

False paracarpy in *Seemannaralia* (Araliaceae): from bilocular ovary to unilocular fruit

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- **Background and Aims** *Seemannaralia* appears to be fundamentally different from all other Araliaceae in the presence of a well-developed symplicate zone in its gynoecium, as well as in the ovule insertion in the symplicate zone (rather than in the cross-zone). The present investigation re-examined the floral structure of *Seemannaralia* with emphasis on the morphology and evolution of its gynoecium.
- **Methods** Flowers and fruits of *Seemannaralia gerrardii* at various developmental stages were examined using light microscopy and scanning electron microscopy.
- **Key Results** Ovaries in the flowers of *Seemannaralia* are bilocular. Each ovary locule corresponds to a carpel whose ascidiate part is distinctly longer than the plicate part. Each carpel contains one fertile ovule attached to the cross-zone, and one sterile ovule as well. The fruit is unilocular: its central cavity is occupied by a single large seed. In the course of fruit development, the growth of one ovule stops while another ovule develops into the mature seed. When this ovule outgrows the available space in the locule, the septum is ruptured, forming a united cavity of two carpels.
- **Conclusions** Despite literature data, the synascidiate zone is well developed in the gynoecium of *Seemannaralia*, and the ovules are attached to the cross-zone. Its preanthetic and anthetic gynoecium has nearly the same structure as gynoecia of most other Araliaceae. The *Seemannaralia* fruit resembles the paracarpous gynoecium but its ground plan is very different because the central cavity is formed by mechanical rupture of the septum. The term ‘pseudoparacarpy’ (‘false paracarpy’) is proposed to describe this condition, which has not been reported to date for indehiscent fruits in any taxa other than *Seemannaralia*. In this genus, the pseudoparacarpy has probably resulted from a decrease in seed number in the course of the transition from zoochory to anemochory.

Key words: Anatomy, Apiales, Araliaceae, development, flower, fruit, gynoecium, paracarpy, *Seemannaralia gerrardii*, syncarpy.

INTRODUCTION

Although the phylogeny and morphology of the Apiales have been investigated by many botanists, and significant progress has been made in this area of research in recent years (e.g. Plunkett *et al.*, 2004a, b; Nicolas and Plunkett, 2009), some important aspects of floral evolution in the order remain enigmatic. In particular, the largest and obviously closely related families of Apiales, namely Araliaceae, Myodocarpaceae and Apiaceae, are similar to each other in the structure of their gynoecia whereas the Pittosporaceae is very distinct from them. The Araliaceae, Myodocarpaceae and Apiaceae possess mainly bi- or multilocular ovaries in a gynoecium with a long synascidiate zone and a very short symplicate zone, with the ovules inserted at the transition between the two zones, i.e. in a cross-zone (also referred to as a ‘Querzone’; e.g. Magin, 1977; Sokoloff *et al.*, 2007). The few known cases of unilocular ovaries in members of Araliaceae and Apiaceae appear to result from carpel reduction, i.e. these gynoecia are pseudomonomerous (Baumann-Bodenheim, 1955; Magin, 1977, 1980). Unlike

these three families, the symplicate zone in gynoecia of the Pittosporaceae is much longer than the synascidiate zone, and the ovules are arranged along this zone. As a result, members of this family have unilocular ovaries with a single cavity formed between adjacent carpels (e.g. Narayana and Radhakrishnaiah, 1982; Erbar and Leins, 1996).

As these two types of gynoecia are distinctive at the family level, a trend of evolutionary transition between them within Apiales could be of phylogenetic interest. Although no morphological constraints for such transitions have been suggested (Weberling, 1989; Erbar and Leins, 1996, 2004; Leins and Erbar, 2004), it is highly questionable whether the condition found in Pittosporaceae should be regarded as ancestral within the Apiales. As Stevens (2009) suggests, ‘floral morphology of Pittosporaceae is quite probably derived, rather than representing the plesiomorphic condition from which the distinctive flowers of [Apiaceae + Araliaceae] evolved’. Understanding evolutionary transformations of gynoecia in Apiales is in part complicated by the fact that precise relationships between Pittosporaceae and other monophyletic groups within Apiales have not yet been fully resolved. Some molecular data suggest

a basal position for Pittosporaceae in relation to the Araliaceae, Myodocarpaceae and Apiaceae (Andersson *et al.*, 2006; Nicolas and Plunkett, 2009) whereas other phylogenetic studies have placed Pittosporaceae as embedded within the Araliaceae–Apiaceae alliance (Plunkett *et al.*, 1996; Chandler and Plunkett, 2004).

In this context, the genus *Seemannaralia*, a member of Araliaceae that appears to be similar to the Pittosporaceae in the ground plan of its gynoecium, could be important for clarifying the evolutionary pathways of floral features in Apiales. This monospecific South African genus reportedly possesses a unilocular gynoecium that should be regarded as having a well-developed symplicate zone with apically attached ovules (Burt and Dickison, 1975). As the embedded position of *Seemannaralia* within Araliaceae is well confirmed by molecular analyses, and direct relationships to Pittosporaceae are very unlikely (Wen *et al.*, 2001; Plunkett *et al.*, 2004a; Lowry *et al.*, 2004), the structure of its gynoecium should certainly be regarded as derived from the condition which is typical for the majority of Apiales taxa. Therefore, *Seemannaralia* may be highly relevant in showing parallelism in the transformation of the gynoecia in different groups of Apiales. Because *Seemannaralia* remains a relatively poorly known genus and because of its relevance to general questions about gynoecium evolution in Apiales, a detailed study of flowers and fruits of this plant was conducted.

Seemannaralia gerrardii is a small to medium-sized deciduous tree with palmately lobed leaves. The species is restricted to a few localities in the eastern region of South Africa, in the provinces of KwaZulu-Natal and Mpumalanga (Burt and Dickison, 1975). Originally, the species was described by Seemann (1866) as *Cussonia gerrardii* Seem. but was segregated by Viguier (1906) into the monotypic genus *Seemannaralia* R.Vig. *Cussonia* Thunb. is another African genus of Araliaceae. Although *Seemannaralia* obviously differs from *Cussonia* by its imbricate petal aestivation and dry laterally compressed fruit as opposed to the valvate petal aestivation and fleshy globose fruits in the latter genus, a close relationship between these taxa was recently supported on the basis of molecular data (Plunkett *et al.*, 2004b). The placement of *Seemannaralia* within various other groups of Araliaceae as suggested by Viguier (1906) and Hutchinson (1967) is not supported by molecular data (Wen *et al.*, 2001; Plunkett *et al.*, 2004b; Lowry *et al.*, 2004) nor by detailed morphological investigations (Burt and Dickison, 1975).

The isolated taxonomic position of *Seemannaralia* was emphasized by Burt and Dickison (1975), who found that the flowers have a unilocular ovary formed by two fused carpels, i.e. a paracarpous gynoecium. The description of Burt and Dickison (1975) implies that the gynoecium of *Seemannaralia* either lacks a synascidiate zone completely or that the synascidiate zone is very short. Importantly, because the ovule attachment is apical in the ovary of *Seemannaralia*, they must be interpreted as being attached to the symplicate zone. As stated above, this remarkable floral feature is not reported elsewhere within Araliaceae, the majority of whose members have di- to pentamerous (sometimes polymerous) syncarpous gynoecia with separate ovarian locules (Philipson, 1970; Eyde and Tseng, 1971; Nuraliev *et al.*, 2010). In particular, all *Cussonia* species

share dimerous gynoecia. One-seeded fruits in *Cussonia natalensis* (Strey, 1981) are formed from bilocular ovaries (Sonder, 1862; Reyneke, 1981), and their septa between fertile and sterile locules of mature fruits remain intact (A. A. Oskolski, pers. obs.).

The occurrence of unilocular ovaries is reported in a few other members of Araliaceae, such as in *Arthropphyllum* and occasionally in some species of *Osmoxylon*, such as *Osmoxylon micranthum*, and *Cuphocarpus*. Unilocular ovaries of *Arthropphyllum* and *Osmoxylon* (Baumann-Bodenheim, 1955; Philipson, 1970, 1979) are formed by single carpels and it is very likely that the ovaries have a well-developed ascidiate zone. Therefore, these taxa may not be fundamentally different from other Araliaceae in the relative length of ascidiate and plicate zones. The phylogenetic placement of taxa with monocarpellate unilocular ovaries (Wen, 2001; Plunkett *et al.*, 2004b) strongly suggests that the unilocular ovary is derived from bi- or multilocular ovaries in Araliaceae through a reduction in the number of carpels.

As outlined above, *Seemannaralia* appears to be fundamentally different from all other investigated Araliaceae in the presence of a well-developed symplicate zone, with the synascidiate zone being either absent or very short, as well as in the ovule insertion in the symplicate zone (rather than in the cross-zone). The present study provides a re-examination of the floral structure of *Seemannaralia* with emphasis on the morphology and evolution of its gynoecium. This work is part of a general study of meristic trends in floral morphology throughout the Araliaceae (Sokoloff *et al.*, 2007; Nuraliev *et al.*, 2009, 2010).

MATERIAL AND METHODS

Inflorescences of *Seemannaralia gerrardii* (Seem.) R.Vig. were collected by the first and the third authors and B. J. de Villiers in April, 2007 in the KwaZulu-Natal Province of South Africa (collector's no. *B.J. de Villiers 97* and *107*; voucher specimens deposited in JRAU). Flowers and fruits at various developmental stages were fixed in FAA (formalin 5 %, acetic acid 5 %, ethyl alcohol 90 %) and stored in 70 % ethanol. For light microscopy, material was sectioned to 15–25 µm thickness using standard methods of paraffin embedding and serial sectioning. Sections were stained with safranin and alcian blue and mounted in euparal. For scanning electron microscopy, air-dried flowers and fruits were sputter-coated with gold using a JFC-1100 ion-coater, and were observed using a JSM-6380LA scanning electron microscope (JEOL, Tokyo, Japan). Premature flowers and fruits were photographed using a SteREO Lumar V12 (Carl Zeiss, Jena, Germany) photomicroscope fitted with a AxioCam MRc5 digital camera (Carl Zeiss).

RESULTS

Flowers of *S. gerrardii* are aggregated into 20- to 40-flowered open umbellules that are arranged into a terminal frondobracteose inflorescence (Fig. 1). The main axis (10–30 cm long) bears 5–14 second-order axes 10–25 cm long (Figs 1A and 2A) subtended by foliage leaves with trilobate to entire

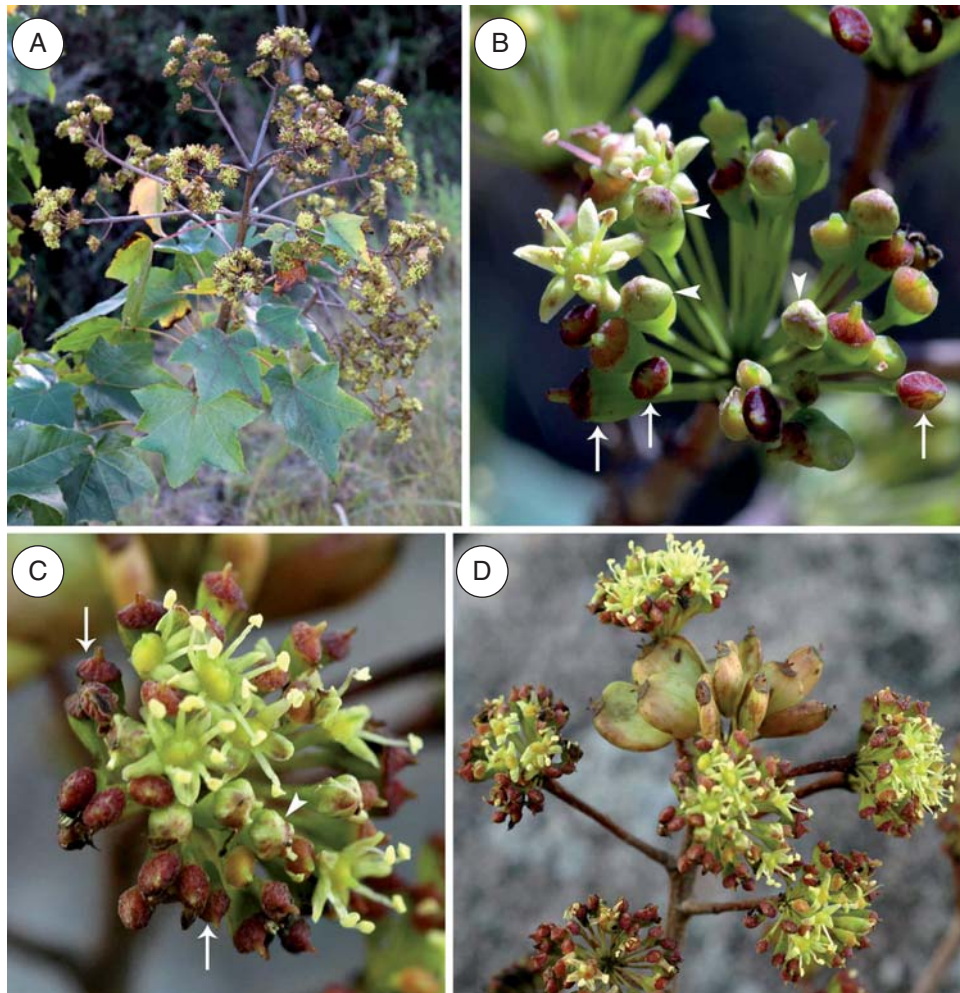


FIG. 1. *Seemannaralia gerrardii*: inflorescences at anthesis. Images taken on 4 April, 2007 at Roselands Farm near Richmond, KwaZulu-Natal, South Africa. (A) General view of a shoot with foliage leaves and a terminal inflorescence. (B, C) Umbellules with anthetic, preanthetic (arrowheads) and postanthetic (arrows) flowers. (D) Distal part of a second-order inflorescence axis with a terminal and several lateral (third-order) umbellules; the terminal umbellule bears immature fruits, while the lateral umbellules bear anthetic and just postanthetic flowers.

(sometimes five-lobate) blades 4–12 cm long on petioles 3–9 cm long. These subtending leaves fall by early anthesis; they are distinct from the foliage leaves situated below the inflorescence; the latter have larger five-lobate blades up to 25 cm long. The internodes in the upper portion of the main inflorescence axis (occasionally also in its middle portion) are shortened. The second-order axes (Figs 1D and 2C) bear terminal umbellules and 3–18 third-order axes (5–12 cm long) subtended by minute (4–8 mm long) triangular bracts, or rarely by small foliage leaves with entire lamina 1–3 cm long. Each third-order axis bears two prophylls inserted at different levels, and a terminal umbellule. Prophylls are caducous and fall off during anthesis.

Each flower is situated in the axil of a narrowly lanceolate bract 0.5–1 mm long. The flowers are hermaphroditic, rather small (flower size at anthesis is approx. 3–5 mm), tetracyclic and have an inferior ovary. Elements of the adjacent whorls alternate with each other. The flowers have five small but conspicuous sepals approx. 0.5 mm long, five free, flat petals (Fig. 1B, C), five stamens and two carpels in a median position. Petal aestivation is imbricate or cochleate.

Ovaries in the flowers of *S. gerrardii* are bilocular (Figs 3 and 4). Each ovary locule corresponds to a carpel whose ascidiate part is distinctly longer than the plicate part. The two laterally compressed carpels are united by their ascidiate parts. The septum between the two locules extends for the full length of the ovary. Each carpel contains one fertile ovule attached to the cross-zone (Fig. 4D–F) and one sterile ovule inserted just above the fertile ovule (Fig. 5A). Because the fertile ovule is pendent, it appears in cross-sections throughout the upper part of the synascidiate zone. The funicle of the fertile ovule is provided with a hairy obturator (Fig. 6A–C). Sterile ovules are much smaller than fertile ovules. The ventral bundles of adjacent carpels are fused in a heterocarpellary position (Fig. 4C–E). Just below the level of ovule insertion, two heterocarpellary ventral bundles unite with each other (Fig. 4F) and then immediately divide in a perpendicular plane, giving rise to two bundles each supplying a fertile ovule. Sterile ovules do not have any vascular supply.

The very short symplicate zone (Figs 4G and 5A, B) forms a roof of the ovary and a massive intrastaminal nectary. Externally, the nectary is covered by relatively long unicellular

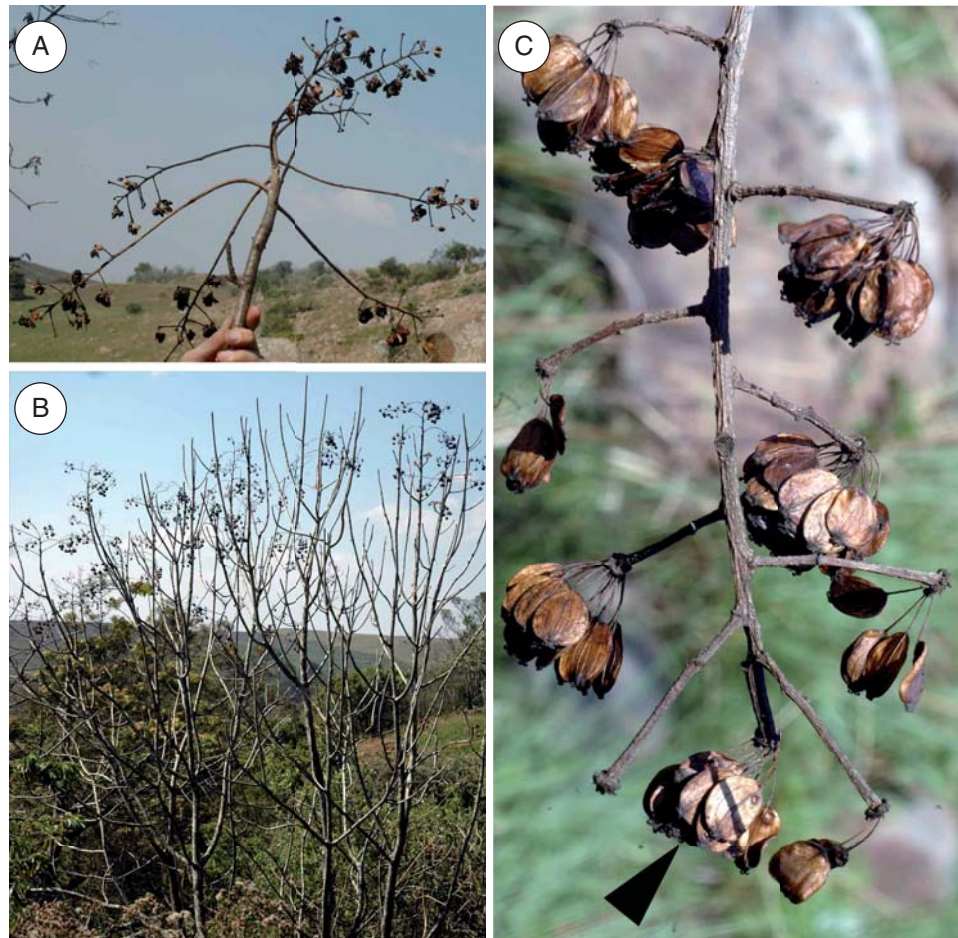


FIG. 2. *Seemannaralia gerrardii*: inflorescences in the dry season, with mature fruits. Images taken on 21 September, 2009, 50 km east of Vryheid, KwaZulu-Natal, South Africa. (A) General view of an inflorescence. (B) General view of an entire plant with numerous fruiting inflorescences. (C) Second-order inflorescence axis with mature fruits (arrowhead = fruits of the terminal umbellule).

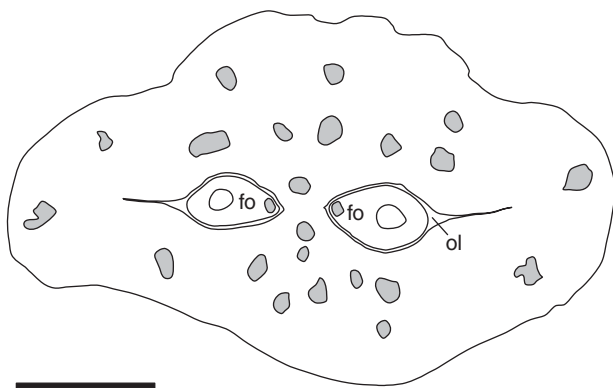


FIG. 3. *Seemannaralia gerrardii*: schematic drawing of a cross-section of just preanthetic flower in the upper part of synasciadiate zone of the gynoecium. Grey areas, vascular bundles; ol, ovarian locules; fo, fertile ovules. Scale bar = 500 μm .

papillae. The surface of each papilla is longitudinally striate. Carpel tips are extended into free plicate stylodia (Fig. 5C) bearing stigmas. Pollen tube transmitting tracts extend from each stylodium downward to the ovules. Just above the cross-zone, the transmitting tracts of adjacent carpels

are united into a short internal compitum that divides beneath into separate transmitting tracts, which reach the ovules of each carpel.

Unlike the flower, the fruit of *Seemannaralia* is unilocular (Figs 6 and 7): its central cavity is occupied mostly by a single large seed but a remnant of a second fertile ovule may also be present. Initially, both fertile ovules of postanthetic flowers grow at an equal rate until they reach 2–3 mm in diameter (Figs 6A, B and 7A). Growth of one ovule then stops whereas the other ovule develops into the mature seed by expanding and elongating, reaching 6–8 mm in length and 4–6 mm in width (Fig. 7B, C). The ovule that develops into a seed can be localized in the abaxial or the adaxial carpel; both variants occur in nearly equal numbers of fruits. When the ovule outgrows the available space in the locule, the septum is ruptured, forming a united cavity of the two carpels. Vestiges of the ruptured septum can be seen as fine sutures on the cavity wall; their scar surface can be distinguished by scanning (Fig. 6D, E) and light microscopy (Fig. 7C). Mature fruits are indehiscent, laterally compressed, elliptical to rounded in outline (Fig. 7D), 9–12 mm in length and 7–10 mm in width. Their abscission is extended over the

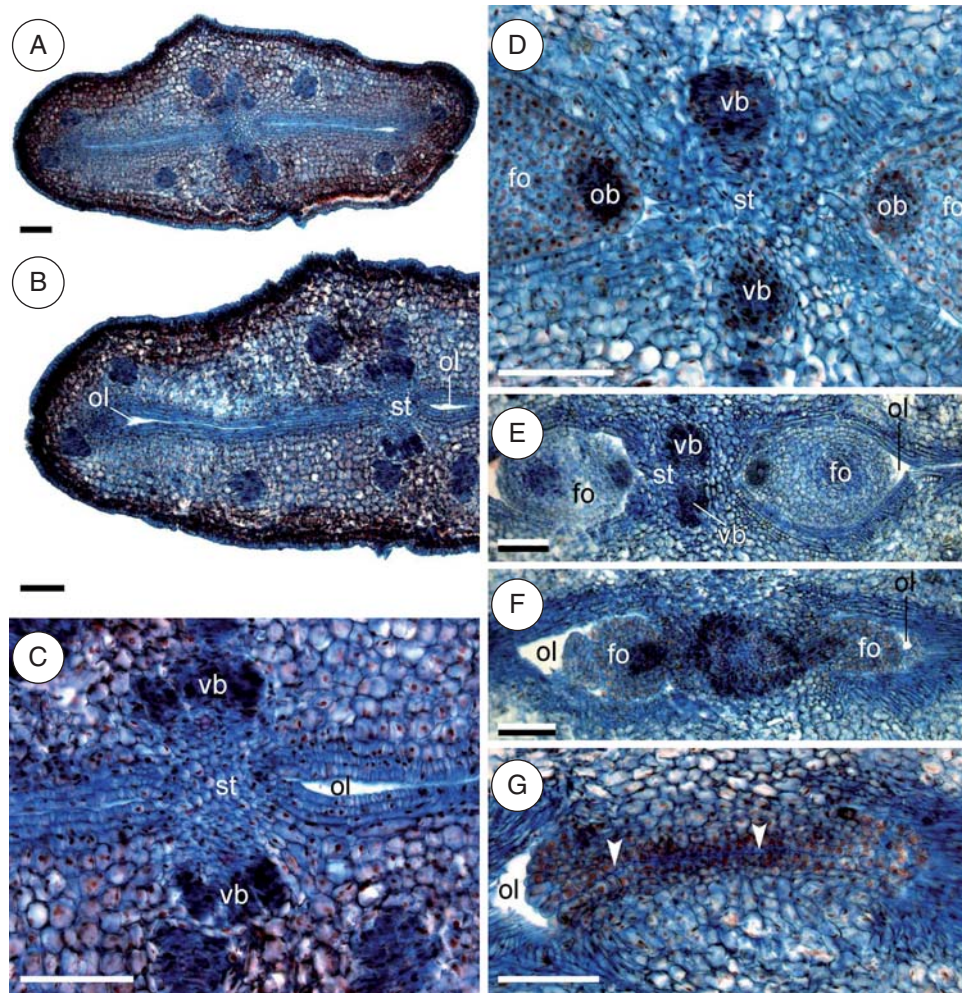


FIG. 4. *Seemannaralia gerrardii*: ascending series of cross-sections of ovary in just preanthetic flower (light microscopy), continued in Fig. 5. (A) Section in lower part of synascidiate zone. (B) Lower part of synascidiate zone, just above (A). (C) Central part of the same section as in (B); note intact septum. (D, E) Central parts of sections in the upper part of synascidiate zone; note intact septum. (D) The same section as illustrated in Fig. 3; heterocarpellary ventral bundles are well separated. (E) Above (D); heterocarpellary ventral bundles are close to each other. (F) Above (E), nearly at the level of fertile ovule attachment (cross-zone); ventral bundles are united. (G) Symplicate zone: above, fertile ovules; below, sterile ovules. Abbreviations: fo, fertile ovule; ob, ovule bundle; ol, ovarian locule; st, septum; vb, ventral bundles; arrowheads, line of postgenital fusion in plicate zone. Scale bars = 100 μ m.

dry season (April–October) with the fruits remaining on the branches after the leaves have fallen (Fig. 2).

DISCUSSION

The present observations show that ovaries in the flowers of *S. gerrardii* are bilocular. The septum between the two locules extends for the full length of the ovary and not only at its apex ‘near the level of ovular insertion’, as Burt and Dickison (1975, p. 457) noted. As far as we are aware ascertain, this is the first record of a phenomenon that could be termed ‘pseudoparacarp’, not only in the Araliales but in the Angiospermae as a whole. The fruit superficially appears to be paracarpous (as is found in Pittosporaceae) but the single locule is formed by mechanical rupture of the septum by the developing seed.

The present data show beyond doubt that the flower of *Seemannaralia* has a bicarpellate syncarpous gynoecium; its ovary contains two locules separated from each other by a

septum. Despite Burt and Dickison’s (1975) records, the synascidiate zone is well developed in this gynoecium and the ovules are attached to the cross-zone rather than to the reportedly long symplicate zone. In the present description, the preanthetic and anthetic gynoecium of *Seemannaralia* has nearly the same structure as gynoecia of most other genera of Araliaceae (including *Cussonia*), Myodocarpaceae and Apiaceae (e.g. Philipson, 1970; Magin, 1977; Reyneke, 1981; Lowry, 1986a, b). Therefore, *Seemannaralia* cannot throw any light on the evolution of the unilocular gynoecium with a well-developed symplicate zone, which is typical for the Pittosporaceae.

The discrepancy between Burt and Dickison’s (1975) results and ours is probably due to the different kind of materials that were used. Burt and Dickison studied dry flowers taken from herbarium collections whereas we used samples fixed in FAA. The ovary septum in *Seemannaralia* (at least that part situated between the heterocarpellary ventral bundles) consists of thin-walled parenchyma that is easily damaged. Like Burt and

Dickison, we observed ‘unilocular ovaries’ (i.e. with split septa) in some transverse sections, but careful observations of serial sections revealed that these cases are localized and represent secondary ruptures of the septa.

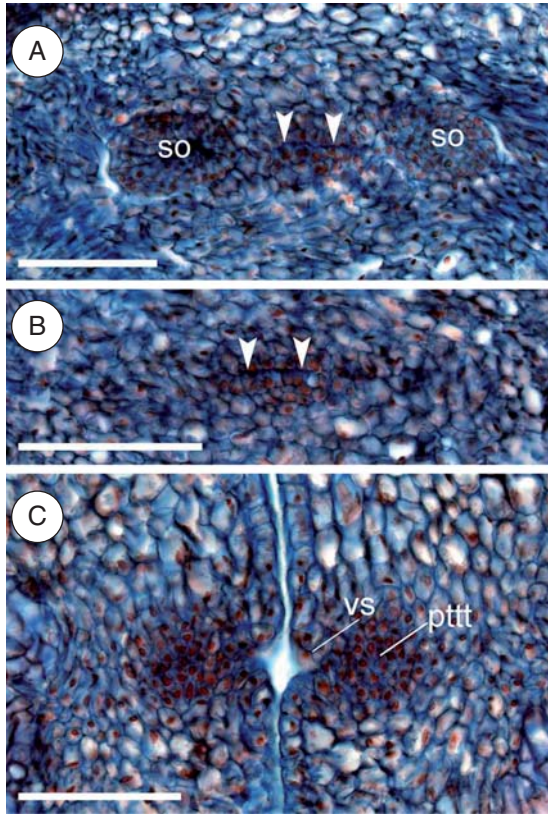


FIG. 5. *Seemannaralia gerrardii*: ascending series of cross-sections of ovary in just preanthetic flower (light microscopy), continued from Fig. 4. (A) Symplicate zone, at the level of sterile ovules. (B) Symplicate zone, above sterile ovules. (C) Plicate zone; carpels free. so, sterile ovule; pttt, pollen tube transmitting tissue; vs, ventral slit; arrowheads, line of postgenital fusion in plicate zone. Scale bars = 100 μm .

The disappearance of the septum and the union of the locules into a common cavity take place in the course of fruit development. The fruit of *Seemannaralia* resembles the paracarpous gynoeceium but its ground plan is very different because the central cavity is formed by mechanical rupture of the septum. The term ‘pseudoparacary’ is proposed here to describe this unusual case of united carpellary cavities.

Among other angiosperms, the destruction of the septa can serve as a mechanism to aid the dehiscence of the fruit in many taxa, for example in *Impatiens* (Caris *et al.*, 2006). Besides, the septa are commonly partly or completely dissolved before or during anthesis in some Caryophyllales (Takhtajan, 1942, 2009; Rohweder, 1967; Bittrich, 1993), a phenomenon used to introduce the term ‘lysicarpous gynoeceium’ (Takhtajan, 1942). Nevertheless, the mechanical rupture of the septum in the course of the development of indehiscent fruit has not been reported to date in any taxa other than *Seemannaralia*.

As Burt and Dickison (1975, p. 460) suggested, the fruit of *Seemannaralia* is functionally equivalent to the typical anemochorous mericarp of Apioideae. In general, seed number in wind-dispersed diaspores tends to be reduced to one, which is the most common condition in anemochorous taxa (Ridley, 1930). Certain adaptive advantages of one-seeded anemochorous diaspores over di- or polyspermous ones have been experimentally demonstrated for *Lonchocarpus pentaphyllus* (Fabaceae), a tropical tree which has indehiscent wind-dispersed fruits containing 0–4 seeds (Augspurger and Hogan, 1983). In this species, the decrease in seed number per fruit is correlated with increases in both seed weight (i.e. improved nutrient storage for the embryo) and dispersal distance. The pseudoparacarpous structure of the fruit in *Seemannaralia* has probably resulted from such a decrease in seed number in the course of a transition from zoochory [as in *Cussonia*, where the fleshy fruits are dispersed by birds (Reyneke, 1981; our pers. obs.)] to anemochory. This suggestion may be tested by detailed studies of fruit dispersion in the two genera.

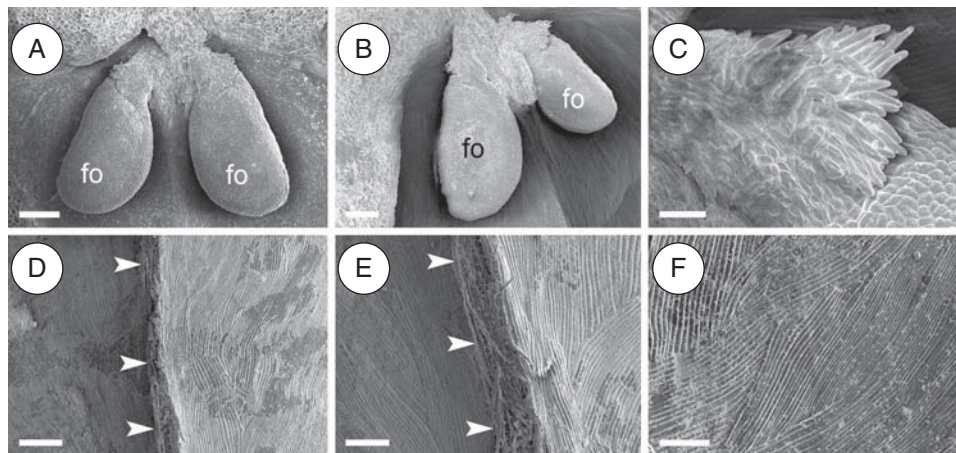


FIG. 6. *Seemannaralia gerrardii*: dissected immature fruits (scanning electron microscopy). (A, B) Upper part of ovary with two fertile ovules visible. (C) Detail of (B) showing obturator. (D, E) Lower part of ovary; inner surface of locules in the area of ruptured septum. (F) Lower part of ovary; inner surface of a locule beside septum. fo, fertile ovule; arrowheads, ruptured septum. Scale bars (A, B, D) = 200 μm , (C) = 50 μm , (E, F) = 100 μm .

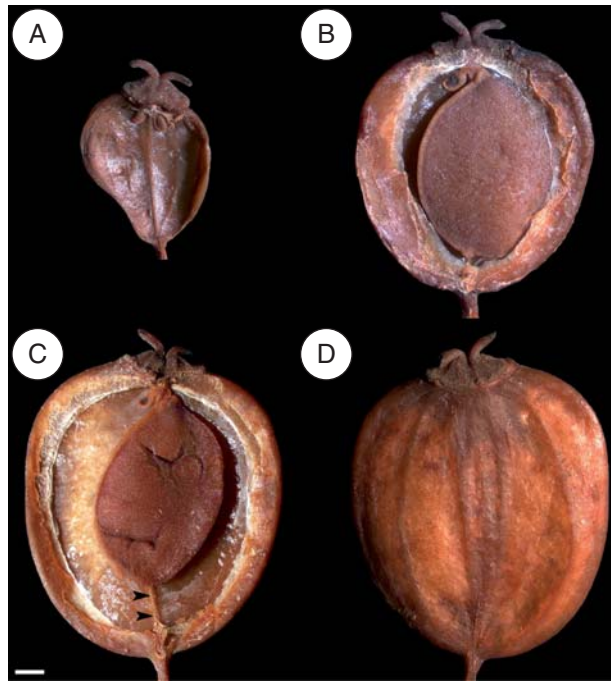


FIG. 7. *Seemannaralia gerrardii*: fruits (light microscopy). (A) Dissected immature fruit with two ovules of the same size. (B, C) Dissected nearly mature fruits with one ovule developing into seed; arrowheads, ruptured septum. (D) Nearly mature fruit: general view. Scale bar common to all figures = 1 mm.

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