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Review paper

Types of organ fusion in angiosperm flowers (with examples from Chloranthaceae, Araliaceae and monocots)

Dmitry D. Sokoloff[1*], Margarita V. Remizowa[1], Alexander C. Timonin[1], Alexei A. Oskolski[2,3], Maxim S. Nuraliev[1,4]

[1]*Faculty of Biology, M.V. Lomonosov Moscow State University, 1, 12, Leninskie Gory, 119234 Moscow, Russia*

[2]*Department of Botany and Plant Biotechnology, University of Johannesburg, PO Box 524 Auckland Park 2006, Johannesburg, South Africa*

[3]*Botanical Museum, V.L. Komarov Botanical Institute, Prof. Popov 2, 197376 St. Petersburg, Russia*

[4]*Joint Russian-Vietnamese Tropical Scientific and Technological Center, Cau Giay, Hanoi, Vietnam*

Summary. Fusion between floral organs or their parts is believed to have played key roles in the origin and subsequent diversification of angiosperms. Two types of fusion can be recognized: postgenital and congenital. Postgenital fusion is readily observable during flower development: primary morphological surfaces of contacting structures meet and join during this process. After *perfect* postgenital fusion, no trace of the original epidermal layers can be recognized, but these remain visible, often in modified form, after *imperfect* postgenital fusion. Congenital fusion cannot be directly observed and takes place due to differential growth. In the case of *complete* congenital fusion, free parts of fused organs cannot be seen at any developmental stages. *Incomplete* congenital fusion implies the presence of free organ parts on the common (united) base; it can be divided into *early* and *late* congenital fusion depending on whether the common base precedes or follows the initiation of free parts during development. Phenomena related to congenital fusion are the development of free organs from common primordia, hybridization of developmental pathways, loss of organ individuality, heterotopies and fasciation. Differences between congenital and postgenital fusion are much more unequivocal than those between the presence and absence of fusion. There is no abrupt boundary between imperfect postgenital fusion and transient contact between organs during development. Structures assumed to be congenitally fused clearly develop as a unit, but it is necessary to demonstrate that these structures indeed belong to different merged organs (instead of being parts of the same organ or two distinct organs on a common base). This only can be done in the framework of comparative morphology. Analyses of both types of fusion involve arbitrary decisions, so it is not appropriate to discard the existence of any type. Conventional interpretations of morphological concepts lie at the base of analyses of character evolution, even if they are performed using maximum parsimony or model based methods and molecular phylogenetic data. Patterns of organ fusion are discussed here using three case studies.

Keywords: androecium, angiosperms, Apiales, Araliaceae, calyx, Chloranthaceae, congenital fusion, corolla, gynoecium, *Hedyosmum*, monocots, postgenital fusion, septal nectaries.

INTRODUCTION

The fusion between floral organs or their parts played key roles in the origin and subsequent diversification of angiosperms (Endress 1990, 2001a, 2006). Indeed, the appearance of fully closed carpels was a major event of angiosperm origin; fusion between carpels is characteristic for many core eudicots and nearly all monocots; sympetalous corolla is a key morphological character of asterids; formation of various types of androecium tubes (in Leguminosae and Asteraceae) and gynostemium (in Orchidaceae) characterizes the most species-rich and ecologically important angiosperm lineages. Despite extensive research in flower morphology since the XIX Century, our knowledge of the diversity and taxonomic distribution of fusions among angiosperms is still incomplete. For example, the most important recent study of angiosperm floral evolution (Sauquet et al. 2017) used only the presence/absence of fusions as observed in anthetic flowers, not taking into account differences between types of organ fusion due to the scarcity of developmental data for so many species, genera and sometimes even families of flowering plants. Apparently, a global analysis of the evolu-

*Corresponding author, e-mail: sokoloff-v@yandex.ru

tion of fusion events in angiosperm flowers requires further explorations of underlying developmental processes and/or refinement of taxon sampling (Sauquet and Magallón 2018), but this task is complicated by the problem of interpretation of empirical data. There are contrasting views on the interpretation and use of observed data on fusion events in plants. For example, one of the most influential and widely used classifications of angiosperm gynoecia (Leinfellner 1950; see also Weberling 1989; Endress 1994) ignores the differences between free and postgenitally united carpels while defining the term syncarpy, whereas at the same time postgenital fusion is frequently viewed as the only recognizable type of organ fusion in plants (e.g., Sattler 1973). One possible way to avoid problems in interpreting types of organ fusion is elimination of the term 'fusion' from the terminology (e.g., Leins and Erbar 2010), but we believe that this way does not simplify analysis of floral evolution.

Verbeke (1992) provided a highly stimulating review on fusion events during floral development and Endress (2006) further outlined the problem. We supplement these accounts to broaden the discussion on morphological aspects of organ fusion in angiosperm flowers. We explore the diversity of the two major types of organ fusion and provide three case studies related to the general issues discussed here. These case studies are based on members of three major groups of flowering plants, namely eudicots, monocots and basal angiosperms. The choice of these particular examples is, however, rather arbitrary and comes from our personal interests and scientific experience.

POSTGENITAL FUSION

The occurrence of fusion is unquestionable when different organs or parts of the same organ are clearly distinct from each other in the beginning of development, but later their surfaces touch each other, adjacent cuticles disappear, cells of contacting epidermal layers dedifferentiate and sometimes (not always!) undergo extensive divisions, and the initially distinct surfaces merge. This process was considered as postgenital fusion (Baum 1948a,b; Boeke 1971; Barabé and Vieth 1979; Verbeke 1992), or sometimes as ontogenetic fusion (Boke 1948) or surface fusion (Sattler 1977). It can take place early or late in flower development, sometimes being completed after anthesis.

The most common and well-known case of postgenital fusion in angiosperm flowers is closure of individual carpels or the entire gynoecium to form a closed ovary locule. The simplest situation is the postgenital fusion of margins in a carpel with a pronounced plicate zone (Baum 1948a; Endress 2015). The plicate zone is horseshoe-shaped in cross section early in development. The process of postgenital closure of its margins leads to formation of a so-called ventral slit. Pronouncedly ascidiate carpels lacking a plicate zone develop as sac-like (ring-like in cross section) structures with an opening at the top. This opening may close postgenitally, but remains open and filled by mucilage in some members of the basal grade of angiosperms (Endress and Igersheim 2000; Endress 2001b, 2015). It is thus concluded that the absence of fusion of carpel margins is an ancestral condition in angiosperms, with independent gains of complete postgenital closure of carpels in the basal angiosperm family Nymphaeaceae and mesangiosperms (Endress and Doyle 2009). In pronouncedly ascidiate (this interpretation is not always clear, see Igersheim and Endress 1998) carpels of Nymphaeaceae, the distal opening is strongly elongate in radial plane at early developmental stages. This elongate shape is conditioned by the presence of numerous congenitally united carpels forming a whorl. The distal opening in carpels of Nymphaeaceae closes postgenitally forming a structure superficially resembling (or homologous to?) a ventral slit in plicate zone of other angiosperms (Igersheim and Endress 1998). Developmentally, the processes of postgenital closure are rather similar in ascidiate carpels of water lilies and in the ventral slits of the carpels of most other angiosperms. Postgenital fusion between the carpels of the same flower is known in many monocots and in a few groups of eudicots (Baum 1948b; Endress et al. 1983; Verbeke 1992; Remizowa et al. 2006b, 2010b; Endress 2010).

Postgenital fusions are well documented in angiosperm androecia. For example, anther tube formation in Asteraceae belongs to this type. Postgenital fusion between distal parts of stamens and carpels leads to the formation of a so-called gynostegium, a structure which is highly important in the pollination biology of Apocynaceae (Endress 1994).

Postgenital fusions are apparently less common in perianth than in androecium and gynoecium (Verbeke 1992). The classical example is fusion between distal parts of keel petals in papilionoid Leguminosae. Other examples are the formation of corolla tubes in some members of the so-called COM-clade (APG IV) of rosids (Matthews and Endress 2002, 2005, 2011). Weberling (1989) provided a review of eudicots with corolla tubes formed by postgenital fusion. The roles of postgenital fusion in the corolla development of Araliaceae are described in a case study below. Like in the case of syncarpy, it is suggested to use the term sympetaly only for corolla tubes formed by congenital fusion (e.g., Endress and Matthews 2012).

Postgenital fusions involving non-floral structures are rather rare. For example, in a species of *Salicornia* (Chenopodiaceae), postgenital fusion between the perianth tube and inflorescence axis is documented (Beer et al. 2010).

The degree of postgenital fusion varies among taxa and organs fused (Baum 1948a,b; Verbeke 1992; Endress and Igersheim 2000). It is therefore useful to distinguish *perfect* and *imperfect* postgenital fusion, even though the differences between them are qualitative rather than quantitative.

After perfect postgenital fusion, no trace of the original epidermal layers can be recognized. Formation of new plas-

modesmata between cells of contacting epidermal layers is documented in the model system of perfect postgenital fusion, *Catharanthus roseus* (Apocynaceae, van der Schoot et al. 1995). The process of perfect postgenital fusion provides examples of apparently the fastest changes of cellular fate reported for any eukaryotic system *in vivo* (Verbeke 1992). In the gynoecium of *Catharanthus roseus*, some fusing cells completely dedifferentiate within 4.3 hours of cell contact, and by 8.9 hours virtually all of the cells have undergone a dramatic change in cell shape and cytological features (Verbeke and Walker 1985).

In the case of imperfect postgenital fusion, the cells derived from the two adjacent epidermal layers can be anatomically identified during all stages of the process. Changes occurring in the contacting surfaces can be of various types, which are specific for certain taxa and organs. As outlined by Endress (2006), postgenital coherence can be realized at different structural levels: (1) at the infracellular level, either by secretion (e.g., in the symplicate zone of the gynoecium of some Lamiales, Hartl 1956) or by interdigitation of cuticular projections (see examples from Araliaceae in our case study below); (2) at the cellular level by interdigitation of epidermal cells (e.g., tepals of Proteaceae, Endress 2006), by hairs or papillae (e.g., El Ottra et al. 2013; sometimes, papillae grow between each other in a manner resembling plectenchyma, Hartl 1956; Webereling 1989); or (3) at the supracellular level by hooking the organs together. Closure of the corolla by multicellular hairs found in some Araliaceae (see our case study below) is intermediate between cohesion at a cellular and supracellular level.

It is difficult to draw a clear boundary between imperfect postgenital fusion of the units and mere appression of their free surfaces. For calyx, corolla and androecium tubes, it is tempting to use the term 'postgenital fusion' only for cases when organs or their parts join each other and remain united by the end of all developmental processes. For example, when all petals of a flower unite by their margins to form a calyptra-like structure which abscises as a single organ at anthesis, it is logical to speak of postgenital fusion between the petals. In contrast, when petals are firmly connected in a flower bud, but still separate from each other at anthesis, it is apparently not convincing to speak of postgenital fusion (Nuraliev et al. 2017). Endress (2006) used a similar criterion discussing transient coherence between sporangiophores of *Equisetum*. On the other hand, adopting this reasoning to gynoecium is apparently problematic. Indeed, postgenitally united ventral margins of the carpels can disjoin again after anthesis in follicles (e.g. *Illicium*: Romanov et al. 2013) and apparently in some other fruit types.

The criterion outlined above leads to the conclusion that postgenital fusion is a widespread case in ovule and seed development. In seed plants, integument develops as an outgrowth bearing a primary morphological surface. In most cases, the (inner) integument tightly adjoins the nucellus and in bitegmic ovules, the two integuments are appressed to each other. In seeds, a common cuticle layer is often present between the derivates of the nucellus and the inner integument and another layer is present between the testa and tegmen (structures derived from the outer and inner integuments, respectively), but it can disappear between the testa and tegmen (e.g. in Lythraceae, Vyshenskaya 1996). We see no reason why these structures constituting ovules and seeds cannot be considered (imperfectly) postgenitally fused to each other.

Endress (2006) highlighted that postgenital coherence is apparently almost restricted to angiosperms. He noted that there are some isolated cases in non-angiosperms but without real fusion, such as transient coherence by interdigitation of the epidermal cells of the contiguous surfaces between sporangiophores of *Equisetum*. Ovule and seed development in gymnosperms merits further attention in this context. For example, micropyle is represented by an open canal at the time of pollination but apparently not so in mature seeds. It is especially tempting to expect the occurrence of postgenital fusion in the region of micropyle in gymnosperms with extensive cell divisions and growth after pollination, such as *Ginkgo*. Among ferns, we see no objection against recognizing postgenital fusion in the process of the closure of soral canals during sporocarp development in *Marsilea* and related genera (Johnson 1898; Goebel 1905).

CONGENITAL FUSION

The term 'congenital fusion' (or 'zonal growth') describes structures whose fused parts initiate as already united. In other words, the process of fusion cannot be directly observed in ontogeny (Verbeke 1992); instead, it is assumed that continuity between fused organs or their parts arose in the course of evolution. This is why the phenomenon is also called 'phylogenetic fusion' (e.g. Cusick 1966). The primary accent on phylogeny is not, however, appropriate in our view. Indeed, De Candolle (1827: 455) worked in the framework of essentialistic (not evolutionary) morphology when he changed the term 'corolla monopetala' (e.g. Rivinus 1690) to 'corolla gamopetala' (i.e., with united petals) for what we currently call sympetalous corolla.

In each particular case, a judgement about the presence of congenital fusion is based on our interpretation of morphological data rather than on our observation of a juncture between individual floral parts. A conclusion that certain organs in certain species are congenitally fused to each other can be made only by means of comparative analysis involving other taxa or a generalized 'ground plan'. Inferring a ground plan is problematic, because this is an ideal construct, and what appears conventional for some scientists may not look plausible for others. For example, in contrast to the conventional concept of leafy shoots, a ground plan proposed by Zhitkov (1983) implies that each leaf whorl in a whorled

phyllotaxy is a split cap-shaped leaf. Many authors take into account methodological difficulties in identification of congenitally fused organs and avoid interpreting this phenomenon as an actual fusion (e.g. Sattler 1973, 1977, 1978; Leins and Erbar 2010; Ronse De Craene 2018).

Barabé and Vieth (1979) summarized the principal differences between views on congenital fusion adopted in the classical XIX Century works of Payer and Van Tieghem. They pointed out that there is a difference, at the theoretical level, between the concepts of *fusion congénitale* as defined by Payer and *concrescence congénitale* formulated by Van Tieghem. The former cannot be observed by definition, while the latter is observable as it is associated with detectable intercalary growth. In contrast to the views of Van Tieghem, subsequent researchers demonstrated that intercalary growth of the tissue of a supporting organ is hardly distinguishable from that of the tissue of a joint basis of united organs (e.g., Bugnon 1928). Thus Sattler (1977) proposed discarding the concept of congenital fusion and describing processes of interprimordial growth instead. He recognized nine patterns of interprimordial growth. Interestingly, Sattler (1977) recognized interprimordial growth along with two other phenomena, namely surface fusion (= postgenital fusion) and heterotopy, which is a change of the site of primordium initiation. However, heterotopy is as unobservable during development as congenital fusion, because it is detectable only by comparison of related taxa (Timonin 2002). This example shows that it is hardly ever possible to propose a terminology free from interpretations (Lubischew 1925).

One of the most widely discussed questions related to the problem of congenital fusion is the morphological interpretation of the inferior ovary wall in various angiosperms (e.g., Eames 1931; Smith and Smith 1942; Douglas 1944, 1957; Kaplan 1967). In a flower with inferior ovary, the locule(s) are located below the level of visible attachment of perianth elements (sepals and petals or tepals) and/or stamens. Much simplifying the discussion, the wall of the inferior ovary can be interpreted (1) as bases of perianth elements and stamens congenitally united with dorsal parts of carpels or (2) as a cup-shaped receptacle congenitally united with dorsal parts of carpels. Furthermore, (3) it is possible to interpret the process of inferior ovary development merely in terms of formation of cup-shaped receptacle resulting from its extensive growth at the periphery, which leads to strongly oblique carpel bases. The latter interpretation fits the processes that can be directly observed in ontogeny, and it does not imply the occurrence of congenital fusion (e.g., Leins and Erbar 2010). An important question in the interpretation of the inferior ovary is recognizing the boundaries of the receptacle. There is no precise way of tracing these boundaries, but examination of the vasculature can help in certain situations. Namely, when so-called recurrent vascular bundles are present in the wall of the inferior ovary, its nature can be recognized as receptacular. The recurrent bundles (Smith and Smith 1942; Douglas 1957) run up to the distal part of the ovary wall and then curve backwards to innervate the ovules. It is assumed that the loop of these bundles indicates the concavity of the receptacle. Although the presence of recurrent bundles is informative for homology assessment, their absence is not informative and provides no support to the idea of the appendicular nature of the inferior ovary wall (hypothesis 1) (e.g., Volgin 1988).

Similar questions have been posed about the nature of the hypanthium (= floral cup, floral tube), which can also be interpreted as congenitally united basal parts of outer floral elements or as a receptacle outgrowth. It is now widely accepted that the nature (homology) of a tube bearing all floral parts excepting the gynoecium (i.e. perianth and stamens) can never be determined (probably except for the case of the occurrence of recurrent bundles in the tube, e.g. Jackson 1934). Particularly, it seems to be impossible to design an investigation that would be of potential help in choosing one of the interpretations. In other words, these hypotheses on the nature of the hypanthium are not falsifiable. For these reasons, the terms "hypanthium" and "floral cup" are now used as synonyms (Leins and Erbar 2010; Ronse De Craene 2010).

Despite all the problems with demarcation between congenital fusion and differential growth (such that discussion on the nature of the inferior ovary was even considered to be fruitless, Endress 1994; Ronse De Craene 2010), the concept of congenital fusion is useful in many situations. Even though we cannot precisely demonstrate the appendicular nature of ab initio continuous calyx, corolla and androecium tubes and syncarpous gynoecia, it is much simpler to operate with these structures assuming that they are products of congenital fusion. In fact, use of terms such as sympetaly and syncarpy does indirectly imply recognizing the phenomenon of fusion. The explicit use of the term congenital fusion clearly demonstrates its problematic background instead of masking it.

Two primary types of congenital fusion can be recognized. In the case of *complete* congenital fusion, no free parts of fused organs can be seen at any developmental stages. For example, carpels of Vitaceae (Gerrath and Posluszny 1989a,b) and a few other eudicots (Endress 2010) and monocots (e.g. *Narthecium*, Remizowa et al. 2006b) are congenitally united up to their tips. In Vitaceae (Gerrath and Posluszny 1989a,b), gynoecium starts its development as a ring-like structure and the common stigma is discoid in anthetic flowers; the bicarpellate nature of the gynoecium is clearly visible in the ovary where the two locules are separated by two one-sided septa postgenitally connected at the centre (though so-called false septa are well-known in some other angiosperm groups, Weberling 1989).

Incomplete congenital fusion implies the presence of free organ parts on the common (united) base; it can be further divided into *early* and *late* congenital fusion. This concept has been developed in extensive studies of corolla

development in asterids, where early and late sympetaly have been recognized (Erbar 1991; Leins and Erbar 1997, 2010).

In the case of late congenital fusion, the free parts of the organs initiate first in flower ontogeny, followed by the development of their common portion. This common portion appears through intercalary growth below the free parts. This is the case of late sympetaly that is common in many families of Lamiales and other lamiids (Leins and Erbar 1997; Erbar and Leins 2011). Late congenital fusion of sepals, stamens and carpels is present in various angiosperms. For example, the tube of androecium in papilionoid Leguminosae develops in this way, as it appears long after free parts of the stamens due to intercalary growth (Tucker 2003). It should be noted that free parts of the organs can subsequently fuse postgenitally. This can be seen in the examples of late congenital fusion between carpels in monocot gynoecia (see below).

In the case of early congenital fusion, a common primordium of the united organs appears first. It is followed by their free parts arising on the common base. In eudicot taxa with early sympetaly (mainly in campanulids), the corolla is ring-like during the earliest developmental stages (girdling primordium, Sattler 1973), and free parts of the petals appear later in development (Erbar 1991; Erbar and Leins 1996; Leins and Erbar, 1997). Only with certain assumptions can the concept of early congenital fusion be viewed as interprimordial growth as described by Sattler (1977). Sattler (1973) viewed a girdling primordium as the borderline case in which the ratio of primordial and interprimordial growth is one (but it seems that this is an interpretative description!).

Patterns of gynoecium development apparently provide examples of the occurrence of early vs. late congenital fusion in taxa with similar definitive structure. For example, the gynoecia of Chenopodiaceae and Piperaceae (except for *Peperomia*) consist of carpels congenitally united into unilocular ovary with one central basal ovule. Distal parts of these carpels are free and form individual stigmas. In both families, the ovule is shared by all carpels (mixomerous gynoecia, Sokoloff et al. 2017). In Chenopodiaceae, gynoecium development starts with a ring-like primordium (e.g., Sattler 1973; Olvera et al. 2008) and free parts of the carpels appear later (early congenital fusion). In Piperaceae, free parts of the carpels appear first (late congenital fusion), at least in *Zippelia* (Liang and Tucker 1995).

The late and early congenital fusion can co-occur in the development of the same structure. For example, the calyx tube of *Coronilla* (Leguminosae) is formed by early congenital fusion between two neighbouring sepals and by late congenital fusion in the rest of the tube. This character is phylogenetically important in the group of genera that includes *Coronilla* (tribe Loteae, Sokoloff et al. 2007a). In some other cases, the combination of late and early congenital fusion is unstable within a species and has no taxonomic value (as in calyculus development of *Tofieldia coccinea*, Tofieldiaceae, Remizowa et al. 2006a).

Differences between early and late congenital fusion can be of taxonomic and evolutionary importance, but it is not always easy to distinguish between them. One reason is that the sequence of developmental events can be very rapid and apparently sometimes not identical in different flowers of the same species (e.g., Degtjareva and Sokoloff 2012). Sometimes, the petal primordia arise on the rim of a plateau, and the extension and connection of the petal bases coincides with the initiation of the stamen primordia (Erbar and Leins 2011). Finally, the occurrence of a ring-like primordium (in the case of early congenital fusion) cannot be properly distinguished from the appearance of a concave receptacle (Ronse De Craene and Smets 2000; Ronse De Craene et al. 2000). Formation of a concave floral apex is characteristic for the early stages of flower development in many angiosperms with inferior ovary. Many campanulids (and some lamiids, including Rubiaceae) with early sympetaly also have an inferior ovary, and it is possible that at least in some cases the ring-like structure observed early in development belongs to receptacle rather than to corolla. There is apparently no way of resolving this problem.

In contrast to postgenital fusion, congenital fusion is widespread among non-angiosperm land plants. Examples are perianthium of liverworts (consisting of three united uppermost leaves), syntelomic leaves of euphyllophytes and ovule integuments of seed plants, fusion between nucellus and integument in various gymnosperms, and seed scale of conifers.

PHENOMENA RELATED TO CONGENITAL FUSION

A common primordium is a primordium that ultimately produces more than one organ (e.g., Tucker 1989; Ronse De Craene and Smets 1993; Endress 1995; Kirchoff 1997; Ferrándiz et al. 1999; Caris et al. 2000; Remizowa et al. 2010a,b). This is exactly what we observe in the case of early congenital fusion. However, the organs developed from a common primodrium not necessarily appear to be united in definitive flowers. For example, Erbar and Leins (1988, 1995, 1996, 2004, 2011) reported the occurrence of a common circular corolla primordium ('early sympetaly') in some asterids having no corolla tube recognizable at later developmental stages. This question is further discussed below in the case study of Araliaceae. Common tepal/stamen primordia are documented in a wide range of monocots (Endress 1995), and we can use this example as an illustration of the phenomenon of common primordia. Each tepal/stamen primordium produces a tepal and a stamen located on the same radius. In many monocots with common tepal/stamen primordia, definitive tepals and stamens are free. This is because after extensive growth of all organs the common tepal/stamen base remains as small as was the common primordium

and thus cannot be recognized anymore. The presence of a common tepal/stamen primordium is therefore neither a necessary nor sufficient condition for the appearance of congenitally united bases of the two organs in anthetic flower (Endress 1995).

The presence of common primordia can be variable within a single species (Remizowa et al. 2005). It seems that the presence of common primordia of inner tepals and inner stamens is intimately linked in monocots with delayed receptacle expansion and delayed carpel initiation. In taxa with delayed receptacle expansion, initiation of (inner) tepals and stamens takes place in very rapid sequence, or almost simultaneously, leading to the appearance of common tepal-stamen primordia (Remizowa et al. 2010a). The appearance of common petal-stamen primordia found in various eudicot families could be interpreted in terms of a gradual regression of the petals linked to their retardation in inception and slower growth (Ronse De Craene and Smets 1993). The delay in inception of the petal primordia is connected with strongly developed antepetalous (primary) stamen primordia and leads to the absorption of the petal primordium by the stamen primordium into a common primordium (Sattler 1962, cited in Ronse De Craene and Smets 1993).

Speculations on common primordia are problematic because most studies consider only their visible appearance during development, though actual patterning (pre-patterning) of organ positions takes place in earlier stages. Remizowa et al. (2010b) attempted to explain the strongly homoplastic occurrence of common tepal-stamen primordia in monocots, hypothesizing that pre-primordial patterning of the floral meristem in most monocots could include identification of sites of six tepal-stamen complexes in two whorls. At later stages, each site then divides into separate tepal and stamen sites, and the actual visibility of common primordia is of secondary importance. This sectorial model could explain both the apparent multiple homoplastic origins of common primordia and the occurrence of intermediate conditions.

There is a problem in distinguishing the occurrence of common primordia as a result of organ fusion from that in the case of organ splitting in the course of evolution (the latter case called dédoublement, reviewed by Ronse De Craene and Smets 1993). The concept of dédoublement is as subject to criticism as the concept of congenital fusion, and the reasons are the same. If, for example, two stamens develop from a common primordium, data from comparative morphology are required to interpret this as evidence of splitting or fusion (see Ronse De Craene and Smets 1993).

Complete congenital fusion shares some features with a phenomenon called hybridization of developmental pathways, which describes a situation when an organ combines characteristics of two organ types, or a mosaic of two developmental programs is realized in organ development (see Lodkina 1983; Sattler 1988; Rutishauser and Isler 2001). For example, it is possible that the earliest Nymphaeaceae possessed small flowers with a moderate number of organs (like in the Early Cretaceous *Monetianthus*, Friis et al. 2009), apparently with clearly distinct stamens and perianth members. With subsequent evolutionary increase of flower size (see Borsch et al. 2008; Doyle and Endress 2014) and an increase in organ number, some Nymphaeaceae acquired flowers with organs intermediate between petals and stamens. These should be interpreted in terms of hybridization of developmental pathways of the two organ types (Meyen 1987; see also recent studies of organ transitions in *Nymphaea*: Volkova et al. 2007; Yoo et al. 2010). In this case, there is no way of mistaking hybridization of developmental pathways with organ fusion. The following two examples are more problematic. (1) In angiosperms, lateral flowers are normally developed in the axils of flower-subtending bracts. In some 'abracteate' monocots, however, an organ is present that combines the positional and developmental characteristics of the flower-subtending bract and the outer median abaxial tepal (Buzgo and Endress 2000; Remizowa et al. 2013). The question then is whether it is a single phyllome developing under control of a mosaic of two developmental programs or two completely congenitally fused phyllomes. Resolving this question is especially problematic in the absence of a series of transitional forms among related taxa, as in *Acorus*, a taxonomically isolated genus appearing sister to all other monocots in most molecular phylogenetic analyses (e.g., Ross et al. 2016). (2) In Polygonaceae, flowers with 2+2, 5 and 3+3 tepals are known (reviewed by Ronse De Craene and Smets 1994; Yurtseva and Choob 2005). Those with 2+2 and 3+3 tepals possess two perianth whorls. When 5 tepals are present, two of them could be interpreted as belonging to the outer whorl, two as belonging to the inner whorl and the fifth as partly belonging to the outer and partly to the inner whorl. Sometimes, the two halves of this tepal differ in morphology accordingly, and two keels can be recognized. However, data on early flower development clearly suggest that this is just a single organ. No developmental evidence for its double origin can be found. We prefer speaking of hybridization of developmental pathways in this case, but another possible interpretation is complete congenital fusion of two tepals. Again, there is no possibility to discard one of these interpretations and prove the other. The question is further complicated by the idea that the perianth of five tepals may be an ancestral condition in evolution of Polygonaceae (Ronse De Craene 2016).

Loss of organ individuality. Certain loss of individuality occurs in any case of congenital fusion, but counting organ number is still usually rather straightforward, even in the case of complete fusion (e.g., in gynoecium of Vitaceae, see above). However, in examples like the unilocular gynoecium of Primulaceae developing as an entire sac-like structure, fused organs have apparently lost their individuality (Endress 2015). Similar 'dissolution' of integrating organs in a

new entity is well-known in the evolutionary morphology of animals (Beklemishev 1964).

Fasciation (e.g., White 1948; Choob and Sinyushin 2012), if viewed as the incomplete separation of organs (or entire flowers), can hardly be distinguished from their congenital fusion (see also Sokoloff et al. 2006, 2007b and the case study of Araliaceae below). Another phenomenon related to congenital fusion is heterotopy (= metatopy, including concaulescence and recaulescence, Troll 1937). This issue is beyond the scope of the present review.

CASE STUDY 1. PERIANTH OF ARALIACEAE

Sympetaly is a key innovation of asterids, especially of euasterids (Endress 2011b). The order Apiales is of interest as a relatively large euasterid clade where flowers with corolla tubes are extremely rare. Araliaceae, one of the largest families in Apiales, shows considerable diversity of perianth morphology (Figs 1-8), though typical tubular corollas with free petal lobes are absent from this family. The case of Araliaceae illustrates how different types of fusion and their combinations condition the ultimate appearance of the perianth and the whole flower. It also shows a kind of hidden perianth diversity, which can only be detected at certain developmental stages.

The calyx in Araliaceae and in its closely related family Apiaceae is uniformly minute, often hardly discernible in mature flowers and never playing evident roles in the pollination process. In both families, the calyx is typically synsepalous, i.e. possesses a tube of congenitally fused sepal bases, and has free sepal lobes (Fig. 1). Various patterns of calyx reduction can be recognized. In some taxa (e.g. *Hydrocotyle* of Araliaceae, Erbar and Leins 1985; Leins and Erbar 2004; Nicolas and Plunkett 2009; *Chaerophyllum* of Apiaceae, Erbar and Leins 1997; Nuraliev et al. 2017), total absence of the calyx whorl was reported: no traces of sepal primordia were found in developmental studies. In several species of Araliaceae, such as *Schefflera actinophylla*, *S. subintegra* (Fig. 7A-C) and *Tupidanthus calyptratus* (Fig. 8A-D), the calyx is represented only by a tube without any free lobes since its initiation (Sokoloff et al. 2007b; Nuraliev et al. 2009, 2010, 2011, 2014, 2017); though of course in this case it is especially difficult to demonstrate that this structure is indeed a calyx tube rather than margins of a concave receptacle. Phylogenetic context (e.g., Plunkett et al. 2005; Nuraliev et al. 2014) suggests interpreting the tubular calyx without free lobes as a result of a transition from incomplete congenital fusion to a complete one. In such situations, it is tempting to speak of complete reduction of the free parts of the fused organs; however, it is apparently impossible to prove (at least in the discussed case) whether the free parts of the fused organs were reduced or became completely fused up to their apices. We argue that in such cases it is more correct to use the terms describing the fusion types rather than the appearance/reduction of parts of organs.

When interpreting these calyces as comprising congenitally fused sepals, one is expecting to outline the fused organs, i.e. to indicate the number of sepals in a calyx. However, it is impossible, at least according to the current state of our knowledge. This calyx also agrees with the situation described above as a loss of organ individuality, which further complicates the evaluation of its evolutionary interpretation. Indeed, the calyces of the above-mentioned taxa lack any traits of individual sepals, even in their anatomical structure. It is possible, therefore, to speculate that the calyx of this morphology does not consist of sepals but represents a unitary structure.

It is important to highlight that an evolutionary switch to the entire calyx has no obvious functional significance. The calyx is small and does not play any role in protection of the flower bud, so it is unclear why the presence of an entire calyx is of a greater adaptive value than the presence of individual tiny sepals. It is more likely that this type of calyx appeared because its developmental program is simpler or because it is developmentally coordinated with a corolla of completely fused petals, and the presence of this corolla type possesses certain adaptive value (in the case of *Tupidanthus* and *Schefflera subintegra*, but not in the case of *S. actinophylla* that lacks corolla tube).

The anthetic corolla of Araliaceae shows considerable diversity, caused by a number of reasons including various patterns of petal fusion. The most common condition in this family is a corolla of free petals, i.e. without con- or postgenital fusion. Erbar and Leins (2004, also Leins and Erbar 2004) described the initiation of corolla in Araliaceae as a low ring primordium that does not grow up forming a tube or as flat shoulders connecting young petals. They consequently identified Araliaceae as characterized by early sympetaly (see also Leins and Erbar 1997). Erbar and Leins (2004) also pointed out that the assumed sympetaly in Araliaceae (and in the same way in Pittosporaceae) appears plausible because of the arrangement of Apiales deep in asterid phylogeny. However, in the majority of Araliaceae, including in the images provided by these authors, the presence of a corolla tube is not obvious even at the stage of petal initiation. Apparently, in some Araliaceae (e.g., *Hedera helix* – Fig. 1 in Erbar and Leins 2004) there is a problem in distinguishing between a circular corolla primordium and the margins of a concave receptacle (as in other asterids with inferior ovary, see above). However, in many Araliaceae, the receptacle is flat and in our view the petals just initiate as distinct primordia (Fig. 1B). We found it groundless to state the presence of organ fusion based exclusively on the observations of the earliest developmental stages (Nuraliev et al. 2017, see also the discussion on common primordia above).

As the calyx in Araliaceae is much shorter than the corolla at most developmental stages and especially in mature

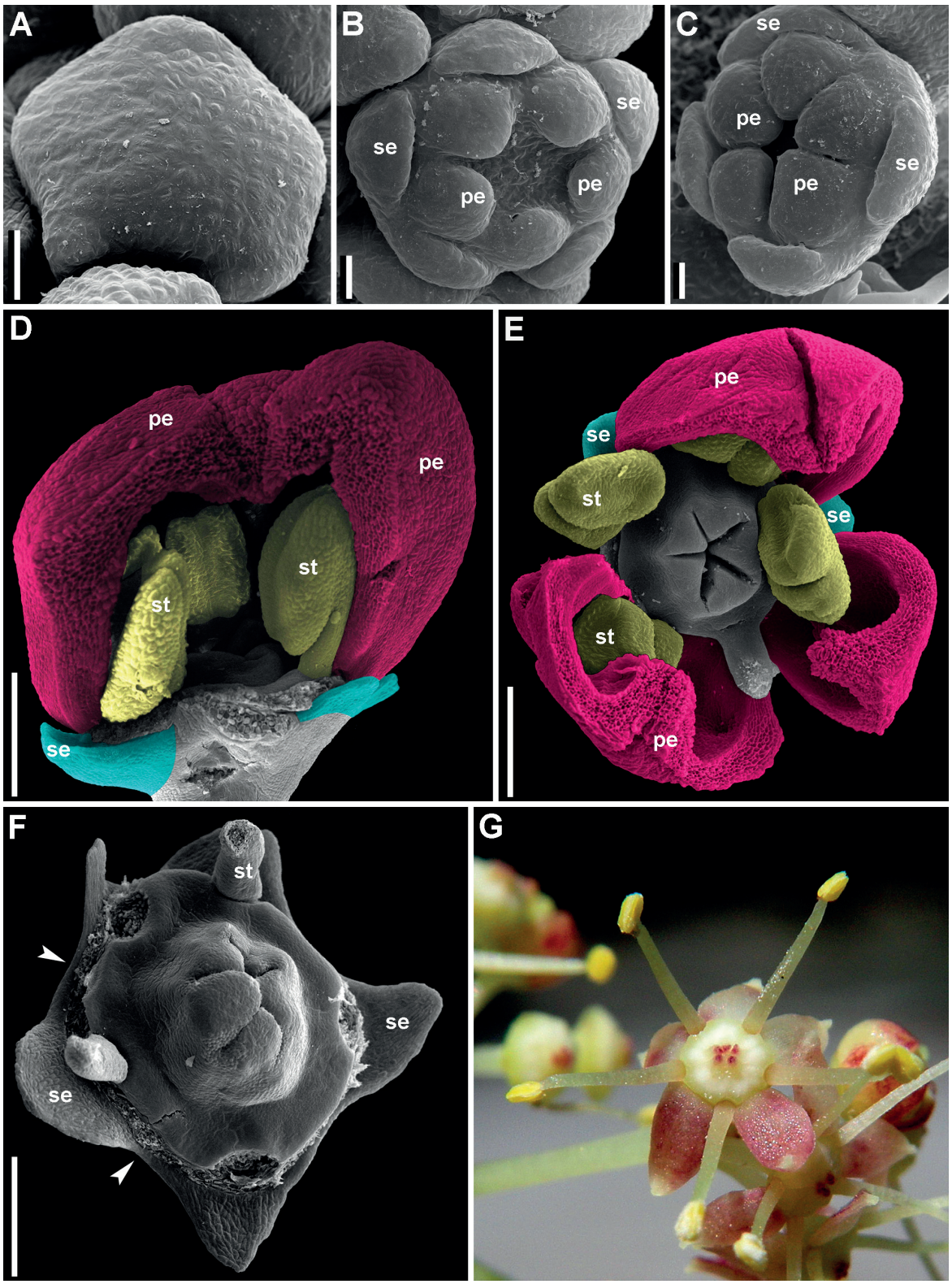

Fig. 1. Flower of *Schefflera leucantha* (Araliaceae) A–F: scanning electron microscopy (SEM), G: photo (modified from Nuraliev et al. 2017). A: Floral primordium. B, C: Perianth initiation. D, E: Late developmental stages; note tightly connected petals (corolla artificially opened in E). F: Almost mature flower; note calyx tube (arrowheads); petals and stamens removed. G: Anthetic flower. pe, petal; se, sepal; st, stamen. (Scale bars: A–C = 30 µm, D–F = 300 µm.)

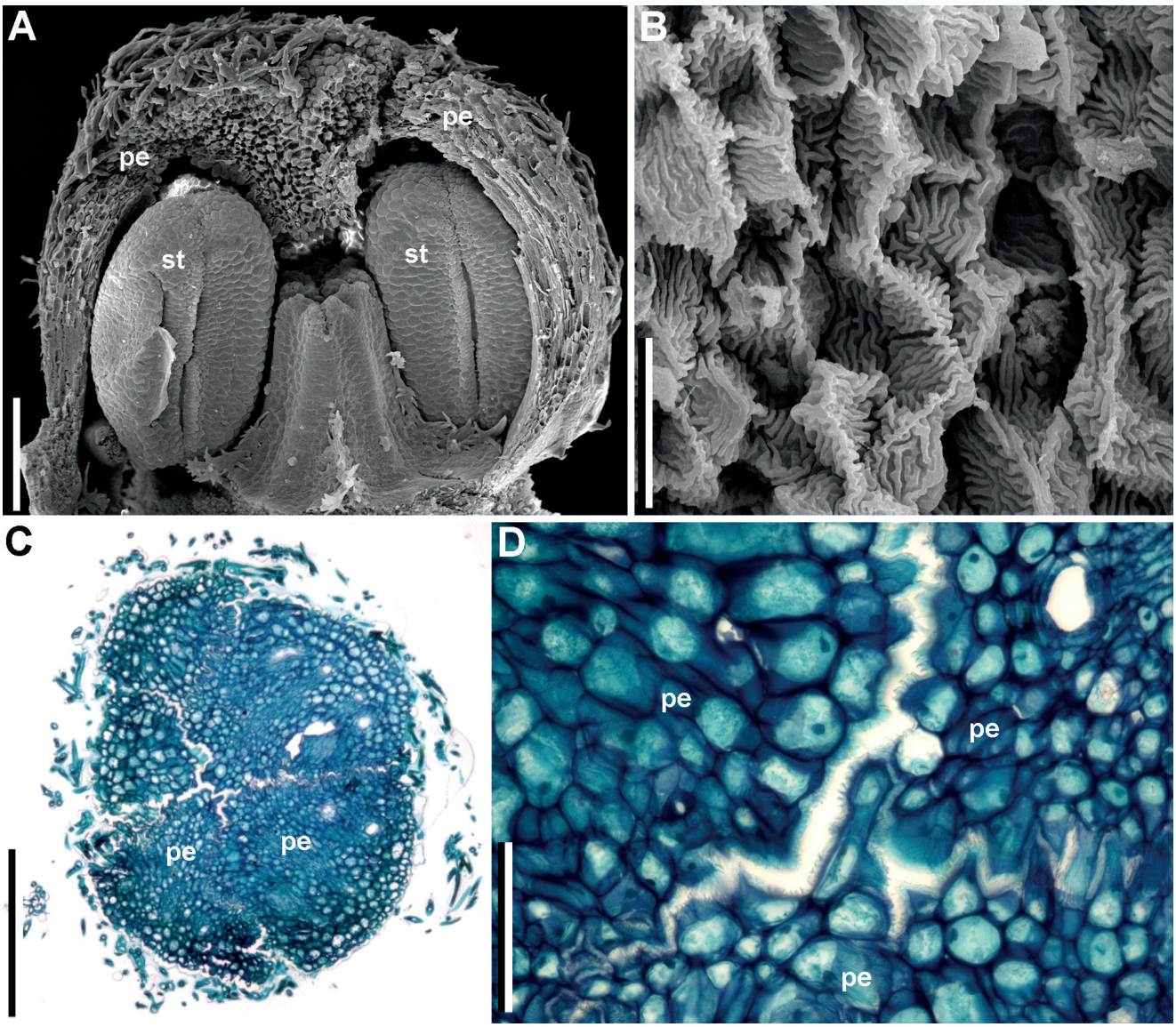

Fig. 2. Flower of *Schefflera macrophylla* (Araliaceae) A, B: SEM, C, D: light microscopy (LM). A: Flower bud; note tightly connected petals. B: Surface of lateral petal side in the region of connection with neighboring petal. C: Cross section of pre-anthetic flower at the level of distal corolla part. D: Central part of a section similar to C; note the cell wall sculpture along the area of petal connection. pe, petal; st, stamen. (Scale bars: A = 300 μm, B = 30 μm, C = 500 μm, D = 100 μm.)

flowers, the corolla plays a main role in protecting the flower bud (Figs 1-8). In corollas without any fusion, the petals stay tightly connected in flower buds via the specialized structure of the cell walls in the epidermal areas involved in this contact (Fig. 1D, E, 2). This situation approaches the idea of imperfect postgenital fusion; however, since the petals are free at anthesis (Fig. 1G), we prefer not to speak of any fusion in this case. There are also representatives of Araliaceae (e.g. *Schefflera schizophylla*, Figs 4-5), which possess the same pattern of corolla development as those with free petals, and even the same corolla structure in the flower bud, but show a different fate of petals at anthesis. In such species, the petals abscise at the time of flower opening and thus are absent in the anthetic flower (Fig. 4D, E). During and after the abscission, the petals stay tightly connected to each other (they only separate from each other in the proximal region). This results in the formation of a calyptra-like structure (not to be confused with the true calyptra described below). This structure seems to be morphologically equal to the corollas of choripetalous species, but the absence of petal separation leads us to the conclusion that this should be regarded as an example of imperfect postgenital fusion.

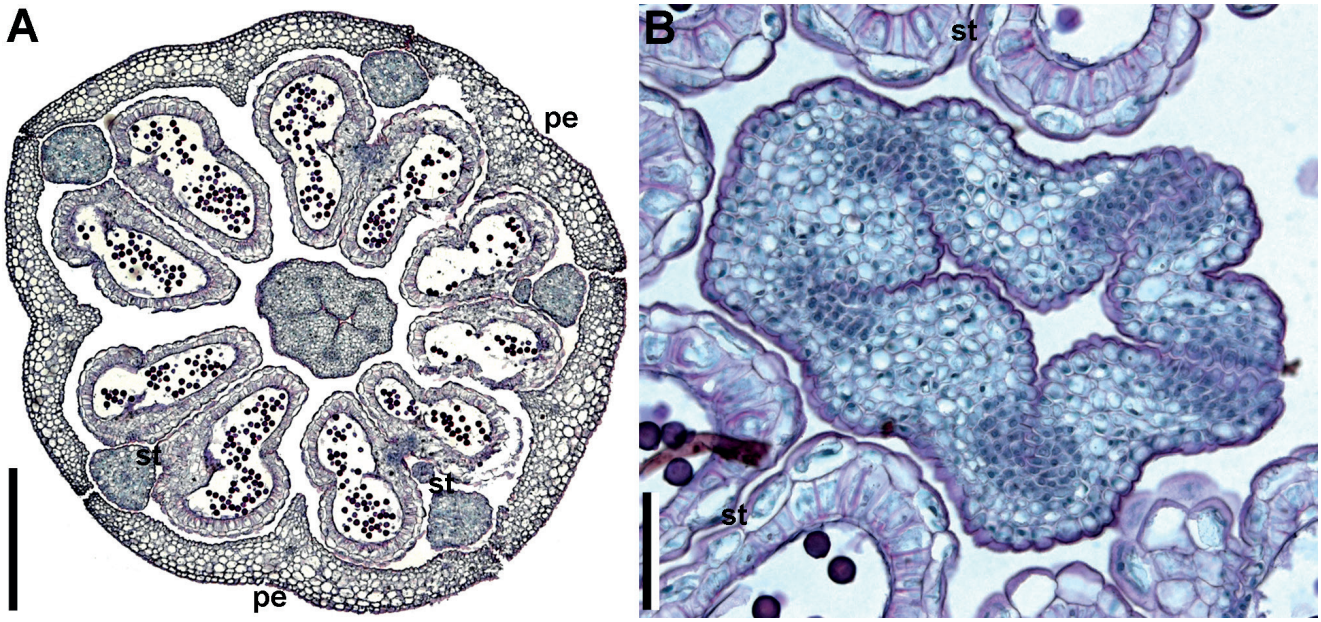

Fig. 3. Flower of *Schefflera delavayi* (Araliaceae; LM; A: modified from Nuraliev et al. 2011). A: Cross-section of pre-anthetic flower at the level of style. B: Cross section of style at a level slightly more proximal than in A; note the five areas of postgenital fusion of carpel ventral slits forming pollen tube transmitting tissue. pe, petal; st, stamen. (Scale bars: A = 500 μm, B = 100 μm.)

Schefflera actinophylla provides an even more striking example of postgenital petal fusion (Fig. 6). The development and morphology of the corolla are again nearly equal here to those of species with free petals and with a calyptra-like structure. The differences appear at the time of flower opening: there are approximately twelve petals in the flower of *S. actinophylla*, and after opening they remain united in groups of two or three. It is most likely that this unusual mode of opening is linked to the high corolla merism: the neighbouring petals are inserted on close radii, almost parallel to each other, and the mechanical forces appearing when the petals turn back are not strong enough to separate them. According to the criterion used in the case of calyptra-like structure (see above), we also assume that this situation is an example of imperfect postgenital fusion. Here, the presence and absence of fusion occur in similar (radially symmetric) regions of the same flower, and even on different sides of the same petal. Moreover, at least at the level of our light microscopic observations of anatomical sections, it is impossible to predict where the connection between petals will remain and can be classified as fusion, and where the petals will separate from each other.

The absence of congenital petal fusion is most likely a plesiomorphic condition in Araliaceae (Nuraliev et al. 2010), but there are a few taxa in this family characterized by a prominent corolla tube (of congenitally united petals). In *Osmoxylon*, the sympetalous corolla is persistent during anthesis (at least during the male stage) and the stamens are exposed through its orifice (Nuraliev et al. 2010). In *Schefflera subintegra* and *Tupidanthus calyptratus*, which were shown to be sister species, the corolla morphology is more complex (Sokoloff et al. 2007b; Nuraliev et al. 2014, 2017). In all three taxa, the corolla initiates as a ring primordium and lacks free petal lobes or any other evidence of individual petals, and therefore the discussion of complete congenital fusion vs. loss of organ identity that was provided above for calyx lacking sepal lobes is fully applicable here. In contrast to *Osmoxylon*, in *S. subintegra* and *T. calyptratus* the orifice of corolla tube closes by means of imperfect postgenital fusion during flower development (Figs 7C, E, 8D). The fusion occurs by the same mechanism as in Araliaceae with the petals fused only postgenitally, i.e. through tight contact between epidermal areas bearing specialized cell wall structures. Additionally, the distal margin of the suture of postgenital closure is covered by multicellular hairs of a special type that do not develop anywhere else in the flower (Figs 7B-D, 8D-E). The combination of con- and postgenital fusion results in the development of massive calyptras, which abscise at the flower opening. The similarities in the mode of corolla closure with more typical members of Araliaceae are of special importance for identification of the calyptra as a modified corolla. Indeed, without special arguments of this sort, one can wonder whether the calyptra is of receptacular origin.

The combination of the congenital and postgenital fusion in the corolla of some Araliaceae is of methodological interest with respect to character scoring in data matrices for analyses of character evolution. Both types of fusion are present here, but only congenital fusion is responsible for

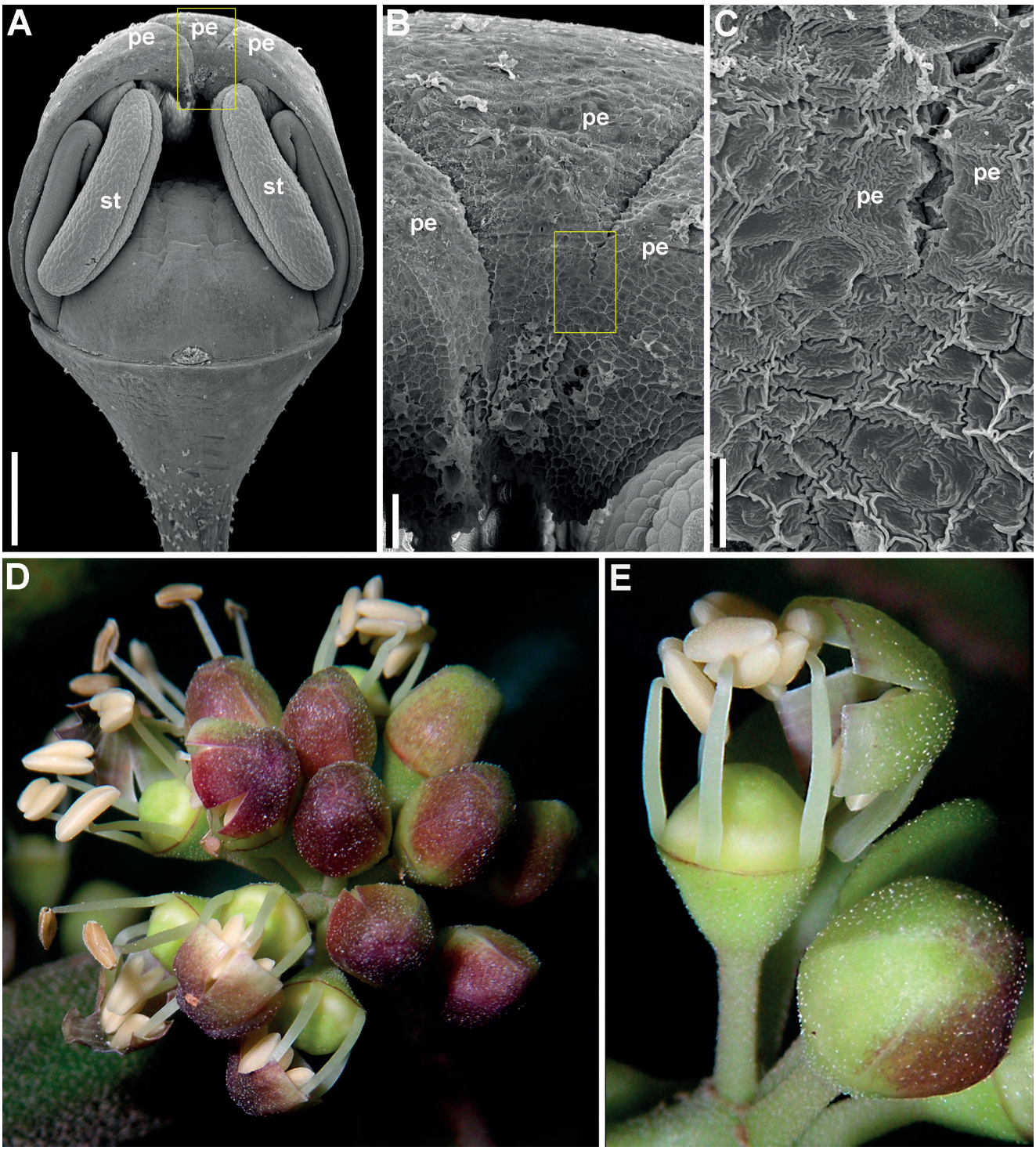

Fig. 4. Flower of *Schefflera schizophylla* (Araliaceae; A–C: SEM, D,E: photo). A: Pre-anthetic flower, lateral view; petals postgenitally fused distally (two petals and one stamen removed). B: Distal portion of corolla contoured with yellow in A. C: Area of postgenital petal fusion contoured with yellow in B; note the sculpture of cell walls. D, E: Opening flower buds; note petals abscising in fused condition, i.e. as a pseudocalyptra. pe, petal; st, stamen. (Scale bars: A = 1 mm, B = 100 µm, C = 30 µm.)

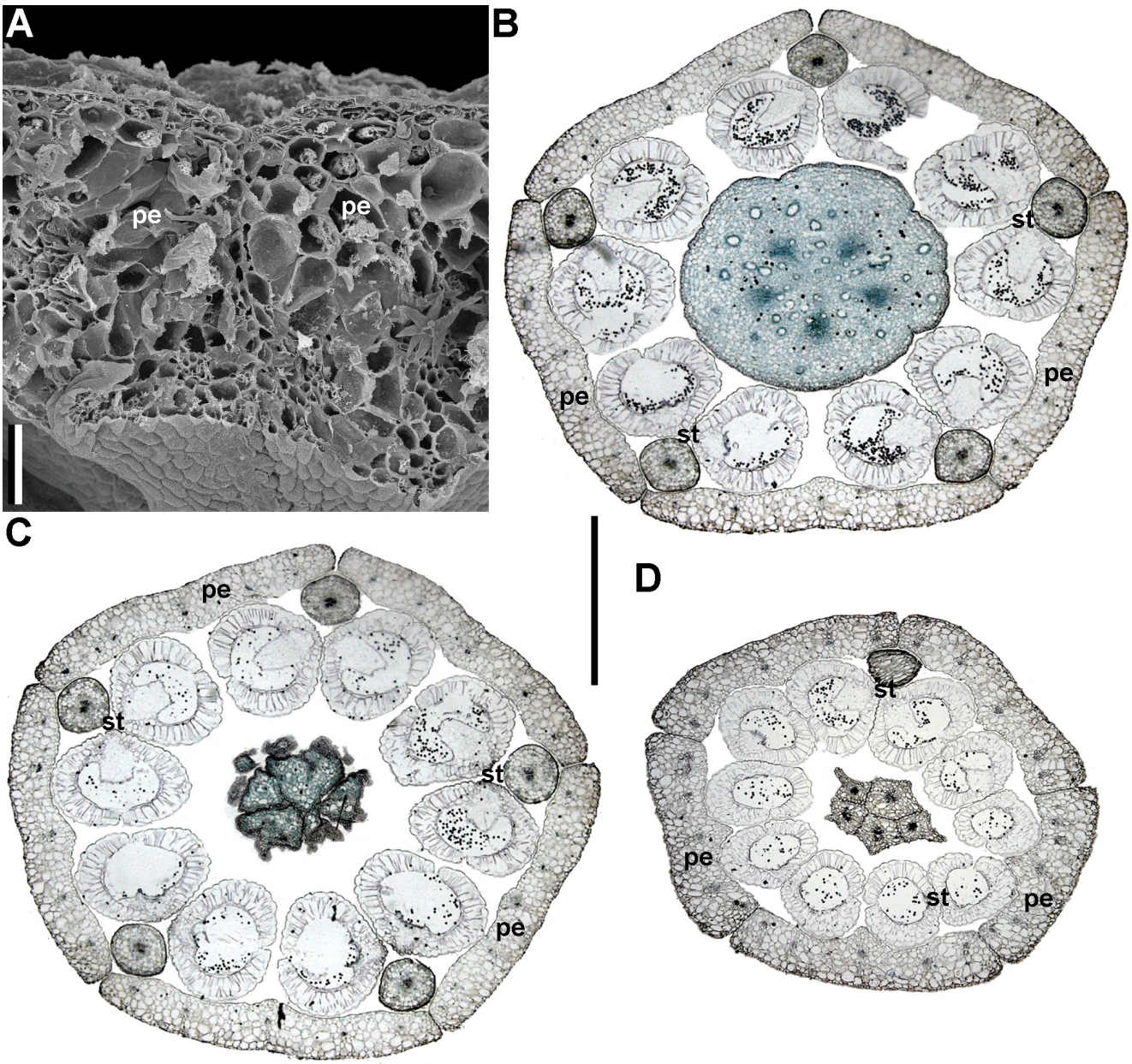

Fig. 5. Flower of *Schefflera schizophylla* (Araliaceae; A: SEM, B–D: LM; B–D modified from Nuraliev et al. 2017). A: Longitudinal section of distal part of corolla in pre-anthetic flower; note the area of fusion between two petals. B–D: Ascending series of cross sections of pre-anthetic flower. B: Section at the level of upper part of gynoecium. C: Section at the level of stigmas. D: Section at the level of petal apices which are bent downwards. pe, petal; st, stamen. (Scale bars: A = 100 μm, B–D = 1 mm.)

the formation of the corolla tube. Postgenital fusion is only responsible for the closure of the orifice of the calyptra. These are two different characters, and postgenital fusion should be considered absent while speaking of formation of the corolla tube. Similar roles of congenital and postgenital fusion can be found in the gynoecium of Araliaceae (and many other angiosperms, e.g. Endress 2015). The fusion between carpels is fully congenital, but postgenital fusion events play role in closing ventral slits of individual carpels (Fig. 3) and, like in the case of the calyptra, allow sealing of the orifice at the top of the gynoecium. This orifice cannot be closed by congenital fusion.

The complex corolla structure is not the only unusual floral feature of *S. subintegra* and *T. calyptratus*: their flowers are also highly polymerous, which is most likely a result of an increase in the number of floral elements in this clade (Sokoloff et al. 2007b; Nuraliev et al. 2014). This evolutionary event, also resembling flower fasciation, possibly affected not

only the number of the floral organs but also the structure of the organs themselves. *Tupidanthus* is unusual among Araliaceae (and most other angiosperms, see Endress 2013) because of the presence of a strongly folded receptacle. This feature allows more compact spacing of the numerous stamens and carpels, forming one whorl of androecium and one whorl of gynoecium. The folded receptacle of *Tupidanthus* resembles structures that can be observed in fasciated flowers and shoots of other angiosperms. Moreover, structures that appear to be two fused flowers sharing the same flower base sometimes occur in the axil of a subtending bract in *Tupidanthus* (Sokoloff et al. 2007b). In this view, the complete congenital fusion in corolla can be regarded to be an effect of fasciation.

The overview presented above shows that the diversity of patterns of fusion in flowers of a particular angiosperm clade appears for two reasons. First, there are fusions that apparently possess some adaptive significance, such as postgenital closure of true calyptras. Second, a number of cases that we here classify as fusions represent no more than direct consequences of some other (basic) evolutionary events, such as reduction (complete congenital fusion in calyx); change in

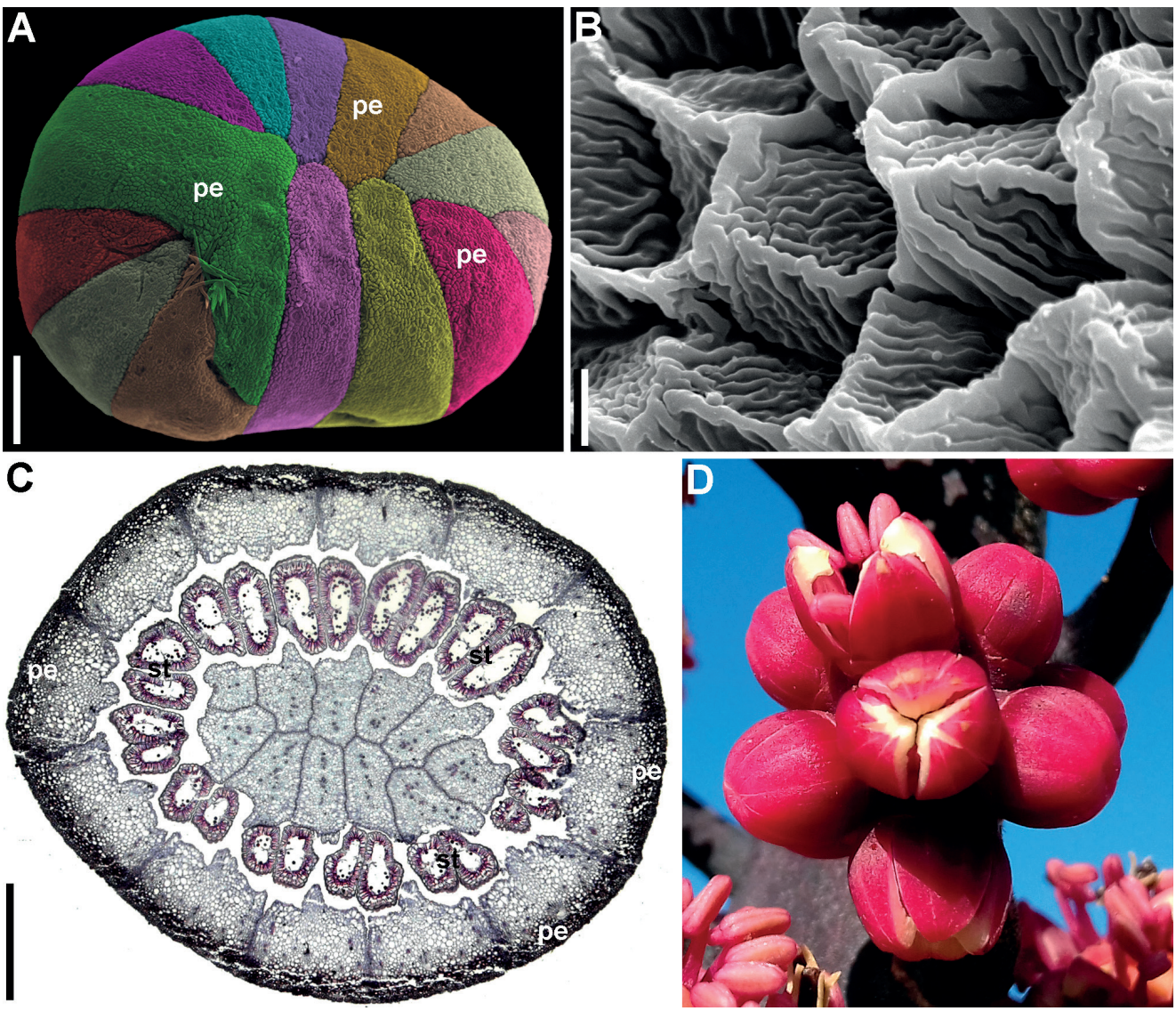

Fig. 6. Flower of *Schefflera actinophylla* (Araliaceae; A, B: SEM, C: LM, D: photo; A, C modified from Nuraliev et al. 2011; B modified from Nuraliev et al. 2017). A: Pre-anthetic flower, top view; each petal is individually colored. B: Lateral petal surface at the area of contact with neighboring petal. C: Cross section at the level of petal apices which are bent downwards. D: Head with flower buds, opening and anthetic flowers; note the petals being postgenitally fused in groups of two or three. pe, petal; st, stamen. (Scale bars: A = 300 µm, B = 3 µm, C = 1 mm.)

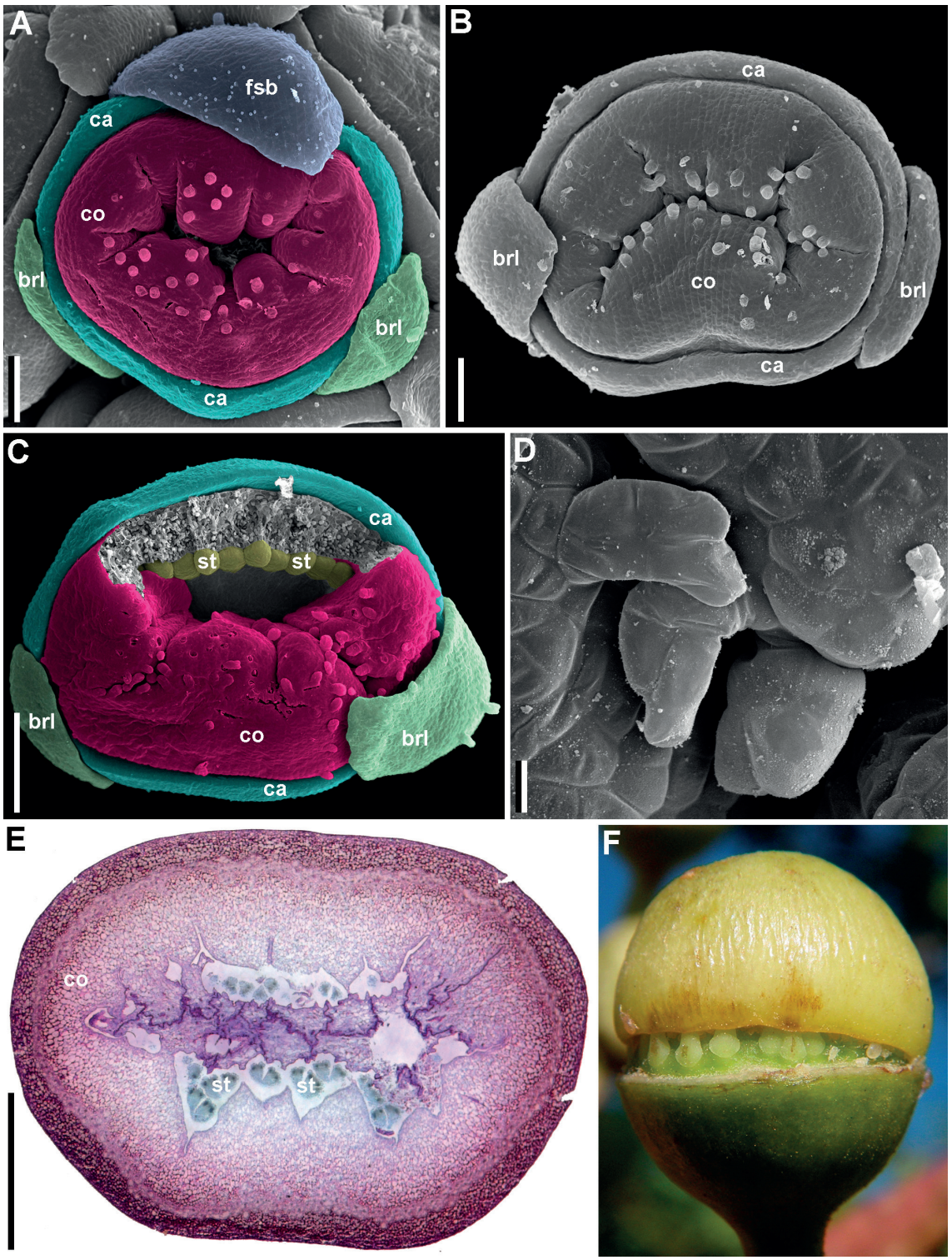

Fig. 7. Flower of *Schefflera subintegra* (Araliaceae; A–D: SEM, E: LM, F: photo; A–D, F modified from Nuraliev et al. 2014). A: Perianth development; note prominent calyx and corolla tubes without evident free lobes of sepals and petals. B: Flower at stage of closure of corolla tube; note hairs developing along the closing orifice. C: Flower at stage of stamen initiation. D: Special hairs covering the corolla suture, top view. E: Cross section of immature flower at the level of distal parts of stamens; note areas of postgenital fusion between the corolla folds bent downwards. F: Opening flower; note the abscising calyptra. brl, bracteole; ca, calyx; co, corolla; fsb, flower-subtending bract; st, stamen. (Scale bars: A, B = 100 µm, C = 200 µm, D = 10 µm, E = 2 mm.)

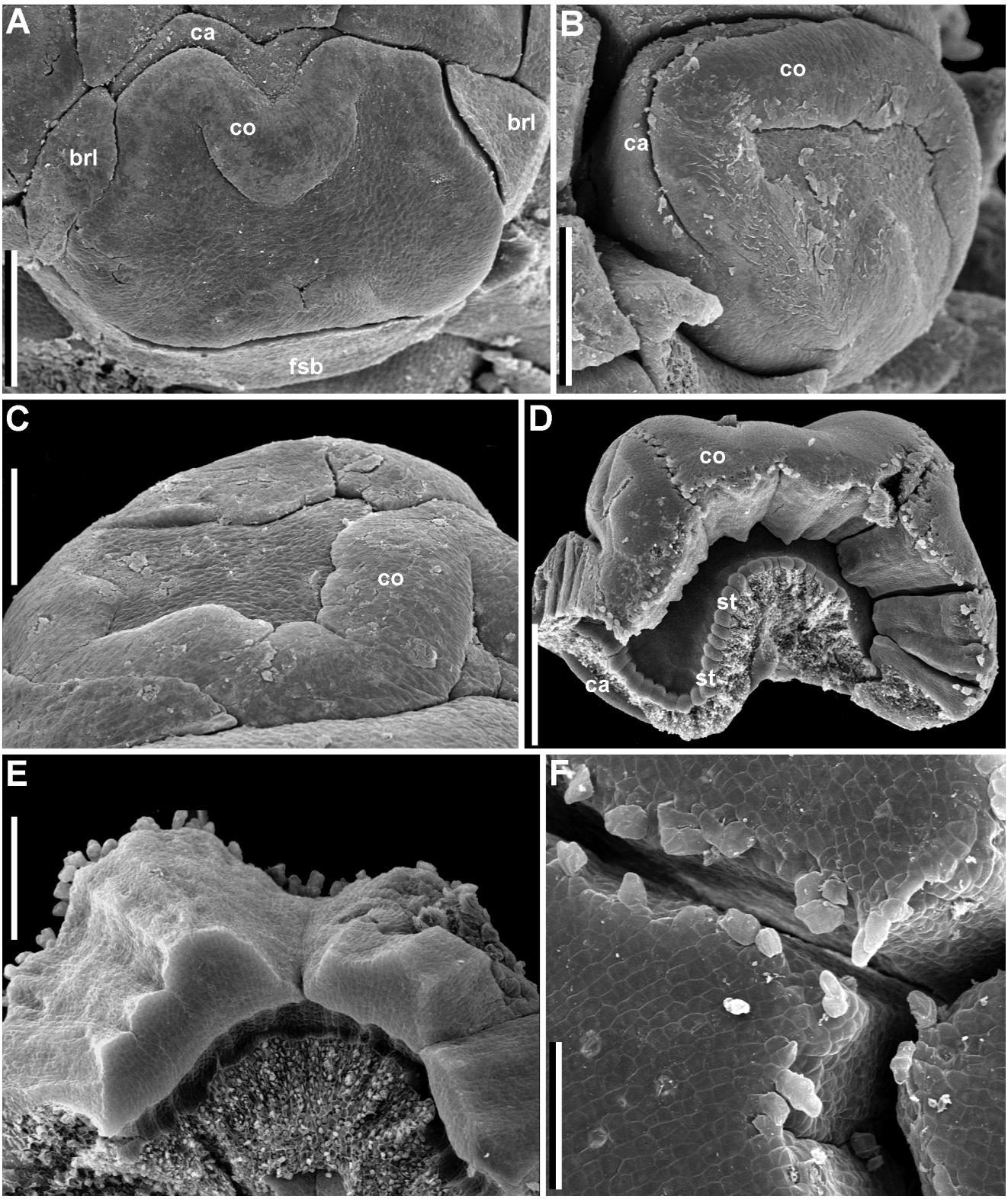

Fig. 8. Flower of *Tupidanthus calyptratus* (Araliaceae; SEM; modified from Sokoloff et al. 2007b). A: Beginning of initiation of calyx and corolla tubes. B: Development of calyx and corolla tubes. C: Oblique view of flower showing corolla tube appressed to floral meristem. D: Flower at stage of stamen initiation; corolla partly removed. E: Part of corolla at nearly the same stage as in D viewed from inside, i.e. from adaxial side. F: Part of developing corolla, top view, with its suture being closed by special hairs along margin. brl, bracteole; ca, calyx; co, corolla; fsb, flower-subtending bract; st, stamen. (Scale bars: A, B = 150 µm, C = 100 µm, D = 400 µm, E = 200 µm, F = 100 µm.)

the timing of abscission of the corolla (one can say that the petals abscise before the opening of the corolla in calyptra-like structures and interpret this as postgenital fusion caused by heterochrony); and flower fasciation (possibly, congenital fusion in calyptrate corollas).

CASE STUDY 2. FLOWERS (?) OF *HEDYOSMUM* (CHLORANTHACEAE)

Chloranthaceae is one of the oldest extant angiosperm families. Data on the morphology of Chloranthaceae are highly important for inferring the early evolution of flowers. Fossils belonging to Chloranthaceae (including beautifully preserved flowers) are known from Early Cretaceous deposits, and members of the family were much more common and widespread on the Earth in the Cretaceous than they are at present (Friis et al. 1999, 2006, 2011; Eklund 1999; Eklund et al. 2004; Doyle and Endress 2014, 2018). Phylogenetic placement of Chloranthaceae remains slightly controversial, but all current hypotheses recognize a clade of mesangiosperms that includes Chloranthaceae, Ceratophyllaceae, magnollids, monocots and eudicots (Endress and Doyle 2009, 2015; Ruhfel et al. 2014; Zeng et al. 2014; APG IV 2016; Soltis et al. 2018). Chloranthaceae share some important characters (e.g., fully ascidiate carpels) with members of the basal angiosperm (=ANITA) grade (Endress and Igersheim 2000; Endress, 2001b, 2015; Endress and Doyle 2009).

Hedyosmum is the largest of the four genera of Chloranthaceae (Endress and Doyle 2015). It includes 44 extant species. *Hedyosmum orientale* grows in Southeast Asia and all other species are restricted to the New World. Here we outline reproductive morphology of *H. orientale* with an emphasis on patterns of organ fusion. The problems discussed here are also relevant to the American species (Endress 1971, 1987; Doria et al. 2012).

The male reproductive units of *Hedyosmum* (Figs 9C-F, 10, 11) are catkins with numerous stamens arranged along the main axis. They clearly show a suite of characters related to pollination by wind. The male units of *Hedyosmum* are most likely inflorescences with each flower reduced up to a single stamen (Endress 1987). Flower-subtending bracts are absent at all developmental stages, at least as visible structures. Stamens are sessile and bear a green and flat apical appendage. The appendage elongates early in stamen development, much before full elongation of the anther. The appendages of all stamens are tightly spaced and act as protecting organs in preanthetic catkins. As suggested by Endress and Doyle (2015) and Doyle and Endress (2018), it is possible that the floral subtending bract has not completely disappeared but is amalgamated with the stamen as the projecting apex. Should this be viewed as congenital fusion or hybridization of developmental pathways? It is difficult to provide plausible arguments pro and contra these hypotheses. The surface of the appendage is similar to that of the leaf teeth (including the presence of stomata), but it also resembles that of a tepal of the female flower. Leroy (1983) hypothesised that the entire multistaminate male unit is a flower homologue, but this view was criticised by Endress (1987) using indirect, but strong arguments.

Below the stamens, the axis of the male unit bears a structure called a collar. This is a group of incompletely congenitally united appendages surrounding the axis. Leroy (1983), in the framework of his ideas of the homologies of the male unit, suggested that the collar is homologous to the perianth (hypothesis 1). Endress (1987) stated that this structure apparently comes across by secondary irregular thickening and space filling of the spike axis below the lowermost stamens, thus functionally comparable to the space filling of the anthers which assume the shape of wedges (hypothesis 2). Doria et al. (2012) suggested that this structure could correspond to the sheathing bases of the ultimate pair of the opposite bracts below the male inflorescence fused together (hypothesis 3). There is also a possibility that this is just one reduced leaf, and its appendages correspond to the teeth of vegetative leaves (hypothesis 4). It is clear that only hypotheses 1 and 3 imply organ fusion, and resolving homologies of the scales forming the collar is essential for resolving the problem. This situation is highly characteristic of all discussions on congenital fusion in plants: it is only possible to recognize this type of fusion in the context of correct organ homology assessment, which is not always an easy task.

The collar appears very early in development of the male reproductive unit. It is already quite conspicuous at the earliest stages of stamen development (Fig. 10D-F). Thus it cannot be called a secondary structure at least with respect of the timing of its initiation, and it is unlikely that physical pressures in the developing male unit are responsible for its appearance. These data support the phyllomic nature of the collar (as in hypotheses 1, 3, 4). At the earliest available stage, the collar was found forming a continuous low belt around the apex of the male unit; no stamens were present at this stage (Fig. 10C). This would allow recognizing early congenital fusion between the appendages (if we can demonstrate that organ fusion takes place here). The belt seen in Fig. 10C is however so low that here (and in other similar situations in different taxa with proposed early congenital fusion) one may question its real continuity.

The collar appendages clearly form one whorl during the observed early stages (Figs 10D-F, 11A). They are usually larger on one side of the male unit early in development (Fig. 10D-F), though these differences are no longer recognizable on subsequent stages (Fig. 11A-E). These data best fit the idea that the collar is formed by just one phyllome (hypothesis 4).

The number of the appendages (or lobes of the collar) tends to be greater in the observed late developmental stages. At least one of our images (Fig. 11B) apparently shows early stages of development of additional appendages out-

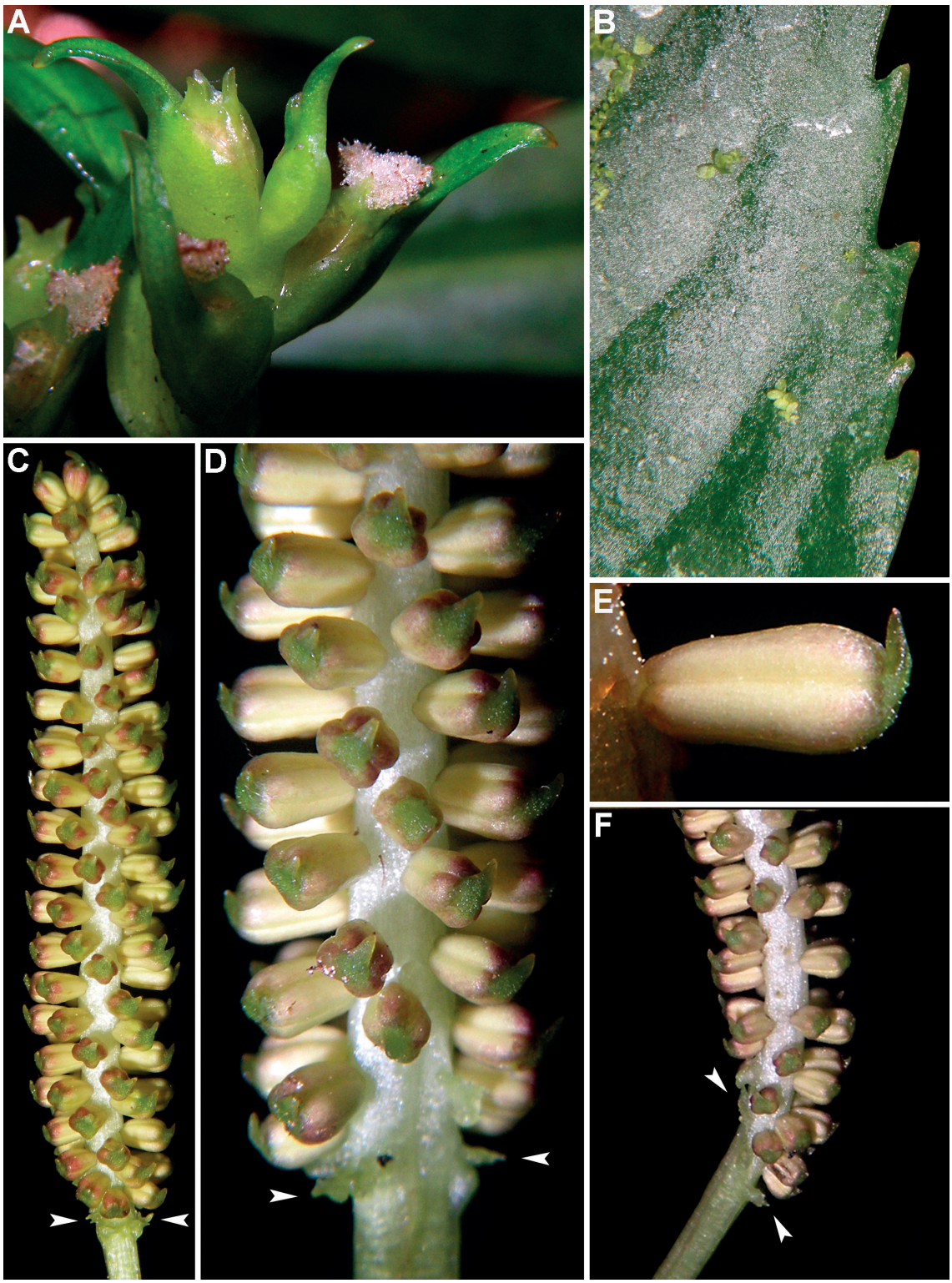

Fig. 9. Morphology of *Hedyosmum orientale* (Chloranthaceae). Photographs taken in nature (Vietnam, Kon Tum prov., Kon Plong distr., Mang Canh municipality) by M.S. Nuraliev. Plants from this population are used for our developmental investigations. A: Female flowers at anthesis with white stigmas. B: Vegetative leaf margin with glandular teeth. C: Male reproductive unit. D: Basal portion of male reproductive unit, note the presence of the collar below the stamens. E: Stamen. F. Basal portion of male unit, image at 90° relative to D, note the oblique nature of the collar. Arrowheads, collar.

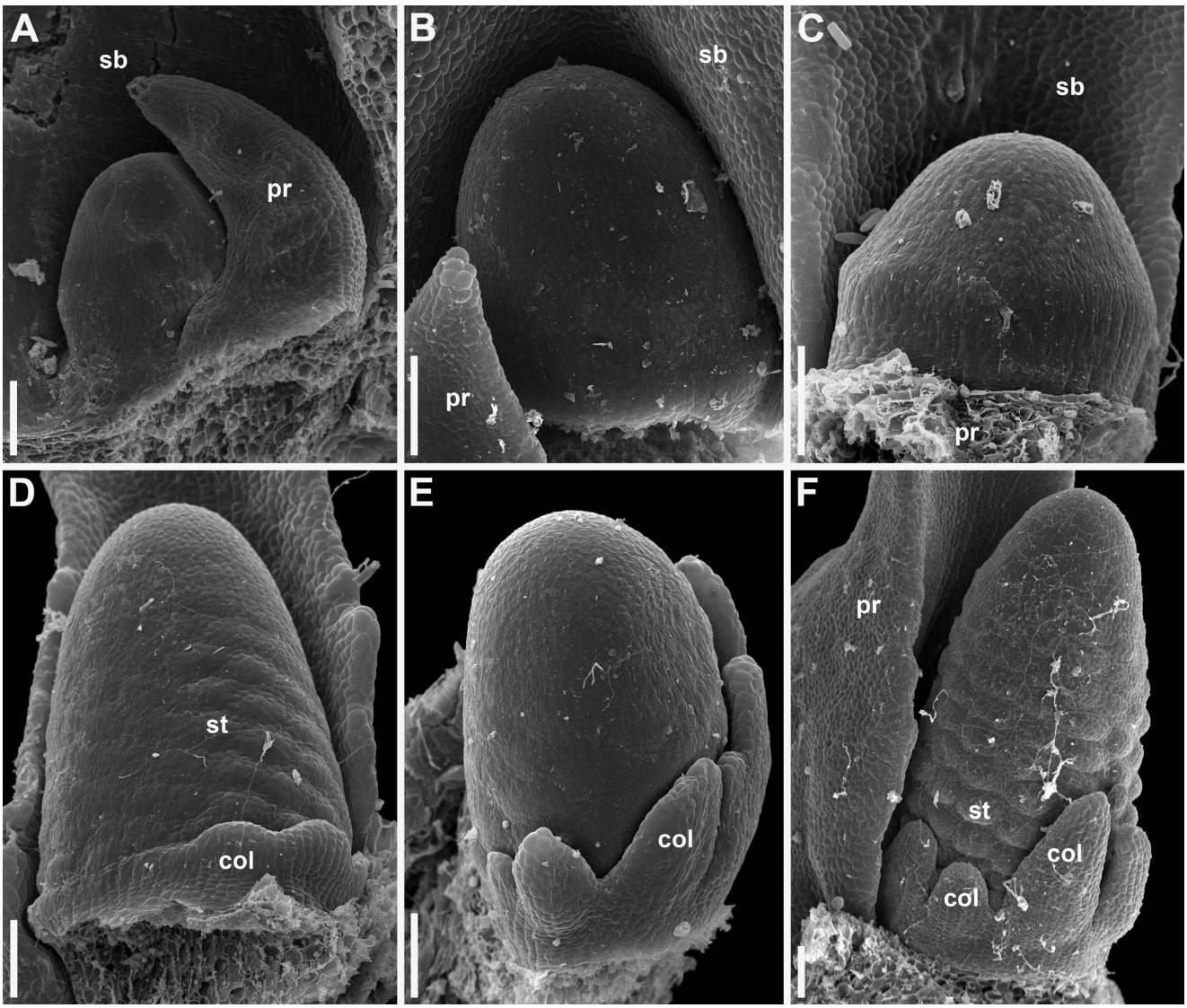

Fig. 10. Early stages of development of male reproductive units (inflorescences?) of *Hedyosmum orientale* (Chloranthaceae, SEM). A, B: Stages before collar and stamen initiation. C: Collar just initiated as a low belt. D: Early stage of collar development, note ab initio united collar appendages and very young stamens. E: Male unit with collar more developed than in D but stamens yet almost absent. F: Lower stamens well initiated but much smaller than the collar appendages. col, collar appendage; pr, prophyll of the axis of the male unit (a next order unit will develop in its axil); sb, subtending bract of the male unit; st, stamen (= reduced male flower?). (Scale bars: A–F = 100 µm.)

side the initial whorl. That these additional appendages do not belong to the initial whorl is also clear during the later stages (Fig. 11C). Sometimes organs intermediate between stamens and collar appendages can be seen below typical stamens (top part of Fig. 11D). These observations do not fit hypotheses 3 and 4. They may support the idea that each appendage is an individual phyllome (hypothesis 1), though it is highly unusual for angiosperm perianth to have a centrifugal pattern of initiation (but it is sometimes present in the so-called epicalyx, Ronse De Craene and Smets 1996). The late initiation of the outermost appendages could be seen as evidence of their non-phyllomic nature (hypothesis 2), but their phyllomic nature is supported by strong microstructural similarities between the tips of the stamens and the collar appendages.

By the time of anthesis, the collar is obliquely inserted on the axis of the male catkin. The obliquity appears because the intercalary elongation rates of the axis are unequal on different sides. At anthesis, the lowermost stamens are attached below the level of attachment of the collar appendages on the opposite side of the catkin axis (Fig. 9F). The one-sided distortion of the initial whorl of the collar appendages some-

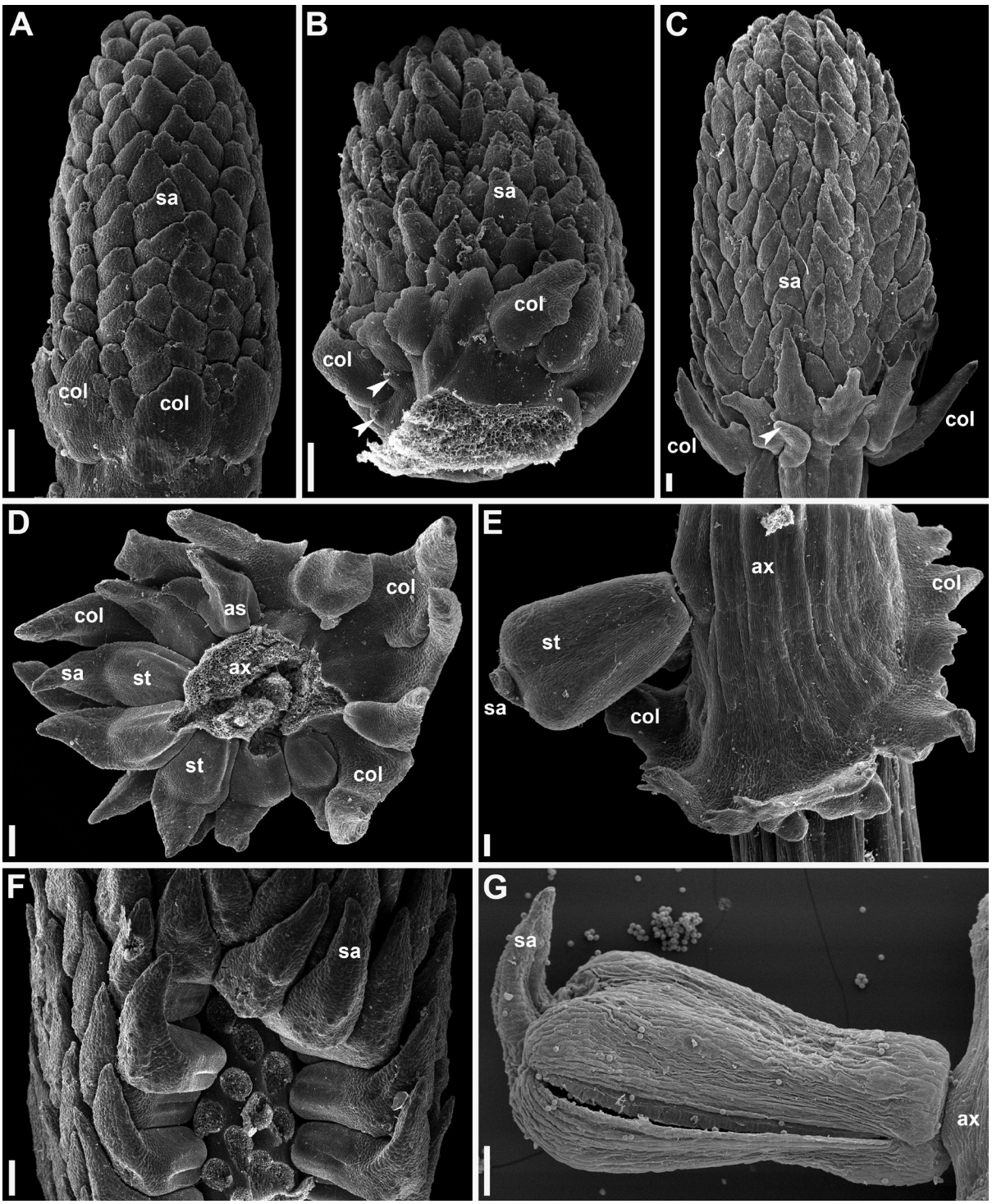

Fig. 11. Late stages of development of male reproductive units (inflorescences?) of *Hedyosmum orientale* (Chloranthaceae, SEM). A–C: Side views of preanthetic male units (C is older than A and B). D: Preanthetic male unit older than in C cut transversally to show the lowermost stamens and the inner side of the collar. Note the united bases of the collar appendages. E: Collar of anthetic male unit with much elongated axis. Only one (the lowermost) stamen is visible. Note that the collar is obliquely inserted on the axis of the male unit. Collar appendages are basally united. F: Detail of side view of male unit at the same stage as in D with some stamens removed. G: Anthetic stamen, side view. as, abnormal bilobed structure with one lobe resembling a collar appendage and another resembling a sterile stamen; ax, main axis of the male unit; col, collar; sa, stamen appendage; st, stamen (= reduced male flower?); arrowheads, collar appendages situated outside the primary whorl. (Scale bars: A–G = 200 μm.)

times breaks the continuity of the shallow sheathing base of the collar (not shown). This is apparently a secondary phenomenon that cannot be used for inferring morphological boundaries between organs.

Summarizing, the homologies of the collar remain unresolved, and because hypothesis 4 remains one possible interpretation, it is unclear whether we can speak of congenital fusion between the collar appendages.

The female flower of *Hedyosmum* (Figs 9A, 12, 13) has a unilocular ovary with one pendent orthotropous ovule and a shortly stalked papillose stigma. There are three appendages at the top of the ovary interpreted as three tepals, a tripartite tepal, staminodes, bract homologues or mere outgrowths of the gynoecium (see Swamy 1953; Burger 1977; Leroy 1983; Endress 1987; Yamazaki 1992; Zhang et al. 2011). Most recent studies describe them as tepals (Endress and Doyle 2009, 2015; Doria et al. 2012; Doyle and Endress 2014). We consider this interpretation plausible, though it is difficult to provide any strong evidence in favour of it, probably except for the apparent presence of the perianth in *Canrightia*, an Early Cretaceous fossil related to Chloranthaceae (Friis and Pedersen 2011; Doyle and Endress 2014; Kvaček et al. 2016). Our data show that epidermal characters of the proposed tepal tips are similar to those of the stamen appendages, collar appendages and leaf teeth, but this is not conclusive. The development of the proposed perianth in the female flowers of *Hedyosmum* does not rely on B homeotic function (the collar of male flowers is not examined!), but this fact does not allow for rejection of tepal homologies (Liu et al. 2013).

The apparent presence of the tepals (which is unique in Chloranthaceae) indicates that the ovary is inferior in *Hedyosmum*. The ovary wall is triangular in cross-section with the angles of this triange alternating with the tepals. Each outer face of the ovary has a peculiar structure called a window (Endress 1971, 1987; Doyle and Endress 2014). The same windows are already present in Early Cretaceous fossils related to *Hedyosmum* (Eklund et al. 2004). The windows are depressions at the outer surface of the wall of the inferior ovary. Their shape is complex, as the entrance to a window is relatively narrow, but the cavity immediately becomes much wider (Fig. 13B-D). In cross-sections, we can see that the outer part of the tissue is attached to the main body of the ovary only through extremely narrow lines along the three ribs of the flower (Fig. 13C, E-G). Thus – in some sense – it is tempting to describe this as a kind of organ fusion. However, no organ fusion can be recognized here. Indeed, the free parts of the tepals are located on the radii of the windows, not the ribs (Fig. 13I), and the structures attached to the ovary through the narrow lines definitely cannot be identified as tepals. Some authors (among them recently Doria et al. 2012) suggested that the windows develop through schizogeny, i.e., disintegration of the primary morphological surface. This interpretation is not supported by earlier (Endress 1971, 1987; Doyle and Endress 2014) and our developmental data, and in fact does not fit the illustrations provided by Doria et al. (2012).

The (free parts of the) tepals are attached to a massive tube above the level of the ovary (Figs. 12I, 13A, E). The opening of this tube is so narrow (Fig. 13A) that it is easily overlooked in the anthetic flower. Is this a perianth tube (of congenitally united tepals) or a concave receptacle? This is a difficult question with respect to all tubular structures found in angiosperms. In the case of *Hedyosmum*, the rim forming the very narrow distal opening of the tube develops due to differential tissue growth that is rather similar to the growth forming the windows of the inferior ovary wall. In both cases, a laminar outgrowth is formed from a very narrow base that covers the surface of the ovary (Fig. 13C, E). Thus, if we interpret the wall of the inferior ovary as receptacular, then the tube should be probably also receptacular (even if the three appendages of the female flower can indeed be interpreted as tepals, see above).

The stigma of *Hedyosmum orientale* is characteristically triangular in cross-section (Fig. 12I). At first glance, this can be viewed as an argument supporting a theory that the gynoecium consists of three united carpels (see Swamy 1953). This theory could find support in the apparent occurrence of syncarpy in the fossil *Canrightia* (Friis and Pedersen 2011). However, the opening of the gynoecium is situated on the ventral side at the base of the triangular stigma rather than on its apex, which is more congruent with interpretation of the gynoecium as unicarpellate (Endress 1971, 1987). It is possible that the triangular shape of the stigma appears due to its relatively late expansion under the physical constraints of the three tepals (Figs 12G-I, 13H-I).

Thus, like the male units, the female flower of *Hedyosmum* provides an example of the difficulties in homology assessment that are related to recognizing the presence or absence of any organ fusion. The total absence of postgenital fusion events in *Hedyosmum* and other Chloranthaceae (probably except the androecium of the fossil *Chloranthistemon endressii*, Eklund et al. 1997; Doyle and Endress 2018) is remarkable.

CASE STUDY 3. CONGENITAL AND POSTGENITAL FUSION IN MONOCOT GYNOECIA

Most angiosperms possess gynoecia with carpels united to each other. In most cases, fusion between the carpels is at least partly congenital (syncarpy). Situations when carpels are postgenitally united thus merit special attention. We illustrate this on the example of monocot gynoecia (Figs. 14-17). Postgenital fusion between carpels (combined with congenital fusion) is found in monocots with septal (also called gynopleural) nectaries (Baum 1948b; Hartl and Severin 1981; van Heel 1988; Simpson 1993; Smets et al. 2000; Kocyan and Endress 2001; Rudall 2002; Remizowa et al. 2006b, 2008,

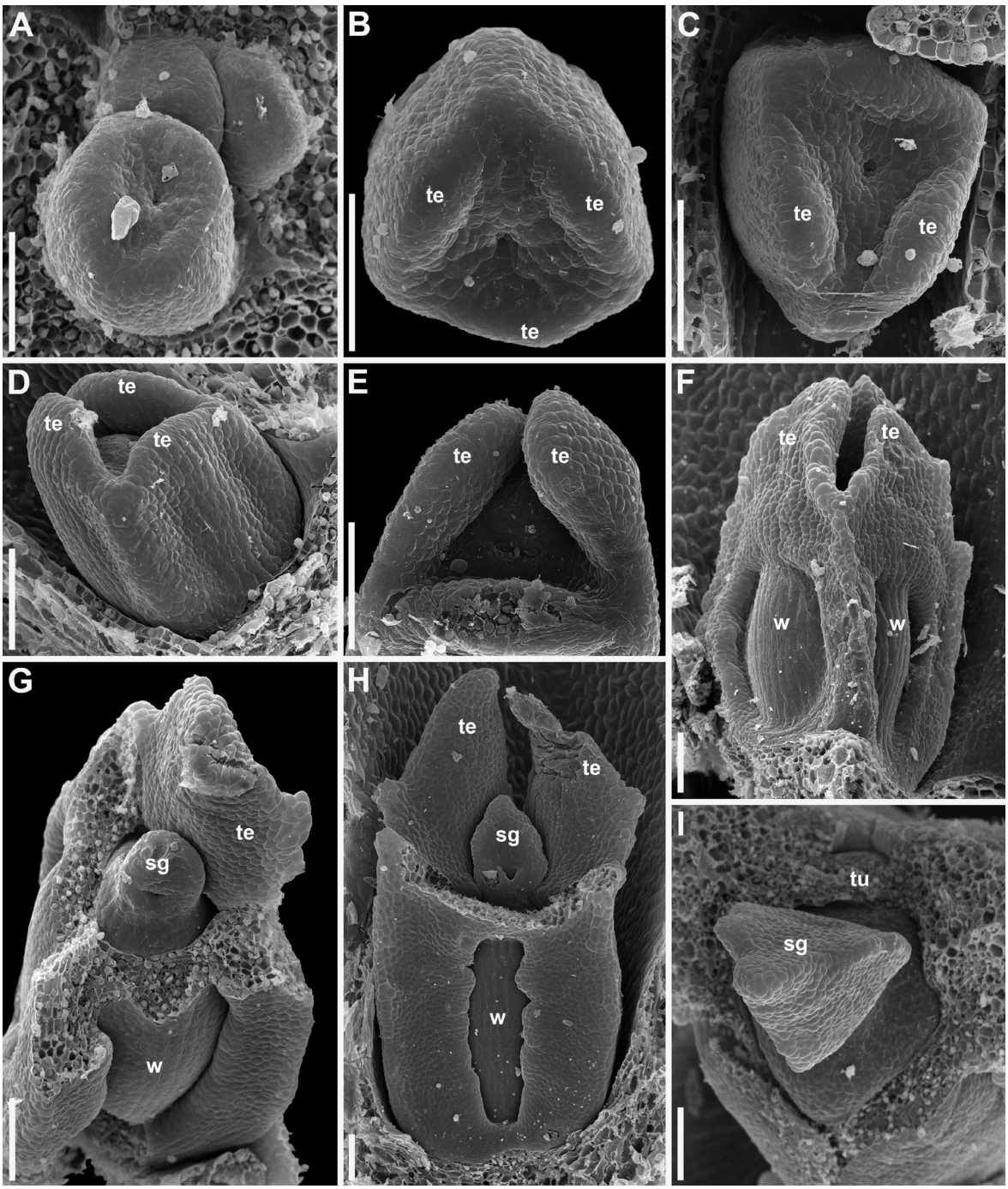

Fig. 12. Female flower development in *Hedyosmum orientale* (Chloranthaceae, SEM). A: Very young stage, top view. There is a very narrow depression in the centre, which is a canal of the developing gynoecium, and an almost entire peripheral ridge that might be interpreted as common primordium of the tree tepals (or as an edge of the concave receptacle). B, C: Slightly older stage with three tepals well recognizable. D: First evidence of differential growth at the surface of the inferior ovary wall. Note that the adaxial tepal is slightly delayed in development. E: Stage similar to D, top view, adaxial tepal removed to show the earliest evidence of stigma (between two other tepals and the orifice of the gynoecium). F: Further differential growth at the surface of the inferior ovary wall, the windows are well recognizable. G: Flower dissected to show developing stigma with the orifice of the gynoecium near its base. H: Side view of flower with well-developed window on the inferior ovary wall; the adaxial tepal is removed to show the stigma with the orifice of the gynoecium near its base. I: Top view of stigma at the stage similar to H. sg, stigma; te, tepal; tu, tubular structure above the ovary (perianth tube?); w, window. (Scale bars: A–I = 100 µm.)

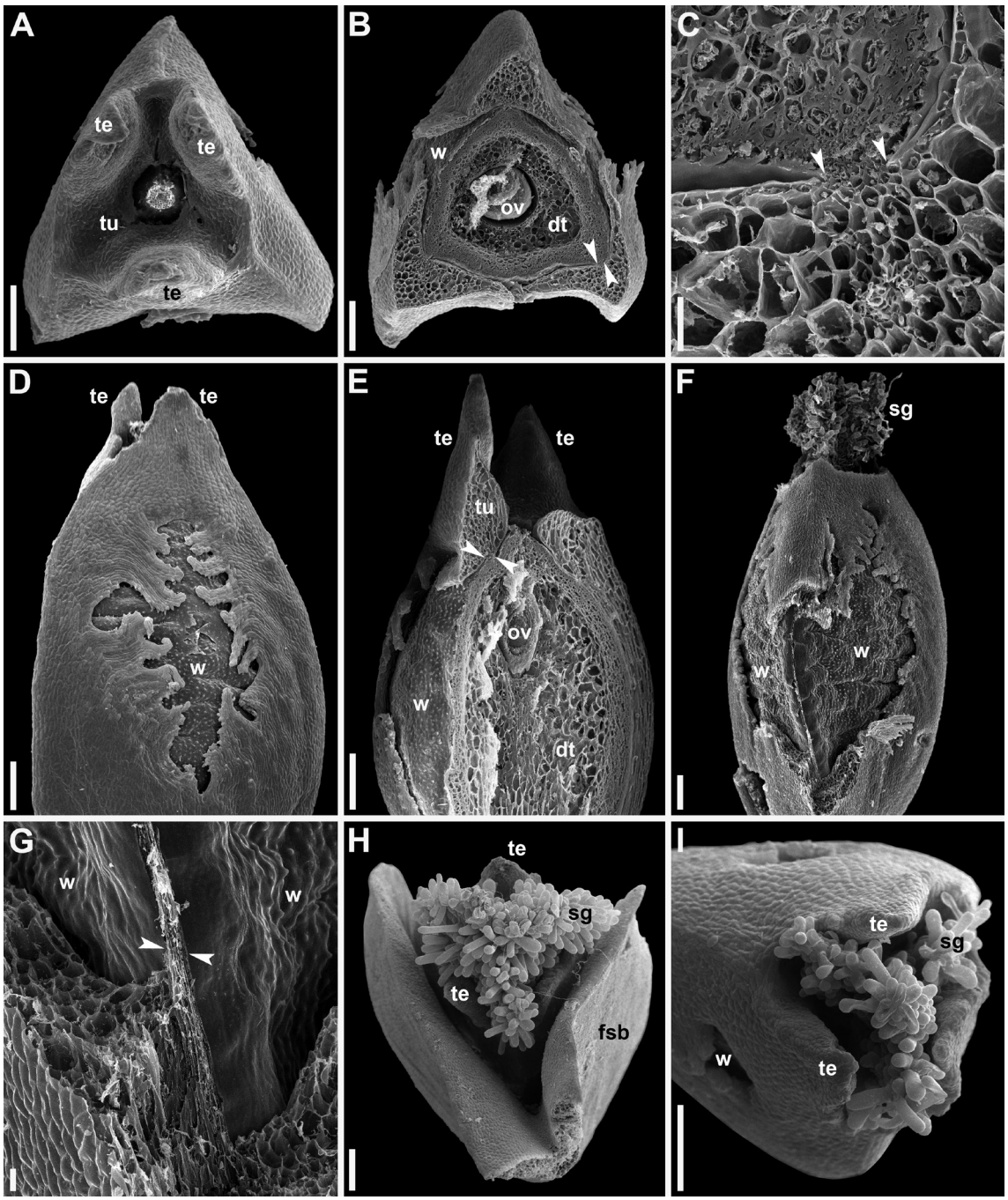

Fig. 13. Structure of female flower of *Hedyosmum orientale* (Chloranthaceae, SEM). A: Top view of flower with stigma abscised. B: Flower cut transversally at the level of the inferior ovary. C: Close up of B showing a narrow belt of tissue connecting the outer and the inner part of the inferior ovary wall. To the left and to the right of this belt (which is cut transversally here) are two windows. D: Side view of postanthetic flower with abscised stigma. E: Flower similar to that in D cut longitudinally. F: Side view of postanthetic flower with tepals removed to show the stigma and the outer part of the inferior ovary wall removed around one the three ribs. G: Close up of F showing a narrow belt of tissue connecting the outer and the inner part of the inferior ovary wall between two windows. H: Top view of anthetic flower situated in the axil of flower-subtending bract. I: Oblique top view of anthetic flower removed from its subtending bract. dt, tissue that will be destroyed during seed development (see Endress 1987); fsb, flower-subtending bract; ov, ovule; sg, stigma; te, tepal; tu, tubular structure above the ovary (perianth tube?); w, window; arrowheads, borders of the narrow belts of tissue connecting the outer and the inner part of the inferior ovary wall. (Scale bars: A, B, D–F, H, I = 150 µm, C, G: 30 µm.)

2010b). This type of nectaries is only found in monocots, but their occurrence is highly homoplastic within the group (Smets et al. 2000; Rudall 2002; Rudall et al. 2003; Remizowa et al. 2010b; Tobe et al. 2018). Septal nectaries differentiate on the lateral abaxial surfaces of adjacent carpels in areas where intercarpellary fusion is absent. The name is referring to the fact that the nectaries often seem to be embedded into septa between the ovary locules. They open by wide or more often narrow canals on the surface of the gynoecium. Septa of such gynoecia form as a result of two phenomena (Hartl and Severin 1981; van Heel 1988; Remizowa et al. 2008, 2010b).

(1) The outer boundary of the nectary is formed by the outer wall of the ovary, without postgenital fusion (Fig. 14). The outer wall develops as a tubular structure that links all of the carpels. Growth of the outer ovary wall extends to the level of the openings of the septal nectaries and determines the position of these openings: the more extensive the growth of the ovary wall, the more distal the nectary openings. Morphological interpretation of the outer ovary wall is problematic; it could represent either the congenitally fused dorsal regions of all of the carpels, or a concave receptacle (see van Heel 1988; Remizowa et al. 2010b).

(2) Above the nectary (and between the nectary and the centre of the flower), a septum is formed by postgenital fusion between adjacent carpels (Fig. 14).

As the vertical position of the nectaries along the gynoecium and the level of their openings differ considerably among monocots, the relative contribution of congenital and postgenital fusion between carpels varies respectively. In some monocots (scattered along the phylogenetic tree), the nectaries are located at the very base or even below the ovary (infralocular nectaries). In the latter case (if openings of the nectaries are also basal), only postgenital intercarpellary fusion is present (Rudall 2002; Remizowa et al. 2006, 2010b).

With apparently very rare exceptions, monocot gynoecia lacking septal nectaries develop without postgenital intercarpellary fusion. Only congenital intercarpellary fusion is present, or the carpels are completely free. As in many cases, the presence or absence of septal nectaries varies within monocot clades, and the presence of postgenital intercarpellary fusion correlates with the presence of this nectary type; therefore, certain functional or developmental links should exist between them (Remizowa et al. 2010b). It appears that the evolutionary loss of septal nectaries is in most cases associated with a loss of congenital intercarpellary fusion. In rare examples, postgenital fusion between carpels can be retained even if the septal nectaries are lacking (*Harperocallis*, Tofieldiaceae). Here, postgenital fusion is replaced by congenital fusion only at the gynoecium base in the area where the nectaries are present in related taxa (Remizowa et al. 2011). This exception thus supports the general rule (see also Ferrari and Oriani 2017 for a similar example in Rapateaceae). From these observations we can conclude that postgenital fusion is a costly process for plants, and where possible plants 'prefer' using a simpler method of congenital fusion (this is also consistent with the presence of congenital fusion between carpels in most eudicots). Indeed, postgenital fusion apparently involves the activity of many genes as de-differentiation of epidermal cells takes place there. Congenital fusion only involves differential growth and thus may be 'simpler' in realization (though this hypothesis should be tested using developmental genetics). However, the question remains: Why is postgenital fusion required in the development of gynoecia with septal nectaries?

In a few monocots, such as *Tofieldia* (Tofieldiaceae, Fig. 15), infralocular nectaries unite in the centre forming an entire triradiate cavity between carpel bases (Rudall 2002; Remizowa et al. 2006). Above the level of the nectary, the carpels are postgenitally united. Because the carpels are free at the base and united further up, gynoecium of this shape technically cannot develop without postgenital fusion between the carpels (unless secondary disintegration of tissue is assumed). Therefore, in the case of *Tofieldia* one can speak of a developmental constraint that requires postgenital intercarpellary fusion.

The triradiate type of septal nectary (Fig. 15) is however relatively rare in monocots. In most cases, the nectaries of the three septa do not unite in the centre of the gynoecium (Fig. 14). In this widespread case, no obvious constraint can be found. There is no clear reason why gynoecia like those of *Metanarthecium* (Nartheciaceae, Remizowa et al. 2008; see Fig. 14) and *Dasypogon* (Dasypogonaceae, Rudall and Conran 2012; see Figs 16-17) cannot develop exclusively by means of differential growth, without postgenital intercarpellary fusion (Remizowa et al. 2010b; see also Odintsova 2013). The shape of the ovary wall in these plants is no more complex than in the example of *Hedyosmum* outlined above. Thus the nature of the apparent constraint governing the correlation between the occurrence of septal nectaries and postgenital intercarpellary fusion is unclear so far. Remizowa et al. (2010b) hypothesized that the early stages of epidermal cell differentiation are similar (i.e., share developmental programs) in the region of future postgenital fusion and future septal-nectary formation. There could be a common large region of epidermal cells that later subdivides into two regions, one consisting of cells that will undergo fusion and the other that will differentiate into a nectary. Early in development, cells of these two types are often similar; before nectar production, adjacent epidermal layers in septal nectaries are in close contact with each other (Remizowa et al. 2010b). This hypothesis (which is testable using methods of developmental genetics) could explain why gynoecia like those of *Metanarthecium* do not develop using exclusively differential growth.

The example of monocot gynoecia shows that the interplay of congenital fusion and postgenital fusion provides all of the diversity of septal nectaries, including the level of

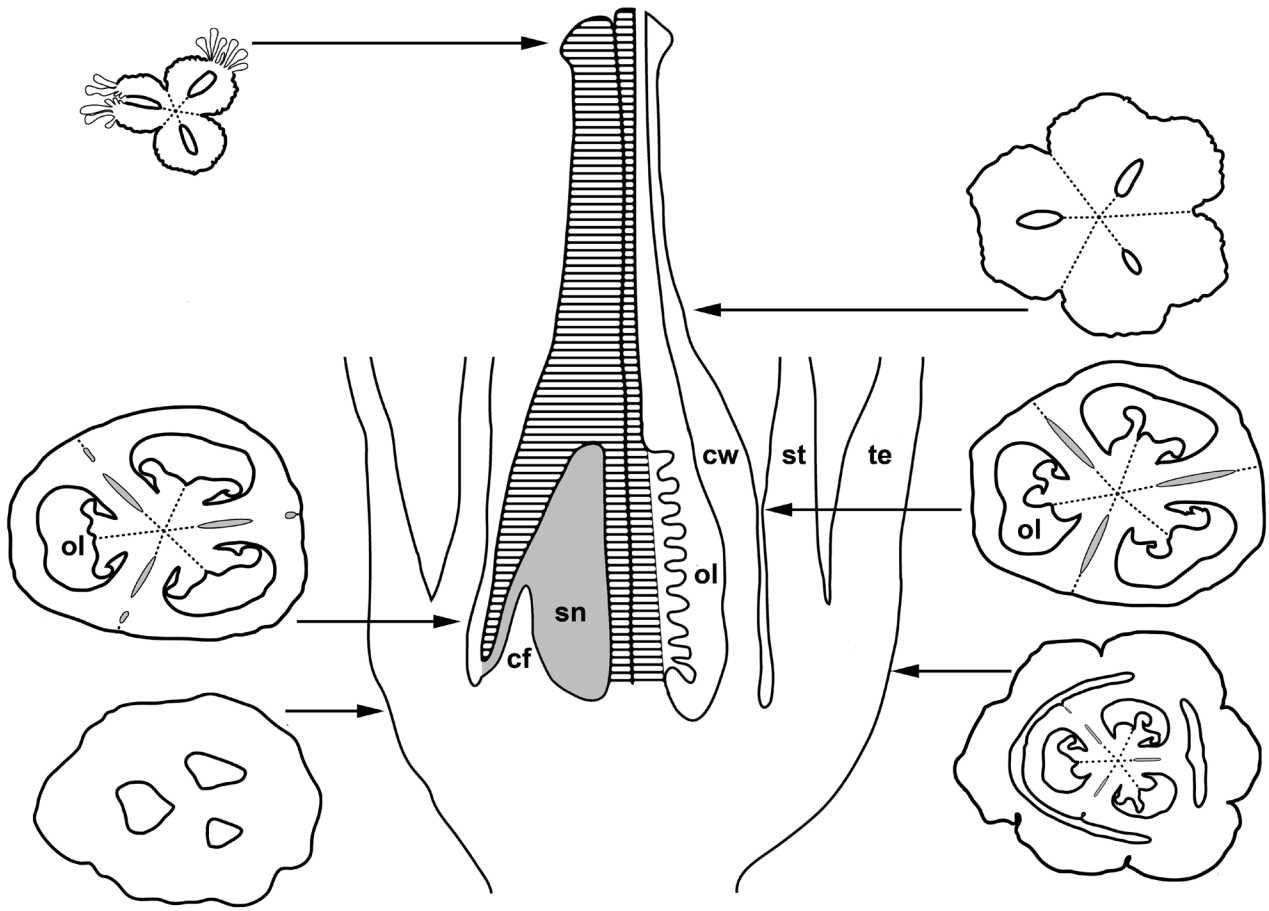

Fig. 14. Diagrams of longitudinal and serial transverse sections of flower of *Metanarthecium luteoviride* (modified from Remizowa et al. 2008). cf, the area of congenital intercarpellary fusion (or this is an outgrowth of the receptacle? – van Heel 1988); cw, carpel wall; ol, ovary locule; sn, septal nectary (also highlighted by gray colour); st, stamen base; te, tepal base; hatched areas of the longitudinal section and dotted lines of transverse sections, postgenitally fused regions. Arrows indicate levels of transverse sections.

their opening, which is of clear ecological and adaptive significance (e.g., Schmid 1985). This should be kept in mind during all reconstructions of character evolution. The area of congenital fusion can be rather small and inconspicuous, especially during early developmental stages, but its presence is of evolutionary significance. For example, early gynoecium development is similar in *Tofieldia* (Fig 15A,B) and *Dasypogon* (Fig. 16A,B), with the carpels completely free from each other. In both cases, the septal nectaries are located at the very base of the gynoecium, but in *Dasypogon*, in contrast to *Tofieldia*, an extremely short zone of congenital fusion appears at relatively late stages of development (Fig. 17A-C). Its presence is important because the ovules are attached at this level (Fig. 17E,F). In attempting to trace the evolution of the presence of congenital fusion between carpels, i.e., what accurately should be called syncarpy (Leinfellner 1950; Endress 2011), *Dasypogon* should be scored as having a syncarpous gynoecium and *Tofieldia* as having an apocarpous gynoecium, at least if only two character states are used. This is significant for resolving the controversial issues of the evolution of syncarpy in Arecaceae (Rudall et al. 2011), as Dasypogonaceae is likely a sister group of palms.

Comparison between *Tofieldia* and *Dasypogon* raises the question of whether we should indeed identify a constraint against congenital intercarpellary fusion in *Tofieldia* due to the presence of a triradiate infralocular nectary. It is possible that the opposite way of reasoning is more plausible: that the presence of postgenital fusion between carpels (which for some reason is associated with septal nectary formation) creates a possibility for the development of triradiate nectary.

CONCLUSIONS

There are two major types of organ fusion (postgenital and congenital). Differences between congenital and postgenital fusion are much more unequivocal than those between the presence and absence of fusion. There is no abrupt boundary between imperfect postgenital fusion and transient

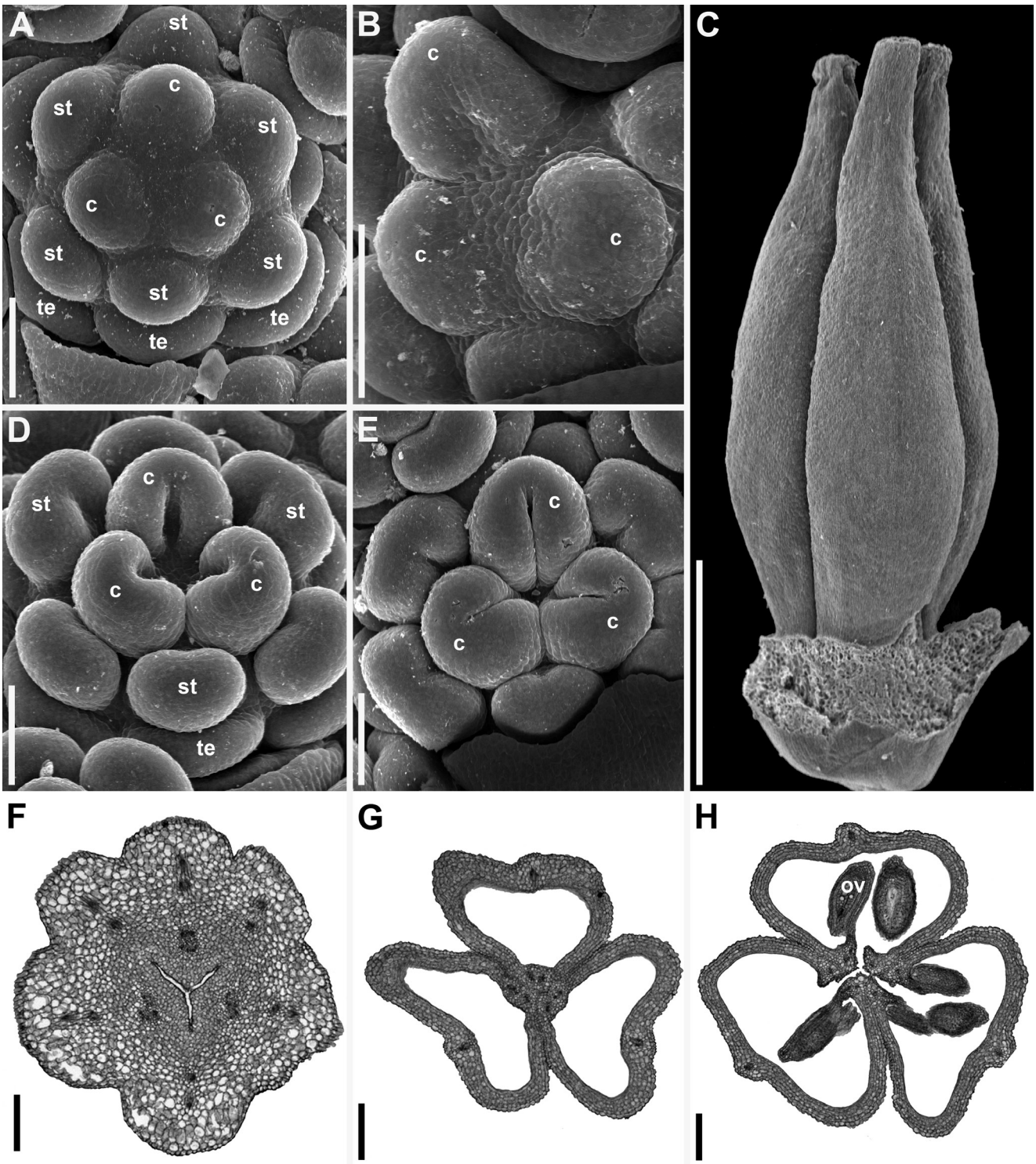

Fig. 15. Gynoecium of *Tofieldia* (Tofieldiaceae). A–E: Flower development of *Tofieldia calyculata* (SEM). A: Flower with carpels just initiated. B: Young free carpels. C: Side view of preanthetic gynoecium. D, E: Young carpels are appressed to each other by their margins, but their actual postgenital fusion takes place on even later stages. F–H: Ascending serial transverse sections of gynoecium of *Tofieldia coccinea* (LM, modified from Remizowa et al. 2010c). F: Flower base with triradiate septal (gynopleural) nectary. G: Postgenitally united sterile ascidiate zones of the carpels. H: Postgenitally united fertile plicate zones of the carpels. c, carpel; ov, ovule; st, stamen; te, tepal. (Scale bars: A, B, D, E: 100 µm, C: 1 mm, F–H: 200 µm.)

contact between organs during development. Structures assumed to be congenitally fused clearly develop as a unit, but it is necessary to demonstrate that these structures indeed belong to different organs merged together (instead of being parts of the same organ or two distinct organs on a common base). This can only be done in the framework of comparative morphology. Analyses of both types of fusion involve arbitrary decisions.

The deeper we look into the patterns of organ fusion, the more we realize that delimitation of these as well as of many other morphological characters is a matter of convention. Careful explication and unification of these conventions is a crucial condition of the correct use of characters in evolutionary analyses. Whatever type of analysis we perform (e.g., maximum parsimony or model based), the primary source is a data set with character states attributed to terminal groups. It is impossible to score characters in one terminal group without explicit or inexplicit use of comparative (and interpretative) morphology (e.g., Sokoloff et al. 2018).

Despite all of the problems with demarcation between congenital fusion and differential growth, we believe that the former concept is useful in many situations. Moreover, we believe that explicit use of the term congenital fusion clearly demonstrates its problematic background instead of obscuring it.

Analyses of evolution of postgenital and congenital fusion come close to the problem of functional and developmental constraints. What are (if any) the adaptive aspects or constraints governing the occurrence of postgenital or congenital fusions? There are two types of structures that for geometrical reasons cannot develop without postgenital fusion events unless schizogeny (disintegration of the primary morphological surface) is involved. (1) The entire structure located on more than one stalk (e.g., anther tube of

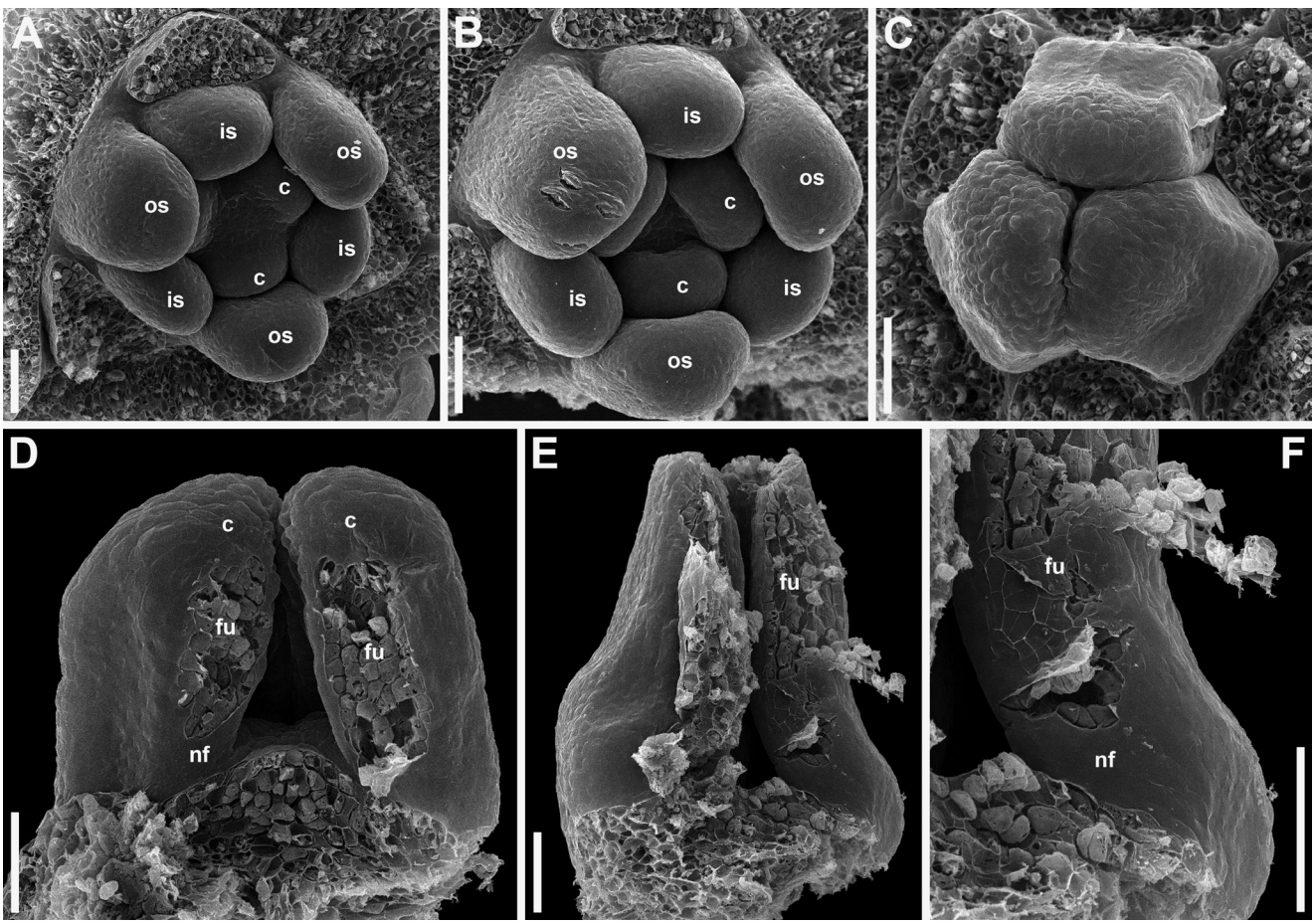

Fig. 16. Early gynoecium development of *Dasypogon* sp. (Dasypogonaceae, SEM). A: Flower with carpels just initiated. B: Further growth of the carpels. C: Top view of gynoecium with postgenitally fused carpels. D: Gynoecium slightly younger than in C with one carpel removed. Note that the carpels are not fused at the base. Septal nectaries will form here. E: Preparation similar to D at a later developmental stage. F: Detail of E showing the area where the carpels are not united. c, carpel; fu, area of postgenital fusion between carpels; is, inner whorl stamen; nf, area where the adjacent carpels are not fused (a septal nectary will form here); os, outer whorl stamen. (Scale bars: A–F = 50 µm.)

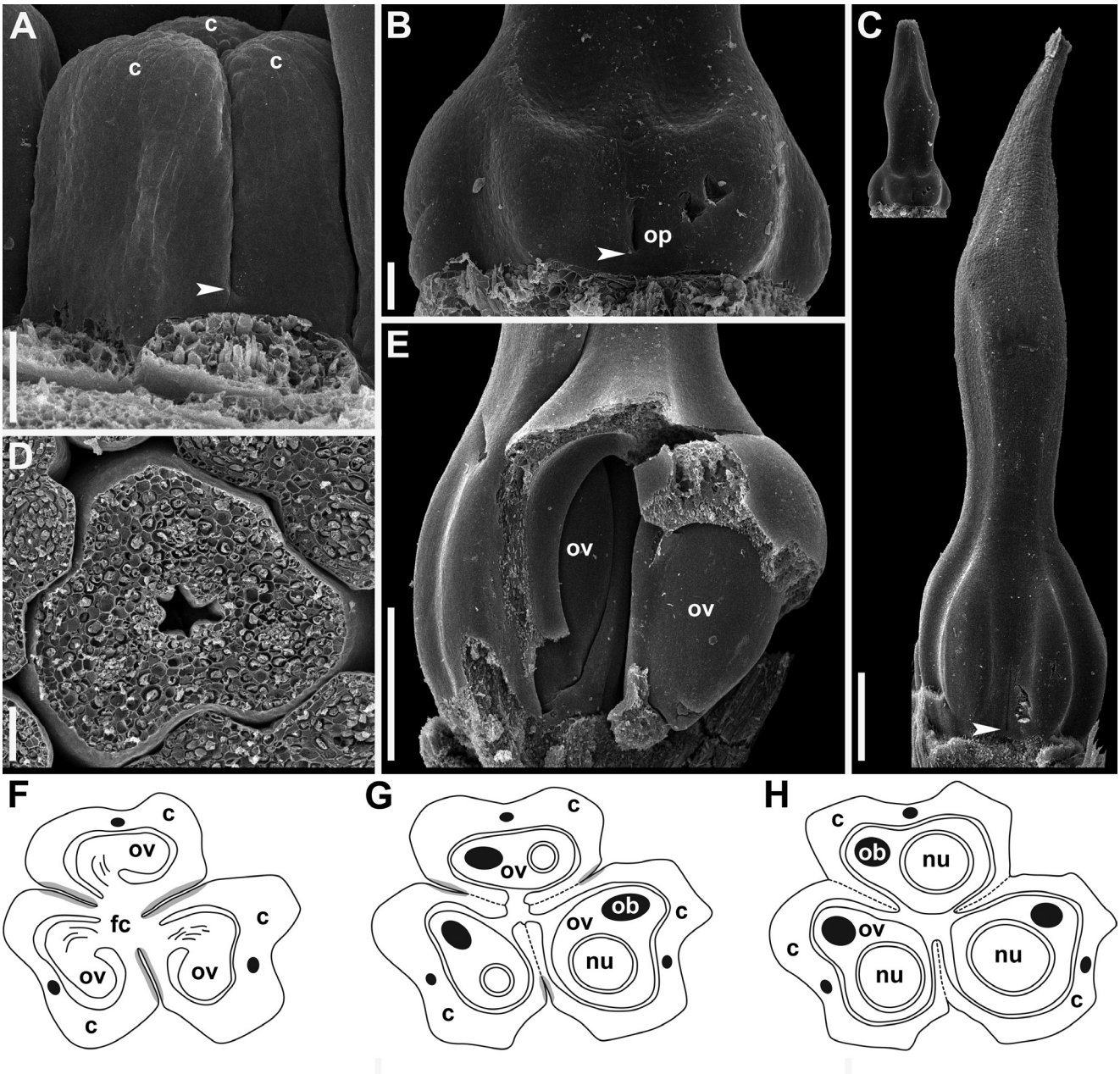

Fig.17. Late gynoecium development and anatomy of *Dasypogon*. A–E, Gynoecium development of *Dasypogon* sp. (SEM). A: Side view of gynoecium with carpels united congenitally at their very bases and postgenitally for the rest of their length. B: Basal part of gynoecium older that in A with opening of septal nectary. Above the opening, the carpels are postgenitally united. C: Gynoecium that is much older than in B (inset shows the entire gynoecium of B at the same magnification). D: Cross section of style with perfect postgenital fusion between carpels. E: Dissected unilocular part of the ovary with ovules (one basally attached ovule in each carpel). F–H: Diagrams of an ascending series of transversal sections of gynoecium (*Dasypogon hookeri*, original drawings based on photographs in Rudall and Conran 2012). F: Flower base with congenitally united carpels and septal nectaries. The ovules are attached at this level. G, H: Unilocular part of the ovary with postgenitally united carpels. c, carpel; fc, flower centre where all carpels are congenitally united; nu, nucellus; ob, ovule bundle; op, opening of septal nectary; ov, ovule; arrowhead, upper border of congenital fusion between carpels; colours on diagrams: black, vascular bundles; gray, epidermal tissue of septal nectaries; dashed line, place of postgenital fusion. (Scale bars: A, B, D = 50 μm; C, E = 500 μm.)

Asteraceae attached to free stamen filaments, keel in papilionoid flower attached to two free petal claws, gynostegium of Asclepiadaceae, monocot gynoecia with triradiate septal nectaries). (2) A closed structure with internal cavity (sporocarps of heterosporous ferns, calyptras of various sorts, angiosperm ovary, some fertilized seed plant ovules). However, postgenital fusions are also found in situations where there is no geometrical constraint for development using differential growth, and the reasons are largely unknown. Recognizing and interpreting the evolutionary constraints related to the occurrence of congenital and postgenital fusion is an important direction of further research.

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