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Cretaceous floral structures from Negev, Israel as evidence of angiosperm radiation in the Gondwana realm*

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ABSTRACT. Inflorescences, flowers and fruits from the Turonian Gerofit locality in southern Negev, Israel are assigned to new genera and species: *Zeevlewya gracilis* gen. et sp. nov. (floral tube of sepals, stamens exserted, basal hypanthium strongly elongated in fruit, supposedly cryptoviviparous), *Minevronia capitata* gen. et sp. nov. (capitate inflorescence of hypanthial flowers), *Eibinevoia chlamydea* (floral tube bracteolate, upper hypanthium persistent in fruit, sepal lobes stalked, hairy, longer then petals), *Lorchiella setosa* gen. et sp. nov. (sepals setose, petals interlocked by marginal hairs in aestivation), and *Shelomonasca caudata* gen. et sp. nov. (floral tube of caudate sepals, with bipartite bracteolate cup at base, petals deciduous), *Seraphocarpus minutus* gen. et sp. nov. (fruit winged over ribs, with a crown of caudate appendages). These morphotypes represent early diversification of a proto-myrtalean stalk, with variously combined characters of the Combretaceae and Rhizophoraceae. Their evolution was related to the early appearance of mangrove communities in the northern Gondwana realm.

KEY WORDS: flowers, fruits, plant evolution, early angiosperms, mangroves, Cretaceous, Gondwana

INTRODUCTION

Cretaceous angiosperms might have spread from a single or several (numerous) diversification centers. The present author advocated the latter view in respect to the mid-Cretaceous Baisian proangiosperms of Transbaikalia (Krassilov & Bugdaeva 1999) and the Siberian ranunculids (Krassilov & Golovneva 2001, 2004). The recently obtain material from the Turonian Gerofit locality in Israel is of a certain significance as evidence of Cretaceous angiosperm evolution in the northern Gondwana realm. Although the palaeogeographic situation is far from clear yet (Krassilov 2003), there must have been a differentiation between the northern (Laurasian) and southern (Gondwana) angiosperms due to seaway barriers and climatic differences. Although leaf morphology does not seem to suggest a far-reached divergence, with *Laurophyllum*, *Sapindopsis*, *Debeya*, *Nelumbites*, etc. reported from both the Laurasian and northern Gondwana floras (Lejal-Nicol & Dominik 1990, Dobruskina 1997, Krassilov & Bacchia 2000), the impression of homogeneity may partly reflect a parallelism of leaf shape evolution rather than taxonomic affinities.

Preliminary reports on fossil plants from Gerofit, listing a few terrestrial and aquatic angiosperms, were published in Eckstein (1963), Lorch (1965), Dobruskina (1997), and Krassilov & Dobruskina (1998). In 2001–2002 a field party including Valentin Krassilov, Zeev Lewy and Shelomo Ashkenazi, the Geological Survey of Israel, collected abundant plant material, which revealed a considerable diversity of the mid-Turonian angiosperms representing several types of coastal wetlands, with a possible mangrove components (Krassilov et al. 2004). It was shown for the first time that the locality

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is rather rich in floral structures. This is the first attempt at their taxonomic treatment that no doubt will be revised with accumulation of relevant material.

MATERIAL AND METHODS

The material came from the Gerofit locality (29°59′10″N, 35°4′15″E) at the base of Gerofit Plateau in southern Negev, Israel (Fig. 1). The mid-Cretaceous deposits of the region, then located on the northern fringe of Gondwana realm, are marine, with lagoonal interbeds. Plant remains occur in the lagoonal deposits of Ora Formation bracketed between the normal marine facies with mid-Turonian (about 90 Ma) ammonites (Freund & Raab 1969, Bartov et al. 1972, Lewy 1985, 1989). The plant remains are ferruginous impressions with patches of mineralized compression film revealing microstructures under scanning electron microscope (SEM).

The most abundant leaves are compound, of pedate architecture, with dichopodial basal segments and with narrow elliptical to elongate entire or serrate leaflets. Similar, perhaps congeneric leaf morphotypes were described from other Cretaceous localities as *Debeya* Miquel, *Dewalquea* Saporta & Marion, *Proteophyllum* Velenovsky, *Manihotites* Berry, etc. (leaf taxonomy will be dealt with elsewhere).

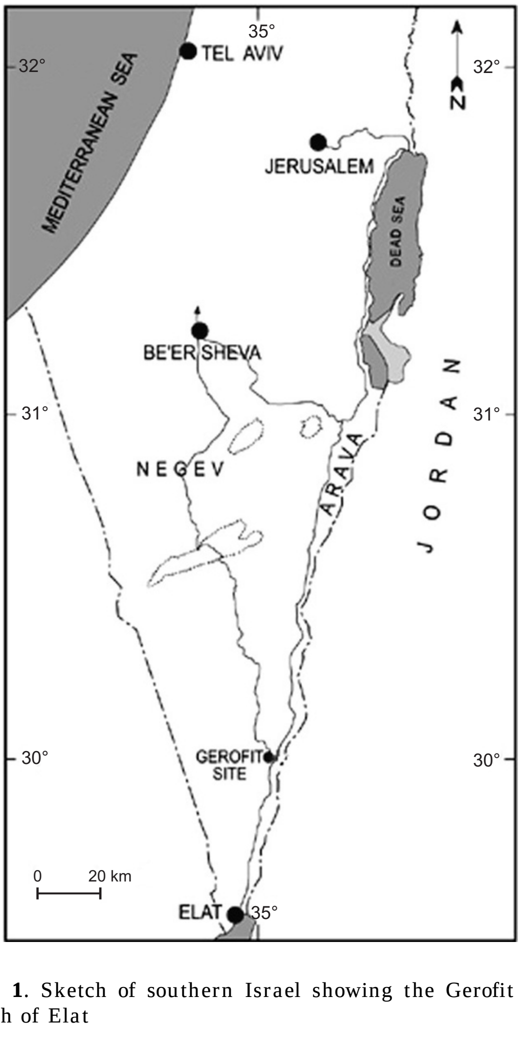

Fig. 1. Sketch of southern Israel showing the Gerofit Site north of Elat

Most of the floral remains were obtained by splitting the fossiliferous clay and clearing the impressions with thin entomological pins in the laboratory. The flowers are fairy common, with fragile parts intact, which suggests a deposition not far from their source plants, perhaps the same as for the associating leaves.

Unfortunately, none of the floral structures are structurally preserved and the attempts at extracting pollen grains failed so far. Yet, the impressions provide morphological information of a certain taxonomic significance. Moreover, it is possible to trace development from flowers to fruits with persistent floral parts and occasionally further to seedlings. It must be noted that bodily preserved floral structures are not necessarily more informative than impressions (see comment on *Esgueiria*, below) and a neglect of the latter amounts to a great loss of palaeobotanical information.

SYSTEMATIC DESCRIPTION

Zeevlewya Krassilov **gen. nov.**

Type. *Zeevlewya gracilis* sp. nov.

Derivation of the name. In honor of Dr. Zeev Lewy, Geological Survey of Israel, in appreciation of his contribution to the Cretaceous palaeontology of Israel and our joint study of Gerofit locality.

Age and geography. Mid-Cretaceous (Turonian) of southern Negev, Israel.

Diagnosis. Flowers monoclinous, epigynous, slightly zygomorphous, shortly pedicellate or sessile with a swollen abscission scar, tubular, slightly curved, about 7 mm long. Floral buds clavate to obovate, obtuse, basally stalk-like, conspicuously expanded in the upper third where the calyx lobes are separated. Hypanthium straight or slightly curved, longitudinally ridged and minutely hairy (with pits of hair bases on impression) over the ovary, narrowly cupuliform or funnel-shaped with 0–6 calyx lobes above. Calyx lobes narrow lanceolate, acuminate, glabrous, one lobe considerably longer than the others, valvate and clasping the stamens in bud, narrowly spreading, deciduous or obliterated later in development. Petals apparently lacking. Androecium of 0–6 stamens with long slender flexible filaments proximally adnate to the calyx tube, unequally exserted. Anthers introrse, elliptical to cordiform, dehiscing into two valves. Filament persistent after shedding the anthers as hooked bristles converging over the tube. Basal hypanthium strongly elongated in fruiting, spindle-shaped, constricted below the shrinking upper hypanthium.

Zeevlewya gracilis Krassilov **sp. nov.**

Pl. 1, figs 1–13; Fig. 2: 1, 2

Holotype. Flower, IG1-322 (Pl. 1, fig. 1).

Type locality. Gerofit, Arava Valley south of the Dead Sea, Israel.

Type horizon. Ora Formation, Middle Turonian.

Derivation of the name. Gracilis (Lat.) graceful.

Diagnosis. As for the genus.

Material. 20 specimens from the type locality.

Description. The holotype (Pl. 1, fig. 1) is a tubular flower, slightly curved, with a conspicuously thickened abscission scar. The hypanthium is horn-shaped, well extended above the ovary, with minute pits of hair bases. The distal lobes are scarcely discernible. The stamens depart above the ovary, their filaments are shortly decurrent down the lower hypanthium. Four stamens are well preserved and two more are faintly marked on the ferruginous impression. The filaments are all well exserted, but of unequal length. Two stamens are considerably longer than the rest, their slender filaments incurved or twisted. The anthers are introrse, relatively massive, elliptical to slightly cordiform (Fig. 2: 1, 2).

The figured paratypes represent various developmental stages of fruiting flowers. One of them (Pl. 1, fig. 2) shows a narrow tubular longitudinally ridged basal hypanthium divided by a constriction zone from the broader upper hypanthium still bearing intact stamens, one of which is much longer than the others, bearing a bivalved dehiscent anther. In two other specimens (Pl. 1, figs 3, 4), most or all the stamens have shed their anthers, the naked filaments persisting as awn-shaped bristles converging over the tube, while the ovaries are conspicuously swollen. In further development (Pl. 1, figs 5–7) the basal hypanthium is strongly elongated (5–6 mm), spindle-shaped, while the upper hypanthium is shrunk to a mere knob still bearing the hooked filaments.

Two germinate fruits (Pl. 1, fig. 8) are entangled by their hooked appendages, both showing lingulate processes that appear as emerging hypocotyls. The structure shown in (Pl. 1, fig. 9) matches the shape and dimensions of the spindle-shaped fruit. It is slightly notched at the apex and bears two lateral rootlets at the lower end and more are developing above, as in dispersed hypocotyls of viviparous mangroves that bear small protuberances of the primordial leaf stipules and are often rooted by the lateral roots rather than the (suppressed) radical.

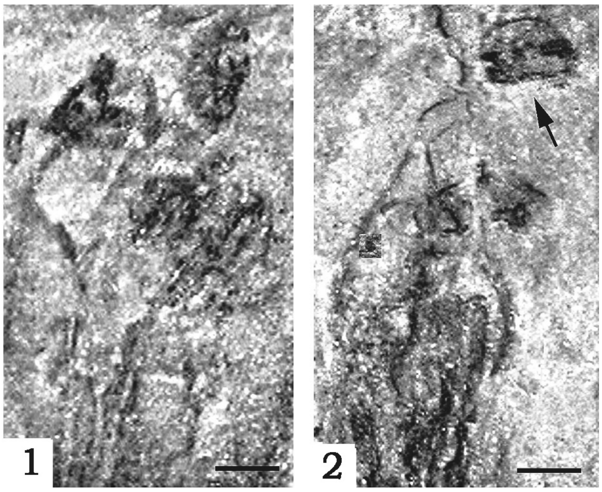

Fig. 2. *Zeevlewya gracilis* gen. et sp. nov., details of stamens: **1** – inserted stamens, counterpart of the holotype (Pl. 1, fig. 2), **2** – stamens with massive bilobed anthers facing floral axis, counterpart of paratype IG0-239a (Pl. 1, fig. 2). Scale bar 0.6 mm

The buds figured in (Pl. 1, figs 10–13) obviously belong to the same species as the fruiting flowers, representing consecutive developmental stages. In the early stage (Pl. 1, fig. 11), the bud is straight, clavate, proximally stalk-like with a basal scar, distally dome-like, with imbricate calyx lobes converging over the androecium. Impressions of anthers inside the hypanthium are at or slightly above the base of the lobes. In the later stages (Pl. 1, figs 10, 12) the buds are slightly curved, with a discernible pedicel. The calyx lobes are slightly separated. They are conduplicately folded clasping the stamens. Few anthers still remain at the base line of the lobes, the others are variously exserted. An immature flower (Pl. 1, fig. 13) shows a funnel-shaped upper hypanthium formed of the narrowly spreading incurved calyx lobes one of which is nearly twice longer than the others rendering the flower slightly zygomorphous. This feature can be seen also in Pl. 1, fig. 12.

Comparison. Similar monoclinous shortly pedicellate hypanthial flowers with floral tube extending above the ovary are most typical for the extant Rhizophoraceae and Combretaceae (Hutchinson 1926, Heywood 1979, Cronquist 1981, Goldberg 1986, Weberling 1989, Zomlefer 1994). In the former family, the flowers often are slightly zygomorphous, with one calyx lobe longer than the others (Ding Hou 1960). The flower buds are naked, obtuse, strikingly similar in shape to the fossil. The stamens have shorter filaments and are epipetalous, but the petals are deciduous. Among the Combretaceae, the apetalous condition is characteristic for the tribe Terminalieae (or Terminaliinae if considered as subtribe) and is less often met in the Combreteae (Exell & Stace 1966). The calyx lobes are commonly conduplicate in bud spreading into a funnel-shaped upper hypanthium divided from the lower hypanthium by a constriction zone and sometimes persistent in fruit (*Guiera*). The stamens are episepalous, exserted, rarely not exserted or variable.

Style is wanting in all the specimens of *Zeevlewya*, which means that it was either deciduous or adnate to the floral tube, as is often the case in the Combretaceae, and concealed in this way. A peculiar feature of *Zeevlewya* is a conspicuous elongation of lower hypanthium forming a stiff spindle-shaped structure while the upper hypanthium still persists. Such a morphology suggests cryptovivipary (with seedling germinating from the seed but remaining inside the fruit before abscission), as in several mangrove genera (Juncosa 1982, 1984, Tomlinson 1994). The germinate fruits float for some time and are often found in groups hooked by their hypocotyls. In the viviparous Rhizophraceae, the excessively developed hypocotyl is abscised from the cotyledons (remaining in the fruit) and, after floating in salt water, is rooted in the mud. Yet in the cryptoviviparous mangroves, such as *Avicennia* or *Aegiceras*, the seedling is shed with the strongly elongated fruit that splits releasing the hypocotyl (Tomlinson 1994). A similar situation is met in *Zeevlewya*, with hypocotyls emerging from germinate fruits entangled by their hooked appendages (Pl. 1, fig. 8) and eventually released. The only comparable fossil structure is a detached hypocotyl of *Ceriops* from the Eocene of England. It is structurally preserved, but rather featureless externally (Wilkinson 1981).

Combretanthites eocenica Berry, a combretaceous flower form the Eocene of North America is apparently staminate, long pedunculate, with relatively short floral tube, deeply divided calyx lobes, long petals and numerous (12) stamens (Berry 1913). It is closer to the extant *Combretum* than to the Cretaceous *Zeevlewya*.

Esquieria, a flower of doubtful combretaceous affinities from the Maastrichtian of Portugal (Friis et al. 1992) and Coniacian of Japan (Takahashi et al. 1999) is distinctive due to the apical feature described as “three styles”, but appearing in the photographs as a short style with three linear stigmatic arms. Androecium is lacking in open flowers – supposedly shed soon after anthesis, a condition quite unlike that in *Zeevlewya*. There is no evidence for the claim that stamens were well excerted in *Esguieria*, which impedes a further comparison with *Zeevlewya*.

Minevronia Krassilov **gen. nov.**

Type. *Minevronia capitata* sp. nov.

Derivation of the name. In honor of Professor Mina Evron, Zinman Institute of Archaeology, University of Haifa, in appreciation of her archaeopalynological research and her interest in palaeobotany.

Diagnosis. Composite inflorescence of a flexible axis bearing floral (fruiting) heads and buds at consecutive nodes, widely spaced. Partial inflorescence of a dichasial structure in bud, surrounded at base by a whorl of partly connate pendent hairy bracts. Floral primordia appearing as minute protuberances on dichasial axes. Mature heads sessile with synchronously developing densely imbricate flowers, about 25 per head. Flowers narrow ovate to fusiform, apically pointed or lacerate, lobes hairy.

Age and geography. Mid-Cretaceous (Turonian) of southern Negev, Israel.

Minevronia capitata Krassilov **sp. nov.**

Fig. 3: 1–5

Holotype. Inflorescence, IG1-209 (Fig. 3).

Type locality. Gerofit, Arava Valley south of the Dead Sea, Israel.

Type horizon. Ora Formation, Cretaceous, Middle Turonian.

Derivation of the name. Capitata (Lat.) clustered in heads.

Diagnosis. As for the genus.

Material. Holotype and counterpart.

Description. The holotype is a composite inflorescence (conflorescence) of meandering axis 90 mm long, 1.5 mm thick, expanded to 2.5 mm at the inflorescence nodes. The nodes are 7 mm apart, the upper one bearing an inflorescence bud, while a fully mature head arises form the lower one. The bud is 3.2 mm long, showing three slender (0.5 mm thick) inflorescence branches, of which the median one is relatively short, unbranched, while the symmetrically developed lateral ones are longer, forked on ends. This dichasial structure is surrounded at base by a whorl of inflorescence bracts that are proximally connate, distally divided into pendent lobes. These latter are broadly triangular, apiculate, slightly upcurved on ends, covered with long hairs. The branches are densely covered with hemispherical protuberances of flower primordia.

The mature head is sessile on the node, 18 mm wide, consisting of the radially spreading imbricate flowers, all apparently at the same developmental stage, although somewhat variable in size (5–6 mm long). Their bases are concealed by overlapping, the free ends are pointed or irregularly lobed (lacerate), with the lobes bearing long hairs. Some of the linear appendages surrounding the flowers might have been bristles arising from the base of hypanthia or from bracteoles, but this could not be verified. Few detached flowers are indistinctly pedicellate or rounded at base, with abscission scars.

Comparison. As their lacerate hairy apices suggest, the flowers might have been hypanthial and basically similar to the group of flower morphotypes described below, in particular to *Lorchiella setosa* gen. et sp. nov. Yet, in *Minevronia*, the nature of bristles is

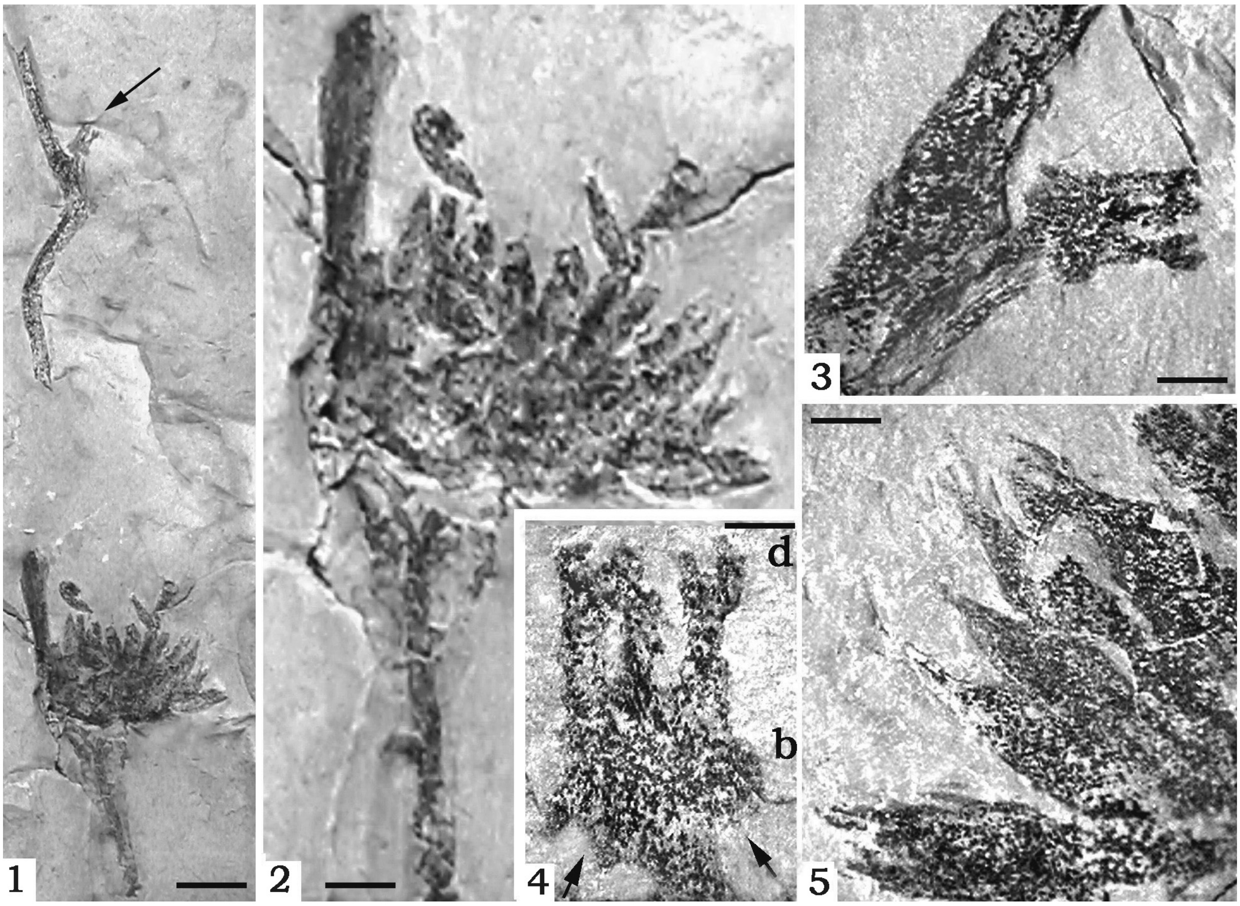

Fig. 3. *Minevronia capitata* gen. et sp. nov., conflorescence of capitate heads, holotype, IG1-209: **1** – conflorescence axis with a head at lower node and a bud (arrow) above, scale bar 7 mm, **2** – head magnified, scale bar 3 mm, **3, 4** – bud magnified, showing a whorl of connate bracts (**b**) and the dichasial branches (**d**) with floral primordia as small protuberances, scale bars 1.6 mm and 0.7 mm, **5** – part of the head showing distinct flowers with hairy hypanthial lobes. Scale bar 1.7 mm

unclear, while the differences in shape and dimensions, as well as the longer apical hairs are against identification of this inflorescence genus with *Lorchiella* or any other flower genus.

Fossil heads of similar general aspect are commonly assigned to *Platanus* or extinct platanoids. Yet in the case of *Minevronia* a platanoid affinity is unlikely on account of flowers with lacerate hairy hypanthia, which are unknown in the platanoids, although few their Cretaceous representatives had calyptrate androecial flowers (Magallon-Puebla et al. 1997). Rather, *Minevronia* can be more favorably compared with *Conocarpus,* a combretaceous genus with hairy calyx lobes, subtended by hairy bracteoles and clustered into small (5 mm) globose heads of about 25 flowers each. *Ramatuella* is another combretaceous genus having globose heads indicating a tendency toward this inflorescence type in the family (Exell & Stace 1966). The bracteate partial inflorescence betrays an essentially dichasial structure, one of the basic in the Myrtales (Leins 1965, Briggs & Johnson 1979).

Eibinevoia Krassilov **gen. nov**.

Type. *Eibinevoia chlamydea* sp. nov.

Derivation of the name. In honor of Professor Eviatar (Eibi) Nevo in appreciation of his contribution to Cretaceous palaeontology of Israel.

Diagnosis. Pistillate flower shortly pedicellate, bracteolate, actinomorphous, epigynous, about 7 mm long, with perianth members proximally connate into a hypanthial tube enclosing the ovary, narrowly cupuliform in the distal part. Bracteole linear with few parallel veins, extending all length of hypanthial tube. Upper hypanthiun persistent in fruit. Sepal lobes stalked, deltoid or spathulate, hairy. Petal lobes relatively short, lingulate, sessile on tube margin, glabrous.

Age and geography. Mid-Cretaceous (Turonian) of southern Negev, Israel.

Eibinevoia chlamydea Krassilov **sp. nov.**

Pl. 2, figs 1, 2

Holotype. Flower in fruit, IG1-364 (Pl. 2, figs 1, 2).

Type locality. Gerofit, Arava Valley south of the Dead Sea, Israel.

Type horizon. Ora Formation, Cretaceous, Middle Turonian.

Derivation of the name. From chlamys (Gr.) cloth, with perianth.

Diagnosis. As for the genus.

Material. Holotype and counterpart. Several fragmentary specimens are tentatively assigned to this species.

Description. The holotype (Pl. 2, figs 1, 2) is a fruiting flower, with the perianth members intact. It shows a short massive pedicel 0.5 mm long, a bulky central part apparently corresponding to the fruit developing from an inferior ovary enclosed by the hypanthial tube, and a single linear bracteole adnate to and as long as the undivided part of the tube. Few short hairs are preserved at the base of the tube. The distally distinct perianth members are spreading at acute angle forming the narrowly cupuliform upper hypanthium. They are differentiated into the morphologically dissimilar outer and inner appendages corresponding to the sepal and petal lobes respectively. The sepal lobes are about 2 mm long, shortly stalked, expanded into a spatulate blade with long curved hairs. Three sepal lobes are preserved on one side of the tube suggesting that their total number should have been no less than four, probably five. The petal lobes are opposite to the sepals, 1–1.3 mm long, sessile on the tube margin, lingulate, slightly incurved, pointed, apparently firm (leathery) and glabrous. There is no evidence of any androecial structures.

Comparison. On account of the pedicellate flower/fruit, inferior ovary of a solitary pistil, adnate bracteole and the perianth tube with distinct lobes in the distal cupuliform part persistent in fruit, this fossil is closer to the Combretaceae than to any other angiosperm group. In the present day Combretaceae, the flowers are tetramerous or pentameous, variable within the tribes (Exell & Stace 1966). The perianth lobes are often deltoid or spatulate and conspicuously pubescent. In *Guiera* and *Bucida*, the calyx lobes are persistent in fruit (Graham 1964, Exell & Stace 1966). Within the family, the Combretoidae is closer in the condition of asymmetrical bracteole than the Laguncularieae with a pair of bracteoles (Exell & Stace 1966). The presence of petals is a diagnostic feature of the tribe Combretae in contrast to the apetalous Terminaliae that differ also in the shorter hypanthium. However, in the Combretaceae, the flowers are monoclinal (bisexual) or (in the Terminaliae) both monoclinal and staminate. Pistillate flowers as in *Eibinevoia* would have been atypical for the extant Combretaceae.

Lorchiella Krassilov **gen. nov.**

Type. *Lorchiella setosa* sp. nov.

Derivation of the name. In honor of Professor J. Lorch whom we owe the first report on the fossil plants from Gerofit.

Diagnosis. Pistillate flower shortly pedicellate, actinomorphous, pentamerous, epigynous. Hypanthia about 7 mm long, elongate-elliptical, ovate in bud, distally lobed and bristled, lacerate at maturity. Petaloid (?) lobes obovate to lanceolate, interlocked by their marginal hairs in aestivation, narrowly spreading, with the hairs mostly deciduous later in development. Sepaloid (?) bristles five, regularly disposed, longer than the lobes, decurrent as longitudinal ridges down the tube.

Age and geography. Mid-Cretaceous (Turonian) of southern Negev, Israel.

Lorchiella setosa Krassilov **sp. nov.**

Pl. 2, figs 3–7; Fig. 4

Holotype. Flower, IG1-297 (Pl. 2, fig. 3).

Type locality. Gerofit, Arava Valley south of the Dead Sea, Israel.

Type horizon. Ora Formation, Cretaceous, Middle Turonian.

Derivation of the name. Setosa (Lat.) bristled.

Diagnosis. As for the genus.

Material. 36 specimens from the type locality.

Description. The holotype (Pl. 2, fig. 3) is an elongate-elliptical flower with a short stout pedicel that is somewhat broader than long. Slender hairs arise on the left side of it. The lower hypanthium is distinctly longitudinally ridged and in the upper quarter divided into the narrowly spreading lanceolate lobes forming the cupuliform upper hypanthium. Five slender bristles diverge at the slightly different levels below the cupule alternating with the lobes and extending well above them. The bristles are traced down the hypanthium as the regularly spaced longitudinal ridges, their radial arrangement indicating actinomorphous symmetry.

The figured paratypes represent various developmental stages, with the hypanthia narrowly ovate in bud, more prominently stalked than in the holotype (Pl. 2, fig. 4), elongate-elliptical and deeply lacerate with maturation (Pl. 2, fig. 7). The apical lobes are interlocked in bud forming a solid conical structure (Pl. 2, figs 4, 5), then slightly separated, exposing their dense interlacing marginal hairs (Pl. 2, fig. 7; Fig. 4). Later in development, the lobes are narrowly spreading, sparsely if at all pubescent, shedding most their hairs at maturity (Pl. 2, fig. 7). The condition of the bristles is also variable. In bud they are bifurcate, adpressed to the tube and intermingled with the apical hairs. An ovate hypanthium (Pl. 2, fig. 4) is longitudinally ridged, but the bristles are not yet separated from the apical cone, whereas in another specimen with the similarly interlocked lobes, a spreading bristle is well-defined on the right side (Pl. 2, fig. 5). An irregularly lacerate hypanthium (Pl. 2, fig. 7) still shows one of the bristles intact.

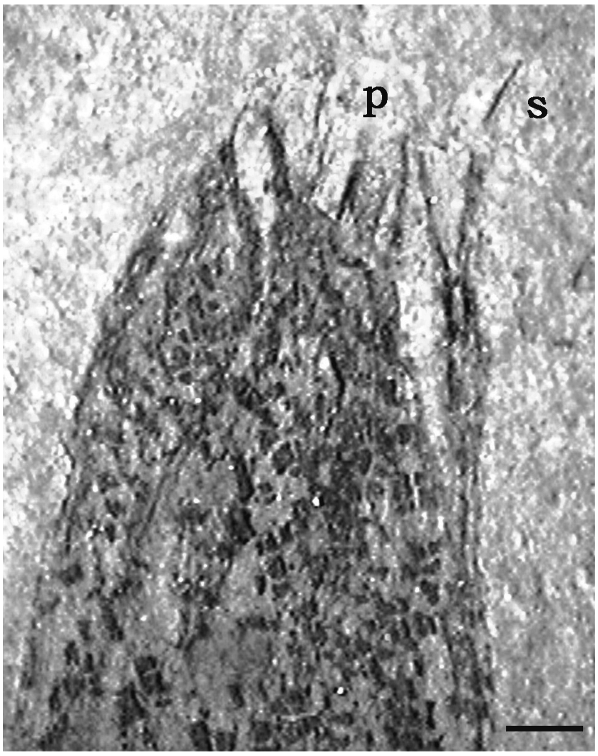

Fig. 4. *Lorchiella setosa* gen. et sp. nov.: details of hairy petals (**p**) and a setose sepal (**s**) in bud, paratype IG1-317. Scale bar 0.4 mm

Comparisons. This flower type is similar to *Eibinevoia chlamidea* sp. nov. (above) in the outline and dimensions of the hypanthia and their pedicels. In *Lorchiella setosa*, the hypanthial bristles topologically correspond to the stalked sepals in *Eibinevoia chlamidea*. These structures might have been homological rendering a transformation of laminar sepal lobes into slender bristles a primary distinction between the two forms. Yet there are additional distinctions (bracteoles occur in *Eibinevoia*, but are lacking in *Lorchiella*; petal lobes are glabrous in *Eibinevoia*, hairy in *Lorchiella*) making them readily separable at the generic level.

Interlocking of hypanthial lobes by their marginal hairs is typical of the extant Rhizophoraceae (Pl. 2, fig. 8). In *Rhizophora*, the flowers are essentially tetramerous, but the sepals are 4 (5), with a prominent longitudinal ridge, usually longer than the petals. These features match the fossil flower, which, however, does not show a bracteolate cup characteristic of the extant genus.

Shelomonasca Krassilov **gen. nov.**

Type. *Shelomonasca caudata* sp. nov

Derivation of the name. In honor of Shelomo Ashkenazi, Geological Survey of Israel, in appreciation of his help in collecting at the Gerofit locality; nascens (Lat.) emerging.

Diagnosis. Pistillate flower pedicellate, actinomorphous, 5–6 mm long, tetramerous, epigynous with a bracteolate cup and basal hairs. The hypanthial tube is ovate to obovate, distally cupuliform. Calyx deeply incised into long caudate lobes. Corolla of shorter lobes, membranous, glabrous, deciduous at maturity.

Age and geography. Mid-Cretaceous (Turonian) of southern Negev, Israel.

Shelomonasca caudata Krassilov **sp. nov.**

Pl. 2, figs. 9, 10; Fig. 5

Holotype. Flower, IG1-360 (Pl. 2, fig. 10).

Type locality. Gerofit, Arava Valley south of the Dead Sea, Israel.

Type horizon. Ora Formation, Cretaceous, Middle Turonian.

Derivation of the name. Caudata (Lat.) with a tail-like process.

Diagnosis. As for the genus.

Material. 14 specimens from the type locality.

Description. The holotype (Pl. 2, fig. 10) shows a swollen bulbous pedicel and a well-developed bipartite bracteolate cup at the base. The cup consists of four lanceolate lobes, upcurved and shortly bristled at the end (Fig. 5). Few basal hairs emerge from the cup. The hypanthium is broadly ovate, divided down to the middle into the erect caudate lobes. Two lobes are seen in the front view and one more is partly immersed in the rock matrix. Only one petal is discernible on the right side.

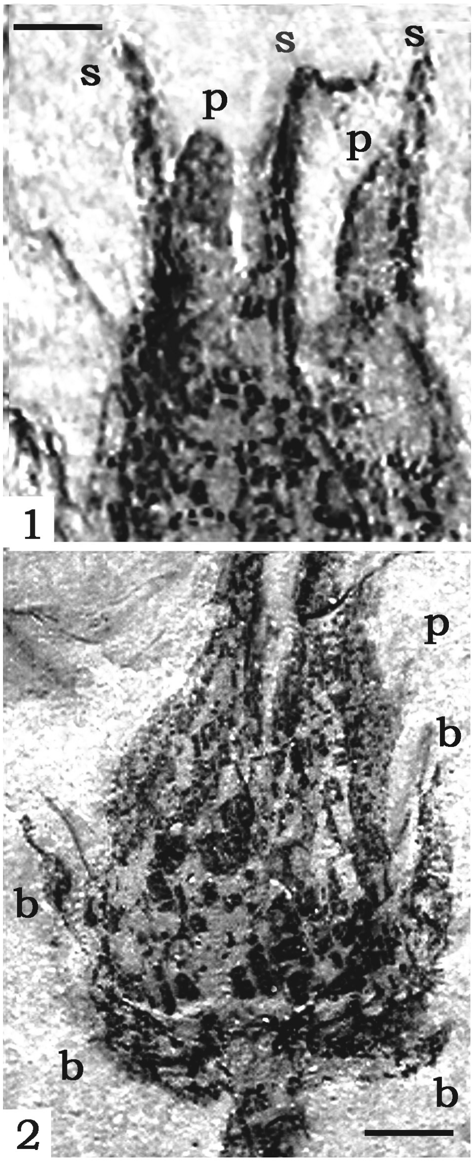

Fig. 5. *Shelomonasca caudata* gen. et sp. nov.: **1** – details of hypanthial cupule with caudate sepals (**s**) and thin lingulate petals (**p**), paratype IG1-359, **2** – details of 4-lobed bracteole (symbol **b** at each lobe), holotype IG1-360. Scale bar 0.5 mm

The cupuliform upper hypanthium is better preserved in the figured paratype (Pl. 2, fig. 9; Fig. 5) in which the lobes are slightly spreading, with the caudices outcurved, apparently stiff, although the middle one is brocken at the end. The structure is described as actinomorphous, because all the lobes are equally developed. The petals emerge in between the caudices, are much shorter than these, obtusely lingulate, flat, membranous, finely longitudinally striate. They appear thin and brittle. This specimen retained basal hairs, but the bracteolate cup is missing. In other specimens the bracteolate cup is variably preserved and the petals are missing or only occasionally present, which suggests that both the bracteoles and petals were deciduous.

Comparison. Although obviously belonging to the same group as *Eibinevoia* and *Lorchiella*, this flower morphotype differs in having the well-developed bracteolate cup, as well as the caudate hypanthial lobes. In *Eibinevoia*, the bracteole is adnate to the hypanthium, the calyx lobes are laminar and hairy. In *Lorchiella* there is no evidence of bracteoles, the calyx lobes are reduced to slender bristles, whereas the corolla lobes are thick and hairy. Bracteolate cup is characteristic of *Rhizophora* in which it is often, but not always, bipartite (making specific distinctions: Ding Hou 1960). Also typical of the Rhizophoraceae (as compared with related myrtalean groups) are the thick persistent sepals and the shorter deciduous petals. On account of these features, *Shelomonasca* seems to have been closer to Rhizophraceae than Combretaceae.

Seraphocarpus Krassilov **gen. nov**.

Type species. *Seraphocarpus minutus* sp. nov.

Derivation of the name. From seraph (Heb.-Gr.) winged creature and carpus (Gr.-Lat.) fruit.

Diagnosis. Fruit small, ellipsoid, slightly flattened, shortly stalked, longitudinally ribbed, winged over the ribs, with a crown of convergent caudate appendages. Wings six, radially spreading, unequally developed, narrow crescent-shaped, membranous, finely transversely striate.

Age and geography. Mid-Cretaceous (Turonian) of southern Negev, Israel.

Seraphocarpus minutus Krassilov **sp. nov.**

Pl. 2, figs 11, 12

Holotype. Fruit, IG1-113 (Pl. 2, fig. 11).

Type locality. Gerofit, Arava Valley south of the Dead Sea, Israel.

Type horizon. Ora Formation, Cretaceous, Middle Turonian.

Derivation of the name. Minutus (Lat.) minute.

Diagnosis. As for the genus.

Material. Four complete fruits and several fragments from the type locality

Description. The holotype (Pl. 2, fig. 11) is an elliptical fruit, 9 × 4.5 mm, with a short curved stalk, crowned with six convergent and tightly adpressed, yet distinct caudate appendages about 2 mm long. The fruit surface is traversed by thick regularly disposed longitudinal ribs. Four ribs are seen on the impression and the symmetry requires two more on the other side. Two wings in front view are symmetrically developed, crescent-shaped, 1 mm wide, finely transversely striate. Two ribs in the front view show shorter wings, less than one half of the body length. The figured paratype IG1-295 (Pl. 2, fig. 12) is of the same shape and dimensions. It shows one wing in the median plane and another, somewhat narrower, obliquely spreading. This specimen adds to the species characters the faintly areolate surface pattern probably reflecting a spongy tissue.

Comparison. This fruit type is fairly distinct due to the symmetrically arranged winged ribs and the distal appendages that might have remained from caudate calyx lobes (as in *Shelomonasca caudata*, above) converging in fruit. These features are typical of the Combretaceae in which the fruits are variously flattened, often winged in the median plane, as in *Conocarpus* or *Laguncularia*, or additionally over the side ribs, as in *Combretum grandifolium* G. Don. (Exell 1931). Fruits with radially spreading membranous wings are common in the Rhamnaceae (*Gouania*) and Sapindaceae (*Koelreuteria*), but the wings are broader and their surface pattern is different. In the Combretaceae, winged fruits occur in species of open landscapes and are dispersed by wind or water, having a spongy tissue in the latter case.

DISCUSSION

The Turonian plant assemblage of Gerofit, southern Negev, contains floral morphotypes not known from the Cretaceous of Laurasian realm, although probably related to some geologically younger fossils from northern continents (Berry 1913, 1934, Friis et al. 1992, Takahashi et al. 1999). Four types of hypanthial flowers are recognized, all with the fully inferior ovary and with the floral tube extending well above it. The bracteoles are variously developed, forming a bipartite cup in *Shelemonazia*. The upper cupuliform hypanthium is persistent in fruit. It is formed of the calyx or corolla or both (*Eibinevoia*). In the former case, the corolla is lacking (*Zeevlewya*) or reduced, with thin deciduous petals (*Shelomonasca*). Otherwise, the sepals are wanting or reduced to bristles, whereas the corolla is relatively massive, with the petals interlocked in bud by their interlacing marginal hairs (*Lorchiella*). The stamens, when present, are well, but unequally exserted. In *Minevronia*, the flowers of the same basic type are clustered in capitate inflorescences, dichasial and bracteate in bud. The dispersed fruits *Seraphocarpus* are ribbed with narrow wings and a crown of hypanthial appendages. Major distinctions between four types of superficially similar flowers are summarized in Table 1.

The closest affinities of these floral structures are with the myrtalean families Combretaceae and Rhizophoraceae (in recent systems, the latter is commonly considered as representing a monotypic order Rhizophorales placed next to the Myrtales, Cronquist 1981). Not only the general morphology of epigynous flowers, but also such structural details as the bipartite bracteolate cup (*Shelomonasca*), unequally developed hypanthial lobes (*Zeevlewya*) or interlocked petals (*Lorchiella*) find their equivalents in the extant combretaceous or rhizophoraceous genera. These findings suggest that both families evolved from a common stock. However, the Cretaceous floral structures combined characters of different myrtalean families perhaps not yet separable into distinct classification units at that time.

Several shared features (the conflorescences of capitate heads, tetramerous flowers, hypanthia) suggest an affinity with the Cretaceous platanoids. Remarkably, the endocingulate pollen grains, characteristic of the Rhizophoraceae, first appeared in some platanoids (Krassilov & Shilin 1995, Krassilov 1997).

Comparing fossil evidence with evolutionary trends postulated for the myrtalean families on purely morphological grounds (Exell 1962, Exell & Stace 1966, Briggs & Johnson 1979), we find that (1) the capitate inflorescences have appeared early in evolution of the group rather than representing an advanced condition; (2) the upper hypanthium was better developed and was more often persistent in the Cretaceous forms than in the extant allies; (3) the stamens were few rather than numerous; (4) the fully inferior, rather than semi-inferior ovaries were the ancestral condition and (5) the nectariferous disks might have appeared later in the history as a feature of new pollination syndrome.

Although fully deserving generic status according to classification criteria applied to the extant angiosperms, all the floral morphotype described above are basically similar, representing variation of the same theme. Their diversity is rather high for a fossil plant assemblage with a limited number of leaf morphotypes. This situation suggests a recent

Table 1. Comparison of four flower morphotypes from Gerofit.

Genus	Androecium	Bracteoles	Sepals	Petals
Zeevlewya	stamens long inserted, filaments persistent in fruit	wanting	free lobes glabrous, one much longer than the rest, deciduous at fruit	free lobes wanting
Eibinevoia	wanting	linear asymmetrical	free lobes longer than corolla, spathulate, hairy	free lobes thick glabrous
Lorchiella	wanting	wanting	free lobes long setose	free lobes hairy, interlocked at bud
Schelomonasca	wanting	cupular, 4-lobed	free lobes long caudate	free lobes short membranous

diversification of floral morphology ahead of the respective vegetative morphology.

It seems, therefore, justified to postulate a basic diversification of the proto-myrtalean stalk in the northern Gondwana realm, perhaps in relation to the initial development of angiosperm mangrove communities (Krassilov et al. 2003). In Laurasia, fossil plants taxonomically related to extant mangrove genera, in particular the distinctive fruits of *Nypa*, the mangrove palm, are known since the Early Eocene, about 55 Ma (Dolianiti 1955, Chandler 1957, Collinson 2000) and the reliable palynological records are of nearly the same age (Graham 1955, 1977, Muller 1961, 1970, Jaramillo 1998), although occasional finds of pollen grains go back to the terminal Cretaceous (Muller 1970). The Cretaceous origins of mangroves have been previously deduced from the present day geographic distribution (Duke 1995). Mangrove origins on the Gondwanic shores of the Tethys also has been postulated on phytogeographic grounds (Mepham 1983, Lacerda et al. 2002). Through the mid-Cretaceous, the early angiosperm evolution might have proceeded more or less independently in the southern and northern realms, the floristic exchanges between them becoming more active toward the end of the period and through the early Palaeogene.

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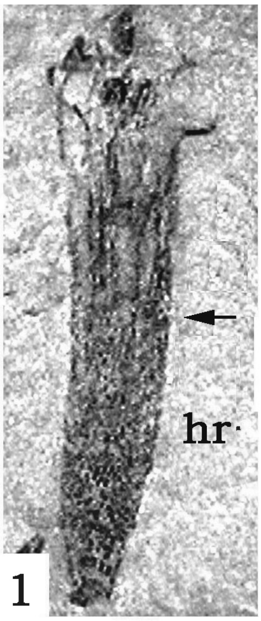
PLATES

Plate 1

Zeevlewya gracilis gen. et sp. nov.

Scale bar to all figures 0.8 mm. Abbrevetions: **a** – anther, **c** – cupuliform upper hypanthium, **f** – filament, **fr** – fruit, **h** – hypocotyls, **hr** – hairy part of hypantium, **l** – long perianth lobe, **lr** – lateral roots

1. Flower with stamens exserted over the floral tube, arrow at the boundary of the pitted lower hypanthium and the base line of decurrent filaments, holotype IG1-322
2. Flower with strongly elongated lower hypanthium, few stamens persist, the longer one bearing a dehiscent anther; arrow at the boundary of the lower and upper cupuliform parts of hypanthium, paratype IG1-239a
3. Flower with the lower hypanthium swollen over the developing fruit and the stamen filaments converging over the tube, paratype IG1-318
4. Flower with hook-like stamen filaments, paratype IG1-171a
5. Spindle-shaped fruit with upper hypanthium intact, paratype IG1-374a
6. Germinate fruit with hypocotyls emerging through the persistent upper hypanthium with a few hooked filaments, paratype IG1-208a
7. Longitudinally ridged fruit with residual stamen filaments, paratype IG1-212a
8. Two germinate fruits entangled by their hooked appendages, both with emerging hypocotyls, paratype IG1-4
9. Detached hypocotyl with lateral roots, paratype IG1-366
10. Floral bud showing anthers at the base of lobes and variously exserted, paratype IG1-292
11. Floral bud at an earlier stage with anthers at the base of hypanthial lobes, paratype IG1-375a
12. Small bud and an opening flower with diverging hypanthial lobes of unequal length, paratype IG1-319
13. Young flower with diverging hypanthial lobes, note a longer lobe on the left side, paratype IG1-239b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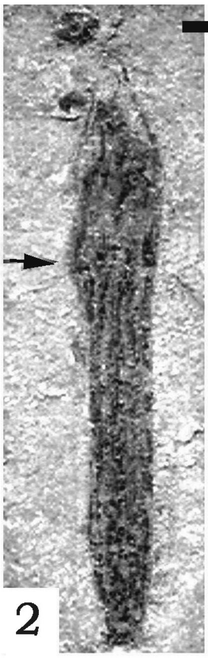
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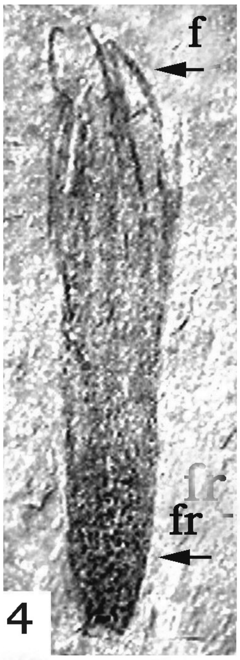
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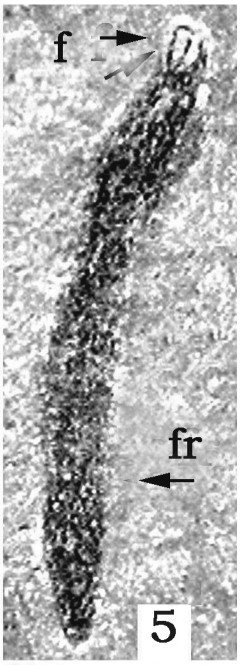
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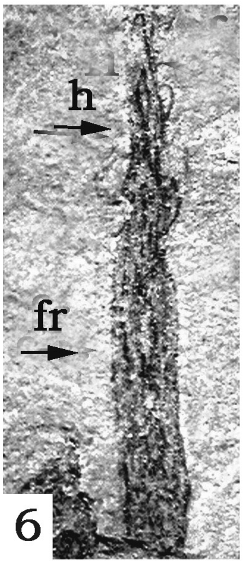
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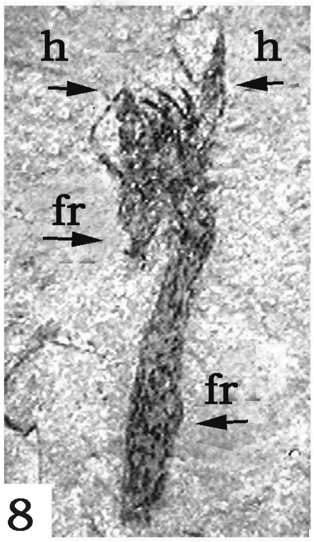
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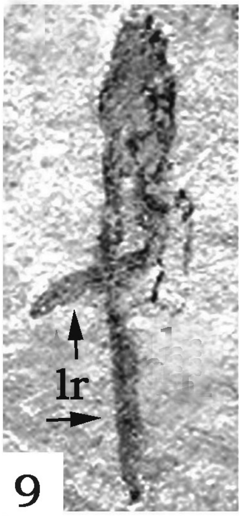
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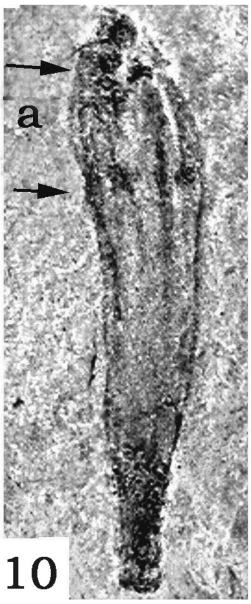
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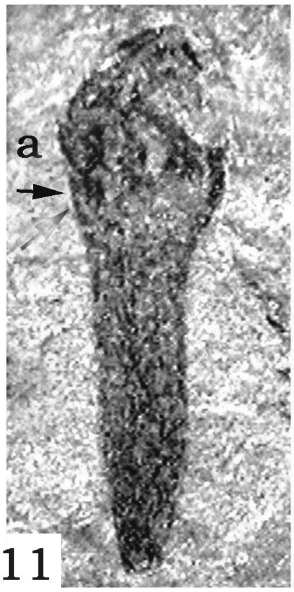
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Plate 2

Scale bar 0. 6 mm (fig. 1), 0.8 mm (figs 2–8), 1.1 mm (figs 9–11). Abbrevations: **b** – bracteole, **p** – petal, **s** – sepal or sepaloid bristle

Eibinevoia chlamydea gen. et sp. nov.

1, 2. Flower in fruit and the upper hypanthium magnified, showing bract (**b**), hairy calyx lobes (**s**) and glabrous petal lobes (**p**), holotype IG1-364a

Lorchiella setosa gen. et sp. nov.

3. Flower with sepaloid bristles (**s**) and narrowly diverging petaloid hypanthial lobes (**p**), holotype IG1-257
4. Bud with petals and bristles interlocked into a solid conical structure, paratype IG1-320
5. Bud with bristles separating from the upper hypanthium, paratype IG1-323
6. Opening bud revealing petals and a sepaloid bristle still interlocked through the apical hairs, paratype IG1-317
7. Lacerate hypanthium, paratype IG1-387

Bruguiera cylindrica (L.) Bl.

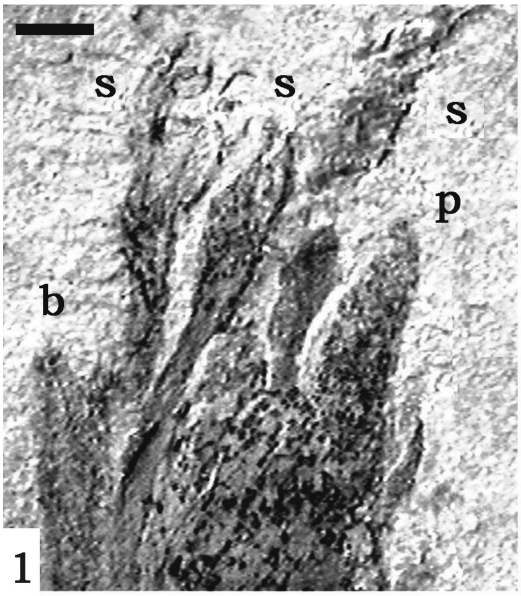
8. Hairy petals (interlocked by hairs in bud) of extant species (the Maldives)

Shelomonasca caudata gen. et sp. nov.

9. Upper hypanthium with caudate calyx lobes (**s**) and two petals (**p**) preserved, paratype IG1-359
10. Flower with a well-developed bracteolate cup (**b**) at base, caudate calyx lobes (**s**) and one petal (**p**) preserved, holotype IG1-360

Seraphocarpus minutus gen. et sp. nov.

11. Fruit with narrow wings over the longitudinal ribs and with a crown of caudate appendages, holotype IG1-113
12. Fruit showing an areolate pattern (spongy tissue) between the ribs, paratype IG1-295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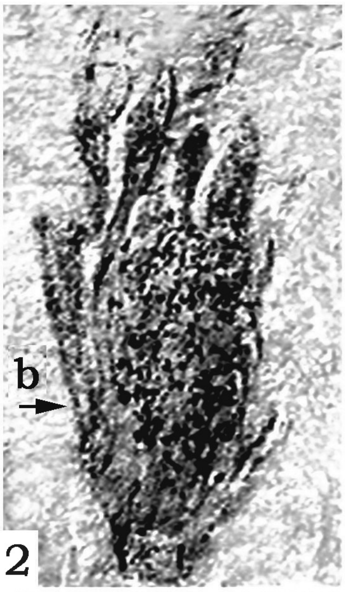
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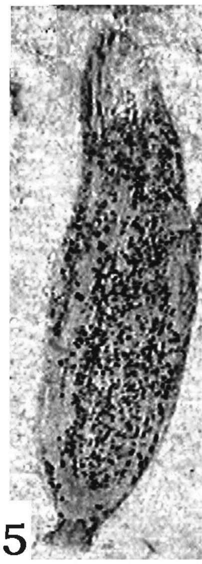
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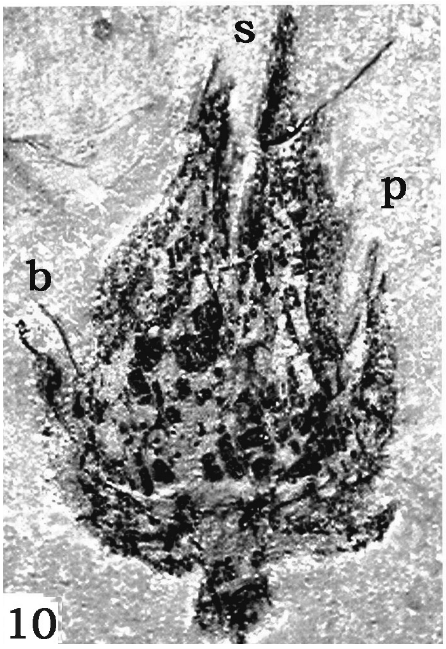
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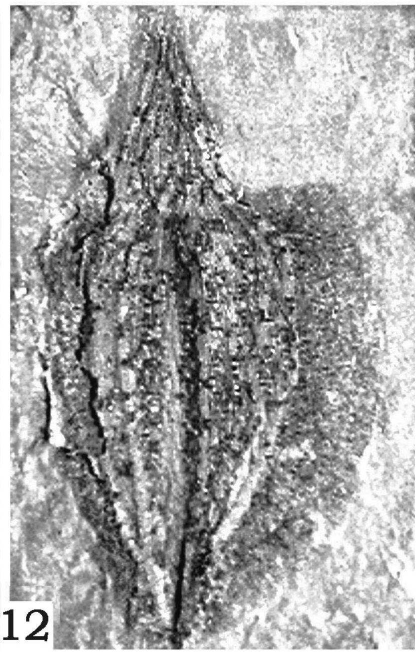
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