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The relationship between nectaries and floral architecture: a case study in Geraniaceae and Hypseocharitaceae

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• **Background and Aims** Flowers of Geraniaceae and Hypseocharitaceae are generally considered as morphologically simple. However, previous studies indicated complex diversity in floral architecture including tendencies towards synorganization. Most of the species have nectar-rewarding flowers which makes the nectaries a key component of floral organization and architecture. Here, the development of the floral nectaries is studied and placed into the context of floral architecture.
• **Methods** Seven species from Geraniaceae and one from Hypseocharitaceae were investigated using scanning electron microscopy and light microscopy. Samples were prepared and processed using standard protocols.
• **Key Results** The development of the nectary glands follows the same trajectory in all species studied. Minor differences occur in the onset of nectarostomata development. The most striking finding is the discovery that a short anthophore develops via intercalary growth at the level of the nectary glands. This anthophore lifts up the entire flower apart from the nectary gland itself and thus plays an important role in floral architecture, especially in the flowers of *Pelargonium*. Here, the zygomorphic flowers show a particularly extensive receptacular growth, resulting in the formation of a spur-like receptacular cavity (‘inner spur’). The nectary gland is hidden at the base of the cavity. Various forms of compartmentalization, culminating in the ‘revolver flower’ of *Geranium maderense*, are described.
• **Conclusions** Despite the superficial similarity of the flowers in Geraniaceae and Hypseocharitaceae, there is broad diversity in floral organization and floral architecture. While the receptacular origin of the spur-like cavity in *Pelargonium* had already been described, anthophore formation via intercalary growth of the receptacle in the other genera had not been previously documented. In the context of the most recent phylogenies of the families, an evolutionary series for the floral architecture is proposed, underscoring the importance of synorganization in these seemingly simple flowers.

Key words: Floral organization, synorganization, flower morphology, nectary development, ontogeny, anthophore, *Geranium*, *Erodium*, *Pelargonium*, *Monsonia*, *Hypseocharis*.

INTRODUCTION

The Geraniaceae comprise about 830 species in five genera (*Erodium*, *Geranium*, *Monsonia*, *Pelargonium* and monotypic *California*) in their most recent circumscription (Albers and van der Walt, 2007). Monotypic *California* was segregated from *Erodium* (Aldasoro *et al.*, 2002). It appears to be the sister group to the remaining *Erodium* species (Fiz *et al.*, 2006). There are two centres of diversity: *Geranium* and *Erodium* are most diverse in the Mediterranean areas of the northern hemisphere, while *Pelargonium* and *Monsonia* are mainly restricted to southern Africa, with only a few species of *Pelargonium* present on Madagascar, the Arabian Peninsula and Australia (Fiz *et al.*, 2008). The phylogenetic sister group to the Geraniaceae are the monogeneric Hypseocharitaceae with 2–6 species. *Hypseocharis* is mainly distributed in the high Andean regions of central South America (Slanis and Grau, 2001). Hypseocharitaceae are often included in the family Geraniaceae (Albers and van der Walt, 2007; APG IV, 2016).

Various aspects of the flowers of these two families have been studied (e.g. Brunies, 1900; Narayana and Arora, 1963; Labbe, 1964; Kumar, 1976; Link, 1989, 1994; Devi, 1991; Struck, 1997; Aldasoro *et al.*, 2001). Several authors investigated the ontogeny, anatomy and morphology of the floral nectaries in the Geraniaceae and related families and genera (e.g. Link, 1989, 1994; Vogel, 1998; Ronse Decraene and Smets, 1999; Jeiter *et al.*, 2017). Flowers of species from both families are shown in Fig. 1.

All five genera of the Geraniaceae and the one of Hypseocharitaceae have flowers that reward nectar. The position of the nectaries at the base of the antesepalous filaments between the bases of the neighbouring petals is conserved within both families (Jeiter *et al.*, 2017). The only apparent exception is found in *Pelargonium*, where the nectar is hidden in a spur-like cavity on the adaxial side of the flower.

The morphology of this spur-like cavity is often described as ‘fused sepal spur’ or ‘hypanthium with adnate spur’ (e.g.

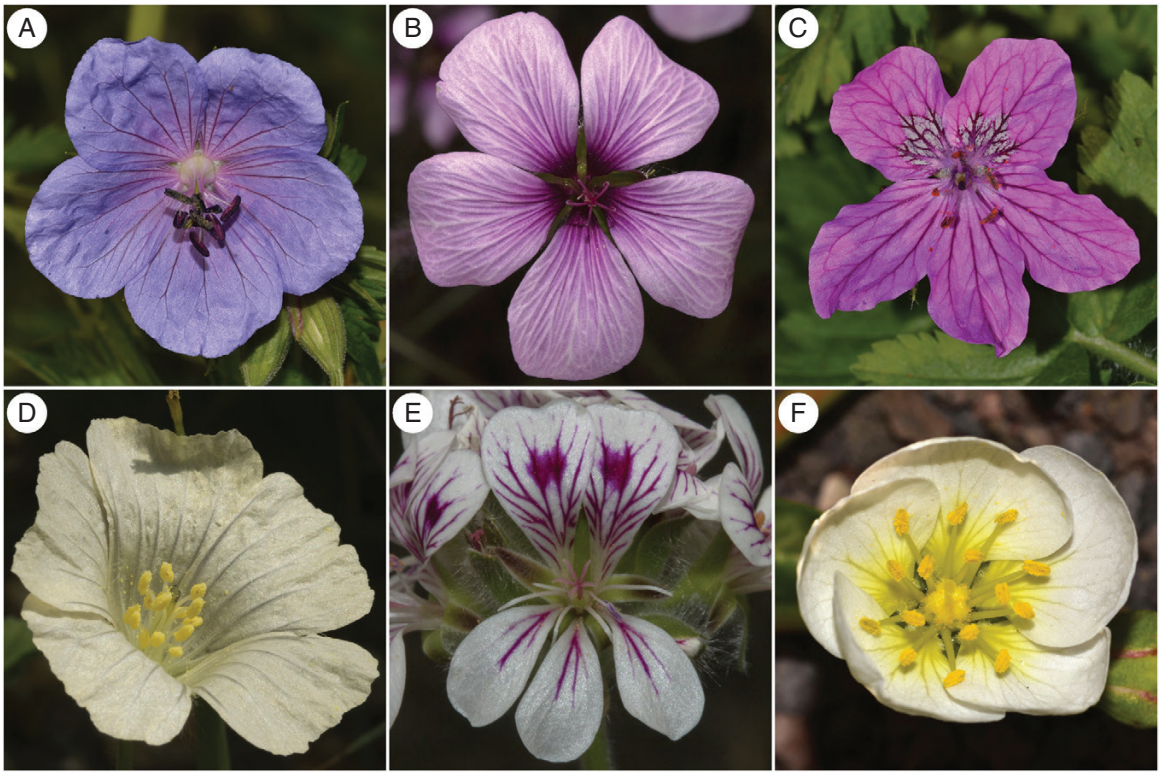

FIG. 1. Floral organization and architecture of some of the species studied in Geraniaceae and Hypseocharitaceae. (A–E) Geraniaceae: (A) *Geranium pratense* (*BONN-3785*); (B) *Geranium maderense* (*GHB 49664*); (C) *Erodium manescavi* (*BONN-3787*); (D) *Monsonia emarginata* (*GHB 44182*); and (E) *Pelargonium australe* (*GHB 36554*). (F) Hypseocharitaceae: *Hypseocharis bilobata* (*Ortuño 2361*).

Sauer, 1933; Röschenbleck *et al.*, 2014), a 'spur formed half by the receptacle and half by the adaxial sepal' (Payer, 1857), 'receptacular spur' or 'receptacular tube' (Japp, 1909; Labbe, 1964; Link, 1989, 1994; Tsai, 2016), or – with no interpretation – simply as 'spur' (e.g. Price and Palmer, 1993; Struck, 1997). Similar structures are present in some species of *Monsonia* (Kers, 1971; Link, 1989, 1994). Unlike the single 'spur' in *Pelargonium*, the actinomorphic flowers of *Monsonia* have five spur-like cavities which are shorter compared with those present in most species of *Pelargonium*.

Apart from nectary development, floral architecture and synorganization are poorly studied in Geraniaceae and Hypseocharitaceae, and incompletely understood in angiosperms in general. There are several misconceptions regarding terms such as 'floral architecture', 'floral structure', 'floral organization' and 'synorganization'. Often these are even used as synonyms, which makes it difficult to pinpoint a clear definition.

The clearest definitions and relationships between those terms have been given by Endress (1994, 1996). According to him, floral structure can be approached on different levels: floral organization, floral architecture and floral mode. 'Floral organization' may be synonymized with floral morphology. Independent organs may be synorganized. 'Synorganization' is the 'spatial and functional connection between organs of the same or different kind leading to homogeneous functional structures' (Ronse De Craene, 2010, p. 412). Common examples of synorganization are fusions between organs of the same or different whorls as in most asterids. Synorganization, fusions and differential growth rates lead to structures of higher order which are described as 'floral architecture'. Structures of higher order exceed the function of the individual or collective of floral organs of which they are composed, and introduce new or modified functions. Finally, the interactions of flowers, for example during pollination, constitute the 'floral mode'.

Synorganization is well known for asterids, where it is usually represented by the fusion of various floral organs (e.g. sympetalous corolla fused with androecium), without explicitly mentioning it under this term [e.g. Asterales (Leins and Erbar, 2006); but see Endress, 2016]. Conversely, synorganization has been rarely studied in rosids, which usually have free petals and separate stamens.

The most detailed study on floral architecture in Geraniaceae was provided by Endress (2010). He described the synorganization in the flowers of *Geranium robertianum* and found a 'revolver architecture' (formation of regular and independent nectary compartments without strict fusion). His study focused on floral organization and floral architecture. Similar studies are available especially for *Pelargonium* (e.g. McDonald and van der Walt, 1992; Struck and van der Walt, 1996; Struck, 1997) but, in contrast to the study by Endress (2010), these focus mainly on the length and shape of the entrance of the spur-like cavity and its relationship to flower–pollinator interaction. The emphasis of these studies is on floral organization and floral mode. A particularly nice example where minute changes in organ shape have major consequences for the organization

and floral mode is found in *Erodium* where zygomorphy arose several times independently (Fiz *et al.*, 2006). These changes towards zygomorphy are mainly due to the presence of glandular trichomes or coloured spots on individual petals, or slight changes in the size relationship between the petals and/or nectary glands of the flower.

We hypothesize that the flowers of Geraniaceae and Hypseocharitaceae, although superficially similar in organization, show divergent architectures, which are the result of various levels of synorganization. Since the presentation of nectar is strongly related to floral mode, which results from changes in floral architecture, we follow a two-step approach: (1) we study the development of the nectary glands in Geraniaceae and Hypseocharitaceae; and (2) we combine our developmental data with detailed observations of the anthetic functional unit.

MATERIALS AND METHODS

Flowers in various developmental stages, including anthetic flowers, of five genera from the Geraniaceae (*Erodium*, *Geranium*, *Monsonia* and *Pelargonium*) and Hypseocharitaceae (*Hypseocharis*) (Table 1) were collected in the Botanical Garden Berlin, Germany and the Botanical Gardens of the University of Bonn, Germany. The material was fixed in formaldehyde–acetic acid–ethanol (FAA; 2 % formaldehyde, 2 % acetic acid, 70 % ethanol) for at least 1 week.

For electron microscopy, the samples were rinsed with ethanol (70 %) and dissected under a stereomicroscope. They were then transferred into FAA for at least 1 h and afterwards dehydrated using formaldehyde dimethyl acetal (FDA; 99.0 %, Sigma-Aldrich Chemie GmbH, Munich, Germany) and finally stored in acetone (protocol modified after Gerstberger and Leins, 1978). Critical point drying (CPD 020, Balzers Union, Liechtenstein) followed the standard protocol. Dried specimens were mounted on aluminium stubs using conductive carbon cement (Leit-C, PLANO GmbH, Wetzlar, Germany) and final preparations were conducted. The mounted specimens were coated with gold or palladium in a sputter coater (SCD 040, Balzers Union) for 1.5 min up to 3 min (depending on the structural complexity of the specimen) at 30 mA. Images were taken in a Stereoscan 200 electron microscope (Cambridge, UK) at 10–15 kV. Contrast and brightness of the images were partially improved using standard image editing software.

For light microscopy, the material was dehydrated using an increasing ethanol to isopropanol to butanol dehydration series. The butanol was gradually replaced with Paraplast© (Leica Biosystems Nussloch GmbH, Nussloch, Germany) and finally stored at 60 °C for at least 2 weeks. The samples were then moulded in blocks, which were trimmed and mounted on wooden blocks. The sectioning was performed using a rotary microtome (Rotationsmikrotom 1515, Leitz, Wetzlar, Germany). The sections were stained in Safranin red and Astra blue. Sections were documented using a light microscope (Axio Scope.A1, Carl Zeiss microscopy GmbH, Jena, Germany) with a digital camera (AxioCam ERc5s, Carl Zeiss microscopy GmbH). Images were partially improved using standard image editing software.

Table 1. *Species studied, vouchers and voucher locations*

Species	Family	Voucher*	Herbarium
Hypseocharis bilobata Killip	Hypseocharitaceae	*Ortuño 2361*	BONN
Erodium manescavi Coss.	Geraniaceae	*BONN-3787*	BONN
Geranium maderense Yeo	Geraniaceae	*GHB 49664*	B
Geranium pratense L.	Geraniaceae	*BONN-3785*	BONN
Monsonia brevirostrata Knuth	Geraniaceae	*GHB 44350*	B
Monsonia emarginata L'Hér.	Geraniaceae	*GHB 44182*	B
Pelargonium australe Willd.	Geraniaceae	*GHB 36554*	B
Pelargonium reniforme (Andrews) Curtis	Geraniaceae	*GHB 8138*	B

*GHB, Garten Herbar Beleg.

RESULTS

Nectary gland development

The development of the nectary glands in the five species studied is shown in Figs 2–6. In all species studied, gland development starts at late stages of floral development, as is common for nectarial tissues. At the onset of nectary gland development, the anthers and ovary are already differentiated. The ovary is still open and a common style is not yet developed.

Geranium pratense (Fig. 2). The development of the nectary gland starts from small, shallowly bilobed bulges below the base of the antesepalous stamen (Fig. 2A–C). The development of the nectary glands is strongly linked with the development of the receptacle below all floral organs except the calyx (Fig. 2C–I). The glands start to develop at the same level as the petals (Fig. 2B, C). Below this region, a circular constriction forms (Fig. 2C, D, I). The resulting column elongates, forming a short anthophore ('extension of the receptacle between the calyx and the rest of the organs in a flower', Ronse De Craene, 2010, p. 404; Fig. 2E, F). The nectarostomata (open, nectar-secreting stomata; nectary-modified stomata; Smets, 1988) are mainly localized at the portion of the gland which faces the base of the flower (Fig. 2D, E). At the final stages of development, shortly before anthesis, the anthophore broadens, shifting the zone with nectarostomata towards a distal position (Fig. 2F). The formation of the nectarostomata happens simultaneously with the development of simple trichomes which arise at the apical and apicolateral area of the gland (Fig. 2C–F).

Erodium manescavi (Fig. 3). The nectary gland initiates its development as a small bulge of tissue at the base of the antesepalous stamen and between the antepetalous stamens (Fig. 3A, B). In later stages, this bulge forms a clear edge at its base, separating it from the base of the sepal and receptacle (Fig. 3C, D). With continuing development, the gland first broadens and finally grows apically (Fig. 3C–F). The five nectary glands vary in size: the most prominent gland is that in the adaxial position (Fig. 3F), and the smallest are on the abaxial side. The adaxial gland shows a strong apical growth. While growing, it covers parts of the base of the adaxial, antesepalous filament. Besides the growth of the glands, the receptacle lifts the inner floral organs only slightly, forming a very short undifferentiated anthophore. The petals stay at the same level during the entire development of the flower (Fig. 2A–E). The glands are glabrous (Fig. 3F). Nectarostomata become visible shortly before

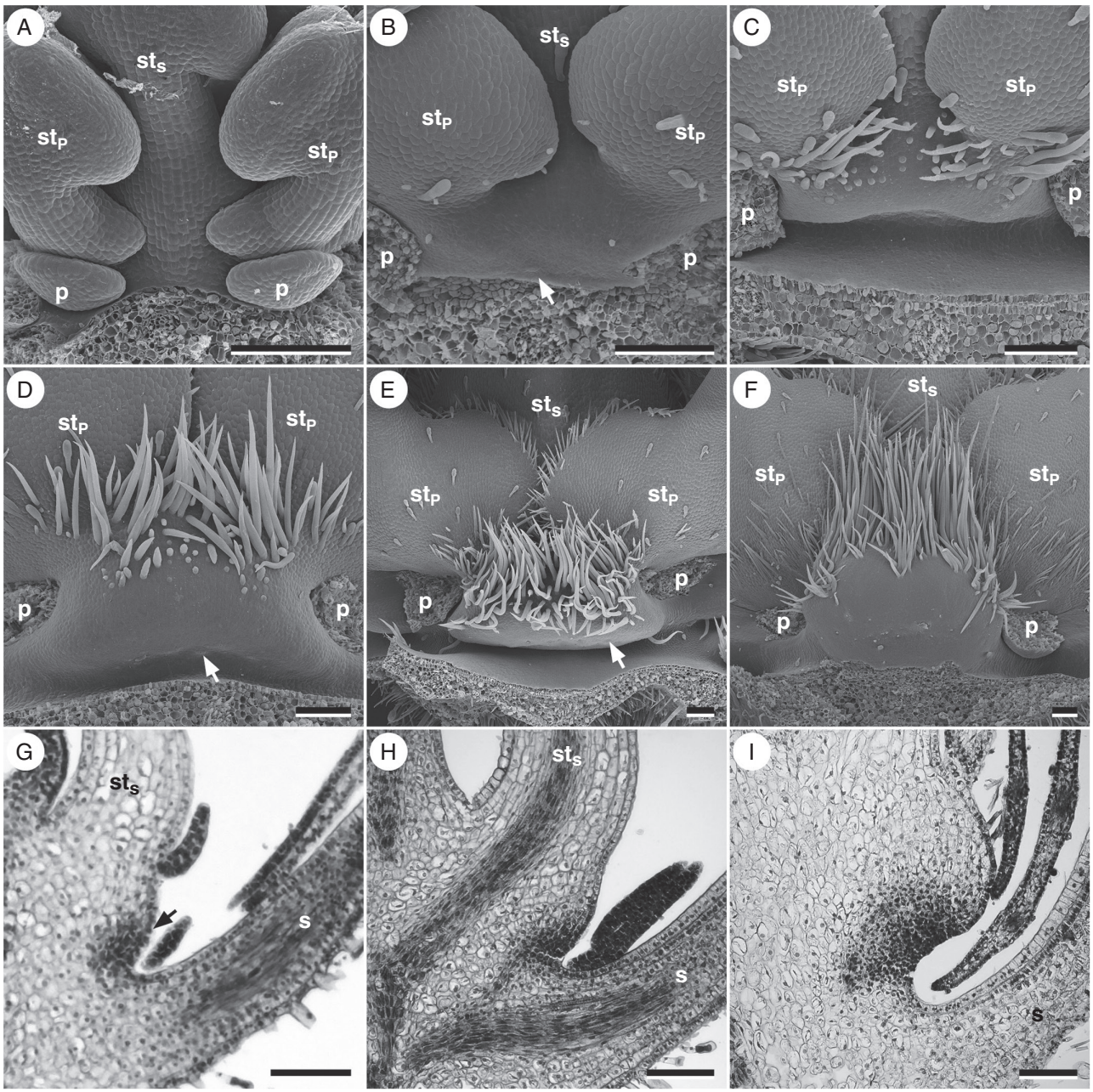

FIG. 2. Nectary gland development in *Geranium pratense*. (A–F) Micrographs obtained using scanning electron microscopy. (G–I) Longitudinal sections. (A) Base of the antesepalous stamen before insertion of the nectary gland. (B) First bulging of the developing gland. The arrow indicates the first bulging of nectary gland tissue. (C) Formation of the anthophore and onset of trichome development. (D) Onset of nectarostomata development. The arrow is pointing to one nectarostoma. (E) Onset of development of circular constriction of the anthophore. The arrow is pointing to one nectarostoma. (F) Nectary gland at anthesis. (G) Longitudinal section through the state corresponding to (B). The arrow indicates developing glandular tissue. (H) Longitudinal section through the state corresponding to (C). (I) Section through an almost anthetic flower. Perianth organs removed. p, petal; s, sepal; st_p, antepetalous stamen; st_s, antesepalous stamen. Scale bars in (A–I) = 100 μm.

anthesis. They are slightly immersed into the epidermis of the glands (Fig. 3F).

Pelargonium australe (Fig. 4). The single nectary gland in *P. australe* also develops late, but along a different trajectory compared with the other Geraniaceae. The distance between the adaxial petals as well as the size of the adaxial sepal is significantly larger than the distances between the other petals and sepals, respectively (Fig. 4A, D). In the space between the adaxial sepal and the adaxial antesepalous stamen, a small number of nectarostomata develops. While the number of nectarostomata increases, a bulge of tissue is formed. At this point, intercalary growth of the surrounding tissue now overtops the nectary, which thus 'sinks' into a tube-like structure (Fig. 4B, E, F). In longitudinal section, a secondary meristem at the base of all floral organs (including the sepals) becomes

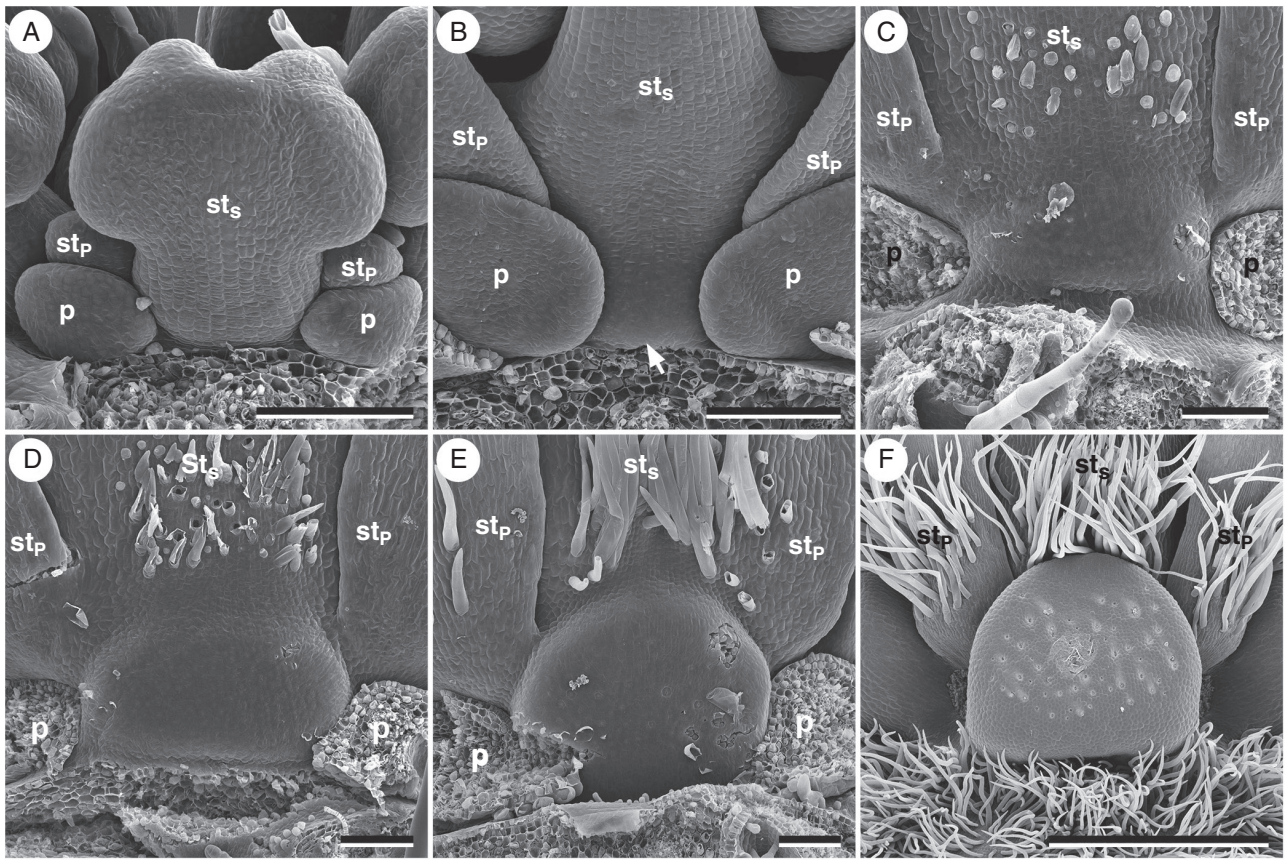

FIG. 3. Nectary gland development in *Erodium manescavi*. (A) Antesepalous stamen before the onset of nectary gland development. (B) Onset of nectary gland development. The arrow indicates the earliest observed stage of nectary gland development. (C) The gland broadens laterally, and trichomes begin to develop. (D) Gland and trichome development progresses. (E) First nectarostomata develop. (F) Adaxial nectary gland in the anthetic flower. Perianth organs removed. p, petal; s, sepal; st_p, antepetalous stamen; st_s, antesepalous stamen. Scale bars in (A–E) = 100 µm, (F) = 1 mm.

visible. This meristem produces regularly shaped cells which elongate subsequently or after a short delay. This elongation process occurs at late stages of floral development, right before anthesis. No secondary meristem is initiated under the nectary gland, so this is the only area retaining its original level (Fig. 4E, F). The gland at the base of this tube-like structure develops a conical shape (Fig. 4C, F). The nectarostomata are located on the ventral (proximal) surface of the gland. The 'sinking' of the nectary gland is thus actually an overtopping of the gland by the surrounding tissue. The entrance of the tube-like structure and the base where the gland is located enlarge during the final stages of development (Fig. 4C, F).

Monsonia brevirostrata (Fig. 5). In the early developmental stages, the glands of *M. brevirostrata* develop similarly to those of *G. pratense*; below the base of the glands and all other floral organs (except for the sepals), a short anthophore is formed (Fig. 5E). After onset of development, the glands become increasingly bilobed (Fig. 5D–F). Nectarostomata develop late and are at first restricted to the part of the gland above the anthophore (Fig. 5A–D, G, H). Shortly before anthesis, the basal part of the gland emerges from the anthophore (Fig. 5E, F). At anthesis the nectary gland shrinks and the zone of nectarostomata becomes enclosed by the basal and apical parts of the nectary gland, while the anthophore is not involved in this shrinking process (Fig. 5E, F). At the same time, the triplet of stamens is tilted distally (Fig. 5I).

Hypseocharis bilobata (Fig. 6). The formation of the nectary glands in *H. bilobata* starts with the emergence of nectarostomata at the base of the triplet of antesepalous and antepetalous stamens (Fig. 6A). After development of several nectarostomata, the upper part of this zone bulges, so that a cleft between the base of the sepal and the nectary gland is formed (Fig. 6B, C). The growth of the upper part of the gland continues and at anthesis the zone of nectarostomata is almost completely hidden between the rest of the gland, the receptacle and the sepal bases, respectively (Fig. 6–F). Nectary glands and the other floral organs are slightly lifted by receptacular growth. The sepal bases form shallow pockets into which the nectary glands protrude (Fig. 6F).

Floral architecture and synorganization

Floral organization is similar amongst Geraniaceae and Hypseocharitaceae (Fig. 1). Apart from changes in symmetry, which are related to receptacle and nectary gland development, variation occurs almost exclusively within the androecium. The number of stamens is usually ten (*Geranium*, *Erodium* and *Pelargonium*) or 15 (*Hypseocharis* and *Monsonia*). Fertile stamens range between five and 15.

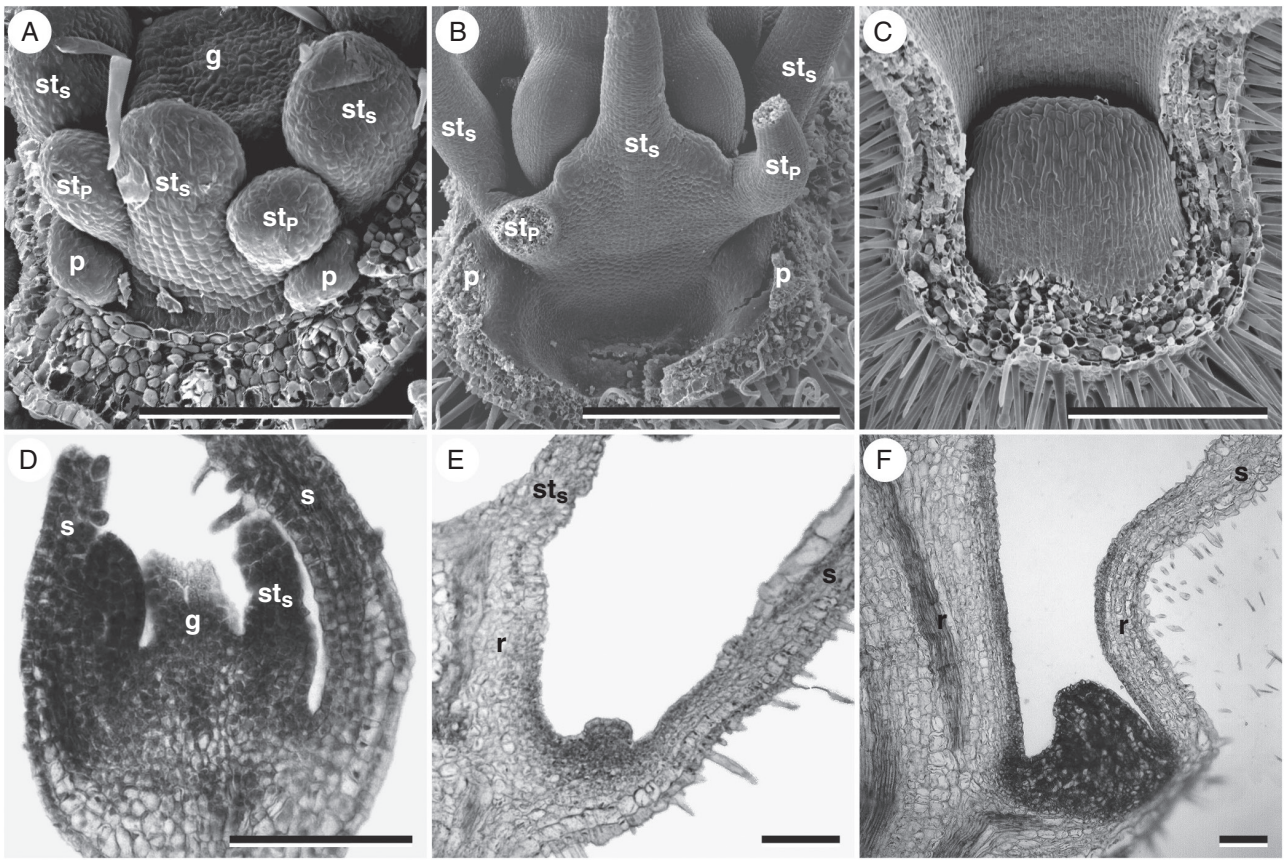

FIG. 4. Nectary gland development in *Pelargonium australe*. (A–C) Micrographs obtained using scanning electron microscopy. (D–F) Longitudinal sections. (A) Adaxial side of the flower before onset of nectary gland development. (B) Tube formation by growth of the receptacle. (C) Nectary gland at the base of the tube of an anthetic flower. (D) Longitudinal section through the developmental state similar to (A). (E) Developmental state similar to (B). (F) Anthetic flower. Perianth organs and wall of the tube in (C) removed. g, gynoecium; p, petal; r, receptacle; s, sepal; st_p; antepetalous stamen; st_s, antesepalous stamen. Scale bars in (A, D–F) = 100 µm, (B, C) = 500 µm.

Geranium pratense (Fig. 1A). The flowers are bowl-shaped. The bases of the filaments, the apical parts of the glands and the bases of the petals are covered with simple trichomes (Fig. 2C–F). Nectar is secreted through nectarostomata at the lower part of the gland (Fig. 2F). A common inner space is formed through the circular constriction of the anthophore and above the bases of the sepals (Figs 1F and 6A). This space may function as a nectarotheca (nectar holder). It is only compartmentalized above the anthophore by the bases of the petals (Fig. 7B, C).

Geranium maderense (Figs 1B and 7D–F). The bases ('claws') of the petals form two ridged, longitudinal protrusions which fit around the central part of the filaments of the antepetalous stamens (Fig. 7F). Additional to the central protrusions of the petal bases, recurved lobes are present, which enclose the glands (Fig. 7E). Below the points of petal attachment to the receptacle, the petals form a distinct tip which fits into the circular constriction of the anthophore. This elaboration of the petals leads to the compartmentalization of the flower. Apart from paired petals, the flattened filaments of three stamens and one sepal are involved in the formation of a compartment (Fig. 7F). Each of these compartments contains one nectary gland. A short anthophore is formed and a circular constriction is present, but the basolateral lobes of the petals prevent the formation of a common space. The inside of the flower is completely glabrous (with the exception of the gynoecium, which is not directly involved in the formation of the compartments).

Erodium manescavi (Fig. 1C). The slightly zygomorphic flower of *E. manescavi* is bowl-shaped. The sizes of the nectary glands differ between small on the abaxial side to two to four times larger on the adaxial side. The petals show distinct, almost claw-like bases. The distance between the adaxial petals is significantly larger compared with the distances to and between the other three petals. Additionally, they show white nectar guides with dark purple veins. The formation of a short anthophore leads to a common space between the insertion of the floral organs and the bases of the sepals. This space is densely filled with simple trichomes emerging from the surrounding organs (Fig. 2F). Above the point of petal and nectary gland insertion, trichomes are present on the filaments. These trichomes form a 'zone' above the glabrous nectary glands (Fig. 2F). The petal bases are covered with the same type of trichomes as present on the filaments. The staminodes are variable in their appearance. In many flowers, only a few staminodes were present.

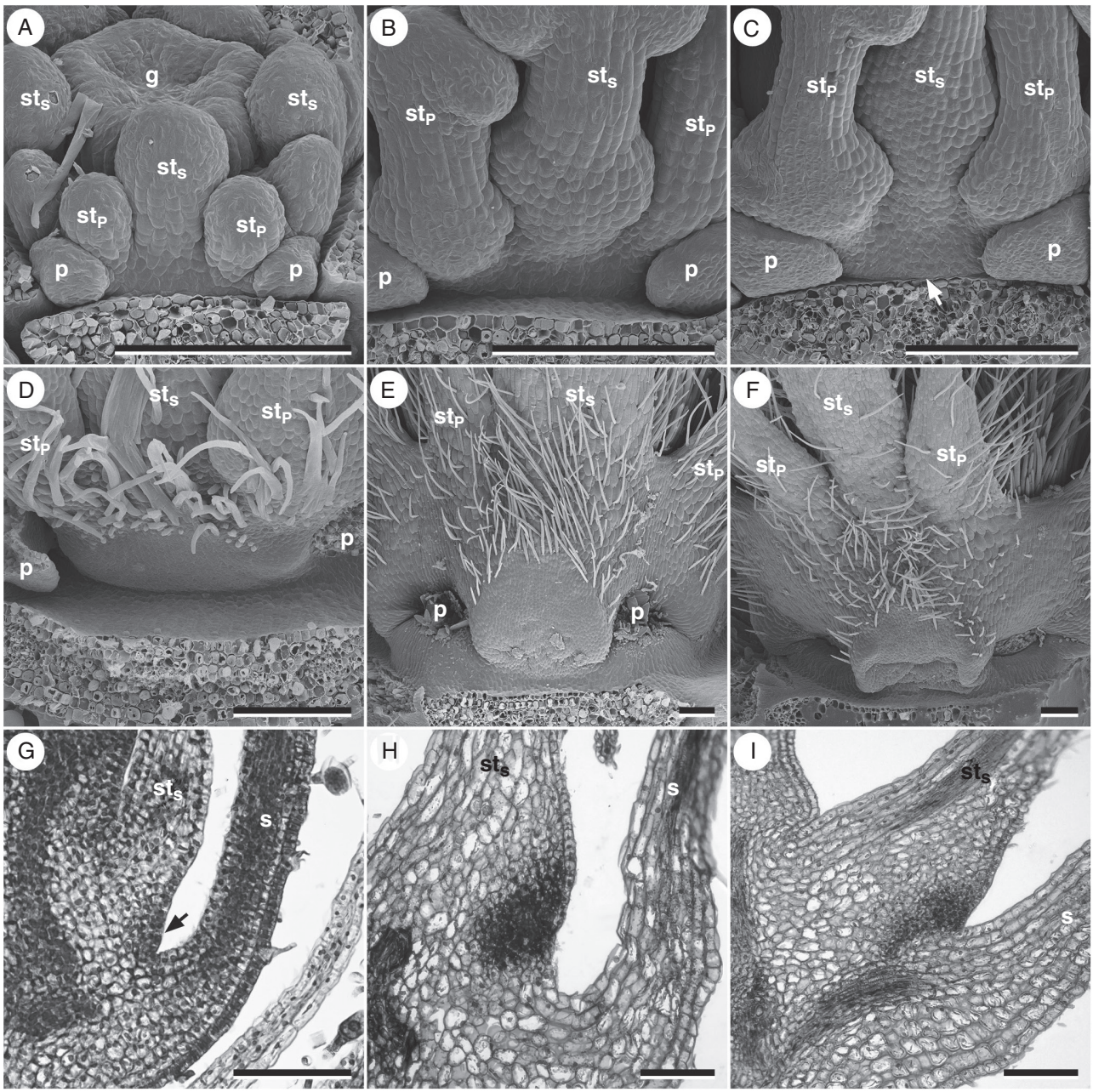

FIG. 5. Nectary gland development in *Monsonia brevirostrata*. (A–F) Micrographs obtained using scanning electron microscopy. (G–I) Longitudinal sections. (A) Young flower showing the early formation of stamen triplets. (B) Stamen base before the onset of nectary gland development. (C) Onset of nectary gland development. (D) Slightly bilobed young nectary gland and onset of anthophore development. (E) Gland shortly before anthesis. (F) Partially collapsed nectary gland and anthophore of an anthetic flower. (G) Longitudinal section through a nectary gland in a corresponding stage to (C). (H) Similar stage to (E). (I) Gland in an anthetic flower. Arrows indicate the earliest observed stage of nectary gland development. Perianth organs removed. g, gynoecium; p, petal; S, sepal; st_p, antepetalous stamen; st_S, antesepalous stamen. Scale bars in (A–I) = 100 µm.

Monsonia emarginata (Fig. 1D) and *M. brevirostrata*. In *Monsonia*, the antepetalous staminal whorl has ten stamens, while the antesepalous whorl has only five. All filaments are basally fused, and those of the antesepalous stamens are longer than those of the antepetalous stamens. The antesepalous stamens form triplets with the adjacent antesepalous stamens. These triplets are fused up to half of their length. Each petal base has two lateral lobes which partially enclose the neighbouring nectary glands. The sepals bend upwards slightly, while the petals and stamen triplets bend outwards through the partial shrinking of the nectary glands and anthophore. This bending leads to an increased distance between the entry zones and the nectary glands. The apicolateral parts of the glands, the petal bases and the filaments are scarcely covered with simple trichomes.

Pelargonium australe (Fig. 1E). The single nectary gland is hidden in a tube-like cavity on the adaxial side of the flower

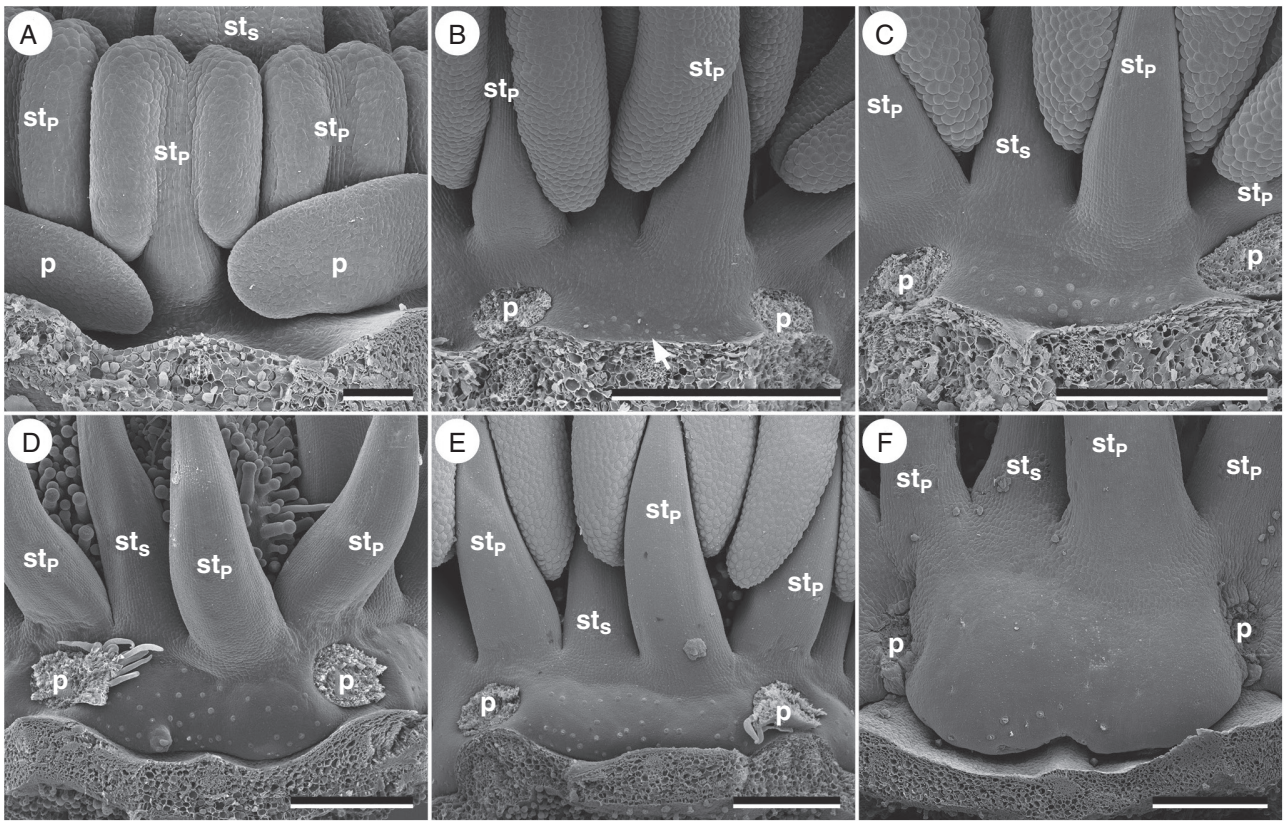

FIG. 6. Nectary gland development in *Hypseocharis bilobata*. Micrographs obtained using scanning electron microscopy. (A) Androecium before onset of nectary gland development. (B) Onset of nectary gland development as a field of nectarostomata. (C) First bulging of the nectary gland. (D) Growth of the nectary gland and the neighbouring receptacle. (E) Continuing growth of the nectary gland. The field of nectarostomata is shifted towards its basipetal position. (F) Nectary gland of an anthetic flower. Arrows indicate the earliest observed stage of nectary gland development. Perianth organs removed. p, petal; s, sepal; st_p, antepetalous stamen; st_s, antesepalous stamen. Scale bars in (A) = 100 µm, (B–F) = 500 µm.

(Fig. 4C, F). The broad opening tapers gradually into a constricted part before it widens again and forms a basal, almost globular compartment in which the nectary gland is localized (Fig. 4F). All floral organs, with the exception of the gynoecium, are glabrous. The abaxial and the lateral antesepalous stamens are staminodial. Their shape ranges from filament-like to triangular with a single large trichome emerging from the tip. All stamens and staminodes are basally fused. The two fertile antepetalous stamens on the adaxial side form a triplet with the adaxial antesepalous stamen. The filament of the latter stamen abruptly broadens towards the fused part of the androecium, forming two 'shoulders' (Fig. 4B). The receptacle below the insertion point of the adaxial petals forms a ring, which constricts the entrance of the cavity (Fig. 4F). In longitudinal sections, a clear difference between the ventral epidermis of the adaxial sepal and the inner epidermis of the cavity is visible (Fig. 4F).

Pelargonium reniforme. The development is similar to that of *P. australe*. The entrance to the spur-like receptacular cavity is surrounded by the partially fused stamen triplet on the proximal side, the erect adaxial sepal on the distal side and the bases of the adaxial petals, demarcating the entrance laterally (Fig. 7H, I). The massive nectary gland is present at the base of the cavity (Fig. 7G).

Hypseocharis bilobata (Fig. 1F). The flowers are bowl-shaped. The nectary glands in *H. bilobata* are located at the bases of 3–4 stamens (Fig. 6). The antepetalous staminal whorl has ten stamens, while the antesepalous has only five. One of the antepetalous stamens is in the antepetalous position, and the second one is shifted towards one of the neighbouring nectary glands. The antesepalous stamens are positioned closer to the centre of the flower. The zone of the nectary glands which is covered with nectarostomata faces towards the base of the sepals (Fig. 6F). The sepals form shallow basipetal protrusions, right in front of the nectary glands (Figs. 6F, 7J). The floral organs are glabrous, possessing simple trichomes only laterally at the bases of the petal (Fig. 7J, K).

DISCUSSION

The study of nectary development adds important information for our understanding of floral organization and floral architecture. The present study of nectary ontogeny in Geraniaceae and Hypseocharitaceae shows that the overall nectary development and floral organization is similar across the taxa studied. They are classified as axial (receptacular) nectaries (Smets, 1988; Smets and Cresens, 1988; Jeiter *et al.*, 2017). Apart from differences in shape and size, major differences occur in the timing of the development of the nectarostomata, through which nectar is

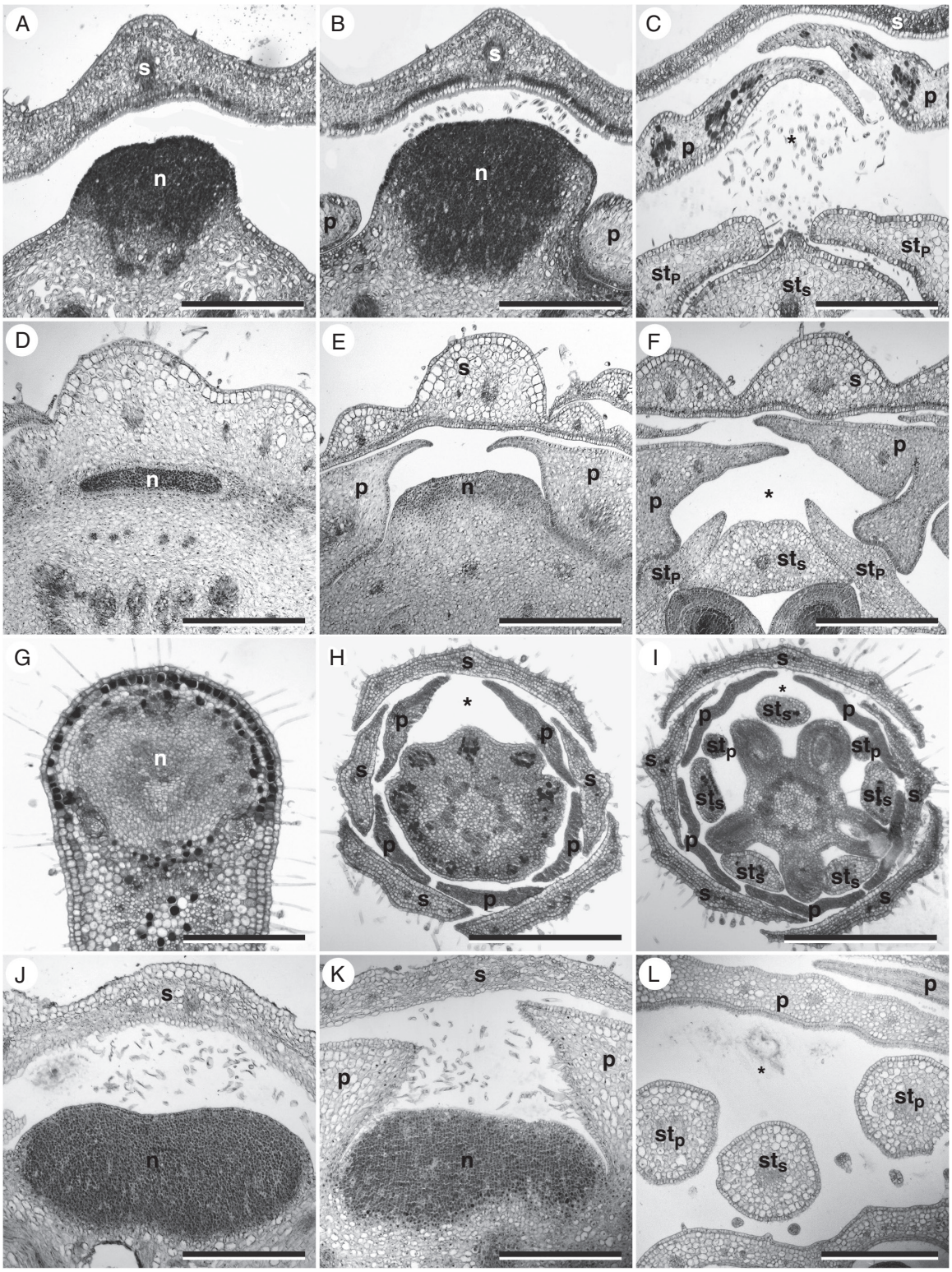

FIG. 7. Floral architecture: cross-sections through mature flowers. (A–C) *Geranium pratense*. (A) Level of circular constriction below petal. (B) Level of petal insertion. (C) Level above nectary gland. (D–F) *Geranium maderense*. (D) Base of the flower and insertion of the nectary gland. (E) Level of petal insertion. (F) Level above the nectary gland. (G–I) *Pelargonium reniforme* (pre-anthetic flower). (G) Level at the base of the receptacular cavity and the base of the gland. (H) Level above the entrance of the cavity. (I) Level of the ovaries. (J–L) *Hypseocharis bilobata*. (J) Level below petal insertion. (K) Level at petal insertion. (L) Level above the nectary gland. n, nectary gland; p, petal; s, sepal; st_p, antepetalous stamens; st_s, antesepalous stamens, *Position of the nectary gland in lower levels. Scale bars in (A–I, K, L) = 500 µm, (J) = 250 µm.

exudated (early in *Hypseocharis*, *Geranium* and *Pelargonium*, and late in *Erodium* and *Monsonia*).

Possibly the most surprising discovery of this study is the presence of a non-nectariferous receptacular structure below the level of petal and anther insertion. This is an anthophore similar to what is found in Caryophyllaceae (e.g. *Lychnis flos-jovis*; Weberling, 1981, p. 30). Anthophore development is the result of intercalary growth of the receptacle and it has two consequences: (1) the size of the nectary glands increases; and (2) the inner volume of the flower increases. Both changes may result in a higher amount of nectar produced and held by the flower. A higher inner volume of the flower may be especially relevant in *G. pratense*, where the anthophore shows a circular constriction. A floral organization and floral architecture similar to that of *G. pratense* have been beautifully illustrated for *G. sylvaticum* (Nilsson, 1984).

Some studies found a positive correlation between the amount of nectariferous tissue and the volume of nectar exudated (e.g. Petanidou *et al.*, 2000). The amount of nectar held by a flower has been found to correlate with the duration of pollinator visit and ultimately with pollination success and seed set (e.g. Manetas, 2000). Increasing the amount of nectar offered is one possible strategy to prolong the time a pollinator spends on a flower. An alternative way to prolong handling time could be compartmentalization of the flower. We found an increased floral complexity in *G. maderense* with five separate nectary compartments formed by a total of six organs from four different whorls. A pollinator would have to probe all five compartments to collect the complete reward of the flower. This form of floral architecture, called 'revolver flower', has been previously described for *G. robertianum* (Endress, 2010). Compartmentalization of the flower is realized through two longitudinal ridges on the base of the petals. This kind of modification appears to be systematically relevant as we confirmed its presence in other species of *Geranium* section *Robertium* (Picard) Rouy & Fouc. (Yeo, 1984), such as *G. reuteri*. This floral architecture is striking because it represents an extreme degree of synorganization in the absence of organ fusion.

Flower compartmentalization is known from several other plant groups either with [e.g. *Brugmansia sanguinea*, Solanaceae (Endress, 1994); Codonaceae (Jeiter *et al.*, 2016)] or without fused organs (e.g. *Aquilegia*; Willmer, 2011), or with a combination of free and fused organs (e.g. Loasaceae; Weigend and Gottschling, 2006). In the case of *Aquilegia*, compartmentalization is realized by individual nectary organs ('Honigblätter'). In the Geraniaceae and Hypseocharitaceae studied, we found a tendency towards the formation of stamen triplets around the nectary gland. Our findings concur with those of Endress (2010), who demonstrated that the formation of (nectar) guide rails in *G. robertianum* is facilitated by the obdiplostemonous organization of the androecium and the formation of stamen triplets. We propose an evolutionary series for the floral architecture (and synorganization) focusing on the occurrence of stamen triplets and nectary position in the Geraniaceae and Hypseocharitaceae (Fig. 8). Selected morphological features are presented in the context of our current understanding of Geraniales phylogeny (Fig. 9). The phylogeny of the Geraniaceae is fully resolved, and the sister group relationships between Hypseocharitaceae and Geraniaceae and to the rest of Geraniales are well supported (Fiz *et al.*, 2008; Palazzesi *et al.*, 2012). Sister to these two families is a well-supported clade comprising the three families Melianthaceae, Francoaceae and Vivianiaceae (Palazzesi *et al.*, 2012). The relationships amongst these three families remain uncertain (Palazzesi *et al.*, 2012), but phylogenies are present for each genus of the Geraniaceae [e.g. *Erodium* (Fiz *et al.*, 2006); *Monsonia* (Touloumenidou *et al.*, 2007); *Pelargonium* (Röschenbleck *et al.*, 2014); *Geranium* (Marcussen and Meseguer, 2017)]. According to APG IV (2016), Myrtales is the sister group of Geraniales, but the relationships between the orders of the rosids remain poorly resolved.

Our results show two character sets which are partially correlated: (1) the androecium and (2) the receptacle including the nectary glands. Within Geraniaceae and Hypseocharitaceae there appears to be a high degree of plasticity in the number of fertile and sterile stamens. The numbers range from five fertile stamens in *California macrophylla* (Aldasoro *et al.*, 2002), to 15 in *Hypseocharis* and *Monsonia*. Additionally, there is variation within genera. In *Pelargonium*, the number of fertile stamens ranges from two to seven while in *Hypseocharis tridentata* only five fertile stamens are present. Considering the common number of ten stamens in Geraniaceae and other genera of the Geraniales (Jeiter *et al.*, 2017), a hypothetical common ancestor with a pentacyclic flower seems to be more likely than one with a tetracyclic flower with one whorl of five stamens as proposed by Ronse De Craene and Bull-Hereñu (2016).

Surprisingly, the seemingly derived receptacular cavity found in *Pelargonium* is linked to several taxa with depressions or cavities formed by the receptacle. Apart from the receptacular cavity in *Pelargonium*, there are depressions in *Hypseocharis*, and the basal clade of *Monsonia* shows several species with tubular receptacular/axial structures (Kers, 1971; Link, 1989; Touloumenidou *et al.*, 2007). We propose a hypothetical ancestor with similar depressions in the receptacle.

Most of the species in this study across *Geranium*, *Erodium* and *Monsonia* show different levels of complexity of floral architecture, synorganization and compartmentalization, but *Pelargonium* represents an entirely different type of floral organization. In the zygomorphic flowers of *Pelargonium*, four of the five nectary glands, present in the other genera, have been lost (Jeiter *et al.*, 2017). The intercalary growth of the receptacle here also includes the bases of the sepals. The only organ that 'remains' in its original position is the nectary gland on the adaxial side of the flower. The intercalary growth results from cell division and subsequent cell elongation (Tsai, 2016). There is considerable variation in the spur length amongst the *Pelargonium* species, ranging from 1 to 100 mm (Bakker *et al.*, 2004). Differences in length appear to be the result of differences in duration of activity of the intercalary meristem; however, the spur-like receptacular cavity growth has so far only been studied in two *Pelargonium* species (Tsai, 2016). In comparison with the often bowl-shaped (and rarely hypocrateriform) flowers of the other genera of the Geraniaceae and Hypseocharitaceae, most *Pelargonium* species show a tubular overall architecture. A similar mechanism of receptacular cavity formation can be assumed for some species of *Monsonia*. The actinomorphic flowers have five independent receptacular cavities, each with one nectary gland (Kers, 1971; Link, 1989). The formation of a tube via intercalary growth of almost the complete receptacle is a rare phenomenon. Endress (1994, p. 115) reports only a few cases where

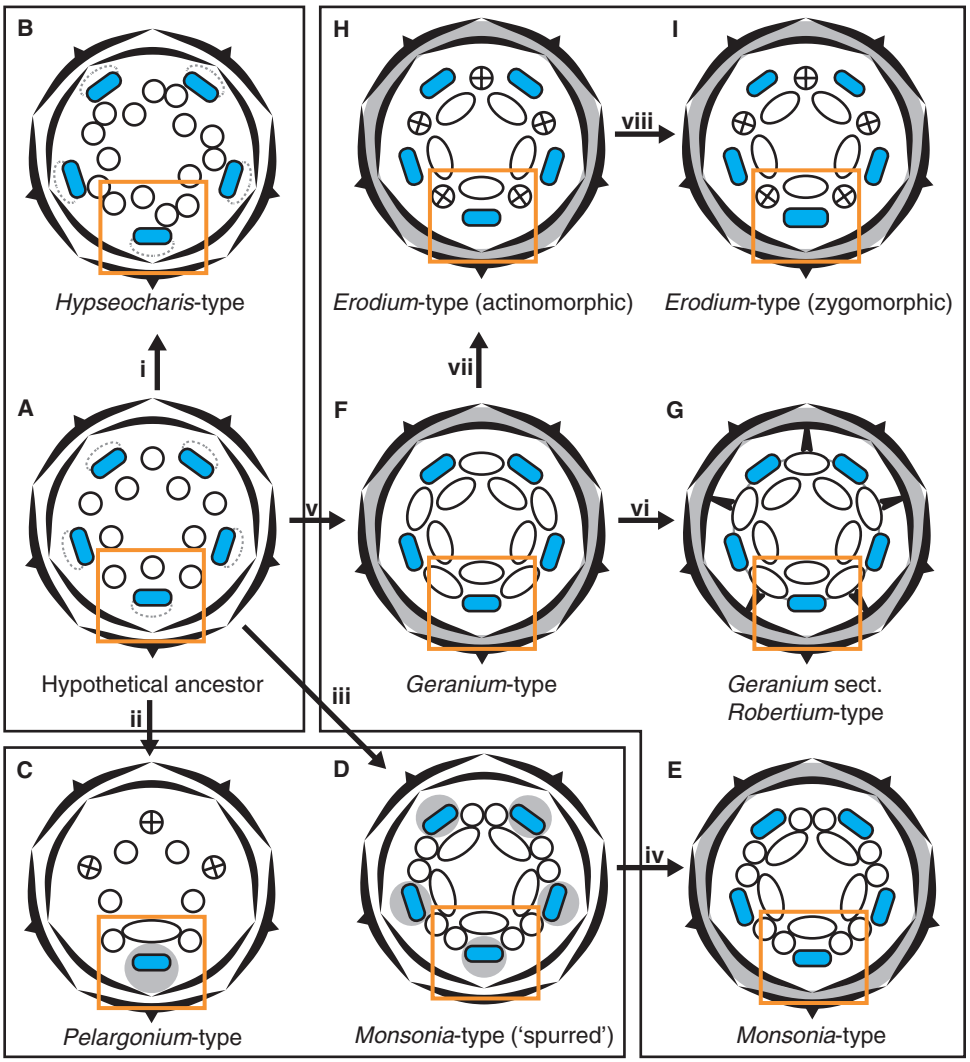

FIG. 8. Schematic representation of the assumed evolutionary series of androecial floral organization in Geraniaceae and Hypseocharitaceae. (A) Type of organization as assumed for the hypothetical ancestor. Nectaries are slightly sunken into the receptacle. (i) Dédoublement in the antepetalous whorl of stamens. (B) *Hypseocharis*-type. (ii) Reduction of four nectary glands and three anthers and the formation of a receptacular cavity through intercalary growth. (C) *Pelargonium*-type. (iii) Dédoublement in the antepetalous androecial whorl and formation of receptacular cavities. (D) *Monsonia*-type with five receptacular cavities ('spurred'). (iv) Reduction of receptacular cavities. (E) *Monsonia*-type. (v) Lateral broadening of the filaments and formation of an elaborate anthophore. (F) *Geranium*-type. (vi) Formation of basal outgrowth of the petals and elaborate synorganization and compartmentalization of the flower. (G) *Geranium* sect. *Robertium*-type. (vii) Reduction of the anthers of the antepetalous stamens. (H) Actinomorphic *Erodium*-type. (viii) Elaboration of the adaxial side of the flower. (I) Slightly zygomorphic *Erodium*-type. Black structures, perianth organs; white circles/ellipses, stamens; crossed circles, staminodes; blue rectangles, nectar glands; small grey circles with dashed line around nectary glands, slightly sunken nectary glands; grey areas, areas which are not affected by intercalary growth of the receptacle; orange boxes, functional unit formed around the nectary gland; black boxes, denote types with similar morphological configuration of the receptacle. Gynoecium not shown.

such 'inner spurs' occur. A 'free receptacular spur' has been described for *Tropaeolum* (Ronse Decraene and Smets, 2001). Tubular structures as such are, of course, common in angiosperm flowers and can be formed by individual organs (usually referred to as 'spurs', e.g. *Aquilegia*; Tucker and Hodges, 2005), by the formation of a hypanthial (receptacular) tube (e.g. *Oenothera*; De Vos, 1981) or by fused sepals or petals (e.g. *Lithospermum*; Cohen, 2016). Variations in length and concomitant shifts in pollinators seem to represent parallel ecological adaptations (Bakker *et al.*, 2004; Whittall and Hodges, 2007; Cohen, 2012).

Interestingly, the function of the unique spur-like receptacular cavity in *Pelargonium* as a key innovation has been rejected (Hodges and Arnold, 1995; Hodges, 1997). The main reason is that a key innovations test is based exclusively on species numbers of sister groups (Slowinski and Guyer, 1993). Considering the number of species present in the sister group, the simplistic view of their diversity in floral architecture, the divergence of dispersal modes, vegetative morphology and the vastly different geographical range of the sister taxa, there may be several 'hidden key innovations' masking the importance of the spur-like receptacular cavity in *Pelargonium*. Comparing the number of species per unit area and coexisting species, *Pelargonium* far exceeds those of the sister group (especially those of *Geranium*). Considering the broad range of pollination

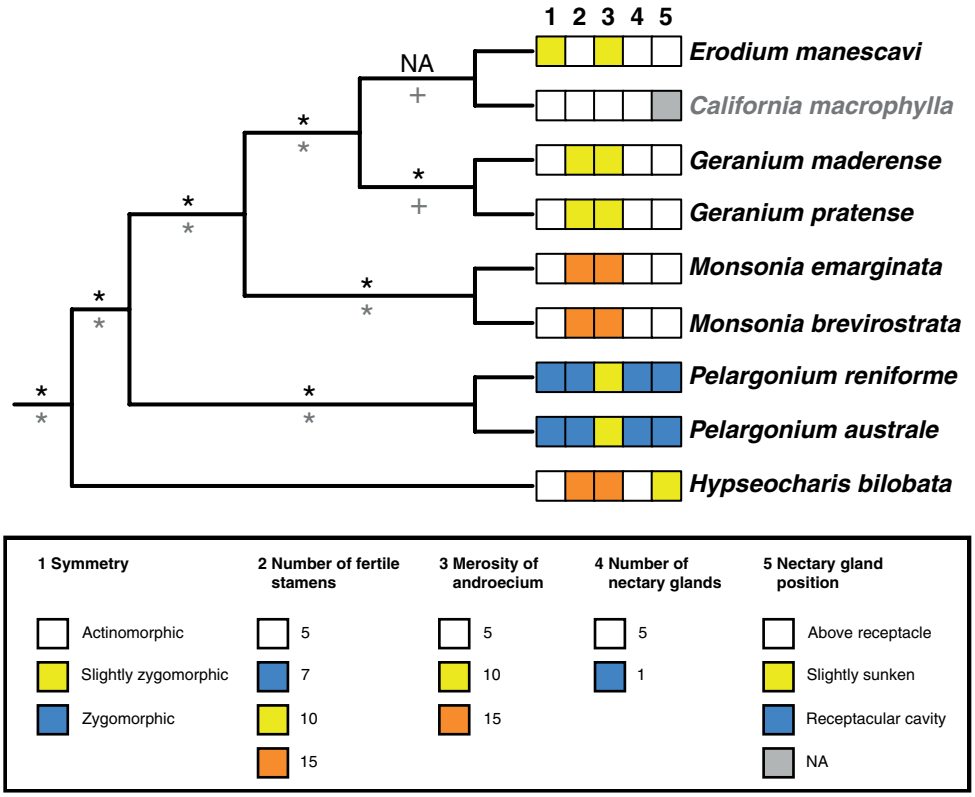

FIG. 9. Phylogenetic relationships and selected character states of the species studied. The topology is based on Palazzesi *et al.* (2012) and Fiz *et al.* (2008). Black labels above the branches refer to support values from Palazzesi *et al.* (2012). Grey labels below the branches refer to support values from Fiz *et al.* (2008). Asterisks (*) indicate bootstrap support values of 100 % and a posterior probability of 1. Pluses (+) indicate a bootstrap support between 50 and 75 % and a posterior probability of 1. *California macrophylla* was not included in the sampling of Palazzesi *et al.* (2012) which is why there are no support values given (NA). The morphological data for *California macrophylla* come from Aldasoro *et al.* (2002) and personal observations. For character coding, please refer to the key.

syndromes documented for *Pelargonium* – vs. a relatively small range in the sister taxa – the specific functional divergence facilitated by the 'inner spur' may well be a key innovation.

Erbar and Leins (1996) underscore the evolutionary significance of sympetaly based on intercalary growth of the stamen–corolla tube. We here demonstrate that part of the floral diversification of Geraniaceae, particularly in the species-rich genus *Pelargonium*, goes back to the hitherto overlooked form of anthophore formation via receptacular, intercalary growth. This expands our appreciation for the importance of intercalary growth contributing to floral architecture and thereby floral mode in highly diversified plant groups.

We further demonstrate that the complex floral synorganization first reported for *G. robertianum* by Endress (2010) is not unique to that species, and a superficial survey indicates that functional floral morphology in *Geranium* may actually be more complex and diverse than generally assumed. A broader sampling of the genus *Geranium* would be particularly interesting for understanding its evolutionary success with >460 species and a sub-cosmopolitan distribution. Jeiter *et al.* (2017) could demonstrate the morphological coherence of flowers across the superficially very different genera of the order Geraniales. The present study illustrates the degrees of freedom obtained by relatively minor changes as a result of intercalary growth or displacement within the rigid constraints of a fairly conserved floral organization.

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