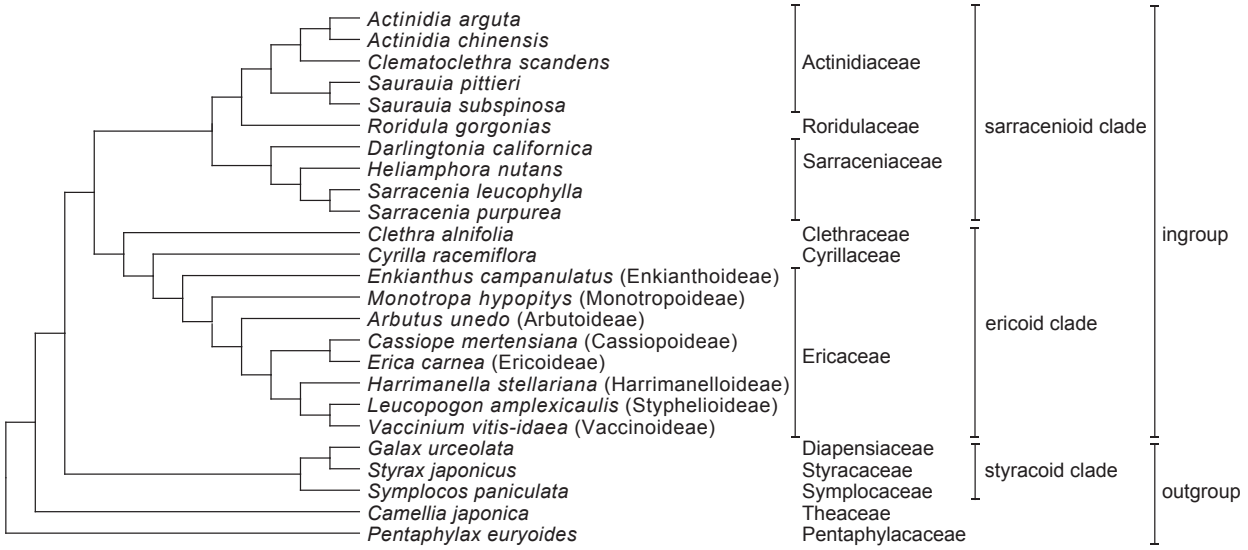


Figure 2. Tree utilised for ancestral state reconstructions. Based on a pruned topology retrieved from the combined analyses. Ericoid species were sampled and inserted following the study by Kron & al (2002). Outgroup species were sampled and inserted following the study by Magallón & al. (2015).

The ancestor of the clade containing Theaceae, the styracoids and core Ericales was reconstructed to have had the following floral morphological traits: petal bases that are thinner than the sepal bases (Fig. 3C); a polystemonous androecium with the stamens arranged in a single whorl (Fig. 4A, B); an abaxially positioned anther attachment (Fig. 4C); absence of anther inversion (Fig. 3D); completely united styles (Fig. 4E); absence of a depression at the ovary–style transition (Fig. 4F); and synlateral vasculature present in the ovary (Fig. 3E). Inferred floral histological character states were: absence of calcium oxalate raphides and mucilage cells in floral tissue (Fig. 3A, B); absence of a secretory inner gynoecium surface (Fig. 3D); and absence of a nucellar hypostase in the ovules (Fig. 3F).

The clade formed by core Ericales and the styracoid clade was characterised by the same floral features with one exception: the loss of polystemony (Fig. 4A). Some further evolutionary changes most likely took place along the stem leading to the ancestor of core Ericales: the anther attachment shifted from an abaxial orientation to an adaxial orientation (Fig. 4C); the anthers started inverting from extrorse to introrse orientation at the onset of anthesis (‘Late anther inversion type A’; Fig. 4D); and a depression appeared at the ovary–style transition (Fig. 4F). Additionally, the ancestor of the ericoid clade and the sarracenioid clade had partially free styles (Fig. 4E) and the ericoid clade gained a second androecium whorl (Fig. 4B).

The ancestor of the sarracenioid clade was characterised by two floral synapomorphies: petals that are proximally as thick or thicker than the proximal region of the sepals (Fig. 3C) and the presence of a nucellar hypostase in the ovules (Fig. 4F; homoplasious with Theaceae). Additionally, the ancestor of the clade was apparently polystemonous, a feature that is also present in Symplocaceae and Theaceae but not in Styracaceae, Diapensiaceae and the ericoid clade (Fig. 4A).

Figure 3. Ancestral state reconstructions for: (A) presence/absence of calcium oxalate raphides in floral tissue; (B) presence/absence of mucilage cells in floral tissue; (C) proximal petal thickness in relation to proximal sepal thickness; (D) presence/absence of a secretory inner gynoecium surface; (E) presence/absence of synlateral vasculature in the ovary; and (F) presence/absence of a nucellar hypostase in ovules.

Figure 4. Ancestral state reconstructions for: (A) presence/absence of polystemony; (B) number of androecium whorls; (C) orientation of anther attachment; (D) presence/absence of anther inversion ('late type A' = inversion from extrorse from introrse anther orientation at the onset of anthesis; 'late type B' = inversion from introrse to extrorse anther orientation at the onset of anthesis; 'late type C' = anthers invert at the onset of anthesis, but a direction cannot be unequivocally assigned; and 'early' = inversion from extrorse to introrse anther orientation early in the floral development); (E) partially free versus completely united styles; and (F) presence/absence of a depression at the ovary–style transition.

The ancestor of the Actinidiaceae–Roridulaceae clade was characterised by the following synapomorphic traits: presence of calcium oxalate raphides in floral tissue (Fig. 3A), presence of mucilage cells in floral tissue (Fig. 3B), presence of a secretory inner gynoecium surface (Fig. 3D), and absence of synlateral vasculature in the ovary (Fig. 3E). Subsequent gains and losses of floral traits in the Actinidiaceae–Roridulaceae clade were inferred as the loss of polystemony in *Roridula* (and, most likely, *Clematoclethra*; Fig. 4A) and styles reverting to completely united in *Clematoclethra* and *Roridula* (Fig. 4E).

Along the stem lineage leading to crown group Sarraceniaceae, a reversal to an abaxial orientation of the anther attachment probably took place (Fig. 4C) with a secondary change in the anthers of *Darlingtonia* (simultaneously one extrorse and one introrse theca per anther). The *Heliamphora–Sarracenia* clade gained a new type of anther inversion, anthers inverting from an introrse to an extrorse orientation at the onset of anthesis ('Late anther inversion type B'; Fig. 4D), while *Darlingtonia* changed to a proximal position of the anther attachment and 'Late anther inversion type C' (Fig. 4D). The *Heliamphora–Sarracenia* clade additionally was inferred to have lost the depression at the ovary–style transition (Fig. 4F) and the styles in *Heliamphora* reverted to completely united (Fig. 4E).

DISCUSSION

MOLECULAR PHYLOGENETIC ANALYSES

The sarracenioid clade was moderately to strongly supported by our analyses (80 / 1.00 / 51), as was the Actinidiaceae–Roridulaceae clade (100 / 1 / 91) and the ericoid clade (89 / 0.99 / 81). These results are compatible with earlier molecular phylogenetic studies of Ericales (Anderberg & al., 2002; Schönenberger & al., 2005) and angiosperms (Soltis & al., 2011; Magallón & al., 2015). Actinidiaceae, Roridulaceae, Sarraceniaceae and Ericaceae were each strongly supported as monophyletic (support for each family 100 / 1.00 / 100), as were the sarracenioid genera (support for each genus 100 / 1.00 / 100, with *Clematoclethra* and *Darlingtonia* being monotypic). These results corroborate earlier analyses of different subclades in the sarracenioids and ericoids (Kron & al., 2002; Li & al., 2002; Chat & al., 2004; Ellison & al., 2012; Stephens & al., 2015). For discussions on traits characterising the respective families and clades, see Anderberg & al. (2002), Schönenberger & al. (2005), Löfstrand & Schönenberger (2015), Kubitzki (2004) and the following sections in this study.

Based on karyology, He & al. (2005) suggested a sister group relationship between *Actinidia* and *Clematoclethra,* with *Saurauia* sister to the *Actinidia–Clematoclethra* clade. These relationships might also be hypothesised based on growth habit (lianescent as opposed to arborescent in *Saurauia*), ecological niche and geographical distribution (mainly temperate East Asia as opposed to predominately highland, tropical New World, Asia and Oceania for *Saurauia*) and fruit dehiscence (indehiscent as opposed to dehiscent in *Saurauia*; Kubitzki, 2004; Löfstrand & Schönenberger, 2015). However, this is the first study to test the sister group relationship of *Actinidia* and *Clematoclethra* using molecular phylogenetic methods, and equally to test the sister group relationship between the *Actinidia–Clematoclethra* clade and *Saurauia*. Earlier molecular phylogenetic studies in Actinidiaceae have focused on infrageneric relationships in *Actinidia*, including *Clematoclethra* and *Saurauia* as outgroups (*e.g.* Li & al., 2002; Chat & al., 2004). Because of the limited taxon sampling, the monophyly of *Actinidia*, while not questioned, has until now been unconfirmed using molecular phylogenetic methods (Li & al., 2002; Chat & al., 2004). The infrageneric relationships and support values in *Actinidia* (Appendix 4) are largely similar to the two most recent phylogenetic studies (Li & al., 2002; Chat & al., 2004). Neither the respective study by Li & al. (2002) and Chat & al. (2004), nor the present study, supports the most recent supraspecific classifications in *Actinidia* (based on mainly leaf morphology and histology; Cui & al., 2002; Li & Li, 2010). All currently accepted sections in the genus (*Actinidia* sect. *Actinidia*, *Actinidia* sect. *Strigosae*, *Actinidia* sect.

Leiocarpae and *Actinidia* sect. *Vestitae*) are strongly supported as non-monophyletic (Fig. 1; Appendix 4; Cui & al., 2002; Li & al., 2002; Chat & al., 2004; Li & Li, 2010).

Within *Saurauia*, which has not been the focus of a molecular phylogenetic study before, our analyses identified two major infrageneric clades with distinct geographical distributions: a Neotropical clade (96 / 1.00 / 98) and an Asian–Oceanian clade (100 / 1.00 / 100). Beyond the monophyly of *Saurauia* and the two geographically distinct clades, resolution among species is low and only a few minor clades are recovered. The latest large-scale taxonomic treatment in *Saurauia* focused on South American species (Soejarto, 1980). An earlier study treated only Mexican and Central American species (Hunter, 1966). In the Asian species, taxonomic treatments have so far been restricted to national floras (*e.g*. Cuong & al., 2007; Li & al., 2007). No comprehensive taxonomic treatment has been performed for the Asian and Oceanian species to date (Conn & Damas, 2013). Soejarto (1980) mentioned the need of a more detailed study of Neotropical species, and *e.g*. Conn & Damas (2013) emphasised that a taxonomic revision of Asian–Oceanian species is greatly needed. There are no previously suggested synapomorphies for the respective geographic lineages, but a few general patterns could be identified in a broad literature review (Backer & Bakhuizen van den Brink, 1963; Hunter, 1966; Soejarto 1969, 1970, 1980; van Royen, 1982; Dressler & Bayer, 2004; He & al., 2005; Cuong & al., 2007; Li & al., 2007; Conn & Damas, 2013). In the Asian–Oceanian clade the petals are generally united for about half of their length, whereas they are usually united for less than 10% (typically displaying no union at all) in the Neotropical species. The Asian–Oceanian species typically have three or five carpels (sometimes 3–5), whereas the Neotropical species typically have five carpels (often variably 3–5 or 5–8 carpels on specimens with predominately five carpels). The styles of the Asian–Oceanian species are typically united for 30–50% of their length (rarely only proximally or almost completely united), whereas the styles of the Neotropical species are typically completely free (rarely united for more than 5%). The basic chromosome number of Asian *Saurauia* is, depending on the source, 10 (Dressler & Bayer, 2004) or 13 (He & al., 2005), whereas the Neotropical species have a basic chromosome number of 15 (Soejarto, 1969, 1970).

The monophyly of Sarraceniaceae and the sister group relationship of *Heliamphora* and *Sarracenia* was established by Ellison & al. (2012), but most infrageneric relationships remained weakly supported in spite of clear morphological differences (Mellichamp, 2009; McPherson & Schnell, 2011; McPherson & al., 2011). More recently, Stephens & al. (2015) provided a tree of *Sarracenia* with good support for various infrageneric relationships. *Sarracenia* is additionally subject to on-going hybridisation and incomplete lineage sorting (Stephens & al., 2015). Several currently accepted species in *Sarracenia* may be untenable, mainly within the disputed [*Sarracenia alabamensis* Case & R.B.Case – *Sarracenia alata* (Alph.Wood) Alph.Wood – *Sarracenia jonesii* Wherry – *Sarracenia leucophylla* Raf. – *Sarracenia rubra* Walter] complex but also regarding the species rank of *Sarracenia rosea* NACZI, CASE & R.B.CASE and the infraspecific taxa in *Sarracenia purpurea* L. (Stephens & al., 2015). In *Heliamphora* a denser sampling is needed before any conclusions on the tenability of current infrageneric taxonomic classifications can be drawn; only seven out of the 23 accepted species have been included in molecular phylogenetic studies (this study; McPherson & al., 2011; Ellison & al., 2012).

ANCESTRAL STATE RECONSTRUCTIONS

Note that the sister relationship between the styracoid clade (Diapensiaceae, Styracaceae and Symplocaceae) and core Ericales is not strongly supported. Similarly, the sister relationship of Pentaphylacaceae and the clade comprising core Ericales, the styracoid clade and Theaceae is not strongly supported. These are, however, depicted in the best working hypothesis for the time being (Soltis & al., 2011; Magallón & al., 2015). Many of the characters (particularly histological characters) discussed as synapomorphic for the clades have not been extensively investigated in Ericales. Additionally, detailed structural studies have only been performed for a handful of species in the sarracenioid clade and the number of androecium whorls has not been

established for *Clematoclethra* and *Sarracenia*. The following discussion should therefore be interpreted as preliminary, pending further investigation.

The presence of calcium oxalate raphides in floral tissue in Ericales is apparently restricted to the Actinidiaceae–Roridulaceae clade (Fig. 3A; Löfstrand & Schönenberger, 2015) and the balsaminoid clade (Balsaminaceae, Marcgraviaceae and Tetrameristaceae; von Balthazar & Schönenberger, 2013). The raphide bundles are easily distinguishable and often visible to the naked eye in dissected floral organs (equally in fresh, alcohol preserved, air dried and critical point dried material; personal observation, S.L.). It therefore stands to reason that such a prominent feature would be mentioned if present in the sampled species (only coded for species where detailed floral histological descriptions are available, otherwise coded as 'missing data'). The needle-like crystalline structure of the individual crystals in calcium oxalate raphides has been suggested to serve as a defence against herbivory by insect larvae in vegetative tissue (*e.g*. Konno & al., 2014), suggesting the same holds true for floral tissue.

The presence of filled and/or striated mucilage cells in floral tissue in Ericales is only known to occur in the Actinidiaceae–Roridulaceae clade and the balsaminoid clade, but the feature is not as prominent as the presence of calcium oxalate raphides (Fig. 3B; only clearly visible in light micrographs; Löfstrand & Schönenberger, 2015). Cells partially filled with mucilage are also present in the stamen filaments of *Polemonium reptans* L. (Polemoniaceae; Schönenberger, 2009). The histological structure of the mucilage cells is clearly different from the surrounding tissue with their thick cell walls and lack of cytoplasm (Stewart, 1919; Matthews & Endress, 2006; Löfstrand & Schönenberger, 2015). We therefore assume that other detailed floral histological studies would mention, at the very least, thick-walled cells devoid of cytoplasm scattered in the parenchymatic tissue (also note that most of the references we used present light micrographs of histological characters). Mucilage cells have been thoroughly studied, *e.g*. in Cactaceae, where one of their suggested functions is water storage (Stewart, 1919). While the ecological niches of cacti are very different to those of Actinidiaceae and Roridulaceae, the study by Stewart (1919) describes cells of almost identical structure to the ones found in the sarracenioid clade, suggesting water storage may be part of the function of the mucilage cells. See Matthews & Endress (2006) for a broad review on the presence of mucilage cells in floral tissue in (mainly) rosids.

Petals that are proximally as thick or thicker than the proximal region of the sepals are apparently rare in Ericales but not exclusive to the sarracenioid clade (Fig. 3C; Löfstrand & Schönenberger, 2015). Massive petal bases, similar to those found in the sarracenioid clade, are, for instance, also present in *Schwartzia brasiliensis* (Choisy) Bedell ex Gir.-Cañas (Marcgraviaceae) and *Rhododendron hirsutum* L. (Ericoideae, Ericaceae), but appear to be exceedingly rare in other Ericales (*e.g*. Palser, 1951, 1961; Kavaljian, 1952; Paterson 1961; Dickison, 1993; Sugiyama, 1997; Schönenberger, 2009; von Balthazar & Schönenberger, 2013).

A secretory inner gynoecium surface has been described for the Actinidiaceae–Roridulaceae clade and the balsaminoid clade of the Ericales (Fig 3D; von Balthazar & Schönenberger, 2013; Löfstrand & Schönenberger, 2015). Whether it is also present in other ericalean families remains to be established. In both clades, the secretion of mucilage is particularly abundant in the stylar canal and on the placentae (von Balthazar & Schönenberger, 2013; Löfstrand & Schönenberger, 2015). The mucilage is additionally visible to the naked eye in dissected fresh floral material (personal observation, S.L.). During anthesis, mucilage in the stylar canal and the ovary is generally part of the pollen tube transmitting tract, facilitating pollen tube growth towards the ovules (Endress 1994). Among the ericalean families, fruits with mucilage surrounding the seeds are present in Actinidiaceae, Ebenaceae and Marcgraviaceae and mucilaginous seed coats have been mentioned for Polemoniaceae and Roridulaceae (Kubitzki, 2004; Schönenberger, 2009). The mucilage surrounding the seeds is of placental origin in both Actinidiaceae and Marcgraviaceae, whereas it originates from the endocarp in Ebenaceae (Kubitzki, 2004; Löfstrand & Schönenberger, 2015). The mucilaginous seed coat in Roridulaceae has not been

more precisely described than that they become sticky when wet (Conran, 2004), whereas the mucilaginous seed coats of Polemoniaceae have been more extensively investigated (the mucilage is contained in epidermal seed coat hairs and is extruded when the seeds get wet; *e.g*. Grant, 1959; Grubert & Hambach, 1972). Roridulaceae, unlike Polemoniaceae, have copious secretion of the inner gynoecium surface (Schönenberger, 2009; Löfstrand & Schönenberger, 2015), suggesting that the seed coats in *Roridula* are not necessarily mucilaginous, but rather become sticky upon rehydration of the placental secretion that surrounds the ovules during flower development. In *Saurauia*, the copious placental mucilage surrounding the seeds in ripe fruits is suggested to aid in the dispersal of the seeds (rain dispersed, after the loculicidal fruits dehisce; Hunter, 1966). The mucilage surrounding the seeds of *Actinidia* makes the seeds sticky when drying (personal observation, S.L.), suggesting that the placental mucilage plays a similar role to seed coat derived mucilage. See Western (2012) for a comprehensive account of the role of seed coat mucilage in the dispersal and germination of seeds.

Synlateral vasculature appears to be present in the ovary (Fig. 3E) in most ericalean taxa, except in the Actinidiaceae–Roridulaceae clade (*e.g*. Palser, 1951, 1954, 1961, 1963; Kavaljian, 1952; Paterson 1961; Dickison, 1993; Sugiyama, 1997; Schönenberger, 2009; von Balthazar & Schönenberger, 2013; Löfstrand & Schönenberger, 2015). In *Actinidia*, the lack of synlateral vasculature might be explained by lack of space due to the increased carpel number (generally more than 15; Li & al., 2007), but this fails to explain the missing synlateral vasculature in *Clematoclethra* and *Saurauia* (typically three or five carpels; Hunter, 1966; Soejarto, 1980; Cuong & al., 2007; Li & al., 2007) or *Roridula* (three carpels; Conran, 2004). One potential explanation, albeit untested, is that the synlateral vasculature was lost in a multicarpellate ancestor of the clade. There is no indication of a more abundant lateral (*i.e*. non-synlateral) vascularisation of the ovaries in the Actinidiaceae–Roridulaceae clade compared to, *e.g*., Sarraceniaceae, nor is there any apparent connection to fruit type or free versus united styles (Löfstrand & Schönenberger, 2015).

A nucellar hypostase is present in the ovules of all sarracenioid genera (Fig. 3F; Löfstrand & Schönenberger, 2015) and in Theaceae (Johri & al., 1992), whereas it has not been described for the genera in the ericoid clade, styracoid clade or Pentaphylacaceae (assuming constancy within genera; see Johri & al. (1992) for an overview). Kavaljian (1952) mentions darkly staining areas in the ovules of *Clethra alnifolia*. These areas, however, appear to be non-homologous to nucellar hypostases in terms of structure and position. Additionally, one investigated specimen of *Clethra* sp. (unpublished data; coll. JS 552, Department of Botany and Biodiversity Research, University of Vienna) does not contain a nucellar hypostase in its ovules and Johri & al. (1992) mention no hypostase in their detailed description of *Clethra* ovules. The trait is, however, poorly understood and may turn out to be more common than previously thought once more detailed histological studies of the families in Ericales have been performed. Nucellar hypostases have been assigned multiple functions in different taxa, including storage of lipids, protein and starch; serving as a boundary for the developing embryo sac; stabilisation of water balance in resting seeds; translocation of nutrients from the vascular bundle in the funiculus to the embryo; and enzyme and hormone production for the protection of mature seeds (Bhatnagar & Bhojwani, 2008).

While polystemony is characteristic for five out of the seven genera in the sarracenioid clade and was reconstructed as ancestral for the group, the ericoid clade is clearly non-polystemonous (Fig. 4A). In our reconstruction, polystemony is a synapomorphy for the sarracenioid clade, Symplocaceae and Theaceae (also present in several earlier diverging ericalean families; Kubitzki, 2004). A reversal to haplostemony has apparently occurred in *Roridula*, indicating that polystemony is not an irreversible state. All genera except *Camellia* appear to have a basic androecium organisation corresponding to the merism of the corolla, with primary primordia typically arising in alternipetalous positions with subsequent secondary proliferation of primordia (Caris, 2013; Löfstrand & Schönenberger, Chapter III). The second whorl of stamens

present in some genera typically occurs in antepetalous positions, with or without secondary proliferation of androecium primordia (Brown, 1935; Caris, 2013). In most polystemonous taxa in Ericales, the primordia proliferate centrifugally, whereas they proliferate both centripetally and centrifugally in *Actinidia chinensis* (Caris, 2013). In *Camellia*, the type of polystemony is somewhat unclear, with the ring-like stamen primordia seemingly arising in multiple whorls (Sugiyama, 1991). With regard to the function of the polystemonous state in the taxa included in this study, we assume that the stamens have a pollinator attracting and rewarding function in the open flowers of Actinidiaceae, *Heliamphora*, Symplocaceae and Theaceae. In these groups, the stamen filaments and/or anthers are often of a contrasting colour to the perianth (Wu & Nootebom, 1996; Li & al., 2007; Min & Bartholemew, 2007b; Löfstrand, 2015). *Darlingtonia* and *Sarracenia* of Sarraceniaceae both have stamens concealed by the synorganised sepals and petals (Löfstrand & Schönenberger, 2015). In all sarracenioid species, where pollination has been studied, pollen is the main reward, further explaining the utility of the many androecium organs and large pollen production even in functionally female flowers of Actinidiaceae (Löfstrand & Schönenberger, 2015).

The number of androecium whorls is variable in Ericales with several shifts between one and two whorls (Fig. 4B; Schönenberger & al., 2005). The ancestor of the sarracenioid clade was reconstructed to have had one whorl of androecium organs. The number of androecium whorls number in *Clematoclethra* and *Sarracenia* have not been unequivocally determined, therefore the interpretation of androecial evolution in the sarracenioids may change once these have been established. The ancestor of the ericoid clade, contrastingly, had two androecium whorls, with loss of the antepetalous whorl in *Cyrilla* (Cyrillaceae) and *Leucopogon* R.Br. (Styphelioideae, Ericaceae). The ancestor of core Ericales and the styracoid clade alike had one androecium whorl, with the Diapensiaceae–Styracaceae clade acquiring a second whorl (Fig. 4B; Kubitzki, 2004; Caris, 2013). Theaceae have one to many androecium whorls and Pentaphylacaceae have one or two androecium whorls (Tsou, 1998; Min & Bartholemew, 2007a, b; Zhang & Schönenberger, 2014). Hence, in Ericales, there is no evidence of haplostemony being an evolutionary dead-end without possible reversal to diplostemony; see Ronse Decraene & Smets (1995) for a comprehensive discussion. On the contrary, loss and secondary gain of an inner androecium whorl has probably occurred several times even within core Ericales; most ericalean taxa with two androecium whorls are diplostemonous as opposed to obdiplostemonous and most taxa with a single androecium whorl are haplostemonous as opposed to obhaplostemonous; see Caris (2013) for an overview. In other words, evolutionarily speaking, there is considerable plasticity in the absence versus presence of a homologous antepetalous androecium whorl in Ericales. An alternative explanation would be that numerous occurrences of *de novo* antepetalous androecium whorls arose independently, leading to the diplostemonous lineages present in the order.

The orientation of the anther attachment in the ancestor of core Ericales was inferred to be adaxial (before the anther inversion) with a reversal to abaxial in Sarraceniaceae and Cyrillaceae (Fig. 4C). As opposed to the structural anther attachment (basifixed, dorsifixed or ventrifixed), this secondary trait accounts for the structural direction of anthers and the orientation at which the stamen filament joins the connective tissue. As a result, visual inspection of the stamens is enough to determine the trait, as opposed to the need of microtome series or scanning electron microscopy investigations, as in the case of many taxa with free thecal lobes. In other words, sagittate, basifixed anthers do not necessarily have a proximal orientation of the anther attachment. More importance is put on the macroscopic orientation of the anther attachment; that is, if the filament meets the anther at the abaxial side (seemingly or truly dorsifixed), adaxial side (seemingly or truly ventrifixed) or is unequivocally proximal (filament orientation parallel to anther, seemingly or truly basifixed). A further strength of this trait compared to the structural anther attachment is that botanical illustrations or visual inspection of a flower is enough to determine the state, also making the use of older publications possible. Many publications on

floral morphology in, *e.g.*, Ericaceae do actually use this character to describe the anther shape rather than the structural anther attachment (*e.g.* Palser, 1951, 1954, 1961). An adaxial orientation of the anther attachment was reconstructed as synapomorphic for core Ericales and potentially coevolved with anther inversion from extrorse to introrse anther orientation during flower development, regardless of the stage at which the inversion occurs. Schönenberger & al. (2012) suggested a link between ventrifixed anthers and 'Late anther inversion type A', but many of the species with this type of anther inversion have basifixed anthers (see *e.g.* Copeland, 1941, 1947; Palser, 1951, 1954; Caris, 2013; Löfstrand & Schönenberger, 2015), whereas ventrifixed anthers do occur in some species with 'Early anther inversion' (*e.g.* Palser 1961; Palser & Murty, 1967). In Ericales, ventrifixed anthers are also known from Polemoniaceae, but unlike core Ericales, Polemoniaceae does not have any kind of anther inversion and, unexpectedly, the anthers are introrse regardless of their ventrifixed nature (Schönenberger, 2009; Schönenberger & al., 2010). Cyrillaceae and Sarraceniaceae independently reversed to the plesiomorphic abaxial orientation of the anther attachment position, with a further change to a proximal orientation of the anther attachment in the unusual case of *Darlingtonia*, where the anther orientation can be unequivocally assigned as a result of the complex anther morphology (Löfstrand & Schönenberger, 2015).

Anther inversion during flower development in Ericales is restricted to, and synapomorphic for, core Ericales (Fig. 4D). See Schönenberger & al. (2012), Caris (2013) and Löfstrand & Schönenberger (2015) for most the recent accounts and discussions of the trait. 'Early anther inversion' is present in Cassiopoideae, Ericoideae, Harrimanelloideae, Styphelioideae and Vaccinioideae of Ericaceae; 'Late anther inversion type A' is present in Actinidiaceae, Roridulaceae, Clethraceae and Arbutoideae, Enkianthoideae and Monotropoideae of Ericaceae; and 'Late anther inversion type B' is present in *Heliamphora* and *Sarracenia*. *Darlingtonia* has anthers that invert at the onset of anthesis, but this is due to it complex anther morphology, which is characterised by a larger theca that is extrorse during development and hence inverts to an introrse orientation at anthesis and a smaller theca that is introrse during development and hence inverts to an extrorse orientation at anthesis ('Late anther inversion type C'; Löfstrand & Schönenberger, 2015). In *Saurauia subspinosa*, the anthers partially invert from the developmental extrorse orientation to an introrse orientation prior to anthesis (yet clearly later than the members of crown-group Ericaceae); see Caris (2013) and Löfstrand & Schönenberger (2015). In *Cassiope* (Cassiopoideae, Ericaceae), anther inversion is initiated early in the development of the floral bud, but either never completes the inversion to an introrse orientation, or is only completed at the beginning of anthesis (Palser, 1951). Additionally, some Ericaceae with early anther inversion have an apical, rather than introrse, anther orientation at anthesis (Caris, 2013). To further confuse the matter, some *Actinidia* species have variable proportions of extrorse, introrse and latrorse anthers in the same flower during floral development and some of the anthers never invert at the onset of anthesis; during development, the majority of the anthers are more or less extrorse and at anthesis the majority of the anthers invert to more or less introrse (Löfstrand & Schönenberger, 2015). What seems clear is that 'Late anther inversion type A' is synapomorphic for core Ericales and 'Late anther inversion type B' is synapomorphic for the *Heliamphora–Sarracenia* clade (Fig. 4D). In addition, 'Early anther inversion' is clearly synapomorphic for crown group Ericaceae. Also, there is a general association of adaxial orientation of the anther attachment (seemingly or truly ventrifixed anthers) and the inversion from extrorse to introrse anther orientation at some point during the flower development (Figs 4C, D).

Partially free styles (Fig. 4E), suggested by Anderberg & al. (2002) as a potential synapomorphy for the sarracenioid clade (with reversals to completely united styles in *Clematoclethra*, *Heliamphora* and *Roridula*) is a somewhat complicated issue. Clethraceae and Cyrillaceae, like *Actinidia*, *Saurauia*, *Darlingtonia* and *Sarracenia*, have partially free styles but in the former two families the free part of the styles is generally much shorter than among the

members of the sarracenioid clade (Qin & Fritsch, 2005; Tucker & Jones, 2009; Lemke 2009; Löfstrand & Schönenberger, 2015). In Clethraceae and Cyrillaceae, the styles are less than 10% free and more or less erect, whereas the styles in the sarracenioid clade are typically free for at least 20% and distally spreading (Qin & Fritsch, 2005; Tucker & Jones, 2009; Lemke 2009; Löfstrand & Schönenberger, 2015). As the degree of within whorl organ union is highly variable in Ericales and relatively few taxa in these families have been studied in detail (Kavaljian, 1952; Copeland, 1953; Dute & al., 2004; Löfstrand & Schönenberger, 2015), we applied a conservative approach distinguishing only between completely united and partially or completely free styles. Based on this definition of the trait, the ancestor of the sarracenioid clade indeed had free styles, but the trait is reconstructed as a parallelism with the ancestor of the ericoid clade, whereas the ancestor of core Ericales appear to have had completely united styles (Fig. 4E). Additionally, *Clematoclethra* (Actinidiaceae), *Heliamphora* (Sarraceniaceae), *Roridula* (Roridulaceae), and Ericaceae all reverted to the completely united styles, further reinforcing the plasticity of organ union both within and among families.

A depression at the ovary–style transition, was inferred as a synapomorphy for core Ericales (Fig. 4F). However, such a depression is lacking in the *Heliamphora–Sarracenia* clade, in *Clethra,* in *Arbutus*, and in functionally male flowers of *Actinidia* (Kavaljian, 1952; Palser, 1954; Löfstrand & Schönenberger, 2015). While the data are fragmentary in much of Ericales, the trait appears to be uncommon, if at all present outside core Ericales (Kubitzki, 2004). Within the clade, the size of the depression may be minute, as in *e.g. Roridula gorgonias,* or deep and conspicuous, as in *e.g. Darlingtonia californica* (Löfstrand & Schönenberger, 2015). A possible explanation for the depression is the collapse of the tissue during ovary development due to the incompletely septate carpels characterising the clade (Löfstrand & Schönenberger 2015). This could explain why the depression is lacking in male *Actinidia* flowers (no incomplete septation present in the ovary) and is minute in species with an intermediate degree of incomplete septation, such as functionally female *Actinidia*, and prominent in species with a large void formed by the incomplete septation, as it is present in *e.g. Darlingtonia* (Löfstrand & Schönenberger, 2015). It does however not explain why other taxa with incomplete septation of the ovary outside core Ericales, among others Symplocaceae (Fritsch & al., 2008), do not display a depression at the ovary–style transition.

SIMILARITIES TO FLORAL MESOFOSSILS

Two late Cretaceous mesofossil genera with well-preserved flowers have tentatively been placed in or close to Actinidiaceae: *Parasaurauia* Keller, Herendeen & Crane and *Glandulocalyx* Schönenberger, von Balthazar, Takahashi, Xiao, Crane & Herendeen (Keller & al., 1996; Schönenberger & al., 2012; Löfstrand & Schönenberger, 2015). Of the characters investigated here, an adaxial orientation of the anther attachment and partially free styles link both fossil genera to extant Actinidiaceae (Keller & al., 1996; Schönenberger & al., 2012). *Glandulocalyx* is additionally polystemonous and *Parasaurauia* displays a depression at the ovary–style transition, both characters common in extant Actinidiaceae (Keller & al., 1996; Schönenberger & al., 2012; Löfstrand & Schönenberger, 2015). Both species also have trimerous gynoecia, linking them to *Roridula* or *Saurauia*, while they share more morphological similarities with the latter genus (Keller & al., 1996; Schönenberger & al., 2012). Two characters shared by *Parasaurauia*, *Glandulocalyx* and *Saurauia* are conspicuous, pluriseriate trichomes present on sepals and capitate stigmas with ventral grooves (Keller & al., 1996; Schönenberger & al., 2012).

CONCLUDING REMARKS

The monophyly of all sarracenioid families, the Actinidiaceae–Roridulaceae clade, the *Actinidia–Clematoclethra* clade, the *Heliamphora–Sarracenia* clade and all sarracenioid genera was confirmed. Additionally, two distinct geographical clades were identified in *Saurauia*. These lineages may be characterised by generally different degrees of organ union in the petals and styles, differences in the most common gynoecium merism and differences in basic chromosome numbers. A need for modern taxonomic revisions is highlighted for *Saurauia* and supraspecific taxa in *Actinidia*, potentially also for *Sarracenia*.

Our ancestral state reconstructions showed that the following floral characters are synapomorphic for core Ericales: an adaxial orientation of the anther attachment (with independent reversals to an abaxial orientation in Sarraceniaceae and Cyrillaceae); anther inversion from an extrorse to an introrse position at the onset of anthesis (with subsequent changes to other patterns of anther inversion in Sarraceniaceae and many Ericaceae, and a reversal to non-inverting anthers in Cyrillaceae); and the presence of a depression at the ovary–style transition (with independent reversals in the *Heliamphora–Sarracenia* clade and in Clethraceae). Floral synapomorphies for the sarracenioid clade are: petals that are proximally as thick or thicker than the proximal region of the sepals; presence of a nucellar hypostase in ovules; and polystemony (with a reversal to haplostemony in *Roridula* and, potentially, diplostemony in *Clematoclethra*). Floral synapomorphies for the Actinidiaceae–Roridulaceae clade are: presence of calcium oxalate raphides in floral tissue; presence of mucilage cells in floral tissue; presence of a secretory inner gynoecium surface; and absence of synlateral vasculature in the ovary.

To affirm the evolutionary origin of anatomical, histological and morphological characters investigated in this study, a larger sampling, both within and outside the sarracenioid clade, is needed in future studies.

ACKNOWLEDGEMENTS

We thank the herbaria E and MO for access to herbarium material; UniVie Botanical Garden, Peter Brownless at RBGE, Eric La Fountaine at UBC Botanical Garden and Agneta Julia Borg for new collections; Michael Barfuss and Elfriede Grasserbauer for assistance in the lab. We are additionally grateful to Aelys Humphries at Stockholm University for suggestions on text improvements.

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Appendix 1. Sampled taxa, voucher information and GenBank accession numbers. Newly generated sequences are indicated with an asterisk (*).

Species Author, *voucher specimen* (herbarium), ITS, *rbcL*, *rpl32–trnL*, *trnK*, *trnL–F*

Actinidia arguta Miq., *Brownless 201* (E), KR819506*, KR819563*, KR819614*, KR819663*, KR819713*; *Actinidia callosa* Lindl., *Wang & al. 169* (E), KR819507*, KR819564*, KR819615*, KR819664*, KR819714*; *Actinidia chinensis* Planch., *Huang & al. 123* (MO), KR819508*, KR819565*, KR819616*, KR819665*, KR819715*; *Actinidia chrysantha* C.F.Liang, AF323797, AJ549035, -, AF322603, AJ548990; *Actinidia cylindrica* C.F.Liang, AF323806, AJ549040, -, AJ548995, AF322605; *Actinidia eriantha* Benth., AF323800, AJ549051, -, AF322605, AJ549006; *Actinidia fulvicoma* Hance., AF323799, AJ549057, -, AF323968, AJ549012; *Actinidia glaucophylla* F.Chun, AF323798, AJ549043, -, AF322604, AJ548998; *Actinidia hemsleyana* Dunn, AF323802, AJ549036, -, AF322608, AJ548991; *Actinidia indochinensis* Merr., -, AJ549054, -, -, AJ549009; *Actinidia kolomikta* Maxim., *Brownless 204* (E), KR819509*, KR819566*, KR819617*, KR819666*, KR819716*; *Actinidia latifolia* (Gardner & Champ.) Merr., AF323825, AJ549037, -, AF322610, AJ548992; *Actinidia macrosperma* C.F.Liang, AF323833, AJ549053, -, -, AJ549008; *Actinidia melanandra* Franch., AF323808, AJ549050, -, AF322600, AJ549005; *Actinidia melliana* Hand.-Mazz., AF323820, AJ549067, -, AF322609, AJ549022; *Actinidia persicina* R.H.Huang & S.M.Wang, AF323814, AJ549068, -, AF322611, AJ549023; *Actinidia pilosula* (Finet. & Gagnep.) Stapf., *Li & al. 12959* (E), KR819510*, KR819567*, KR819618*, KR819667*, KR819717*; *Actinidia polygama* Franch & Sav., AF323796, AJ549071, -, AF322601, AJ549026; *Actinidia rubricaulis* Dunn., *Cuong 2051* (MO), KR819511*, KR819568*, KR819619*, KR819668*, KR819718*; *Actinidia rudis* Dunn., *Cuong 2047* (MO), KR819512*, KR819569*, KR819620*, KR819669*, KR819719*; *Actinidia rufa* Franch. & Sav., *Brownless 199* (E), KR819513*, KR819570*, KR819621*, KR819670*, KR819720*; *Actinidia sabiifolia* Dunn, AF323812, -, AJ549039, -, AF322607, AJ548994; *Actinidia strigosa* Hook.*f.* & Thomson, *Noshiro & al. 9240547* (E), KR819514*, KR819571*, KR819622*, KR819671*, KR819721*; *Actinidia styracifolia* C.F.Liang, AF323822, AJ549033, -, AF322612, AJ548988; *Actinidia valvata* Dunn, AF323842, AJ549052, -, AF322602, AJ549007; *Actinidia venosa* Rehder, *Aldén & al. 1723* (E), KR819515*, KR819572*, KR819623*, KR819672*, KR819722*; *Actinidia zhejiangensis* C.F.Liang, AF323817, -AJ549038, -, AF322613, AJ548993; *Arbutus canariensis* Duhamei, -, L12597, -, U61345, -; *Archeria comberi* Summerh. ex Orr, **-, U79741, -, AF015632, -;** *Camellia japonica* L., -, AF380035, AF396225, AF380074, -; *Cassiope fastigiata* D.Don, *Crawford & al. 630* (MO), KR819516*, KR819573*, KR819662*, KR819673*, KR819723*; *Chimaphila maculata* Pursch, -, KF613044, -, AF440414, -; *Clematoclethra scandens* subsp. *actinidioides* (Maxim.) Y.C.Tang & Q.Y.Xiang, AF323805, -, Z80172, -, AF322618, AJ549032; *Clematoclethra scandens* subsp. *hemsleyi* (Baill.) Y.C.Tang & Q.Y.Xiang, *Straley 5519* (UBC), KR819517*, KR819574*, KR819624*, KR819674*, KR819724*; *Clethra arborea* Aiton, -, -, HM850891, AY190593; *Cyrilla racemiflora* L., -, -, AF380080, AJ430872; *Darlingtonia californica* Torr., *Löfstrand 4* (W), KR819518*, KR819575*, KR819625*, KR819675*, KR819725*; *Enkianthus campanulatus* G.Nicholson, -, L12616, -, U61344, -; *Gaultheria procumbens* L., -, KJ841345, -, AF366643, JF801637; *Harrimanella hypnoides* (L.) Coville, -, U82766, -, U61315, -; *Heliamphora heterodoxa* Steyerm., JQ218242, -, -, -, JQ218258, -; *Heliamphora ionasi* Maguire, *Löfstrand 6* (W), KR819519*, KR819576*, KR819626*, KR819676*, KR819726*; *Heliamphora minor* Gleason, *Löfstrand 7* (W), KR819520*, KR819577*, -, KR819677*, KR819727*; *Heliamphora neblinae* Maguire, -, -, -, JQ218260, -; *Heliamphora nutans* Benth., *Löfstrand 8* (W), KR819521*, KR819578*, -, KR819678*, KR819728*; *Heliamphora pulchella* Wistuba, Carow, Harbarth & Nerz, *Löfstrand 9* (W), KR819522*, KR819579*, -, KR819679*, KR819729*; *Heliamphora tatei* Gleason, L42188 & L42202, -, -, -, -; *Rhododendron ferrugineum* L., -, KF602219, -, AB012741, AF394254; *Roridula dentata* L., AY950689, -, -, JQ218262, -; *Roridula gorgonias* Planch., *Löfstrand 3* (W),

KR819523*, -, KR819627*, KR819680*, KR819730*; *Sarracenia alabamensis* Case & R.B.Case, *Löfstrand 10* (W), KR819524*, KR819581*, KR819628*, KR819681*, KR819731*; *Sarracenia alata* (Alph.Wood) Alph.Wood, *Löfstrand 11* (W), KR819525*, KR819582*, KR819629*, KR819682*, KR819732*; *Sarracenia flava* L., *Löfstrand 12* (W), KR819526*, KR819583*, KR819630*, KR819683*, KR819733*; *Sarracenia jonesii* Wherry, JQ218238, -, -, JQ218248, -; *Sarracenia leucophylla* Raf., *Löfstrand 13* (W), KR819527*, KR819584*, KR819631*, KR819684*, KR819734*; *Sarracenia minor* Sweet, *Löfstrand 14* (W), KR819528*, KR819585*, KR819632*, KR819685*, KR819735*; *Sarracenia oreophila* Wherry, *Löfstrand 15* (W), KR819529*, KR819586*, KR819633*, KR819686*, KR819736*; *Sarracenia psittacina* Michx., *Löfstrand 16* (W), KR819530*, KR819587*, KR819634*, KR819687*, KR819737*; *Sarracenia purpurea* subsp. *purpurea* L., *Löfstrand 17* (W), KR819531*, KR819588*, KR819635*, KR819688*, KR819738*; *Sarracenia purpurea* subsp. *venosa* (Raf.) Wherry, JQ218230, -, -, JQ218246, -; *Sarracenia rosea* Naczi, Case & R.B.Case, *Löfstrand 18* (W), KR819532*, KR819589*, KR819636*, KR819689*, KR819739*; *Sarracenia rubra* Walter, *Löfstrand 5* (W), KR819533*, KR819590*, KR819637*, KR819690*, KR819740*; *Saurauia aspera* Turcz., *Meyer 9964* (MO), KR819534*, KR819591*, KR819638*, KR819691*, KR819741*; *Saurauia biserrata* Spreng., *Croat 57648* (MO), KR819535*, KR819592*, KR819639*, KR819692*, KR819742*; *Saurauia bullosa* Wawra, *Rubio & al. 2234* (MO), KR819536*, KR819593*, KR819640*, KR819693*, KR819743*; *Saurauia chaparensis* Soejarto, *Teran & al. 603* (MO), KR819537*, KR819594*, KR819641*, KR819694*, KR819744*; *Saurauia choriophylla* R.E.Schult. & G.Gut., *Fonnegra & al. 5699* (MO), KR819538*, KR819595*, KR819642*, KR819695*, KR819745*; *Saurauia conferta* Warb., *Bau & al. 84182* (E), KR819539*, -, -, -, KR819696*; *Saurauia fasciculata* Wall., *Noshiro & al. 9755133* (E), KR819540*, KR819596*, KR819643*, KR819697*, KR819746*; *Saurauia ferox* Korth., *Mantor 130145* (E), KR819541*, KR819597*, KR819644*, KR819698*, KR819747*; *Saurauia kegeliana* Schltdl., *Rodríguez & al. 747* (MO), KR819542*, KR819598*, KR819645*, KR819699*, KR819748*; *Saurauia leprosa* Korth., *Middleton & al. 3543* (E), KR819543*, KR819599*, KR819646*, KR819700*, KR819749*; *Saurauia macrotricha* Kurz., *Cuong 2040* (MO), KR819544*, -, -, -, -; *Saurauia magnifica* Soejarto, *Harling & Anderson 12675* (MO), KR819545*, KR819600*, KR819647*, KR819701*, KR819750*; *Saurauia malayana* Hoogland, *Julius & al. 57477* (E), KR819546*, -, -, -, -; *Saurauia montana* Seem., *Schönenberger 908* (W), KR819547*, KR819601*, KR819648*, KR819702*, KR819751*; *Saurauia napaulensis* DC., *Gaoligong Shan Biodiversity Survey 23389* (E), KR819548*, KR819602*, KR819649*, KR819703*, KR819752*; *Saurauia novoguineensis* Scheff., *Regalado & Sirikolo 786* (MO), KR819549*, -, KR819650*, -, KR819753*; *Saurauia oreophila* Hemsl., *Ávila & al. 3238* (MO), KR819550*, -, -, -, KR819754*; *Saurauia parviflora* Triana & Planch., *Croat & Gaskin 80128* (MO), KR819551*, KR819603*, KR819651*, KR819704*, KR819755*; *Saurauia pedunculata* Hook., *Cruz Paredes 147* (MO), KR819552*, KR819604*, KR819652*, KR819705*, KR819756*; *Saurauia pentapetala* (Jack) Hoogland, *Middleton & al. 3501* (E), -, KR819605*, KR819653*, KR819706*, KR819757*; *Saurauia pittieri* Donn.Sm., *Borg 17* (S), KR819553*, KR819606*, KR819654*, KR819707*, KR819758*; *Saurauia polyneura* C.F.Liang & Y.S.Wang, *Li & al. 8725* (MO), KR819554*, KR819607*, KR819655*, KR819708*, KR819759*; *Saurauia roxburghii* Wall., *Newman & al. 2339* (E), KR819555*, KR819608*, KR819656*, KR819709*, KR819760*; *Saurauia scabrida* Hemsl., *Gómez Chagala 822* (MO), KR819556*, -, KR819657*, -, KR819761*; *Saurauia spectabilis* Hook., *Fuentes & al. 10418* (MO), KR819557*, KR819609*, KR819658*, KR819710*, KR819762*; *Saurauia subspinosa* J.Anthony, *Löfstrand 2* (W), KR819558*, KR819610*, KR819659*, KR819711*, KR819763*; *Saurauia tewensis* Korth., *Burley & al. 3345* (E), KR819559*, KR819611*, KR819660*, -, KR819764*; *Saurauia ursina* Triana & Planch., *Gentry & al. 76191* (MO), KR819560*, -, -, -, KR819765*; *Saurauia waldheimia* Buscal., *Stevens & al. 29397* (MO), KR819561*, KR819612*, KR819661*, KR819712*, KR819766*; *Saurauia yasicae* Loes., *Aguilar 5581* (MO), KR819562*, KR819613*, -, -, KR819767*.

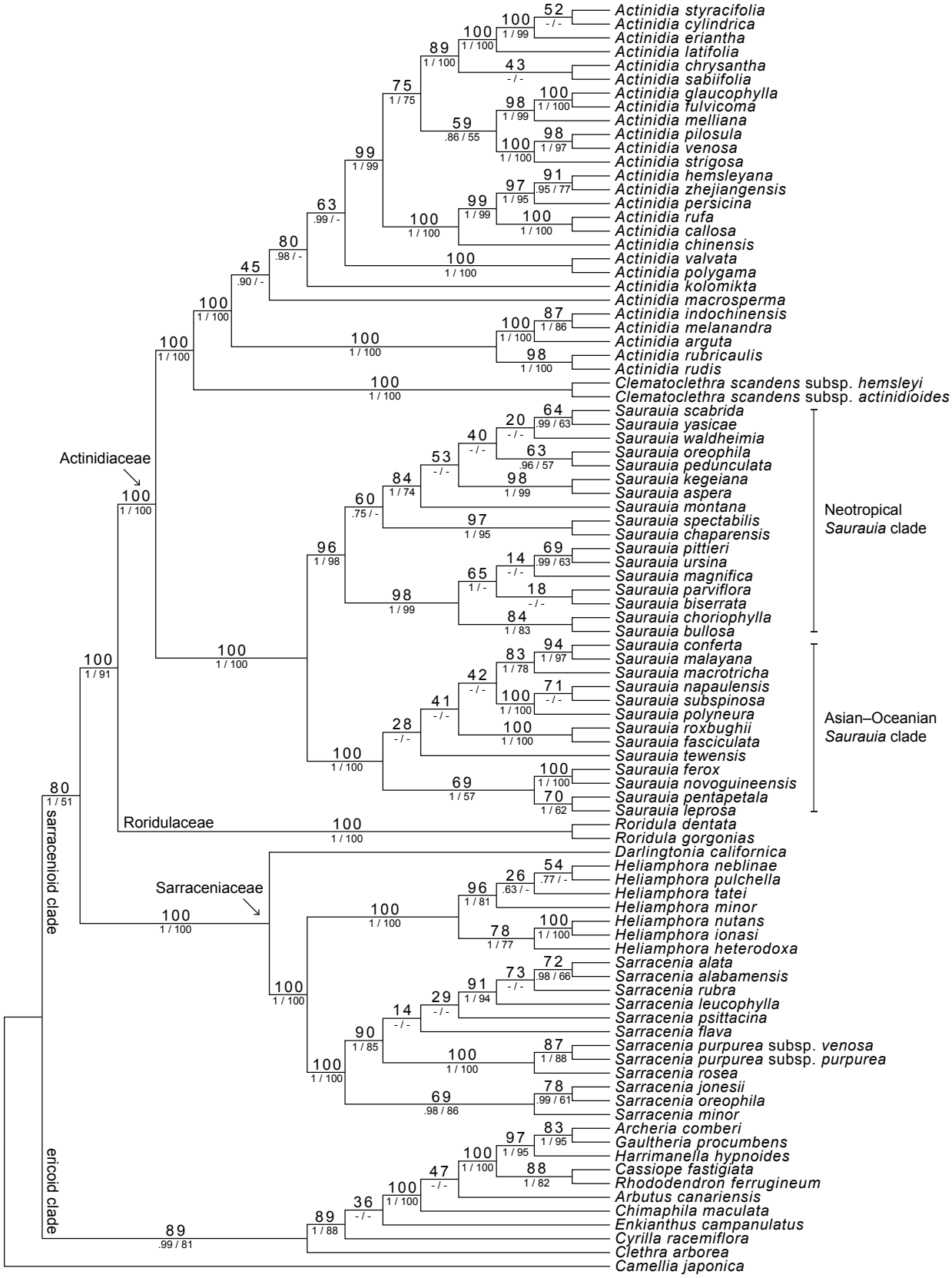
Appendix 2. Details of primers used in this study; matK160R (located in the 5' end of the *matK* gene) was designed by Sutee Duangjai (Department of Forest Biology, Kasetsart University, Thailand); ITS-5c (located in the 3' end of the 18S gene) was designed by Michael H.J. Barfuss (Department of Botany and Biodiversity Research, University of Vienna, Austria). Abbreviations: A = amplification; S = sequencing. Annealing temperatures: 1F+1460R: 48°C; rpl32F+trnL$^{(UAG)}$: 48°C; trnK-3914F+matK160R: 48°C; 80F+matK880R: 48°C; 800F+1710R: 48°C; c+f: 49°C; ITS-5C+26S R: 55°C.

Region	Primer	Usage	Primer sequence from 5' end	Reference
rbcL	1F	A+S	ATG TCA CCA CAA ACA GAA AC	Fay & *al.* (2002)
	1460R	A+S	TCC TTT TAG TAA AAG ATT GGG CCG AG	Fay & *al.* (2002)
	636Fn	S	TAT GCG TTG GAG AGA CCG TTT C	Fay & *al.* (2002)
	724R	S	TCG CAT GTA CCT GCA GTA GC	Fay & *al.* (2002)
rpl32–trnL	rpL32-F	A+S	CAG TTC CAA AA A AAC GTA CTT C	Shaw & *al.* (2007)
	trnL$^{(UAG)}$	A+S	CTG CTT CCT AAG AGC AGC GT	Shaw & *al.* (2007)
trnK	trnK-3914F	A+S	GGG GTT GCT AAC TCA ACG G	Johnson & Soltis (1994)
	matK160R	A+S	AGT AAT TAA ACG TTT CRC ART TAG	This study
	80F	A+S	CTA TAC CCA CTT ATC TTT CGG GAG T	Samuel & *al.* (2005)
	matK880R	A+S	CCA GAA ATT GAC AAG GTA ATA TTT CC	Duangjai & *al.* (2009)
	800F	A+S	CAT GCA TTA TGT TAG GTA TCA AGG	Samuel & *al.* (2005)
	1710R	A+S	GCT TGC ATT TTT CAT TGC ACA CG	Samuel & *al.* (2005)
trnL–F	c	A+S	CGA AAT CGG TAG ACT CTA CG	Taberlet & *al.* (1991)
	f	A+S	ATT TGA ACT GGT GAC ACG AG	Taberlet & *al.* (1991)
	d	S	GGG GAT AGA GGG ACT TGA AC	Taberlet & *al.* (1991)
	e	S	GGT TCA AGT CCC TCT ATC CC	Taberlet & *al.* (1991)
ITS	ITS-5c	A+S	AGA GGA AGG AGA AGG CGT AAC AA	This study
	26s R	A+S	GGA CGC TTC TCC AGA CTA CAA TT	Gruensteudl & *al.* (2009)
	5.8s F	S	ACT CTC GGC AAC GGA TAT CTC GGC TC	Gruensteudl & *al.* (2009)
	5.8s R	S	ATG CGT GAC GCC CAG GCA GAC GTG	Gruensteudl & *al.* (2009)

Appendix 3. Morphological character matrix. **A:** *Calcium oxalate raphides in floral tissue* (0 = absent, 1 = present). **B:** *Mucilage cells in floral tissue* (0 = absent, 1 = present). **C:** *Proximal petal thickness* (0 = thinner than sepal bases, 1 = equal to or thicker than sepal bases). **D:** *Secretory inner gynoecium surface* (0 = absent, 1 = present). **E:** *Synlateral vasculature in ovary* (0 = absent, 1 = present). **F:** *Nucellar hypostase in ovules* (0 = absent, 1 = present). **G:** *Polystemony* (0 = absent, 1 = present). **H:** *No. androecium whorls* (0 = one, 1 = two, 2 = irregular). **I:** *Orientation of anther attachment* (0 = abaxial, 1 = adaxial, 2 = proximal). **J:** Anther inversion (0 = late type A, 2 = late type B, 3 = late type C, 4 = early). **K:** Style union (0 = completely united, 1 = partially free). **L:** Depression at ovary–style transition (0 = absent, 1 = present).

SPECIES	A	B	C	D	E	F	G	H	I	J	K	L
Actinidia arguta	1	1	1	1	0	1	1	0	1	1	1	1
Actinidia chinensis	1	1	1	1	0	1	1	0	1	1	1	1
Clematoclethra scandens	1	1	1	1	0	1	0	?	1	1	0	1
Saurauia pittieri	1	1	1	1	0	1	1	0	1	1	1	1
Saurauia subspinosa	1	1	1	1	0	1	1	0	1	1	1	1
Roridula gorgonias	1	1	1	1	0	1	0	0	1	1	0	1
Darlingtonia californica	0	0	1	0	1	1	1	0	2	3	1	1
Heliamphora nutans	0	0	1	0	1	1	1	0	0	2	0	0
Sarracenia leucophylla	0	0	1	0	1	1	1	?	0	2	1	0
Sarracenia purpurea	0	0	1	0	1	1	1	?	0	2	1	0
Clethra alnifolia	0	0	0	0	1	0	0	1	1	1	1	0
Cyrilla racemiflora	0	0	0	0	1	0	0	0	0	0	1	1
Enkianthus campanulatus	0	0	0	0	1	0	0	1	1	1	0	1
Monotropa hypopitys	0	0	?	0	1	0	0	1	1	1	0	1
Arbutus unedo	0	0	0	0	1	?	0	1	1	1	0	0
Cassiope mertensiana	0	0	?	0	1	0	0	1	1	4	0	1
Erica carnea	0	0	0	0	?	0	0	1	1	4	0	1
Harrimanella hypnoides	0	0	0	0	1	0	0	1	1	4	0	1
Vaccinium vitis-idaea	0	0	?	0	1	0	0	1	1	4	0	1
Leucopogon amplexicaulis	0	0	0	0	1	0	0	0	1	4	0	?
Galax urceolata	0	0	0	0	1	0	0	1	2	0	0	0
Styrax japonicus	0	0	0	0	1	0	0	1	2	0	0	0
Symplocos paniculata	0	0	0	0	1	0	1	0	0	0	0	1
Camellia japonica	0	0	0	0	1	1	1	2	0	0	0	0
Pentaphylax euryoides	?	?	?	?	?	0	0	0	0	0	0	0

Appendix 4. Best scoring maximum likelihood tree (cladogram) from the combined analysis (rooted with *Camellia*). Maximum likelihood bootstrap support above branches; Bayesian posterior probability and parsimony bootstrap support values below branches. Hyphens (-) denote Bayesian posterior probability or parsimony bootstrap support < 50.



CONCLUDING DISCUSSION

METHODOLOGY

MORPHOLOGICAL TECHNIQUES (CHAPTERS II, III)

Taxon sampling was based on the inclusion of at least one species per extant genus in the sarracenioid clade, earlier collected material and availability in botanical gardens.

For the structural study (Chapter II), the investigations were primarily based on light microscopy (LM) studies of microtome section series; the technique is unsurpassed in detail for internal morphological and histological characters, as well as anatomy. LM studies were additionally used as a complement in Chapter III. For the developmental study (Chapter III), the principal investigation technique was scanning electron microscopy (SEM; also used for morphology and external histology in Chapter II). The technique allows for great magnification of structures in sharp contrast, allowing studies of micro morphological and micro histological studies of external structures (also used to study placentation patterns and ovule structure in Chapter II). Microcomputer X-ray tomography (Micro-CT) was used for three-dimensional studies of the complicated gynoecial structure in *Sarracenia*. The technique is excellent as a non-destructive way to study rare or fragile material, as well as three-dimensional studies, allowing for detailed measurements, but the resolution is often not sufficient for the study of micro morphological and micro histological characters. For details on LM, SEM and Micro-CT methodology, see Chapter II, Igersheim (1993), Weber & Igersheim (1994), Igersheim & Cichocki (1996), Fischer *et al*. (2012) and Staedler *et al*. (2014).

MOLECULAR TECHNIQUES (CHAPTER IV)

Taxon sampling was based on availability in the herbaria E and MO, earlier collected material, availability in the Botanical Garden of the University of Vienna and previously published sequences in GenBank. Region sampling was based on availability in GenBank and high potential for informative content. Standard techniques were employed for DNA extraction, amplification and sequencing. Because of low toxicity, high yield and reproducibility, extraction kits, clean-up kits and sequencing kits were used; see Chapter III for details.

For reproducibility and to avoid the risk of arbitrary alignment positions, sequence alignments were carried out in MUSCLE (Edgar, 2004). Because phylogenetic analyses of DNA sequence data are sensitive to the selected nucleotide substitution model (particularly when using a Bayesian approach for phylogenetic inference; *e.g*. Erixon *et al*., 2004), models were selected under the corrected Akaike information criterion (AICc) as implemented in jModelTest (Darriba *et al*., 2012; Guindon & Gascuel, 2003).

Phylogenetic reconstructions were mainly based on a maximum likelihood approach with bootstrapping (using RAxML; Stamatakis, 2006), supported by Bayesian inference of posterior probability (using MrBayes, Ronquist et al., 2011) and parsimony with bootstrapping (using PAUP*; Swofford, 2002). The use of maximum likelihood as the principal method for phylogenetic inference was based mainly on the low sensitivity to sampling errors and model of nucleotide substitution (*e.g*. Stamatakis, 2006). However, the approach is potentially sensitive to the relative content of missing data (*e.g*. Simmons, 2011, 2014; Jiang *et al*., 2014) and was therefore complemented with other phylogenetic approaches. Bayesian inference, similarly to maximum likelihood inference, includes a model of nucleotide substitution in the analysis (*e.g*. Ronquist *et al*., 2011). However, the approach is sensitive to incorrectly selected nucleotide substitution models and has been proposed to over-estimate statistical support for incorrect clades (*e.g*. Zander, 2004; Simmons & Norton, 2014). Parsimony is widely used in plant systematics, but does not include models of nucleotide substitution in the analysis and is, under

certain circumstances, not statistically consistent, most well known is perhaps the phenomenon of 'long branch attraction' (*e.g*. Felsenstein, 1978; Swofford, 2002).

ANCESTRAL STATE RECONSTRUCTIONS

Ancestral state reconstructions of floral characters (Chapter IV) were conducted in Mesquite (Maddison & Maddison, 2015). A maximum likelihood approach was selected for the reconstructions because of the lesser sensitivity to (potentially incorrect) topology and the additional indication of statistical support (*e.g*. Cunningham *et al*., 1998; Li *et al*., 2010; Maddison & Maddison, 2015).

Ancestral state reconstructions are sensitive to taxon sampling and, naturally, the phylogenetic relationships (topology) in the studied group (*e.g*. Cunningham *et al*., 1998; Li *et al*., 2010). The results of the ancestral state reconstructions in Chapter IV should therefore be viewed as preliminary, pending studies in a larger phylogenetic context (with well-established phylogenetic relationships in Ericales). Additionally, some of the histological characters with inferred evolution are not widely investigated in Ericales and may turn out to be also present in other ericalean families (Chapters II, IV).

DEVELOPMENTAL AND STRUCTURAL EVIDENCE

The following discussion will mainly focus on floral characters deemed to be of systematic significance in Chapters II–IV. The potential functions of the characters will not be discussed here (see Preamble, Chapters II–IV and references for more comprehensive accounts).

GENERAL FLORAL STRUCTURE

Flowers in the sarracenioid clade are actinomorphic with superior ovaries (subinferior in *Roridula*; Chapter II); they are solitary (*Darlingtonia* and *Sarracenia*) or borne on few to many flowered inflorescence branches (Actinidiaceae, *Roridula*, *Heliamphora*; Chapters II, III; Macfarlane, 1908; Gilg & Werdermann, 1925; Diels, 1930). Flowers are structurally bisexual, but often functionally unisexual in *Actinidia* and *Saurauia* (Macfarlane, 1908; Diels, 1930; Soejarto, 1969, 1980; Cuong *et al*., 2007; Li *et al*., 2007). The perianth is two-whorled and typically pentamerous (di- to trimerous in *Heliamphora*; Chapters II, III), although variable in *Actinidia* and *Saurauia* (Chapters II, III; Macfarlane, 1908; Diels, 1930; Soejarto, 1980; Li *et al*., 2007). In non-pentamerous perianths of Actinidiaceae, paired organs ('dédoublement') are common (Chapters II, III; Caris, 2013). Androecia are polystemonous in all sarracenioids except *Clematoclethra* (ten stamens) and *Roridula* (five stamens; Chapters II–IV; Macfarlane, 1908; Gilg & Werdermann, 1925; Diels, 1930). The stamens are arranged in one whorl-like structure (but borne on a ring primordium) in most polystemonous species, although some *Actinidia* and *Saurauia* have stamens arranged in two or more whorl-like structures (Chapters II, III; Macfarlane, 1908; Dickison, 1972; Berry *et al.,* 2005; Li *et al*., 2007; Caris, 2013). In *Sarracenia* (and less clearly in *Darlingtonia*), the stamens are arranged in groups, but the early androecium development is unknown (Chapters II, III; Mellichamp, 2009). Gynoecia have three (*Roridula, Heliamphora* and *Saurauia p.p*.; Chapters II, III; Macfarlane, 1908; Diels, 1930; Li *et al*., 2007), five (*Clematoclethra*, *Saurauia p.p*., *Darlingtonia*, *Sarracenia*; Chapters II, III; Macfarlane, 1908; Soejarto, 1980) or numerous (*Actinidia*; Chapters II, III; Li *et al*., 2007) carpels, although carpel merism is variable in *Saurauia* (Chapters II, III; Hunter, 1966; Soejarto, 1980; Cuong *et al*., 2007; Li *et al*., 2007). Ovaries are syncarpous, but style union varies in the clade: *Clematoclethra*, *Roridula* and *Heliamphora* have completely united styles (Chapter II; Macfarlane, 1908; Gilg & Werdermann, 1925; Diels, 1930); *Darlingtonia*, *Sarracenia* and *Saurauia p.p*. have partially united styles (Chapters II–IV; Macfarlane, 1908; Cuong *et al*., 2007; Li *et al*., 2007); and *Actinidia* and *Saurauia p.p*. have almost completely free styles (Chapters II, III; Soejarto, 1980; Li *et al*., 2007). In sum, the flowers of the sarracenioids is similar to that of

many other Ericales, with the exception of the multicarpellate gynoecia in *Actinidia* and largely free styles in most species (Chapters II–IV; Kubitzki, 2004).

All sarracenioids are characterised by tanniferous floral tissue (Chapter II), a common enough floral trait in Ericales (*e.g.* Palser, 1951, 1961; Kavaljian, 1952; Paterson 1961; Dickison, 1993; Sugiyama, 1997; von Balthazar & Schönenberger, 2013), but a more interesting character from a systematic point of view is the presence of condensed tannins in most floral tissue (Chapter II). The only other ericalean species known to contain similar histological structures in the cells is *Pelliciera rhizophorae* Planch. & Triana (Tetrameristaceae; unpubl. data: M. von Balthazar & J. Schönenberger). However, data is fragmentary in Ericales and more detailed histological studies are needed for most families in order to determine the systematic significance of condensed tannins (Chapters II, IV).

The floral tissue in the Actinidiaceae–Roridulaceae subclade is further characterised by the: presence of calcium oxalate raphide bundles and mucilage cells (Chapter II). The only other ericalean group known to have both these floral histological traits is the balsaminoid clade (Balsaminaceae, Marcgraviaceae and Tetrameristaceae; von Balthazar & Schönenberger, 2013), although *Polemonium reptans* L. (Polemoniaceae) also contains mucilage in the stamen filaments (Schönenberger, 2009). While detailed floral histological investigations are still lacking for many ericalean families and genera, it stands to reason that these characters would, if present, be mentioned in floral morphological studies. The calcium oxalate raphide bundles are very prominent, equally visible by sight in fresh, alcohol preserved, air dried and critical point dried material, they additionally have a tendency to dull the microtome blade and rip sections (Chapter II; personal observation). The mucilage cells, although not as distinct as the raphide bundles, are hard to miss when dissecting material (fresh or alcohol preserved) and additionally stain characteristically pink when exposed to ruthenium red (Chapter II; personal observation; von Balthazar & Schönenberger, 2013). Even if another staining protocol is less prone to visualise them, the characteristically thick cell walls and lacking cytoplasm makes them easy to distinguish (Chapter II; personal observation). As expected, based on the rarity of these traits in Ericales (Chapter II; Schönenberger, 2009; von Balthazar & Schönenberger, 2013), they were supported as synapomorphic for the Actinidiaceae–Roridulaceae clade in Chapter III.

PERIANTH

The sarracenioid clade is characterised by two alternating (isomerous) perianth whorls (Chapters II, III; Macfarlane, 1908; Gilg & Werdermann, 1925; Diels, 1930). The perianth in *Heliamphora*, traditionally interpreted as a single whorl of petaloid tepals (*e.g.* Macfarlane, 1908; Berry *et al*., 2005), is now re-interpreted as having a distinctly two-whorled perianth: a peripheral whorl of typically two sepals and a more central whorl of two to three petals (Chapters II, III). Another partial exception is the occasional presence of an additional, incomplete whorl of petaloid organs alternating with the petals in *Actinidia chinensis* Planch. (Chapter II; Li *et al*., 2007). However, these organs appear to be of androecial origin (based on vasculature; Chapter II) and are always much smaller than the primary petal whorl (Chapter II; Li *et al*., 2007). In all taxa except *Heliamphora*, the respective perianth whorls are easily distinguishable from one another by shape, size, colour and/or histological characters: in Actinidiaceae and Roridulaceae the outer perianth whorl is clearly sepaloid and often covered in multicellular hairs (Chapter II; Gilg & Werdermann, 1925; Diels, 1930), whereas both perianth whorls are petaloid in Sarraceniaceae. However, the sepals and petals in *Darlingtonia* and *Sarracenia* have vastly different shapes (lanceolate–ovate sepals; pandurate petals) and are often differentiated by colour (Chapter II; Macfarlane, 1908; Mellichamp, 2009). In *Heliamphora* the differences are more discrete, but the sepals are larger and wider, have clearly different vascular patterns in the floral base and have more numerous stomata (Chapters II, III; Berry *et al*., 2005).

The perianth is initiated in a clockwise or anticlockwise spiral sequence with distinct plastochrons between successive organs (indicated by size differences between successive young organs) in all sarracenioids (Chapter III; Caris, 2013). The spiral insertion continues with distinct (subequal) plastochrons and more or less equal divergence angles between successive organs throughout the entire perianth except for the corolla in *Saurauia* (Chapter III). The divergence angles between successive perianth organs approaches a Fibonacci spiral (*c*. 137.5°), albeit with adjusted divergence angles as a result of growth processes and displacements of earlier emerging organs (Study II; Hofmeister, 1868). A spiral initiation with distinct plastochrons between successive sepals is common in eudicots, but less common closer to the floral centre (Endress, 2011). Like in almost all eudicot flowers, the arrangement of the perianth organs in mature flowers, irrespective of the spiral initiation pattern, conforms to a whorled phyllotaxis (Studies I, II; Gilg & Werdermann, 1925; Diels, 1930; Mellichamp, 2009; Endress, 2011; Caris, 2013). The differences in organ size and divergence angles among the organs during the early stages of a given whorl are levelled out during later floral development leading to a typical eudicot perianth with alternating whorls of sepals and petals (Studies I, II). In mature flowers, the quincuncial perianth aestivation (in both respective whorls) in pentamerous flowers is the only visible remnant of the spiral initiation of organs (Chapters II, III, Endress, 1994, 2011); non-pentamerous flowers are imbricate with other aestivation patterns (Chapters II, III; Macfarlane, 1908; Gilg & Werdermann, 1925; Diels, 1930). In Ericales, spirally initiated corollas in whorled flowers are only known from the sarracenioid families (Study II; Caris, 2013), Fouquieriaceae (Schönenberger & Grenhagen, 2005; Caris, 2013), Pentaphylacaceae (Zhang *et al*., 2007, 2008; Zhang & Schönenberger, 2014) and Theaceae (Erbar, 1986; Sugiyama, 1991; Tsou, 1998); none of these families are closely related to the sarracenioids, suggesting the trait may have evolved independently in the respective groups (Study II; Schönenberger *et al*., 2005).

Another uncommon floral trait in Ericales but shared by most sarracenioids are petals that are proximally thick to massive, often markedly thicker than the proximal region of the sepals (Chapters II, IV; Palser, 1951, 1961; Kavaljian, 1952; Paterson 1961; Dickison, 1993; Sugiyama, 1997; Schönenberger, 2009; von Balthazar & Schönenberger, 2013).

ANDROECIUM

All sarracenioid taxa except *Clematoclethra* and *Roridula* are polystemonous (*Clematoclethra* has ten stamens, *Roridula* has five; Chapters II–IV; Macfarlane, 1908; Gilg & Werdermann, 1925; Diels, 1930). In *Actinidia*, *Saurauia*, *Darlingtonia* and *Heliamphora*, the stamens are arranged in a whorl-like structure, occasionally in numerous whorl-like structures in Actinidiaceae (Chapters II, III; Hunter, 1966; Dickison, 1972; Soejarto, 1980; van Heel, 1987). In *Clematoclethra* five stamens are positioned in a more peripheral, alternipetalous position and five stamens in a more central, antepetalous position (Studies I, II). In *Roridula* the five stamens are inserted in alternipetalous positions (Chapters II, III). In *Sarracenia*, the stamens are most commonly arranged in five more peripheral alternipetalous groups and five more central antepetalous groups (Chapters II, III). Anthers are basifixed or ventrifixed and extrorse–latrorse in Actinidiaceae and Roridulaceae, basifixed or dorsifixed and introrse–latrorse in *Heliamphora* and *Sarracenia* and basifixed, simultaneously introrse and extrorse in *Darlingtonia* (Chapters II, III; Macfarlane, 1908; Gilg & Werdermann, 1925; Diels, 1930). Stamens are free from each other and the petals (less than 5% united; Chapters II, III)

Based on stamen organisation, vascular patterns in the floral base, early androecium development and ancestral state reconstructions (Chapters II–IV; van Heel, 1987; Schönenberger, 2005), *Actinidia*, *Saurauia*, *Roridula* and *Heliamphora* appear to be haplostemonous or haplostemony-derived polystemonous. Secondary stamen primordia arise on a ring primordium with leading stamens in alternipetalous positions, thereafter primordia emerge in a lateral sequence (towards an antepetalous position; Chapter III; van Heel, 1987).

Darlingtonia, contrastingly, has five, weakly defined, antepetalous groups of stamens (Chapters II, III), suggesting an obhaplostemony-derived polystemony, but the early androecium organisation is not known. Antepetalous groups of stamens (but no alternipetalous groups) are reasonably common in Ericales, but not in the immediately related families; the pattern, although different from *Darlingtonia*, is present in, among other families, Pentaphylacaceae, Symplocaceae and Theaceae (Erbar, 1986; Tsou, 1998; Caris, 2013; Zhang & Schönenberger, 2014). The developmental origin of the ten stamens in *Clematoclethra* are, as of yet, unclear and a developmental study is needed to determine if the androecium consists of one whorl (potentially a ring primordium) with ten stamens or two whorls of five stamens each (Chapters II, III). In *Sarracenia*, the stamens are arranged in ten (to 17) weakly distinguished groups (Chapters II, III; Shreve, 1906; Mellichamp, 2009). Shreve (1906) found the stamens to arise in a single whorl, with two groups of stamens in every alternipetalous position, in sharp contrast to the arrangement of stamens in later stages, where five groups are clearly alternipetalous and five groups clearly antepetalous (Chapter III). The stamen arrangement in mature flowers appears to most commonly be similar to the findings of Chapter III (Chapter II; personal observation), indicating that the stamens either arose as five groups each in two whorls, or as ten groups in a single whorl (potentially on a ring primordium). While polystemony is characteristic for five out of the seven genera in the sarracenioid clade, the closely related ericoid clade is clearly diplostemonous (rarely haplostemonous; Chapters II–IV; Leins, 1964; Caris, 2013). In the ancestral state reconstructions of Chapter IV, polystemony is reconstructed as synapomorphic for the sarracenioid clade, but also for Symplocaceae and Theaceae. A reversal from polystemony to a lower stamen number has apparently occurred twice in the sarracenioid clade: once in *Clematoclethra* and once in *Roridula*, indicating that polystemony is not an irreversible state, also extensively discussed by *e.g*. Ronse Decraene & Smets (1995, 1998).

An interesting peculiarity of the stamens in the sarracenioid clade is the inversion of anthers in late floral development (Schönenberger, 2012). In Ericales, anther inversion is restricted to core Ericales, with a few different main patterns present: the anthers in Actinidiaceae, Roridulaceae, Clethraceae and early diverging Ericaceae invert from an extrorse to an introrse orientation late in the floral development (Chapters II–IV; Schönenberger, 2012); the anthers in *Heliamphora* and *Sarracenia* invert in the opposite direction, from an introrse to an extrorse orientation, late in the floral development (Chapters II–IV; Schönenberger, 2012); the anthers in *Darlingtonia* invert late in the floral development, but the direction cannot be assigned because of the unique anther morphology (Chapters II–IV); and the anthers in crown group Ericaceae invert from an extrorse to an introrse orientation early in the floral development. Anther inversion from an extrorse to an introrse orientation is apparently linked to ventrifixed or deeply sagittate, basifixed and extrorse anthers (Chapters II–IV; Matthews & Knox, 1926; Copeland, 1941, 1947; Palser, 1951, 1954, 1961; Leins, 1964; Caris, 2013). Both states are inferred as synapomorphic for core Ericales in Chapter IV with a reversal to dorsifixed or basifixed, introrse anthers in Cyrillaceae and Sarraceniaceae (the anthers in Cyrillaceae do not invert and the anthers in Sarraceniaceae invert in other directions). The only other group in Ericales where ventrifixed anthers are represented is Polemoniaceae, but unlike core Ericales, Polemoniaceae does not have any kind of anther inversion and the anthers are introrse despite their ventrifixed nature (Schönenberger, 2009; Schönenberger *et al*., 2010).

GYNOECIUM

Carpel merism is variable in the sarracenioid clade: *Clematoclethra, Darlingtonia, Sarracenia* and *Saurauia p.p.* are pentamerous, *Heliamphora, Roridula* and *Saurauia p.p*. are trimerous and *Actinidia* is multicarpellate (typically 15–30 carpels; Chapters II, III; Li *et al.,* 2007; Endress 2014). Other carpel numbers than three and five are also relatively common in *Saurauia*, varying even between flowers in the same inflorescence (Chapters II, III; Hunter, 1966; Soejarto, 1980; Cuong *et al*., 2007; Li *et al*., 2007). All sarracenioids have carpels arranged in one whorl

(Chapters II, III; Brundell, 1975; van Heel, 1987; Caris, 2013; Endress, 2014). The gynoecia are syncarpous at least in the ovary: *Clematoclethra*, *Heliamphora* and *Roridula* are completely syncarpous (only minute stigmatic lobes are free), *Darlingtonia* and *Sarracenia* have distally free styles and *Actinidia* and *Saurauia* have free to proximally united styles (up to *c*. 50% of total style length in Asian species; Chapters II–IV; Hunter, 1966; Soejarto, 1980; Cuong *et al*., 2007; Li *et al.*, 2007). Partially free styles appear to be a parallelism with the ericoid clade (Clethraceae and Cyrillaceae have partially free styles; Chapter III; Kubitzki, 2004), with a reversal to completely united styles in *Clematoclethra*, *Heliamphora, Roridula* and Ericaceae (Chapters II–IV; Kubitzki, 2004).

A depression at the ovary–style transition is common in the sarracenioid clade (Chapter II), and inferred as a synapomorphy for core Ericales (Chapter IV). However, such a depression is lacking in the *Heliamphora–Sarracenia* clade, *Clethra, Arbutus* and functionally male flowers of *Actinidia* (Chapters II–IV; Kavaljian, 1952; Palser, 1954). Outside core Ericales, a depression at the transition from ovary to styles appears to be uncommon (Kubitzki, 2004).

The Actinidiaceae–Roridulaceae clade is further characterised by a secretory inner gynoecium surface and the lack of synlateral vasculature in the ovary (Chapters II, IV). A secretory, inner gynoecium surface is, in Ericales, only known for the Actinidiaceae–Roridulaceae clade and the balsaminoid clade (Chapter II; von Balthazar & Schönenberger, 2013), and most ericalean taxa appear to have synlateral vasculature in the ovaries (Chapter II; Palser, 1951, 1954, 1961, 1963; Kavaljian, 1952; Paterson 1961; Dickison, 1993; Sugiyama, 1997; Schönenberger, 2009; von Balthazar & Schönenberger, 2013). Unsurprisingly, as a result of the rarity of the traits in Ericales, both are reconstructed as synapomorphic for the Actinidiaceae–Roridulaceae clade (Chapter IV).

A nucellar hypostase is present in the ovules of all sarracenioid genera and in Theaceae (Chapters II, IV; Johri *et al*., 1992), whereas it has not been described for most other ericalean families (Johri *et al*., 1992). Accordingly, it is reconstructed as a synapomorphy for the sarracenioids, and equally, for Theaceae (Chapter IV).

PHYLOGENETIC RELATIONSHIPS

The monophyly of core Ericales (albeit not thoroughly tested in these analyses), the sarracenioid clade, all sarracenioid families, the Actinidiaceae–Roridulaceae clade, the *Actinidia–Clematoclethra* clade, the *Heliamphora–Sarracenia* clade and all sarracenioid genera were confirmed (Chapter IV). Additionally, two distinct geographical clades were identified in *Saurauia* (Chapter IV). These results are compatible with earlier molecular phylogenetic studies of Ericales (Anderberg *et al*., 2002; Schönenberger *et al*., 2005), *Actinidia* (Li *et al*., 2002; Chat *et al*., 2004) and Sarraceniaceae (Ellison *et al*., 2012; Stephens *et al*., 2015). In the following section, most emphasis is put on novel findings (*i.e*. potentially synapomorphic characters and previously untested or unknown phylogenetic relationships). For an overview on the taxonomic history of the sarracenioids, see Preamble and Chapters II–IV.

Core Ericales has long been acknowledged as a natural group (*e.g*. Chase *et al*., 1993; Anderberg *et al*., 2002) and is supported both by molecular phylogenetics and several morphological characters (Chapters II, IV). Potential and inferred floral synapomorphies for core Ericales include: abaxial orientation of anther attachment (not present in Sarraceniaceae and Cyrillaceae; Chapters III, IV), anther inversion (not present in Cyrillaceae; Chapters II–IV), depression at ovary–style transition (not present in Clethraceae and a few members of Ericaceae; Chapters II, IV), and partially free styles (not present in *Clematoclethra*, *Roridula*, *Heliamphora* and Ericaceae; Chapters II, IV).

The monophyly and suprafamilial relationships of the sarracenioid clade have also long been established with molecular phylogenetics (*e.g*. Anderberg *et al*., 2002; Schönenberger *et al*.,

2005; Ellison *et al*., 2012), although Chapter IV is by far the most extensively sampled study including all three families. Potential and inferred floral synapomorphies for the sarracenioid clade include: condensed tannins in floral tissue (Chapters II, IV), spirally inserted corolla (not present in *Saurauia*; Chapters II, III), proximally thick petals (Chapters II, IV), androecium formation on a ring primordium (haplostemonous whorl in *Roridula*; unclear in *Clematoclethra*, *Darlingtonia* and *Sarracenia*; Chapter III), polystemony (absent in *Clematoclethra* and *Roridula*; Chapters II–IV), and presence of a nucellar hypostase in ovules (Chapters II, IV). Potential and inferred floral synapomorphies for the Actinidiaceae–Roridulaceae clade include: calcium oxalate raphides in floral tissue (Chapters II, IV), mucilage cells in floral tissue (Chapters II, IV), absence of synlateral vasculature in gynoecium (Chapters II, IV) and a secretory inner gynoecium surface (Chapters II, IV).

The monophyly of Actinidiaceae and its genera has before my studies, although not questioned, not been tested using molecular phylogenetic techniques. He *et al*. (2005) suggested a sister group relationship between *Actinidia* and *Clematoclethra,* with *Saurauia* sister to the *Actinidia–Clematoclethra* clade based on karyology, affirmed by the findings of Chapter IV. These relationships might also be hypothesised based on growth habit (*Actinidia* and *Clematoclethra* are lianescent, whereas *Saurauia* are arborescent; Gilg & Werdermann, 1925), ecological niche and geographical distribution (*Actinidia* and *Clematoclethra* are mainly native to temperate East Asia, whereas *Saurauia* are mainly native to highland tropical New world, Asia and Oceania; *e.g*. Hunter, 1966; Soejarto, 1980; Tropicos, 2015) and fruit dehiscence (fruits are indehiscent in *Actinidia* and *Clematoclethra*, whereas they are dehiscent in *Saurauia*; Chapter II; Soejarto, 1980). The monophyly and infrageneric relationships of *Saurauia* have, before my studies, never been investigated using a molecular systematic approach (Chapter IV). Vegetative and, to some extent, floral morphology of the Neotropical species has been studied by Hunter (1966) and Soejarto (1969, 1980), whereas the Asian species have mostly been treated in national floras (*e.g*. Cuong *et al*., 2007; Li *et al*., 2007); relatively little is known about the Oceanian species. Additionally, the genus appears to be in dire need of a taxonomic revision (*e.g*. Soejarto, 1980; Conn & Damas, 2013). My studies affirm the monophyly of *Saurauia* and identifies the two above mentioned distinct geographical clades (Chapters III, IV), but a larger sampling, both in terms of sampled species and in terms of DNA regions would be desirable for further infrageneric studies. My studies combined with a broad literature review (Backer & Bakhuizen van den Brink, 1963; Hunter, 1966; Soejarto 1969, 1970, 1980; van Royen, 1982; Dressler & Bayer, 2004; He *et al*., 2005; Cuong *et al*., 2007; Li *et al*., 2007; Conn & Damas, 2013) identifies the following characterising traits for the respective *Saurauia* clades: Asian–Oceanian species mostly have a sympetalous corolla, whereas it is mostly choripetalous in Neotropical species (Chapters II–IV); Asian species have centrifugal proliferation of stamen primordia, whereas the Neotropical species do not (Chapter III; Brown, 1935); anthers partially invert during floral development in Asian species, whereas the inversion is initiated at anthesis in Neotropical species (Chapters II–IV); Asian–Oceanian species typically have three or five carpels, whereas Neotropical species mostly have five (Chapters III, IV); Asian–Oceanian species typically have partially united styles, whereas Neotropical species typically have almost completely free styles (Chapters II–IV); and the basic chromosome number of Asian *Saurauia* is, depending on the source, 10 (Dressler & Bayer, 2004) or 13 (He *et al*., 2005), whereas Neotropical species have a basic chromosome number of 15 (Soejarto, 1969, 1970). The androecium proliferation patterns, initiation timing of anther inversion and chromosome numbers are not known for the Oceanian *Saurauia* species, but they are, based on phylogenetic relationships and other shared morphological traits (Chapters III, IV), most probably similar to the Asian *Saurauia* species.

CONCLUSIONS

In sum, the studies included in this thesis identified several structural characteristics of the sarracenioid clade, the Actinidiaceae–Roridulaceae subclade and the infrageneric groups in *Saurauia* (Chapters II–IV). Several of these traits were additionally inferred as synapomorphic for the sarracenioids and the Actinidiaceae–Roridulaceae clade respectively (Chapter IV). However, many of the characters (particularly histological characters) discussed here as characteristic (or synapomorphic) for the sarracenioid clade and its subclades are not extensively investigated in Ericales and all of the discussed traits need to be tested in a larger phylogenetic context to be affirmed as truly synapomorphic. Irrespective of an apomorphic or plesiomorphic nature of the characters, they add vital information to our understanding of floral evolution in Ericales.

Furthermore, the monophyly of the sarracenioid clade and the Actinidiaceae–Roridulaceae subclade, as well as all families and genera, was affirmed (Chapter IV). The phylogenetic analysis also stresses the need of taxonomic revisions in *Saurauia* and the supraspecific classifications in *Actinidia*.

The studies presented here further reinforce the notion that floral characters traditionally considered of high taxonomic value (*e.g.* number of stamens, number of carpels, union of organs and integument number) often turn out to be homoplasious when considered in a large phylogenetic framework, whereas anatomical, histological and phytochemical characters, appear to be of considerable when circumscribing higher taxa. On a final note, detailed comparative structural and developmental studies, such as Chapters II and III, may help to refine hypotheses of floral evolution in higher taxa, as well as the investigation of floral disparity analyses (*e.g.* morphospaces) and provide a basis for fossil placement analyses. This in turn, may be of use in neighbouring fields of research, such as determining the age and biogeography of Ericales, evo-devo study on floral development or pollination biology.

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CURRICULUM VITAE

STEFAN D. LÖFSTRAND

Date of birth: 10 February 1985

Nationality: Swedish

Address: Dampfschiffstraße 12/1/11; 1030 Wien; Austria

E-mail: stefan@lofstrand.net

Phone: +43 (0) 660 391 00 61

EDUCATION

2012–present Ph.D. studies. University of Vienna, Austria

2011–2012 Part time studies (evening courses). Geological science and environmental science. Stockholm University, Sweden.

2010–2011 M.Sc. Thesis 'Evolutionary relationships in the tribe Naucleeae (Rubiaceae, Cinchonoideae)'. Bergius Foundation, The Royal Swedish Academy of Sciences, Sweden.

2005–2010 Undergraduate studies. Major in biology (botany). Stockholm University, Sweden.

2004–2005 Undergraduate Studies. Swedish Red Cross University College, Sweden.

EMPLOYMENT HISTORY

2012–present University Assistant Prae Doc. University of Vienna, Department of Botany and Biodiversity Research, Division of Structural and Functional Botany, Austria.

2011–2012 Project Assistant. Bergius Foundation, The Royal Swedish Academy of Sciences, Sweden.

2009–2011 Teaching assistant (part time). Stockholm University, Department of Botany, Sweden.

SCIENTIFIC AWARDS

2013 Best student poster (Löfstrand SD, Schönenberger J. *Comparative floral structure in the sarracenioid clade (Actinidiaceae, Roridulaceae and Sarraceniaceae)*. Svenska systematikdagarna 2013, Sweden.

PUBLICATIONS

Löfstrand SD, Schönenberger J. 2015. Comparative floral structure and systematics in the sarracenioid clade (Actinidiaceae, Roridulaceae and Sarraceniaceae) of Ericales. *Botanical Journal of the Linnean Society* **178:** 1–46.

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