

A New Order of Heterosporous Plants from the Late Cretaceous of the Kem' River, Western Siberia

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Abstract—Remains of a heterosporous plant from the Late Cretaceous of the Tchulymo-Yenisey Basin, Western Siberia, are peculiar in having solitary sporangia on the laminar sporophyll pinnules. The sporangia produce a large number of megaspores in the symmetrically developed tetrads. Microspores are enveloped in the laesural outgrowths of the megaspores. These characters substantiate a new order of pteridophytes representing a special direction in the evolution of heterosporous plants.

INTRODUCTION

The remains of a heterosporous plant recently found in the collection of Late Cretaceous flora from the Kem' River Basin are of outstanding interest owing to their unique preservation and the peculiarity of the spore-bearing structures that allows us to consider these plants as representing a new pteridophytic order.

Heterosporous pteridophytes first appeared in the mid-Devonian. They flourished in the Carboniferous after which their diversity gradually declined in favour of woody lycopsids and their derivative pleuromeids, which in turn suffered extinctions through the Permian and Triassic. Only four genera of heterosporous lycopsids survived in the Late Mesozoic, three of them are aquatic or semiaquatic forms (Krassilov, 1982; Krassilov and Makulbekov, 1996). In the Cretaceous they were joined by aquatic heterosporous ferns. Their macrofossils appear in the Albian. Even the earliest forms are comparable with Recent genera. New findings reported below not only show an increase in the range of taxonomic diversity of heterosporous plants, but also evidence of peculiar extinct forms, with no close analogues in the modern flora but with probable mid-Paleozoic phylogenetic roots.

MATERIAL

The remains of a new heterosporous plant are housed in the paleobotanical collection of the Botanical Institute, Russian Academy of Sciences, St. Petersburg (BIN, no. 1198) obtained in 1995 from the deposits of Kemsкая Formation in the Tchulymo-Yeniseysk Basin, Western Siberia. The locality occurs on the right bank of the Kem' River 15 km downstream of the village of Podgornaya. The Kemsкая Formation here consists of the soft white to light gray caolinitic sands and clays that are overlain by the Tertiary deposits of the Varakovskaya Formation consisting of ferruginous

sandstones and conglomerates. The Kemsкая Formation is tentatively dated as the Cenomanian (Nagorskiy, 1939; Lebedev, 1958).

SYSTEMATIC PALEONTOLOGY

Order Heroleandales Krassilov et Golovneva, ordo nov.

Etymology. From the family Heroleandraceae.

Diagnosis. Plants free-sporing heterosporous. Sporangia epilaminar on sporophyll segments. Megaspores numerous, several hundreds per sporangium. Four megaspores of tetrad equally developed. Microspores occurring in megasporangia, contained in the laesural appendages of megaspores.

Composition. A monotypic order.

Remarks. This order differs from the heterosporous archaeopterids, barinophytes and lycopsids in the sporophyll morphology with pinnate venation of spore-bearing pinnules. It differs from the heterosporous ferns in solitary sporangia, great number of megaspores per sporangium and their equal development in the tetrads (in all the known representatives of the Salviniales and Marsileales the megasporangia contain only one functional megaspore), as well as by amphisporous sporangia that produce morphologically different mega- and microspores. The latter feature occurs in the Barinophytales, an order of leafless Devonian plants that differ from the new order in the morphology of laminate sporophylls, as well as in much fewer megaspores per sporangium.

Thus, the new group is morphologically sufficiently distinct to establish a taxon of the same rank as the order Barinophytales with amphisporous sporangia and the orders Salviniales and Marsiliales of heterosporous ferns.

Explanation of Plate 12

Figs. 1–6. *Heroleandra profusa* Krassilov et Golovneva, gen. et sp. nov., holotype BIN, no. 1198-8-1, megaspore and microspore morphology. SEM: (1) megaspore tetrad, $\times 400$; (2) megaspore, lateral view, $\times 700$; (3) microspore, proximal aspect, $\times 3200$; (4, 5) microspore clumps in laesural pockets of a megaspore, $\times 1100$ and 1800 ; (6) two microspores in the mouth of a laesural pocket, $\times 1800$.

Family Heroleandraceae Krassilov and Golovneva, fam. nov.

Etymology. From the type genus.

Type genus. *Heroleandra*, gen. nov.; Late Cretaceous of Tchulymo-Yeniseysk Basin, Western Siberia.

Diagnosis. As for the order.

Composition. Monotypic family.

Genus *Heroleandra* Krassilov et Golovneva, gen. nov.

Etymology. After the mythological lovers Hero and Leander drowned in the waters of the Hellespont.

Type species. *Heroleandra profusa* Krassilov et Golovneva, sp. nov.; the Kem' River, Tchulymo-Yeniseysk Basin, Western Siberia; the Kems kaya Formation, Upper Cretaceous.

Diagnosis. Sporophyll pinnate with pair or few pairs of lateral pinnules. Sporangia solitary, adaxial on sporophyll pinnules, producing large number of trilete megaspores, all unreduced in tetrad, with laesural appendages bearing monolet microspores.

Composition. Monotypic.

Heroleandra profusa Krassilov et Golovneva, sp. nov.

Plate 12, figs. 1–6

Etymology. From Latin *profusa* (pouring).

Holotype. Botanical Institute (BIN), no. 1198-8-1; Kem' River, Tchulymo-Yeniseysk Basin, Western Siberia; Upper Cretaceous, Kems kaya Formation (Pl. 12, figs. 1–6; Fig. 1d).

Diagnosis. As for the genus.

Description (Figs. 1–3). The collection contains several spore-bearing structures in the form of fragmentary axes with alternate or subopposite abbreviated petiolate pinnules. The largest fragment of the axis is 20 mm long, 0.6 to 0.8 mm thick, straight, longitudinally grooved, striate, slightly expanded at attachment of the pinnules. The pinnules are elliptical, 8–15 mm long, 6–9 mm wide (average dimensions 11×7 mm), attached by a short decurrent petiole up to 2 mm long. They arise at 45 degrees to the axis. As suggested by the impressions, the lamina of the pinnules was thick, coriaceous, flat or folded along the midrib, with a raised marginal flange, symmetrically narrowed to the base and with a rounded apex. The venation is pinnate, with the midrib extending to the apex of the blade and giving off up to 7 pairs of lateral veins. The lateral veins are opposite, seldom alternate, arising at an acute angle and reaching the inner boundary of the marginal flange and terminating in a small tubercle, supposedly glandu-

lar. These veins are relatively thick and prominent in the central part of the blade, but rather indistinct in both the basal and apical parts of it. Occasional lateral veins fork near the base. The impressions, reflecting a fine structure of the leaf surface, show an irregular network of higher order veins that arise from the laterals as well from the midrib between them (Fig. 1e). In one case the blade is longitudinally wrinkled perhaps owing to desiccation of the leaves.

The leaf blade is preserved as a yellowish brown ferrugineous incrustation with impressions of megaspores that under low magnification appear as minute pits. Spore clumps are permanently preserved on the pinnules. In the better preserved sporophylls the entire blade, except the raised marginal flange, is covered with a continuous spore mass filling a solitary sporangium (Fig. 1d).

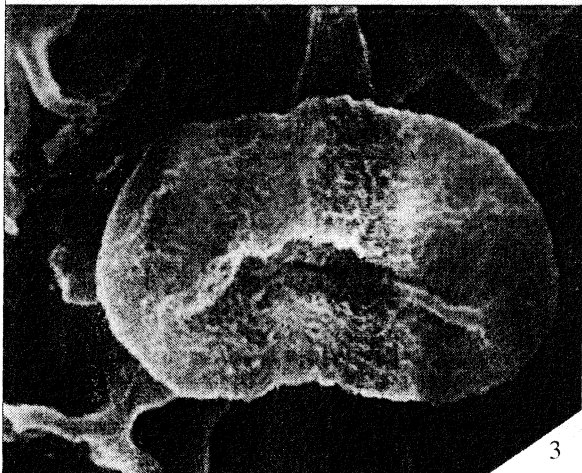
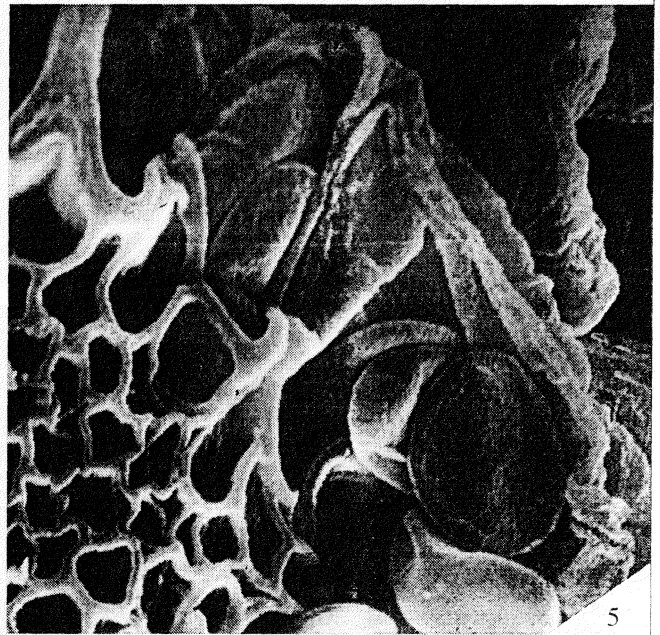
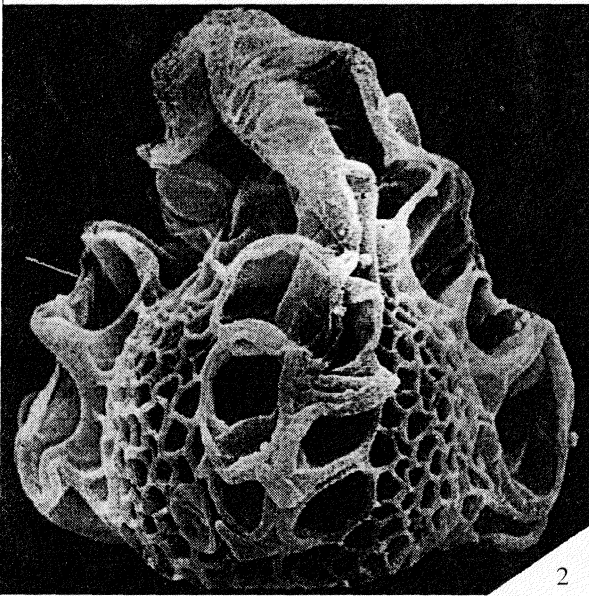
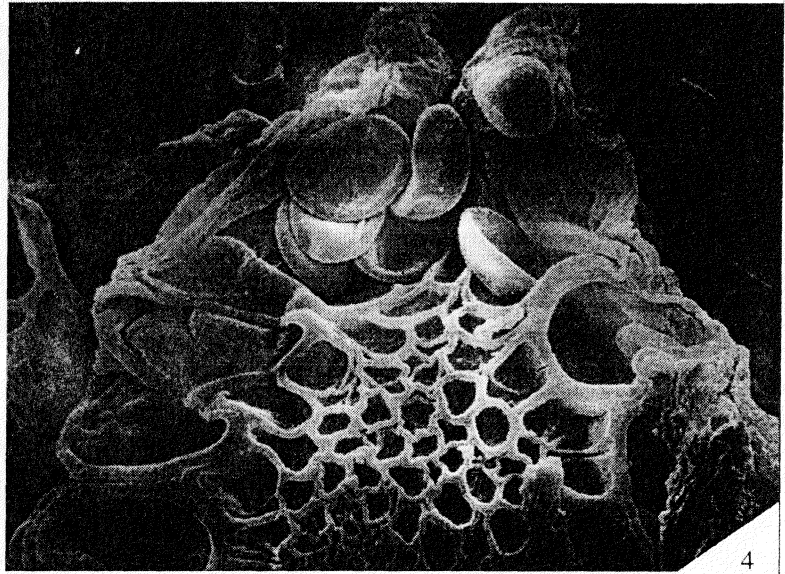
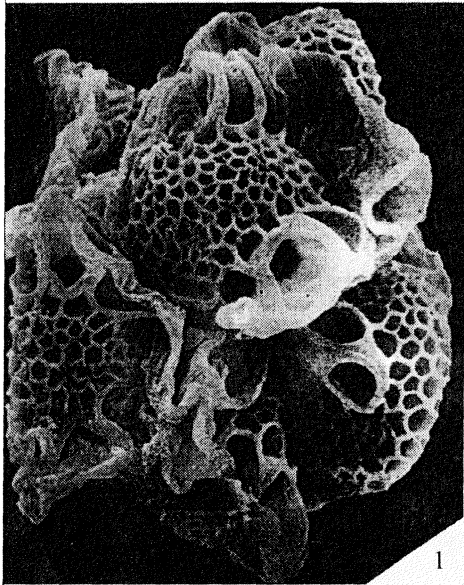
In SEM the sporangia show abundant (several hundred) megaspores. The megaspores are produced in tetrahedral tetrads many of which are preserved intact. However, a great number of tetrads are broken apart or partly so. Most of the dispersed megaspores are solitary, with the tetrad configuration occasionally preserved. In the sporangia we found no evidence of sterile partitions, although the tetrads tend to be arranged in rows parallel to the lateral veins, with occasional slit-like spaces between the rows.

The megaspores are tetrahedral, spherical-prolate, proximally swollen, broadly rounded distally or concave, with slightly convex contact facets (Pl. 12, fig. 2; Figs. 2a–2c). The equatorial aspect is rounded-triangular, with Y-shaped laesurae mark projecting at angles. The lateral aspect is triangular, with a prominent apical extension. The Y-mark laesurae extend to $3/4$ of the spore radius, with large membranous involute lamellae. The apical acrolamellae are nearly of the same length as the polar axis of the spore body, forming a massive conical neck, thickened at the summit, and in the ripe megaspores split into three lobes. Over the laesurae the membranous lamellae are shorter, about $1/4$ to $1/3$ of the equatorial diameter, forming double rows of "pockets"—short tubular appendages with an irregular rounded-polygonal opening. There are three to four such pockets per row.

Dimensions of the megaspores: polar axis without acrolamellae about $70 \mu\text{m}$, equatorial diameter $75\text{--}80 \mu\text{m}$, apical cone $40\text{--}65 \mu\text{m}$ high, laesural pockets $25\text{--}30 \mu\text{m}$ high, their openings $20\text{--}35 \mu\text{m}$ wide.

The megaspore body is reticulate over the distal face and the contact facets. The reticulum is prominent, with irregular-polygonal lumina $5\text{--}6 \mu\text{m}$ wide in the central part of the contact face, increasing toward the laesurae.

Plate 12



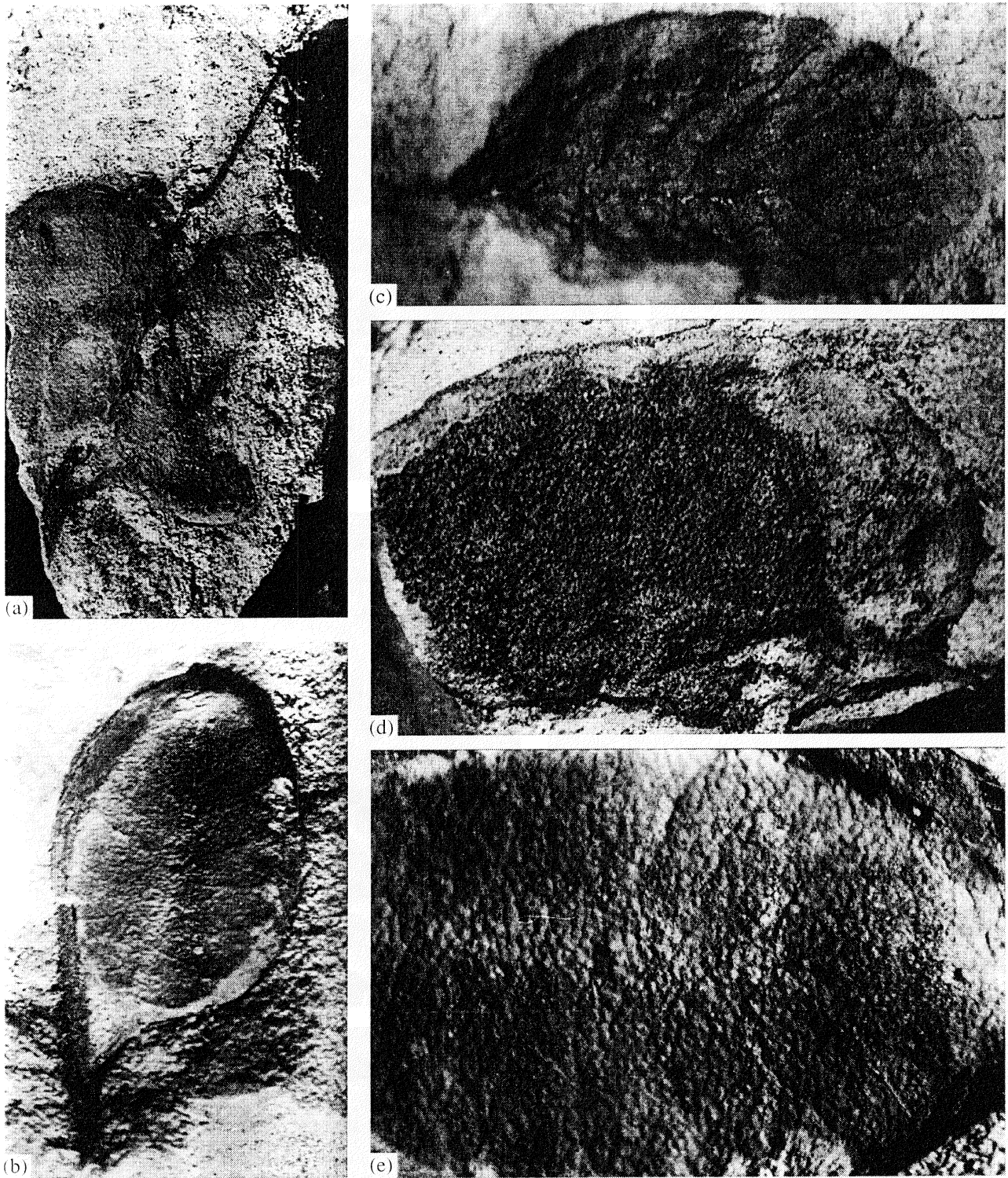


Fig. 1. *Heroleandra profusa* Krassilov et Golovneva, gen. et sp. nov.: (a) holotype BIN no. 1198-8-2, sporophyll with a pair of opposite pinnules, $\times 4.5$; (b) specimen BIN no. 1198-8-3, short petiolate sporophyll pinnule attached to the axis, $\times 9$; (c) specimen BIN no. 1198-8-4, sporophyll pinnule with a broad marginal flange and with folds along the lateral veins, $\times 12$; (d) holotype, specimen BIN no. 1198-8-1, sporangium on the upper side of the pinnule, $\times 20$; (e) specimen BIN no. 1198-8-3, blow-up of sporophyll pinnule venation showing the higher order network, $\times 15$.

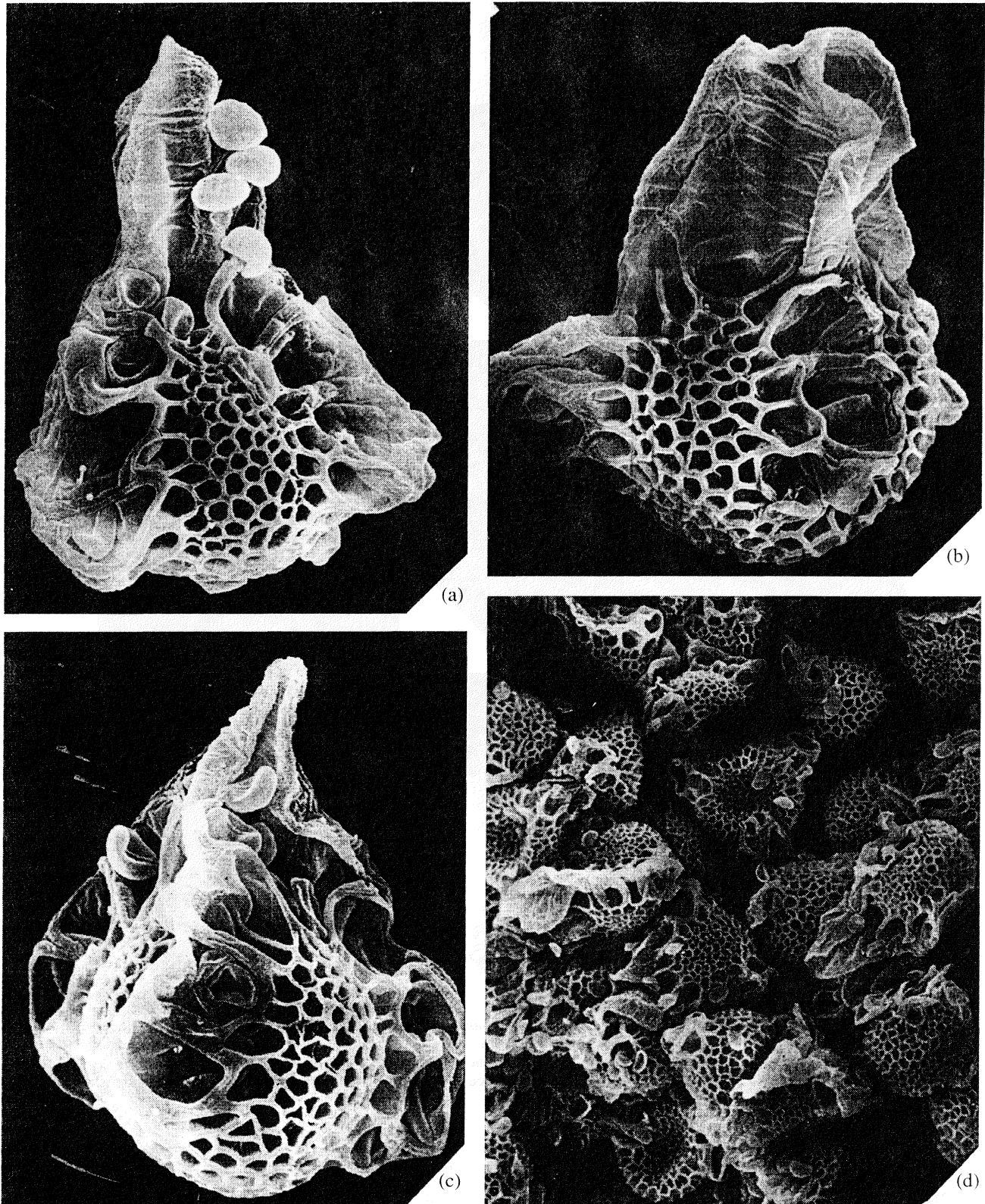


Fig. 2. *Heroleandra profusa* Krassilov et Golovneva, gen. et sp. nov., holotype BIN no. 1198-8-1: (a–c) variability of laesural appendages, some of them containing microspores, SEM, $\times 700$; (d) megaspores inside the sporangium, SEM, $\times 150$.

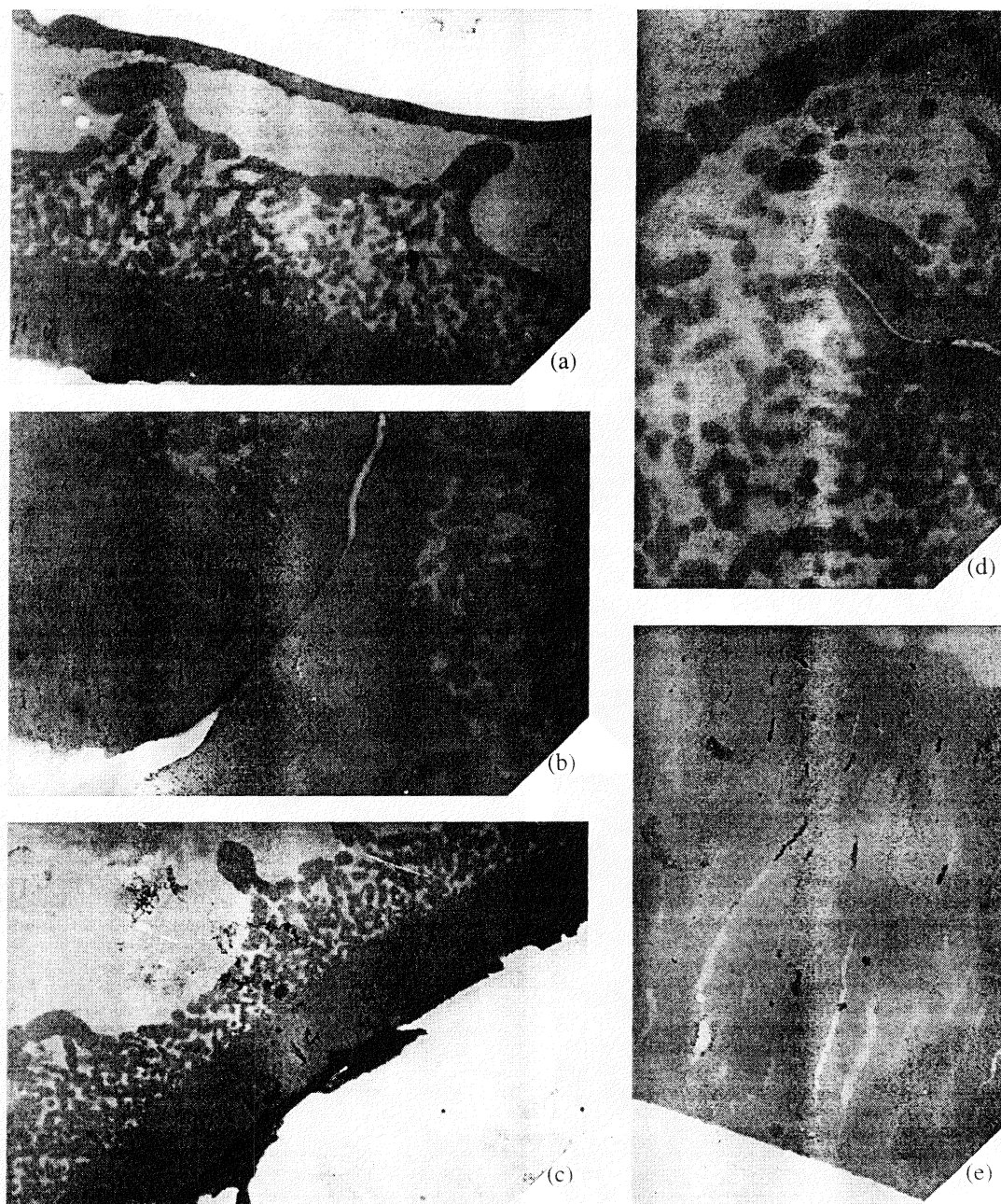


Fig. 3. *Heroleandra profusa* Krassilov et Golovneva, gen. et sp. nov.: (a, c) holotype BIN no. 1198-8-1, ultrathin sections of the megaspore sporoderm: (a, c) sections showing three major layers—the outer homogeneous, the middle spongy and the inner fibrous, TEM, $\times 8000$ and 6000 ; (b, e) fibrous layer showing a thin homogeneous basal zone and a zone of less distinct fibers in the upper part, TEM, $\times 15000$ and 40000 ; (d) outer homogeneous layer pierced by narrow pore canals and the spongy layer beneath, TEM, $\times 15000$.

The peripheral lumina bordering on the membranous acrolamellae are conspicuously stretched. The muri of the reticulum are smooth, with small teeth at the angles. The membranes of the apical acrolamellae and laesural pockets are loosely folded, wrinkled, and pierced with minute pores. In the tetrads, the acrolamellae are folded over the margins of the adjacent megaspore. Ultrathin sections show three sporoderm layers (Fig. 3).

The microspores occur in the apical cone and laesural pockets (Pl. 12, figs. 4–5). They often protrude from the openings of the laesural pockets (Pl. 12, fig. 6) or stick to the lobes of the apical cone. Tetrad configuration is occasionally preserved in the arrangement of microspores. The better preserved microspores are ellipsoid or bean-shaped, proximally slightly concave, with smoothly rounded ends, monolete, with the

median laesura not reaching to equator (Pl. 12, fig. 3). In compressed microspores the exine is folded and sometimes split into halves. The dimensions of microspores are about $15\text{--}21 \times 13\text{--}16 \mu\text{m}$. The laesura is slightly or occasionally strongly curved, shortly split at one or both ends or else overlapped by exinal folds, sometimes widely open. The microspore surface is rugulate, microreticulate with irregular meshes. The exinal folds sometimes resemble a trilete mark. However, not a single specimen with obvious trilete mark was found among several hundred studied microspores.

The spore-bearing structures are associated in the fossil plant bed with sterile pinnules showing an anastomosing dichotomous venation, probably belonging to the same plant.

Remarks. In the shape and venation of the pinnules the sporophylls are comparable with the floating leaves of modern aquatic ferns, as well as with that of the extinct Cretaceous genus *Weichselia*. However, in these latter fern groups the spore-bearing structures are sori that in aquatic ferns develop on submerged leaf lobes or inside sporocarps on the leaf petioles. In the Marsileaceae the sporocarps might derive from leaf lobes. In their shape and arrangement they resemble the sporophyll pinnules of *Heroleandra*. The latter, however, are not transformed into closed structures. They bear a solitary sporangium rather than rows of mega- and microsporangia as in the Marsileaceae. In the Salviniaceae the amphisporangiate sori are relatively rare. More often there are several (in the case of extreme reduction a single pair only) micro- and macrosori with numerous sporangia on long stalks. In this group the mega- and microspores never occur in one and the same sporangium.

Gulate megaspores have hitherto been known primarily in Paleozoic lepidophytes, the megasporangia of which typically contain a single tetrad with a single functional and three aborted megaspores. Very large lepidophytic megaspores with a beak-shaped apical extension, or gula, are assigned to the spore genus *Lagenicula*. This genus includes both glabrous and sculptured morphotypes. In them the apical beaks might serve for anchoring rather than for capturing microspores (Zerndt, 1934).

A closer similarity exists between the megaspores of *Heroleandra* and dispersed megaspores of unknown affinities, such as *Arcellites* Miner first described from the Cretaceous deposits of Greenland (Miner, 1935). Hughes (1955) compared them with Paleozoic *Lagenicula*, as well as the enigmatic Devonian *Kryshfovichia* described by Nikitin (1934). The Cretaceous megaspores are peculiar in having an apical appendage of 3–6 lobes that formed a closed conical structure with a cavity inside. In ripe dispersed megaspores the lobes might diverge. Hughes suggested that the apical structures in *Arcellites* were formed by the outer sporoderm layer above the Y-shaped mark that protruded in the inner cavity and was distinguishable in sections only.

He asserted a similarity of these apical structures with apical "androcameras" of *Kryshfovichia* containing microspores, but refrained from discussing their possible functions, as well as the phylogenetic relationships between the respective plant groups. He simply noted the possibility of their lycopsid affinities. Microspores are not mentioned in this work.

In the 1960s the dispersed megaspores of the same type were found in 33 Early Cretaceous localities in Europe, North America and Australia (Ellis and Tschudy, 1964). All the finds came from freshwater or brackish facies. As for their morphology, Ellis and Tschudy (1964) confirm the location of a Y-shaped mark under the apical appendages as described by Hughes (1954), as well as the derivation of acrolamelae from the outer sporoderm layer. The inner layer is continuous under the gula. In discussing the taxonomic assignment of *Arcellites* these authors support an aquatic fern affinity close to the Marsileales. They observed the microspores *Perrotrilites* lodged between the apical lobes and suggested that in the floating megaspores the apical neck might turn down and open to capture microspores.

Li and Batten (1986) described four groups of *Arcellites*—non-sculptured, rugulate, a group with solitary sculptural elements and a reticulate group with raised angles of the network. The two latter groups comprise most of the known species. Notably, the microspores of the *Crybelosporites* morphotype constantly associate with, and are sometimes attached to, the megaspores from the Cretaceous of China. Their belonging to one and the same plant taxon is confirmed by their sporoderm ultrastructure.

Though species of *Arcellites* differ from megaspores of *Heroleandra* in the short laesurae overlapped by the apical cone, it can be surmised that at least some of them were produced in amphisporous sporangia. The latter might then exist not in a single genus only, but in a diverse group of Cretaceous pteridophytes.

Batten *et al.* (1996) suggested that *Arcellites*-type megaspores were produced by some extinct marsileacean ferns. A similar conclusion was reached by Chitale and Paradkar (1973) in relation to the Paleocene genus *Rhodeites* producing the *Arcellites*-type megaspores.

In the related megaspore genus *Balmeisporites* from the Early Cretaceous of the southern continents and Siberia (Baldoni and Batten, 1991; Dettmann, 1995) the laesural lamellae are deeply invaginate and resemble the laesural pockets of *Heroleandra*. However, in *Balmeisporites* these structures do not contain microspores.

In *Rhodeites* from the Lower Paleocene intertrappean deposits of India the pinnule-like sporocarps contain amphisporangiate sori with a few megasporangia. The latter are preserved as membranous structures enveloping a single functional megaspore. The microsporangia are much more numerous, preserved as compact

microspore masses when their walls are resorbed (Chitale and Paradkar, 1972, 1973). Both mega- and microspores are trilete, the megaspores having the apical laesural appendages as in *Arcellites*. This aquatic Cretaceous fern was previously compared with the extant Brazilian genus *Regnellidium*. However, the distinctions from this and other extant genera are sufficient for separation at generic and even familial level. At the same time, in the morphology of spore-bearing structures *Rhodeites* is closer to the Marsileales than the Cretaceous *Heroleandra*. In the relative development of megaspores and microspores the Indian genus conforms to the mainstream evolutionary trend in heterosporous plants.

Material. The holotype and cotypes BIN, no. 1198-8-2–1198-8-5. Slides 1198a–1198c from the same locality.

MORPHOLOGICAL INTERPRETATION

In *Heroleandra* the spore-bearing pinnules are peculiar in having large solitary sporangia that occupied most of the blade and were apparently covered on the flanks only by the raised margins of the pinnules. Most difficult for morphological interpretation is association of spores of two widely divergent size categories of which the much smaller microspores are found in the cavities of the laesural appendages. In modern plants the development of megaspores and microspores in one and the same sporangium normally does not occur. It rarely occurs also in the fossil record. In fact, amphisporeous sporangia are typical only of the Barinophytales, a small group of primitive heterosporous plants recorded from the Devonian and Lower Carboniferous. Their most completely known genus *Barinophyton* has large sporangia born in two rows on the lateral branches of fertile shoots. The sporangia contained a small number (about 30) of large glabrous megaspores up to 900 μm in diameter, immersed in the mass (several thousand) microspores. Both the mega- and microspores are trilete.

The barinophytes are considered as a separate order or even class (the Barinopsida) probably derived from the Devonian zosterophylls, and considered to be related to the lycopsids by Meyen (1987). However, Brauer (1980) described in the structurally preserved *Barinophyton* from the Devonian of North America the pitted gymnosperm-type tracheids as in progymnosperms. Among the latter the order Archaeopteridales includes both isosporous and heterosporous forms, occasionally with mega- and microspores in the same sporangium, as in the genus *Chaleuria* and a single species of *Archaeopteris* (Medyanik, 1982).

These data show that in the diverse group of Devonian progymnosperms sporogenesis has evolved in several ways: isospory persisted in some of them, while in the others differentiation of morphologically similar mega- and microsporangia took place or, in a fairly iso-

lated line, amphisporeous sporangia appeared for the first time.

Our material suggests amphispority as a mode existing in the Late Cretaceous heterosporous plants. Here the number of megaspores per sporangium was much greater than in the rest of the heterosporous pteridophytes, exceeding the barinophytes by several hundred times, let alone the aquatic ferns in which a single functional megaspore per sporangium is the norm, with three other megaspores either aborted or functioning as floats. In the case of *Heroleandra* such a developmental mode is unlikely to have taken place for there were intact tetrads with four equally developed megaspores. We suggest that in this plant no less than a half of the spore mother cells differentiated as megasporocytes, developing in megaspore tetrads, while the rest of the sporogenous cells, in which meiotic division was probably delayed, produced bilateral microspores.

We have to explain at the first glance improbable, but confirmed by our observations systematic occurrence of microspores in the laesural pockets of megaspores within the amphisporeous sporangia. Except in the Devonian *Kryshfovichia* with its peculiar "androcameras", such structures are virtually unknown in heterosporous pteridophytes. We propose for them a morphological designation "amphisporion". In *Heroleandra* the amphisporions consisted of a megaspore with laesural lamellae forming a hollow apical cone and lateral pockets. These laesural structures bore abundant microspores, the development of which cannot be traced. Hypothetically, in the amphisporion formation the earlier differentiated megaspores produced laesural membranes that penetrated the mass of microsporocytes, a further development of which took place in the cavities of the laesural appendages. Functionally the amphisporions provided for the association of female and male gametophytes in the widely dispersed aquatic plants.

Thus evolutionary trends in heterosporous plants might have been more diverse than previously expected. Alongside with a conventional for heterosporous pteridophytes (including the lycopsids and aquatic ferns), differentiation of mega- and microsporangia, and the reduction of megaspore numbers, there was a quite different trend—a differentiation of mega- and microsporocytes within the amphisporeous sporangia.

Taking into consideration an enormous chronological gap between the Devonian and Cretaceous representatives of amphisporeous structures one is led to suggest their independent origin. In the Devonian barinophytes amphispority was accompanied by a reduction of megaspore numbers compensated by their increase in size. They may have produced amphisporions, but the latter are not yet confirmed. In the Cretaceous line the megaspores were relatively small but neither the number of megaspore tetrads, nor the individual megaspores in tetrads became reduced. The megaspore development

has involved microspores as components of bisexual dispersion units, the amphispores.

With the possible assignment to a new order of the dispersed morphotypes *Arcellites* and *Balmeisporites*, the geological range of the latter would be extended from the Berriassian to the Senonian. The Heroleandres flourished at the onset of a widespread eutrophication of freshwater and brackish reservoirs (supposedly enhanced by the appearance of floating macrophytes). They were forerunners of the great adaptive radiation experienced by aquatic pteridophytes in the mid-Cretaceous. Their extinction at the end of the period correlates with the diversification of aquatic angiosperms. At the same time, the geographical ranges of *Arcellites* and related megaspore genera indicate the possible role of a climatic factor in the terminal Cretaceous decline of the group.

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