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Weedy Albian angiosperms

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ABSTRACT. Two new species of angiosperms from the Early – Middle Albian of Primorye, Far East, are described on the basis of rhizomatous stems with tubers and adventitious roots, irregularly pinnatisect leaves, intact solitary flowers and heads of achenes or follicles. These tiny angiosperms are compared with the extant Ranunculaceae and allied families (ranunculids) on the basis of their growth form and fruit morphology. They are preserved in the tuffaceous deposits of the rising Sikhote Alin Ranges forming a pioneer fern – angiosperm community colonizing ash fallouts. These findings contribute to the mid-Cretaceous diversity of ranunculids, supposedly one of the major stem groups of early angiosperms.

KEY WORDS: early angiosperms, ranunculids, plant morphology, plant paleoecology, angiosperm evolution

INTRODUCTION

Despite the rapid progress of angiosperm palaeobotany in the recent years, early angiosperms are still poorly known as whole plants. Whether they were woody or herbaceous or of initially diverse habits is a matter of opinion. Here we report on new finds from the Albian of Primorye, Far East, and discuss their bearing on the subject.

The Early Cretaceous flora of Primorye comes from the Berriasian – Valanginian marginal marine deposits, the Barremian – Aptian non-marine or partly paralic coal-bearing cyclothems, and the volcanomictic Albian sequences recording an initial phase of the Sikhote Alin orogenic event. Rich pre-Albian flora consists of ferns, cycadophytes and conifers, with several types of peat-building wetland communities reconstructed as fern swamps or marshes, bennettitalean swamps and conifer boglands associated with resinous coals (Krassilov 1967). Two macrofossils from the coal-bearing strata, the linear serrate leaves *Pandanophyllum ahnertii* Krysht. and the pitted fruit-like bodies *Onoana nicanica* Krassilov have been considered as probably angiospermous (Kryshtofovich 1929, Krassilov 1967), but no reliable evidence of angiosperms has ever been found in either macrofossil or palynological records (Krassilov 1967, Markevitch & Shuklina 2005).

A single trilobed leaf collected above the upper coal seam of Partisansk Coal Basin in the eastern South Primorye was described by Kryshtofovich (1929) as *Aralia lucifera* Krysht., the earliest indubitable angiosperm fossil in the Cretaceous of eastern Asia justifying, in Kryshtofovich's opinion, correlation with the Potomac Group of eastern North America. Exact stratigraphic occurrence of Kryshtofovich's find is unknown, but since the coal seams are overlain by the Albian marine *Trigonia* shales, *Aralia lucifera* must have came from this horizon. The assignment to an extant genus, prominent in the living vegetation of the area, was a tribute to a long-standing paleobotanical tradition

Krassilov re-described this material and found two new angiosperm localities in the tuffaceous deposits of Rasdolninsk Coal Basin in the western South Primorye and on the coast of Ussuriysk Bay east of Vladivostok (Krassilov 1965). Both these localities contained fragmented small-leaved angiosperms of more than one species accompanied by a fern, *Anemia* (*"Asplenium"*) *dicksoniana* (Heer) Krassilov and by occasional scale-leaved conifer remains.

About 40 years later, a new locality of Albian angiosperms has been found by Yelena Volynets near Krassilov's Ussuriysk Bay locality and at the same or slightly higher stratigraphic level in the tuffaceous sequence. The locality contains so far the most complete remains of herbaceous angiosperms providing evidence on their growth forms and habitats. It adds to the previous records of small-leaved early angiosperms of ranunculid affinities (Vakhrameev & Krassilov 1979, Krassilov et al. 1983, Krassilov 1997, Krassilov & Golovneva 2001, 2003) supporting the phylogenetic significance of Ranunculidae sensu Takhtajan, 1987 as an ancestral line of angiosperm evolution.

MATERIAL AND METHODS

In the South Primorye Region of the Russian Far East (Fig. 1), thick coal-bearing deposits of Barremian – Aptian age are overlain by the marine *Trigonia* beds, representing a short-time marine ingression and containing an early Albian invertebrate assemblage studied by Valentin Konovalov, a paleontologist of the regional Geological Survey, who unfortunately left only short excerpts of his comprehensive stratigraphic analysis (referred to in Krassilov 1967). *Trigonia* beds and their coeval non-marine black shales to the west are conformably overlain by volcanoclastic deposits marking an initial volcanic phase of the Sikhote Alin orogeny. The tuffaceous sequence is assigned to the early – middle Albian on the basis of its stratigraphic position above the well-dated marine lower Albian and the macrofloral/palynological assemblages (Krassilov 1967, Markevitch & Shuklina 2005). They contain angiosperm leaves in the Rasdolninsk Basin and on the eastern coast of Ussuriysk Bay. The recently found locality is an outcrop of black shales and greenish gray psammitic tuffites exposed on the coastal cliff of Bolshoy Kuvshin Inlet (Fig. 1). The tuffite is speckled with ferrous inclusions and coal grains.

The plant remains are deposited on the bedding planes, as well as imbedded in the coarser tuffaceous matrix. They are brownish or dark gray impressions colored with ferrous infiltrations and dispersed organic matter, yielding no structurally preserved material. The plant remains are folded and sheared by a post-depositional slumping of the sediment, the fragments being displaced few mm apart. Post-depositional fragmentation process is responsible for the impression appearing discontinuous and not exactly in one plane (examples in Pl. 1, fig. 1, Pl. 3, fig. 4, Pl. 4, fig. 3). Nevertheless it is possible to recognize the whole plants, with rhizomes, branching stems, leaves, flowers and fruits intact. Associated with such post-depositionally fragmented material, there are scattered remains of cauline and reproductive organs belonging to the same species as the whole-plant impressions. Two angiosperm species are recognized, accompanied by nearly as numerous or patchily more abundant fern remains and occasional scale-leaved conifer shoots. The material was studied and photographed with a stereomicroscope LEICA MZ6 and a digital camera NIKON DS-Fi1. The collection is deposited in the Institute of Biology and Soil Science, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok (No. 320).

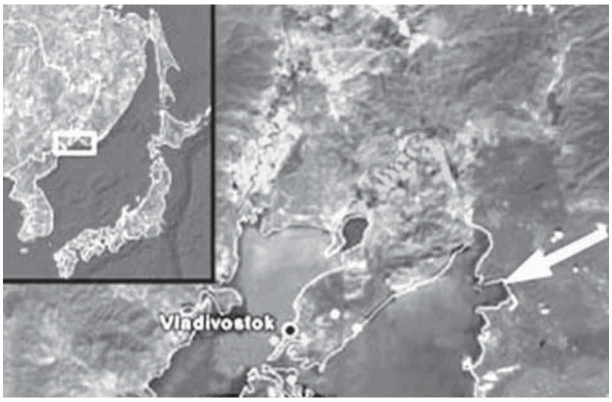

Fig. 1. Study area in the South Primorye. Arrow on the Ussuriysk Bay angiosperm locality

SYSTEMATICS

Genus ***Achaenocarpites*** Krassilov & Volynets, **gen. nov**.

Type species. *Achaenocarpites capitellatus* Krassilov & Volynetz sp. nov. (designated here).

Etymology. Greek *achaiein,* indehiscent and *carpos,* fruit.

Diagnosis. As for the type species.

Species content. The type species only.

Achaenocarpites capitellatus Krassilov & Volynets, **sp. nov.**

Plate 1, figs 1–6, Plate 2, figs 1–7, Plate 3, figs 1–3

Holotype. Institute of Biology and Soil Science, No. 320-9A (Pl. 1, figs. 1–4), designated here.

Type locality and stratum. Primorye Region of Russian Far East, eastern coast of Ussuriysk Bay, Bolshoy Kuvshin Inlet near

Bolshoy Kamen' Village, Early – Middle Albian, tuffaceous horizon of the Kangaus Formation.

Etymology. Latin *capititulum*, small head.

Diagnosis. Rhizome sympodially branched, bearing tubers and filiform adventitious roots. Leafy stems not sharply delimited from the rhizomatous part, slender, with one or a few pairs of cauline leaves and a solitary terminal flower. Leaves stipulate, basically ternate, pinnatisect or 3-lobed, the larger ones with additional proximal lobes. Flower small, actinomorphic, monochlamydeous, developing into a head of achenes, with tepals partly persistent at fruit. Achenes numerous, obovate, minutely mucronate. Seed descending from apical region of achene, anatropous with a distinct raphe.

Description. The holotype represents a whole plant about 30 mm long, which is twisted and cleaved by post-depositional slumping of the rock matrix, so that the rhizomatic part and the leafy axis are not exactly in the same plane. The rhizome bears adventitious roots and a pair of tubers at the base (Pl. 1, fig. 2). The roots arise in a bunch slightly above the tuber node and from the tips of the tubers. They are preserved as slender (0.2–0.3 mm) flexuous dark stripes up to 10 mm long. The tubers are 3 × 2 mm, broadly rounded at the base, tapered to the tips, making deep impressions as of a hulky body. The rhizome is sympodially ramified, with three branches diverging in rapid succession from near the tuber node, spreading to one side at acute angles, proximally smoothly arched, then straight, apparently rigid. They are uniformly 0.5 mm thick, distinctly grooved. The median one is cut shortly above the base, the lateral ones are traceable up to 15 mm, one approaching the leafy stem on the right side of the photograph (Pl. 1, fig. 1).

The stem is only slightly thinner than the rhizome and similarly grooved. It extends for 5 mm before producing a pair of opposite leaves that arise at about 75° bending down in smooth arches. The leaves are incompletely preserved, one traceable for 12 mm, pinnatisect into obcuneate to broadly triangular lobes, decurrent and narrowly webbing the midrib. At the base of each leaf there is a narrow lingulate appendage 1.5 mm long (marked “s” in Pl. 1, fig. 3) onlapping the leaf base and spreading medially between the leaf and the shoot axis. The appendages are well separated and morphologically distinct from the leaf lobes representing a pair of leaf stipules.

Distally, the shoot axis arches down and, six mm above the leaf node, terminates in a flower 3 mm in diameter, in which only half circles of perianth and gynoecial structures are preserved on a relatively massive spherical receptacle. The perianth is represented by two tepals persistent at the gynoecium developing into a head of radially spreading achenes. Missing parts left circular slightly elevated scars on the opposite site of receptacle. The tepals (sepals?) are elliptical, flat, nutant, one onlapping the pedicel. The achenes are obovate, about 1.5 mm long, rounded with a minute mucro or shortly cleft. Their apical regions are strongly concave at the seed locule.

Shed achenes preserved on the same bedding surface (Pl. 2 figs 1–7) are 1.5–1.8 mm long, rather uniformly obovate, wedging to the base, sometimes showing a minute apical beak. Some are split over the beak (Pl. 2, fig. 4). They are finely striate proximally before the locule, whereas their distal shoulders exhibit thick-walled cells with rounded-polygonal lumina (Pl. 2, fig. 3). The pits and minute dents at the margins represent hair bases. A solitary seed is clearly seen in Plate 2, figures 5–7 as a dark inner body descending from the apical region and pointing to the base of the achene. They are ovate, about 1 mm long, rounded and thickened at the chalazal end, gradually pointed, asymmetrically curved on the one side and nearly straight on the other. The epidermal cells are small, rounded, bulging and giving the seed surface a verrucate appearance (Pl. 2, fig. 5). Details of micropyle and hilum are scarcely discernible, but a distinct longitudinal ridge, representing raphe, indicates anatropous polarity of the ovule.

Two heads of achenes in Plate 1, figs 5, 6 are assigned to the same species on account of their similarity in shape and dimensions to the floral receptacle and achenes of the holotype. They are associated on the slab with a pinnatisect leaf of the same type as the leaves of the holotype. The heads are globose, 3.6 and 3.9 mm in diameters, consisting of about 16 radially spreading achenes and a few longer caudate appendages probably representing persistent tepals. The achenes are obovate, apically rounded or shortly mucronate (when the minute mucros are preserved in the coarse-

Fig. 2. Achene of extant *Anemone coronaria* L., extant on Mount Carmel, Israel, cleared to show the position of the seed for comparison with Pl. 2, figs 6, 7

grained matrix), showing a concavity of the seed locule at the distal end, as in the holotype.

In addition to the intact leaves of the holotype, there are numerous impressions of detached leaves of the same type (Pl. 1, fig. 5, Pl. 2, fig. 1, Pl. 3, figs 1–3), ranging from ternate or trilobed, 5 mm long to imparipinnatisect or pinnatifid, up to 50 mm long. The latter are apically trilobed, with one or two pairs of obovate or elliptical proximal lobes. A fragment of bipinnate leaf with a slender webbed rachis (Pl. 3, fig. 2) shows a short trilobed basal leaflet corresponding to the apical trilobed segment of the longer pinnae leaflets. The midribs give off an upcurved lateral branch to each lobe, this running medially or along the basiscopic margin and lost towards the apex. Apical lobes of imparipinnate leave receive two acrodromous branches. Secondary veins are faintly marked, oblique, looping shortly before the margin. In the webbing part of leaf blade, secondary veins arise directly from the rachises, some ascending into the lobes as a slender intramarginal vein (e.g. basal trilobed leaflet in Pl. 3, fig. 2).

Comparison. A rhizomatous habit, with the leafy stems scarcely delimited from the rhizome and with opposite (as in *Clematis* L., Ranunculoideae: Anemoneae) or subopposite ternate compound or pinnatisect cauline leaves is rather typical of the Ranunculales: Ranunculaceae (overviewed in Tamura 1993). A sympodial branching of rhizome is quite common (e. g. *Talictrum* Heintze, Thalictroideae), as are the adventitious roots arising from the rhizome. Tubers are a more specific feature, occurring, among the Ranunculaceae, in *Eranthis* Salisb., Helliboreae, *Barneoudia* C. Gray, Anemoneae, *Isopyrum* L. and *Enemion* Raf., Isopyreae, and less constantly in *Thalictrum*.

Foliar architecture of *Achaenocarpites* is basically ternate, with additional leaflets or lobes appearing on the larger leaves. As ontogenetic studies show (Kürbs 1973; Tamura 1993), this situation is typical of the Ranunculaceae, the leaves of which, though morphologically diverse, are invariably tripartite in early development. Compound ternate leaves are also found in *Hyrcantha* Krassilov & Vachrameev, a fossil ranunculid genus (Krassilov et al. 1983). A Cretaceous leaf morphogenus *Sapindopsis* Fontaine typically has the imparipinnate compound leaves with elongate entire leaflets (morphological analysis in Doyle & Hickey 1976). However, the pinnatisect leaves with trilobed apical leaflets are also included in *Sapindopsis* allegedly confirming its platanaceous affinities, also based on a slab association with fruiting heads (Crane et al. 1993). It must be noted that trilobed leaflets of compound leaves typically occur in Ranunculaceae rather than in Platanaceae. Assignment of *Sapindopsis* to Platanaceae is not so far confirmed by cuticular studies (Krassilov & Bacchia 2000, Carpenter et al. 2005), and small fossil heads of achenes are more probably ranunculoid fruits than platanoid infructescences.

Terminal actinomorphic flowers with a gynoecium of many free uniovulate carpels developing into a head of achenes are rather common among the Ranunculaceae: Ranunculoideae, as well as Thalictroideae. Anatropous ovules pendulous from near the apex of achene occur in the Ranunculoideae: Anemoneae and Ranunculeae (e.g. *Anemone* L. or *Myusurus* L.). *Anemone coronculata* L. produces rather similar hirsute achenes (Fig. 2), but larger, with a longer beak, turgid and readily splitting under slight pressure, releasing the seed.

Among fossil angiosperms, a small basically actinomorphic flower with free carpels occurs in *Callicrypta* Krassilov & Golovneva, but the perianth is relatively large, with three circles of heteromorphic tepals, and the carpels are much fewer than in *Achaenocarpites* (Krassilov & Golovneva 2003). A trilobed leaf or leaflet described by Kryshtofovich (1929) as *Aralia lucifera* Krysht. may actually belong to a congeneric, but specifically different *Achaenocarpites* plant.

Genus ***Ternaricarpites*** Krassilov & Volynets, **gen. nov.**

Type species. *Ternaricarpites floribundus* Krassilov & Volynets, sp. nov. (designated here).

Etymology. Latin *ternarius*, tripartite

Diagnosis. As for the type species.

Species content. The type species only.

Ternaricarpites floribundus Krassilov & Volynets, **sp. nov.**

Plate 3, fig. 4, Plate 4, figs 1–7, Fig. 3

Holotype. Institute of Biology and Soil Science, No. 320-31 (Pl. 3, fig. 4; Fig. 3A), designated here.

Type locality and stratum. Primorye Region of Russian Far East, eastern coast of Ussuriysk Bay, Bolshoy Kuvshin Inlet near Bolshoy Kamen' Village, Early – Middle Albian, tuffaceous horizon of the Kangaus Formation.

Etymology. *Floribundus* (Latin), abundantly flowering.

Diagnosis. Stem slender, basally rhizomatous, sympodially branched. Basal leaves pinnatisect of opposite decurrent lobes. Venation open. Midveins of the lobes running close to the upper margin or acroscopically laminaless, giving off dense oblique lateral veins that in the web arise directly from the axis. Flower terminal on branches, occasionally axillar at branching node, with a slightly zygomorphous perianth of 5 unequal tepals, connate at base. Venation of tepals similar to that of leaf lobes. Fruit a ternate follicetum. Follicles dorsicidal, lacking transverse striation (fibres). Seeds in rows along the abaxial suture.

Description. No less than 20 fruiting axes are exposed on a slab of tuffite, No. 320-31 (Pl. 3, fig. 4; Fig. 3A) Their arrangement may seem haphazard, but actually they belong into three overlapping branching systems (numbered 1–3 in Fig. 3A) forwarded in the same direction as if ascending from a common base. The thicker axes are about 0.8–1.0 mm, decreasing after branching, giving off slender (0.4 mm) branchlets that arise either sympodially, to one side or, at some distal nodes, dichopodially, to both sides of the penultimate axis. The branches depart at about 45°, arch forward and slightly undulate. The intervals between the nodes decrease upwards from about 14 mm to 4 mm. The ultimate branchlets bear terminal fruits of ternate follicles. Fruits are also produced at the axils of terminal branches. They all seem equally developed.

In the central branching shoot (2 in Fig. 3A), a basally attached pinnatisect leaf shows three pairs of proximal lobes on a webbed rachis distally extending as a naked axis. The lobes are opposite, asymmetrical, 3.5–7.0 mm long, with acroscopic margins stretched perpendicular to the axis, basiscopic margins decurrent, apex pointed or bifid. Venation of the lobes consists of a midvein running close to the acroscopic margin or laminaless on the acroscopic side and shortly caudate, giving off dense oblique lateral veins that in the decurrent part arise directly from the axis.

Paratype No. 320-10 is a branching axis, the lower part of which, 1.5 mm thick, with minute scars, probably represents a rhizome. Continuous with it is a slender (1 mm) sympodially branched axis bearing terminal flower subtended by a bract or prophyll (Pl. 4, figs 1, 2). The flower shows a 5-lobed perianth, 5.5 mm wide, somewhat zygomorphic, of unequal lobes that are basally connate for about 1/3 of their length. The larger median lobe is elongate, spread in the bedding plane, with a distinct midrib giving off dense oblique, slightly arching lateral veins reaching to the margin. The lateral lobes appear conduplicately folded, one shortly caudate, another split at the tip. A ternate fruit in the left part of the picture may belong to the same branching system, but actual connection cannot be traced.

Paratype No. 320-52 (Pl. 4, fig. 3; Fig. 3B) is a fruiting shoot arising from a sympodially ramified rhizome. The fruit is axillar at the distal branching node. A pair of minute appendages below the fruit node may represent vestigial cataphylls.

Paratypes 320-25 and 320-30 show fruits of ternate follicles typical of the genus (Pl. 4,

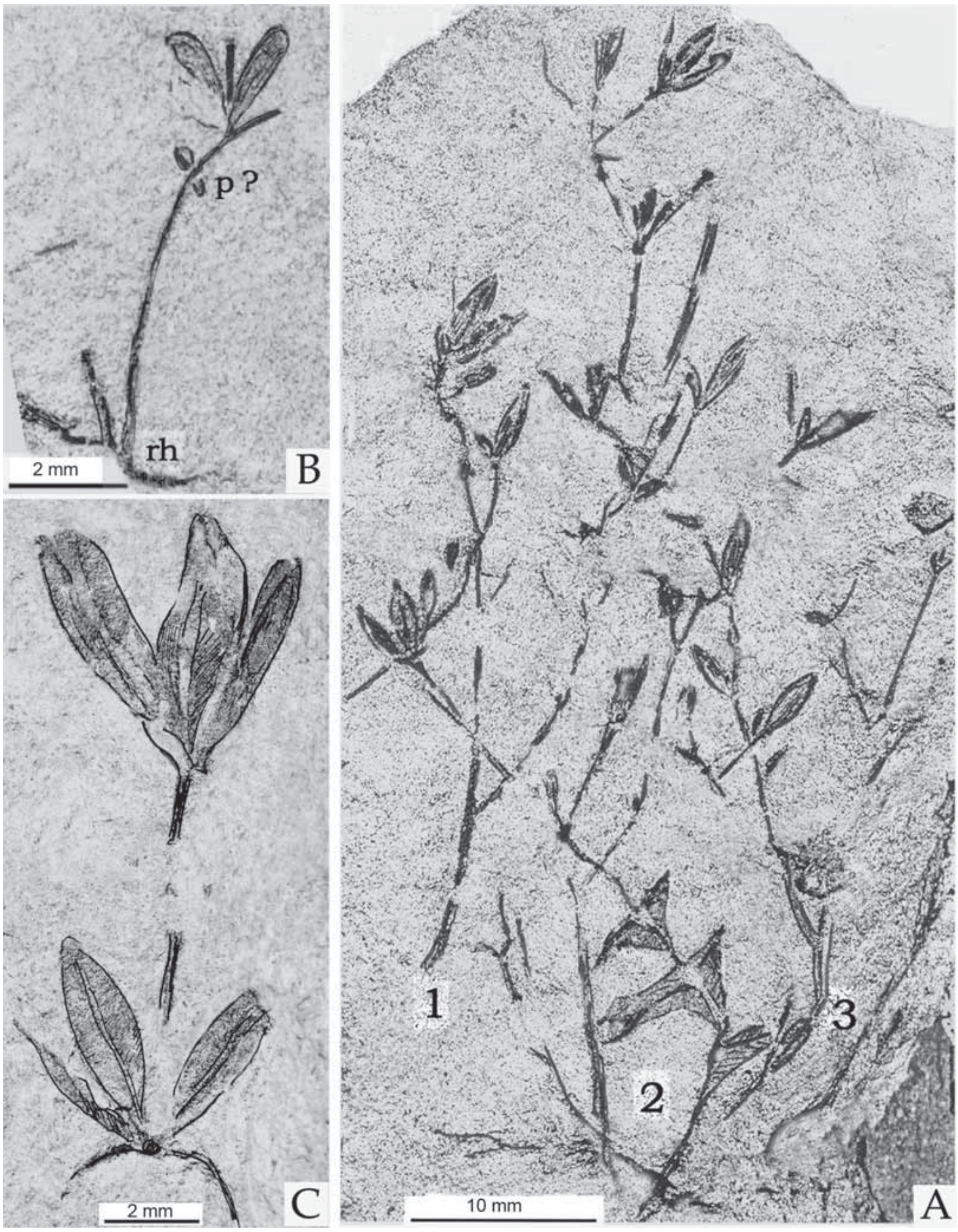

Fig. 3. *Ternariocarpites floribundus* gen et sp. nov., retouched photographs showing the modes of branching and positions of the fruits: **A** – Branching axes with terminal and axillary fruits, one with a basal leaf, 320-31 (Pl. 3, fig. 4); **B** – Sympodially branched rhizome giving off a shoot with an axillary fruit at a branching node, 320–52 (Pl. 4, fig. 3); **C** – Branching shoot with two fruits of ternate dorsicidal follicles, 320-25 (Pl. 4, fig. 4)

figs 4, 5; Fig.3C). The fruits appear terminal and are attached at a slightly expanded node of a slender longitudinally grooved axis. The follicles are elongate, 6–8 mm long, free to the base, shortly stipitate, pointed or cleft at the tip, lacking a transverse tracery of veins or fibres, but with a prominent abaxial keel of two parallel ridges, occasionally gaping and probably representing a dehiscence suture. A dehiscent follicle (enlarged in Pl. 4, fig 5) shows a row of vague elliptical scars (arrows) presumably of seeds aligned with the abaxial suture.

A detached leaf (Pl. 4, fig. 7) essentially similar to the basal leaf of the holotype is found together with fruiting shoots probably representing their cauline foliage. It is impairpnatisect, with a slender almost continuously webbed midrib. The lobes are elongate, basally expanded, distally notched, with an additional lobe or tooth resulting from unequal apical division. Sinuses between the lobes are broadly rounded or somewhat angular. The oblique lateral venation does not show evidence of anastomosing.

Comparison. This plant is interpreted as rhizomatous with pinnatisect leaves and terminal flowers, therefore of a similar growth form and probably related to *Achaenocarpites capitellatus* gen. et sp. nov., but differing in follicular fruits and therefore allied to different groups of ranunculids, i.e. the Ranunculaceae: Helleboroideae and Isopyroideae (the systematics overviewed in Tamura 1993). Perianths of 5 tepals (sepals) occur in *Caltha* L. and some other Helleboreae and are zygomorphous in the Delphineae. The numbers of follicles vary in these groups, but ternate fruits commonly occur in *Trollius* L., *Delphinium* L., *Aquilegia* L., *Kingdonia* Balf. & Smith, and some other helleborid and isopyrid genera. As in the Isopyroideae, transverse fibres are lacking in the follicles of *Ternericarpites*. Open venation is a rare feature in angiosperms known in *Kingdonia* and *Circaeaster* (Foster 1961).

Characters of *Ternaricarpites floribunda* atypical of the present day ranunculids are the sympodial branching of fertile axes, both terminal and axillary flowers (fruits), and the abaxial dehiscence of the follicles. In the Ranunculaceae, solitary flowers are typically terminal, but leaf-opposite in *Ranunculus* subgen. *Batrachium* (DC.) Peterm., and inflorescences can be axillary and sometimes single-flowered. Both ventral and dorsal sutures can be involved in dehiscence of the follicles. Therefore, these features do not preclude a comparison with ranunculids, although they more commonly occur in the other, probably allied families, in particular, *Cercidiphyllum* that differs in decussate arrangement of follicles and their association with a solitary leaf on the short shoot.

In the fossil genus *Hyrcantha* Krassilov & Vachrameev, the fruits are basically ternate, although occasionally pentamerous, differing in the urn-shaped ventricidal follicles, truncate at the broad sessile stigmas (Krassilov et al. 1983). The leaves are ternately compound, similar to those of *Achaenocarpites* (above), and the follicles show the distinctly marked transvers fibres. *Hyrcantha decussata* (Leng et Friis) Dilcher, Sun, Ji & Li from the Early Cretaceous Yixian Formation of northeastern China differs mainly in the decussate arrangement of the carpels (Dilcher et al. 2007).

Leaves of the same morphotype as the basal leaves of *Ternaricarpites floribundus*, but specifically perhaps different were described from coeval deposits of Rasdolninsk Basin, western Primorye as *Sujfunophyllum dichotomum* Krassilov (Krassilov 1967). As a leaf morphogenus, *Sujfunophyllum* is applicable to detached leaves of the type shown in Plate 4, fig. 7.

DISCUSSION

Taphonomically, the Ussuriysk Bay locality represents a re-deposited ash-fall material with imbedded plant debris and coal grains. Preservation of whole plants, as well as the joint occurrences of rhizomes, branching stems, detached leaves, achenocarpic heads and dispersed achenes indicate deposition at or near the growth site, with no or insignificant transportation sorting. Fragmentation of plant material is mostly post-depositional, by slumping and sliding of water-logged tuffaceous sediment. In the slab assemblages, the two species of rhizomatous angiosperms are constantly associated with *Anemia ("Asplenium") dicksoniana* (Heer) Krassilov, a small-leaved representative (or a close ally) of an extant schizaeaceous fern genus, in which creeping forms of open periodically dry to boggy habitats are rather common (Kramer 1990). Both ferns and angiosperms had pinnatisect leaves of a similar general aspect, with slender rachises and decurrent leaflets (pinnules) or lobes. Extant ferns of similar habits are known to be colonizers of ash fallouts in Africa (Kornaś 1978), and the "fern spikes" of the fossil record might have been due to a spread of such habits and habitats during the major volcanic events. Therefore, it seems logical to assume that the Albian fern – angiosperm assemblage corresponds to a pioneer community of a few co-adapted early colonizer species growing on fresh fallouts of a volcanic landscape.

Angiosperms are wanted in the rich Barremian – Aptian flora of Primorye, while the Albian records represent their first regional (although not evolutionary) appearance correlated with a radical change in both sedimentary environments and floristic assemblages. With the rise of Sikhote Alin Ranges and the onset of volcanic activity in the Albian, the peat forming wetlands, in particular the extensive fern marshes were drastically reduced and replaced

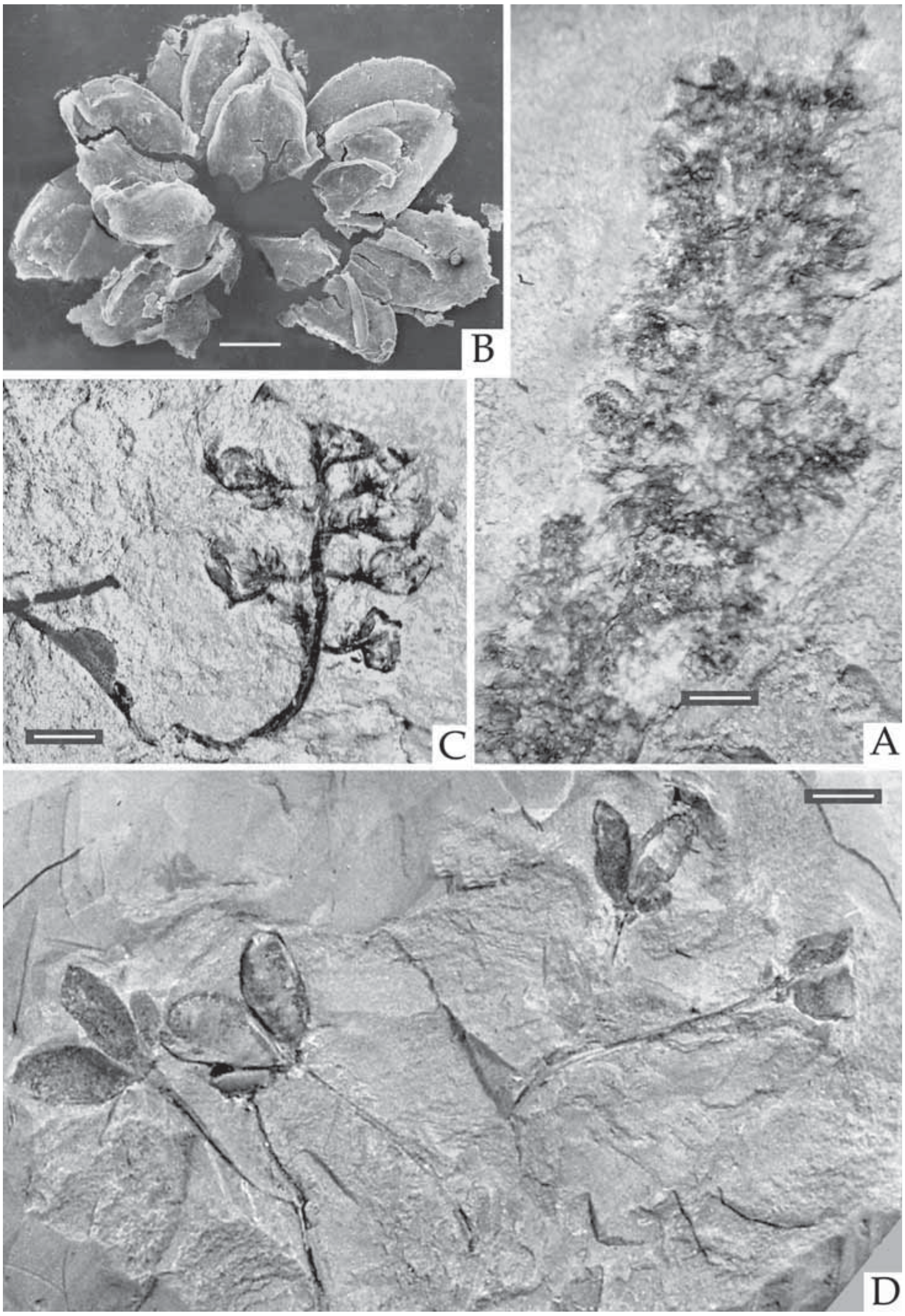

Fig. 4. Ranunculoid angiosperms from the Albian – Cenomanian of Siberia and Kazakhstan: **A** – *Caspiocarpus paniculiger* Krassilov & Vachrameev (Krassilov 1984); **B** – *Callicrypta chlamydea* Krassilov & Golovneva (Krassilov & Golovneva 2004); **C** – *Freyantha sibirica* Krassilov & Golovneva (Krassilov & Golovneva 2001); **D** – *Hyrcantha karatscheensis* (Vachrameev) Krassilov (Krassilov et al. 1983). Scalebars: A – 1 mm; B – 0,3 mm; C, D – 3 mm

by new types of plant communities. A customary notion of early angiosperms entering the Mesozoic fern – gymnosperm communities as solitary newcomers does not comply with the data, because angiosperms in fact failed to penetrate the pre-existing wetlands, but instead participated in the build up of a new herbaceous plant community of early colonizers overgrowing ash fallout substrates and stabilizing them with a turf of rhizomatous stems and roots. Ferns that became members of such early angiosperm communities were not the ferns of the Aptian peat bogs, but likewise the newcomers as *Anemia dicksoniana*, ubiquitous through the Albian and Late Cretaceous and apparently co-adapted with angiosperms of a pioneer habit (Krassilov 1979).

Further inland, in Transbaikalia and Mongolia, replacement of fern marshes by proangiosperms and the first appearing angiosperms took place much earlier being associated with a widespread volcanism over the Jurassic – Cretaceous boundary (Krassilov & Bugdaeva 1999). On the Pacific coast, the Mesozoic type fern – gymnosperm wetlands survived until the Albian, declining with the onset of volcanism and associated environmental changes, which enhanced new floristic and syntaxonomic developments.

The Albian angiosperms from Primorye confirm that herbaceous growth habit appeared early in the evolutionary history of ranunculids and was perhaps primary for the group. It is well known that herbaceous plants are underrepresented in the fossil record. This may explain rarity of fossil ranunculids. However, in the mid-Cretaceous they were more common than afterwards and were represented by a number of morphotaxa suggesting a considerable diversity and morphological disparity. Examples are *Caspiocarpus paniculiger* Krassilov & Vachrameev from the Middle Albian of Kazakhstan, a herbaceous plant with a slender stem bearing a pair of palmately lobate *Cissites*-type leaves and a terminal tripartite paniculate infructescence of small condensed racemose paracladia, each bearing up to ten 1-3-ovulate follicles (Fig. 4A). The ovules are anatropous, bitegmic, ascending from the base. This plant was compared to ranunculids in the widest sense on account of its general habit, leaf morphology, dorsi-ventricidal dehiscence of follicles and the structure of ovules with extremely thin integuments as in the modern Ranunculaceae and Circaeasteraceae. *Hyrcantha karatscheensis* (Vachrameev) Krassilov from the same horizon is represented by slender branched axes bearing biternate leaves and terminal fruits of 3–5 urn-shaped ventricidal follicles crowned with a broad sessile stigma (Fig. 4D) as in the Paeoniaceae, a controversial family morphologically linked to both the Ranunculales and Dilleniales (Cronquist 1981).

Callicrypta chlamydea Krassilov & Golovneva from the Lower Cenomanian of Siberia is an actinomorphic flower less than 2 mm wide (Fig. 4B), functionally pistillate, although found with sticking pollen grains probably produced by a staminode. The perianth is 3-seriate of a relatively massive calyx and a corolla of dimorphous inner and outer petals. The gynoecium is apocarpous of small ascidiform carpels. Our analysis pointed to the Menispermaceae and Arborellaceae as the nearest extant groups, at the same time revealing a significant similarity between the two (*Amborella* has been traditionally assigned to the Monimiaceae, but presently is more commonly placed in the vicinity of the Nymphaeaceae: Mathews & Donoghue 1999, Endress 2001). Pollen grains are of the type found *in situ* in *Freyantha sibirica* Krassilov & Golovneva from a stratigraphically coeval horizon in West Siberia (Krassilov & Golovneva 2001), a racemose staminate inflorescence, terminal on the axis with minute prophylls. The staminate flowers consist of fasciculate stamens subtended by calyptrate bracts (Fig. 4C). The alleged affinities with the Menispermaceae and Sargenthodoxaceae make *Freyantha* assignable to the ranunculid plexus. The recently described carpellate infructescence *Cathiaria* Golovneva & Oskolski, probably belonging to the same plant as *Freyantha*, is a panicle of short racemose paracladia bearing several dorsicidal follicles (Golovneva & Oskolski 2007), comparable to *Caspiocarpus* (above), but with a laminar structure (inflorescence bract or prophyll) adnate to the paracladia in early development.

Teixeiraea von Balthazar, Pedersen & Friis, assigned to the Ranunculales (von Balthazar et al. 2003) is a fragmentary staminate organ, interpreted as a solitary flower, but appearing as a condensed bracteate inflorescence showing stamens produced from the axils of the bracts. The stamens consist of long anthers on a very short filament, a morphology quite atypical of the ranunculids.

Achaenocarpites capitellatus gen. et sp. nov. is perhaps the most confident mid-Cretaceous ranunculid being assigned to this group on the basis of both vegetative and reproductive morphology. Its leaves, basically trilobed, correspond to the basic type of all ranunculids, the diversity of adult leaf morphologies depending on marginal growth (Kürbs 1973).

While *Achaenocarpites* is assigned to achenocarpoid group of ranunculids, typically represented by the Ranunculaceae: Anemoneae, its associate *Ternaricarpites* belongs in the folicetoid line. This genus is significant, in the first place, due to open venation, as in *Kingdonia* grouped with *Circaeaster* with a similar venation or separated into a monotypic family Kingdoniaceae (Foster 1961). Dimorphism of basal and cauline leaves, characteristic of the Ranunculaceae, is not proved, but seem probable in *Ternaricarpites*, the basal leaves of which are of the same general type, but differ in details of lobing and venation from the associated detached leaves. Both terminal and axillary position of flowers (fruits) on the branching shoots in *Ternaricarpites* find its analogy in the floral organography of Isopyreae (Tucker & Hodges 2005). Moreover, the monochlamydeous perianth of five unequal tepals, with the larger one in a median abaxial position may result from an organogenesis typical of this tribe, with a successive helical initiation of sepals reflected in their size differences. Features of adult floral structures in Cretaceous ranunculids preserved in the organogenesis of modern taxa suggest phylogenetic relatedness, although the fossil genus is also comparable to the Cercidiphyllaceae on account of sympodial branching, floral prophyll and dorsicidal carpels.

These findings seem to support the classical "ranalean" theory of angiosperm phylogeny, with the large heterogeneous ranunculid families Ranunculaceae, Menispermaceae, and Berberidaceae, presently forming the bulk of the ranunculids, and a number of not unanimously recognized monotypic families, such as the Kingdoniaceae, Circaeasteraceae, Lardizabalaceae, Sargentodoxaceae, Paeoniaceae, Glaucidiaceae, Amborellaceae, and those to be erected for fossil forms, linking this group to the orders of remote ranunculoid affinities. Yet much more has to be learned of Cretaceous ranunculids before it will be possible to relate the logical schemes of morphological and molecular phylogeny to what actually happened in the course of angiosperm evolution.

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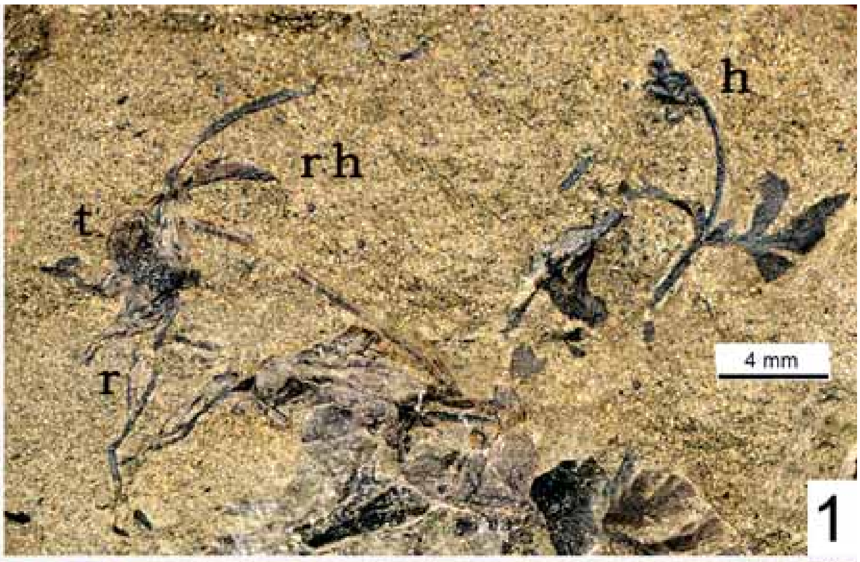
PLATES

Plate 1

Achaenocarpites capitellatus gen. et sp. nov.

1. Branching rhizome **(rh)** with tubers **(t)** and adventitious roots **(r),** supposedly continuous with, but cleaved apart from the leafy stem with a terminal floral structure **(h)**, holotype 320-9A.
2. Tubers enlarged from fig. 1.
3. Stem with a pair of leaves (**s** – leaf stipules) and a terminal head, enlarged from fig. 1.
4. Flower with two persistent tepals **(te)** and gynoecium developing into a head of achenes, enlarged from fig. 1.
5. Leaf of the same morphotype as in the holotype, in association with two heads of achenes, 320-46C.
6. Head enlarged from fig. 5.


2 mm
2


h
rh
t
r
4 mm
1


te
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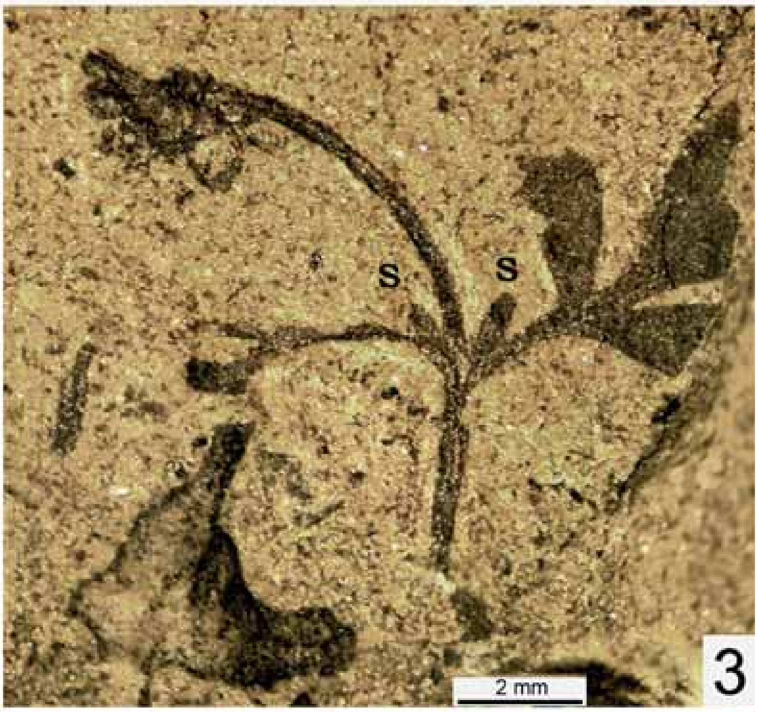
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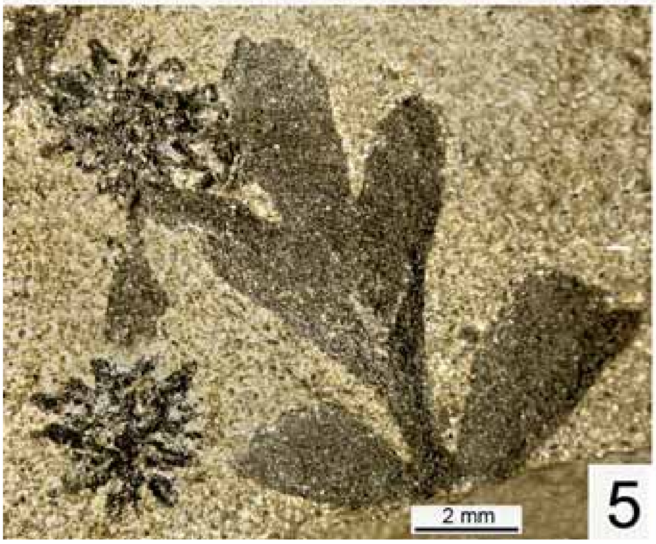
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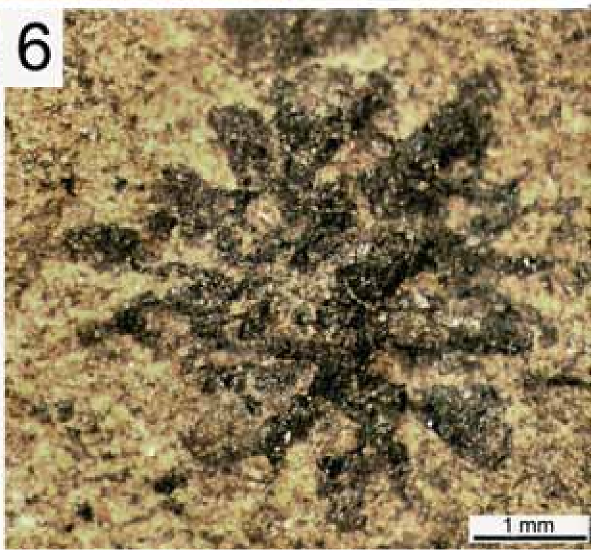
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1 mm

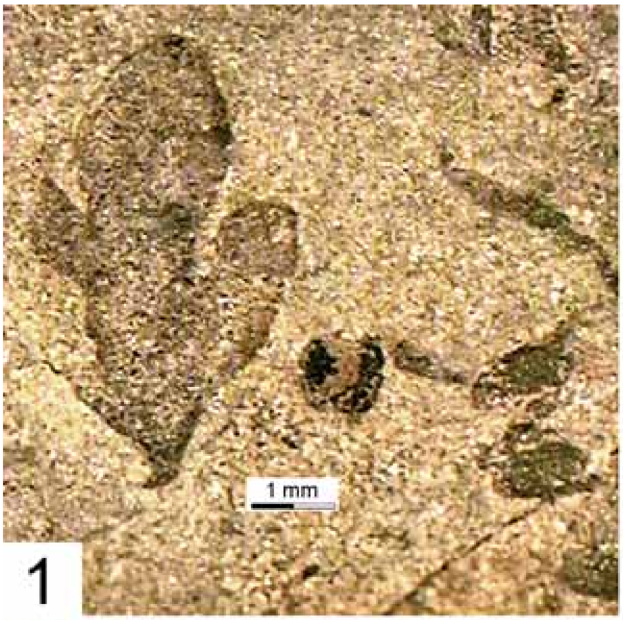
Plate 2

Achaenocarpites capitellatus gen. et sp. nov.

1. Trilobed leaf in association with dispersed achenes, preserved on the same slab as the holotype, 320-9B.
2. Dispersed achenes on the same slab as the holotype N-320-9C, enlarged in figs 3–7.
3. Achene showing polygonal surface cells.
4. Achene cleft at tip.

5–7. Split achene exposing seeds, fig. 5 also showing a prominent longitudinal ridge.

Plate 2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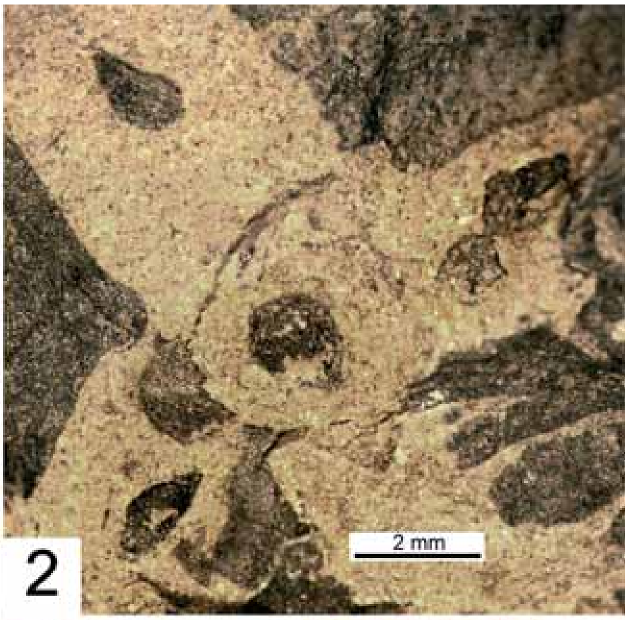
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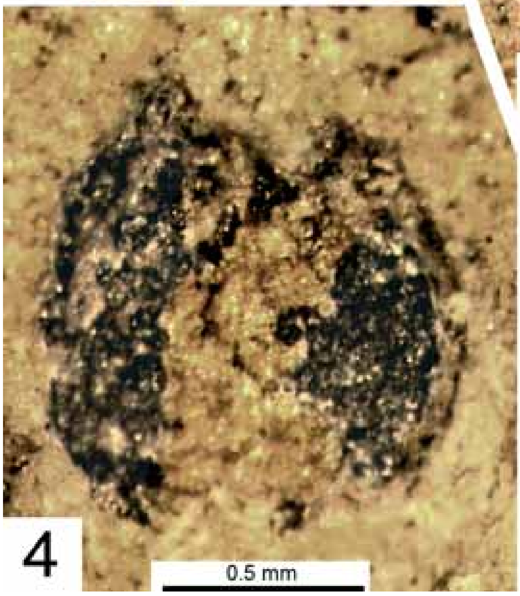
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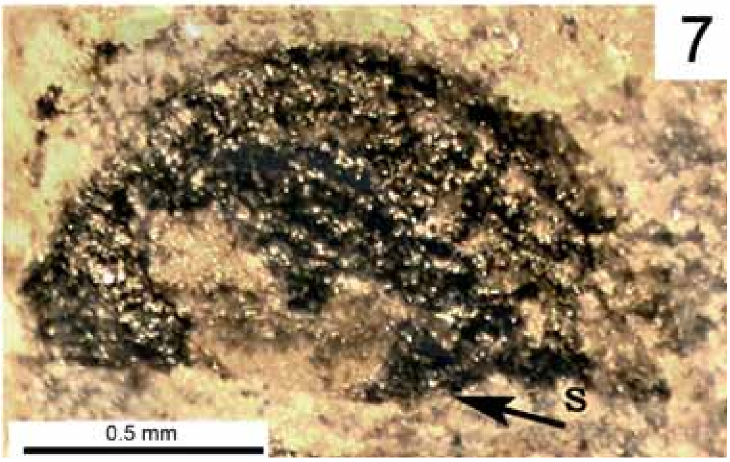
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Plate 3

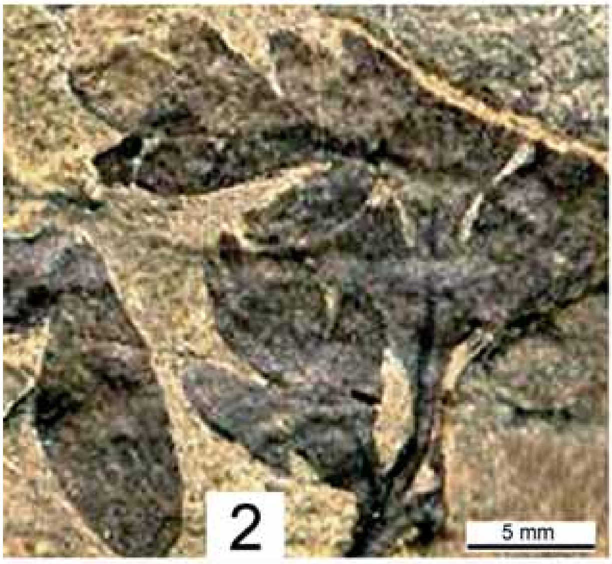
Achaenocarpites capitellatus gen. et sp. nov.

1–3. Leaf fragments, 320-7, 320-4, and 320-26 showing transitions from trilobed to imparipinnate leaflets; details of venation are discernible in the basal trilobed leaflet and a lobe to the left of it on fig. 2.

Ternaricarpites floribundus gen. et sp. nov.

4. Branched fruiting axes representing a single fragmented plant, one axis with a basal leaf (arrow), holotype 320-31.


1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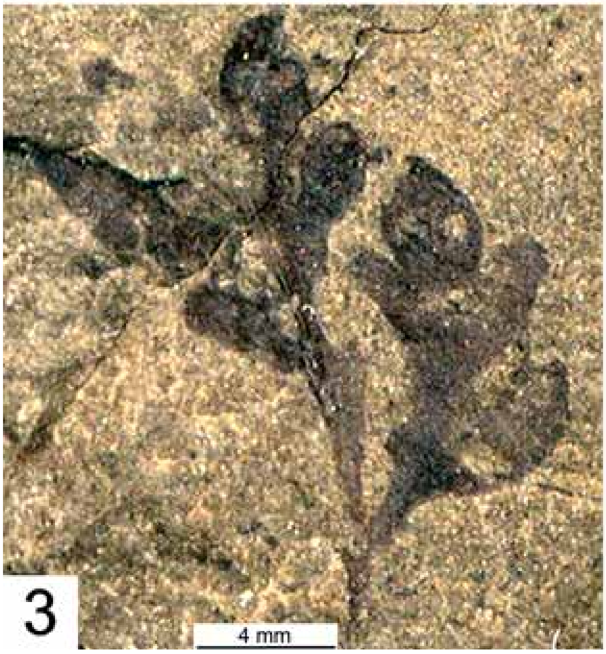
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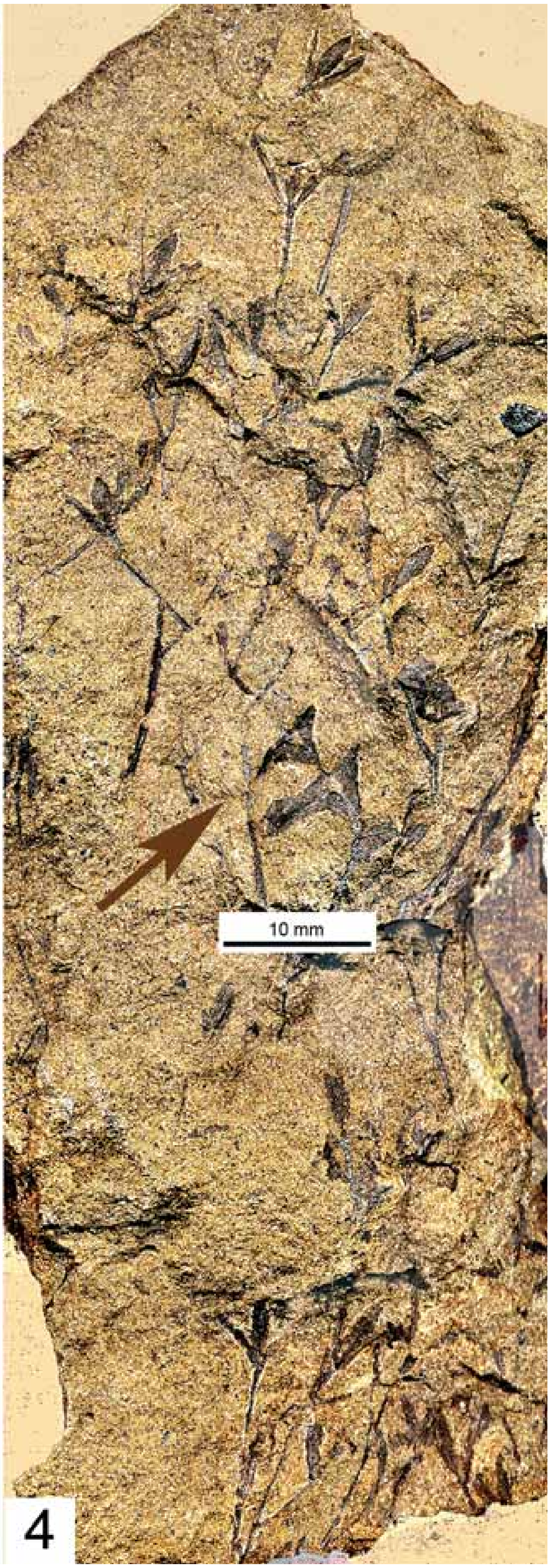
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Plate 4

Ternaricarpites floribundus gen. et sp. nov.

1. Branching axis, thicker and apparently rhizomatous at the base, bearing a terminal flower, 320-10.
2. Flower with a perianth of five unequal tepals subtended by a bract or prophyll **(P)**, enlarged from fig. 1.
3. Sympodially branched rhizome giving off a shoot with an axillary fruit at a branching node, 320-52.
4. Branching shoot with two fruits of ternate follicles, 320-25.
5. Dehiscent follicle with seed impressions (arrows), enlarged from fig. 4.
6. Axis with a fruit of ternate follicles with an adaxial suture marked by a prominent double ridge, 320-30.
7. Isolated pinnatisect leaf of *Suifunophyllum* type (Krassilov, 1967), 320-50, comparable with an attached one, shown in Plate 3, fig. 4 (at arrow).

Plate 4