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CRETACEOUS FLOWERS FROM KAZAKHSTAN

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ABSTRACT

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***Hyrcantha* gen. nov. from the Middle Albian is a paniculate inflorescence. The flowers are bisexual with persistent calyx and apocarpous gynoecium. The carpels are ascidial with broad sessile stigma. The genus is related to the Ranunculaceae and Paeoniaceae. The Late Cretaceous *Sarysua* gen. nov. has cymoid inflorescences of many actinomorphic pentamerous flowers with syncarpous five-lobed ovaries and free styles. A geranialean affinity is suggested. In *Taldysaja* of the same age much reduced pistillate flowers are born in spikelets or solitary on branches of the fasciculate inflorescence. These findings evidence the important role of the ranunculoid—paeonioid complex among ancestral angiosperms and the considerable diversity of the Late Cretaceous flowering structures.**

INTRODUCTION

In recent years several important reproductive structures of early angiosperms have come to light (Dilcher, 1979; Vachrameev and Krassilov, 1979; Friis and Skarby, 1981; Retallack and Dilcher, 1981). A few more finds of this kind are described in this paper. One of them is from the Middle Albian of western Kazakhstan — the same beds which yielded *Caspiocarpus* (Vachrameev and Krassilov, 1979) — while two others are from the Santonian—Campanian of south-central Kazakhstan. See Vachrameev (1952) and Shilin and Romanova (1978) for justification of the age assignments and general description of the fossil floras.

Inflorescences were mentioned in the original descriptions as reproductive structures of unknown nature. Their detailed study is here undertaken for the first time. The Albian inflorescences occur in light-coloured clay as impressions, gray on dispersed coaly substance. The Santonian—Campanian fossils are thin iron oxide incrustations, brown on light-yellow siltstone. No organic matter suitable for maceration is preserved but at places cell outlines are visible on impressions and incrustations.

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SYSTEMATICS

Genus *Hyrcantha* Krassilov et Vachrameev, gen. nov.

Name: Hyrcanian is the ancient name of the Caspian Sea.
Type species: Hyrcantha karatscheensis (Vachrameev) Krassilov et Vachrameev, comb. nov.
Diagnosis: Inflorescence bracteate, paniculate, ultimate branches one-flowered. Flowers terminal, bisexual. Calyx small, persistent, sepals scaly, reflexed. Stamens shorter than carpels. Gynoecium apocarpous, of three or five ascidial carpels dehiscing along the ventral sutures. Stigma terminal, sessile, rather broad.

Hyrcantha karatscheensis (Vachrameev) Krassilov et Vachrameev comb. nov. (Plate 1, 1-5; Plate II, 1-7).

Basionym: Carpotithes karatscheensis Vachrameev, 1952, Regional Stratigraphy of the USSR, p.274, Pl. XLIV, 1-5.

Holotype: N 3302/47, Geological Institute, Moscow (Vachrameev, 1952, pi. XLIV, 3).
Locality: Karatsche-Tau Hill, western Kazakhstan.
Age: Middle Albian.
Description: The best specimen is a part of a paniculate inflorescence (Plate I, 1—3, Fig.l) with a grooved main axis 1.3 mm thick. Minute bracts occur at the nodes and there are also bracteoles on the lateral branches. A lower branch is forking twice in rapid succession, the upper branches are unbranched, one-flowered. They are subopposite, departing at acute angle. The pedicels are thin, about 10—14 mm long. All flowers are evidently at fruiting stage, of equal size, about 13 mm wide. Remains of the calyx are seen in three of them, the better preserved is shown in Plate II, 1, 2. Sepals are scaly, 1.5 mm long, reflexed and more or less appressed to the pedicel. In this specimen there is no unequivocal evidence of androecium.

Gynoecia consist of three ascidial carpels, about 7 mm long, 3 mm wide, sessile on a broad receptacle, free to the base, showing polygonal surface cells and a terminal scar (Plate II, 4—5) or a broad notch (Plate II, 4) probably representing sessile stigma.

PLATE I

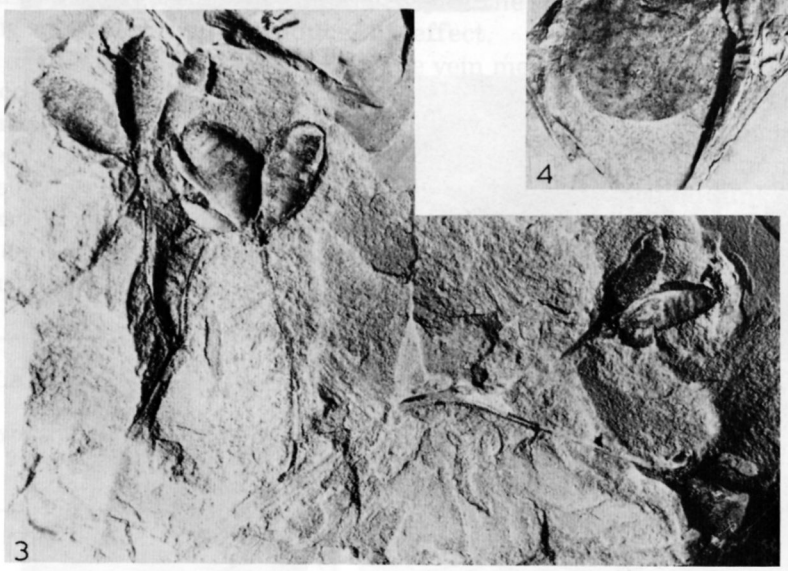
Hyrcantha karatscheensis

1, 2. Lateral inflorescence branches, X 3.
3. Part of a paniculate inflorescence, X 2.
4. Lateral inflorescence branch bearing flower. Leaflets of "*Leguminosites*" *karatscheensis* overlap the axis, X 1.5.

PLATE I


1


2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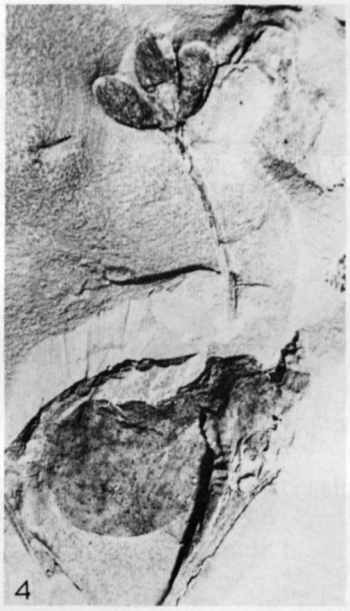
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Most carpels seem to be dehiscent along the ventral suture letting rock matrix fill the locules. The internal casts show a dorsal suture and anastomosing transverse striation (Plate II, 7).

Another specimen (Plate I, 4) is a fragment of the grooved axis 20 mm long, 1.5 mm thick, bearing a single lateral branch terminated by a flower of the same dimensions as in the holotype. This flower is significant in showing, in addition to persistent calyx and tricarpous gynoecium, distinct impressions of stamens (Plate II, 3). The filaments are about 0.5 mm thick, reaching to about mid-length of the carpels. One of them bears a crumpled anther which seems bilocular, but its structure cannot be made out with any confidence.

While flowers in these inflorescences are trimerous, a specimen figured by Vachrameev (1952) pi. XLIV, 3 shows five carpels (Fig.l).

Associated leaves (Plate III, 1—5): Inflorescences regularly associate with compound leaves described by Vachrameev (1952) as *Leguminosites karatscheensis.* In the above described specimen (Plate I, 4) the leaflets overlap main axis slightly above the node. Though they are obviously not in organic connection, the association seems noteworthy.

A few notes can be added to the original description of the leaves. While most fragments of compound leaves are pinnate, some of them (Fig.2 reproduced from pi. XXXIV in Vachrameev, 1952) suggest ternate arrangement of the leaflets. The latter show a mid vein which fades out above the middle. Secondary veins are thin, undulate, oblique to the mid vein, forking once or twice, their branches running to the margin. Tertiary veins are scalariform, straight or bowed. Veinlets of higher order form rounded meshes about 0.1 mm wide. Margins seem entire but on closer inspection show scabrations or even minute prickles on the vein ends (Plate III, 4, 5).

In SEM the leaf impressions show vague outlines of epidermal cells and fairly distinct stomatal pits which are either empty or filled with the puck-like casts of the guard cells. Rapid decay of the stomata penetrated by incrustating substances could produce this effect.

Stomata are scattered within the vein meshes (Plate III, 1, 2) occasionally occurring over the veinlets (Plate III, 2, upper right corner). They tend to be orientated along the secondary veins. The spacing of the stomata is rather regular, paired stomata seen in Plate III, 1 are rather uncommon. The guard cell thickenings are elliptical, 17 jum long, slightly if at all sunken below the leaf surface. There are no indications of specialized subsidiary cells.

Remarks: What we know about *Hyrcanta* is hardly sufficient for exact taxonomic assignment. Similar apocarpous gynoecia of three ascidial follicles

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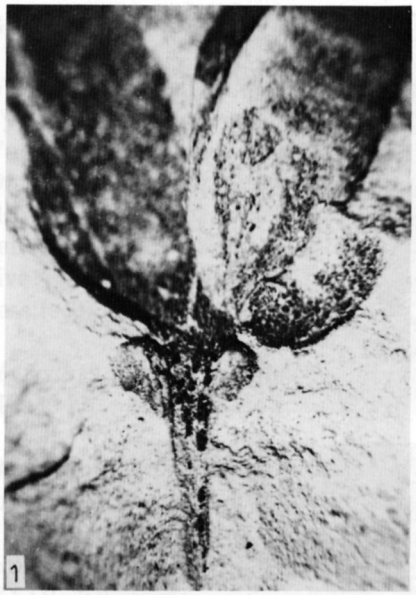
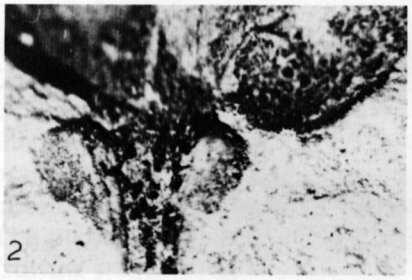
PLATE II

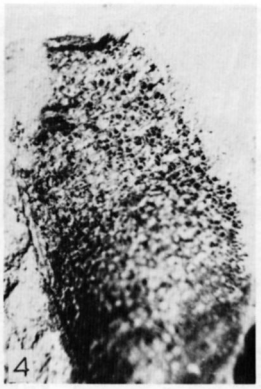
Hyrcantha karatscheensis

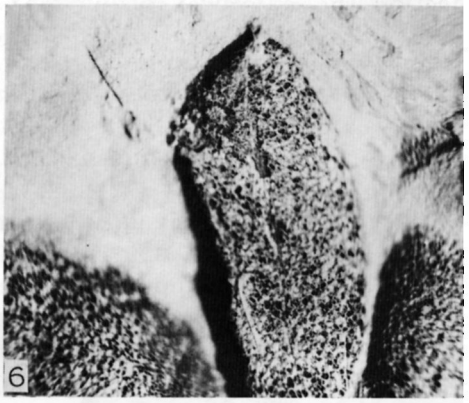
1,2. Flower showing persistent calyx, X 7 and 10.
3. Flower showing stamens, arrow on a crumpled anther, X 7.
4—6. Carpels showing terminal stigmas, X 7.
7. Internal cast of a carpel showing transverse striation, X 10.

PLATE II









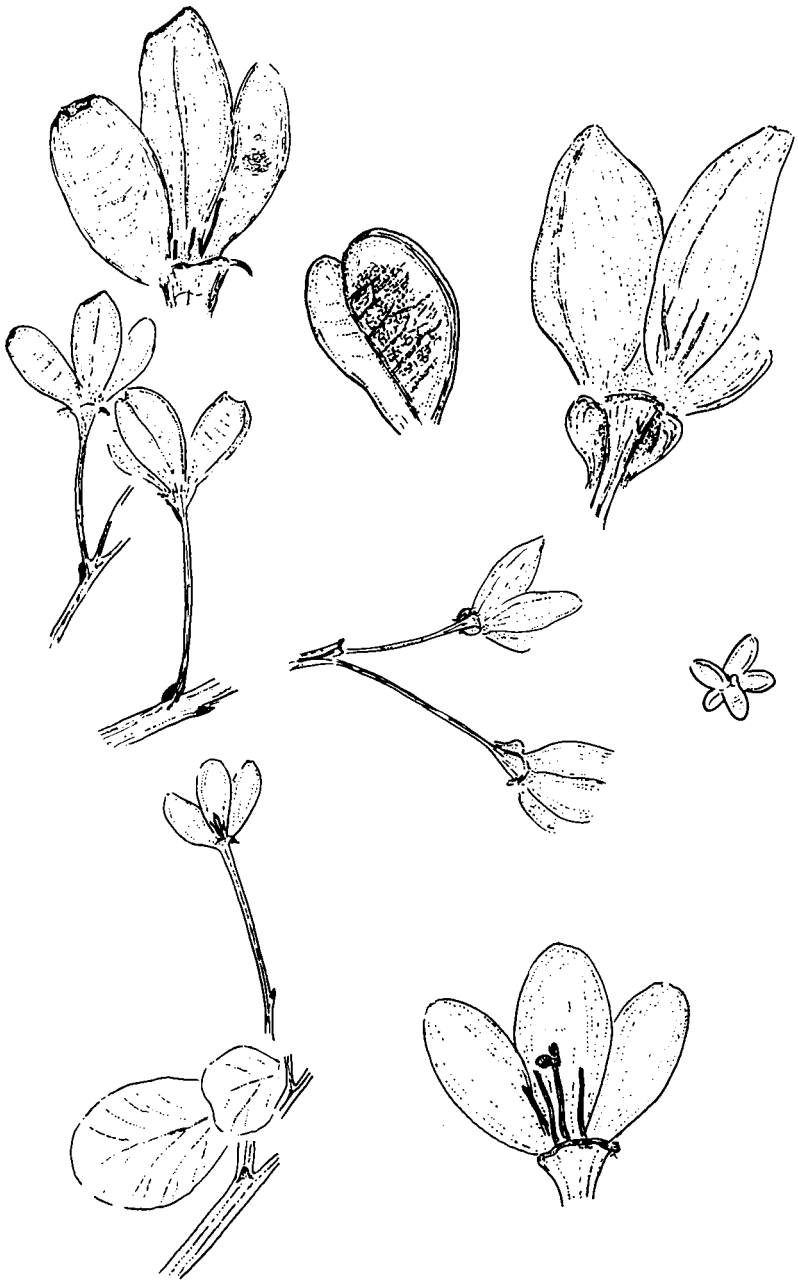
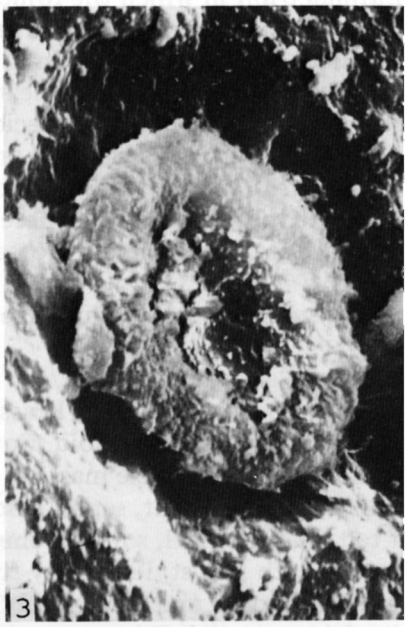
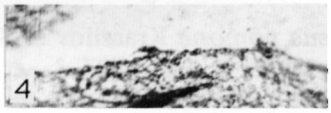
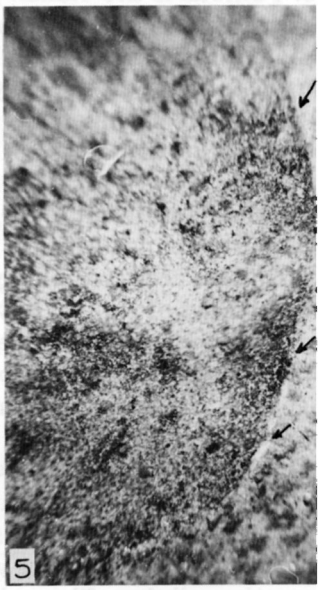


Fig.1. ***Hyrcantha karatscheensis,*** **inflorescence and flowers. A 5-merous gynoecium (middle right) is reproduced from Vachrameev (1952, pi. XLIV, 3).**

PLATE III







are known in the Ranunculaceae and especially in the extant *Thalictrum* subgen. *Euthalictrum* in which the follicles are usually sessile, about 7—8 mm long. Also in *Thalictrum the* styles are often reduced and inflorescences can be paniculate, and bracteate, as in T. *foetidum* L.

At the same time, a broad sessile stigma and persistent calyx are characteristic features of *Paeonia.* Some species of *Paeonia* (e.g. *P. caucasica)* have biternate leaves with ovate leaflets and the leaf margins can be scabrate as in *"Leguminosites" karatscheensis.* Taking all this into consideration, *Hyrcantha* can be tentatively placed somewhere in the vicinity of the Ranunculaceae and Paeoniaceae, reinforcing the often debated links between these families.

Genus *Sarysua* Krassilov et Shilin, gen. nov.

Name: After Sarysu River.
Type species: Sarysua pomona Krassilov et Shilin, sp. nov.
Diagnosis: Inflorescence cymoid, flowers actinomorphic, pedicel shorter than gynoecium, receptacle massive, bearing glands below the whorl of stamens. Calyx persistent, sepals lanceolate, caudate, reflexed. Stamens about ten, in one whorl, some of them reduced to staminodia. Gynoecium syncarpous with free styles. Ovary five-lobed, pubescent. Locules broad at the base but narrow and presumably sterile above. Styles five, of varying length, glabrous, solid. Stigma terminal, capitate.

Sarysua pomona Krassilov et Shilin, sp. nov. (Plate IV, 1—4; Plate V, 1—7; Plate VI, 1 - 5 ; Plate VII, 1 - 4 ; Plate VIII, 1 - 4)

Name: Pomona is the Italian goddess of gardens.
Holotype: N 284/67, now at repository of the Institute of Biology and Pedology, Vladivostok (Plate IV, 4; Plate V, 1, 7).
Locality: Taldysaj on the Sarysu River, south-central Karakhstan.
Age: Santonian—Campanian.
Description: Several siltstone slabs contain crowded flowers of one kind. Those in Plate IV, 1 possibly belong in the same inflorescence. No connecting axes are seen, but the flowers seem to be arranged in a regular manner allowing tentative reconstruction of the inflorescence. In this specimen, most of the 32 flowers are assembled within a rectangle three sides of which are formed by rows of parallel flowers pointing outwards or occasionally inwards. Central group comprises flowers with shorter ovaries and slightly longer styles facing each other. The most probable form of inflorescence suggested by this arrangement is a dichasial cyme (Fig.3).

All the flowers are stalked, with thin pedicels about 3 mm long and relatively massive receptacles 1.5 mm wide. They show a persistent calyx with lanceolate, longly pointed (caudate) reflexed lobes 2 mm long (Plate IV, 3). In most flowers androecium is represented by a few stamens. They are better seen in transfer preparations where the filaments or their stumps often stick up from the cellulose film as hollow cylinders. Plate VI, 1 (see also Fig.3)

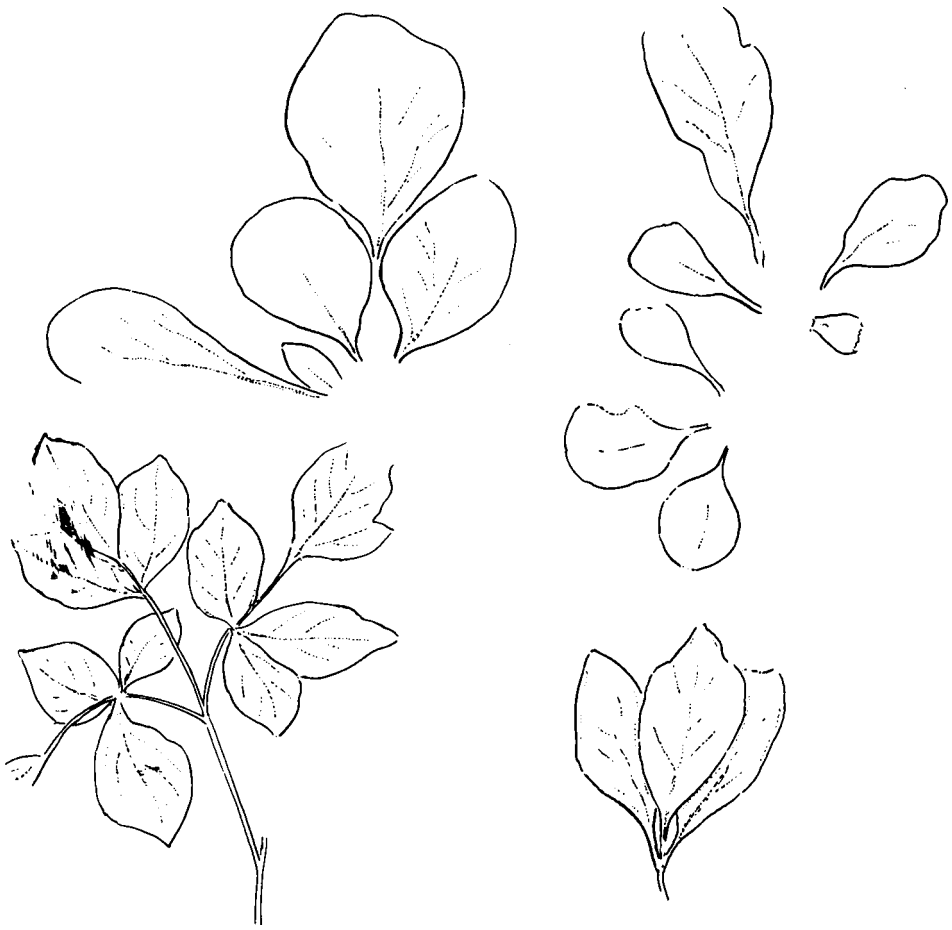


Fig.2. ***"Liguminosites" karatscheensis*****, leaves associating with** ***Hyrcantha karatscheensis,*** **reproduced from Vachrameev (1952, pi. XXXIV). A leaf of the extant** ***Paeonia caucasica*** **N. Schipez. (bottom left) is shown for comparison.**

shows stumps of eight filaments in a single whorl. Judging by their spacing, at least two filaments are missing. Hooked appendage on the left side (Plate VI, 4) could be a staminode. Clavate body seen at the edge below the stamen whorl is supposedly of glandular nature. There are also rounded scars on the receptacle, possibly left by similar glands (Plate VI, 2). In SEM the filaments are ridged, showing rows of elongate cells (Plate VIII, 4).

PLATE ill

"Leguminosites" karatscheensis

1. **SEM of a leaf impression showing stomata, X 180.**
2. **Stomata scattered in the vein meshes and occasionally over the veinlet, X 350.**
3. **Stomatal pit with a cast of guard cell thickenings, X 3000.**
4. **Margin of a leaflet, arrows on scabrations on the ends of lateral veins, X 10.**

Ovaries in most flowers are elongate conical about 7 (6—8) mm long, but the inner group of flowers in Plate IV, 1, shows much shorter ovaries, less than 2 mm long. At the same time their styles are slightly longer than in the larger gynoecia. Impressions of the ovaries show deep folds, possibly exaggerated by compression (Plate V, 4). These folds conceivably mark boundaries of the connate carpels. Ovaries cleaved through the median plane expose wings of two opposite carpels forming septae and between them a portion of the third carpel showing a longitudinal ridge — evidently the ventral suture (Plate IV, 2). Different planes of cleavage expose one of the locules which is broadly ovate at the base but narrow and slit-like in the upper half of the carpel (Plate V, 1, 2, 7). These observations suggest that the carpels were closed (ventral suture) and the upper portions of the locules were most probably sterile.

A bunch of five free styles crowns the ovary. Usually three or four of them are exposed on the rock surface (Plate V, 1—4) while the rest are broken off, leaving stumps or immersed in the rock but they can be revealed by digging with a needle. Styles are curved, about 0.7—0.9 mm long but in the flowers with shorter ovaries up to 1.1 mm long (Plate V, 5). In transfer preparations styles often stick up from cellulose film in the same manner as stamens. Stigmas are terminal, hemisphaerical or slightly concave, papillate.

In SEM the ovaries show coarse pits of the hair bases (Plate VII, 3, 4) while styles are glabrous. Cell outlines are far more distinct in styles than in ovaries. It appears that, for some reason, styles were mineralized to a higher extent than ovaries. It is possible that mineralizing solutions have infiltrated through the transmitting tissue. Epidermal cells of the styles are elongate, forming longitudinal rows. One specimen reveals subepidermal columnar cells of the stylar cortex (Plate VII, 1,2). There are no traces of vascular bundles which in styles are usually confined to the cortex. Also there are no indications of a central hollow, suggesting that the styles were solid (that is, filled with transmitting tissue). SEM of the longitudinally split styles (Plate VIII, 1—3) show what appears to be transmitting tissue. It consists of narrow longitudinally stretched cells forming undulating rows. Rounded bodies within the transmitting tissue such as seen in Plate VIII, 3 could be either secretory cavities or — a fascinating possibility which unfortunately cannot be tested at present — arrested pollen tubes.

Remarks: Surveying the extant genera of angiosperms for combination of such characters as cymoid inflorescence, actinomorphic bisexual pedicelled flower of pentamerous structure, persistent calyx, glands in the staminate

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PLATE IV

Sarysua pomona

1. **Flowers crowded on a rock slab, some of them showing regular arrangement. Note central group of shorter flowers, X 3.**
2. **Flower showing stamens and a ridge on the median carpel, arrow, X 10.**
3. **Flower showing calyx, X 10.**
4. **Group of three flowers, X 3.**

PLATE IV


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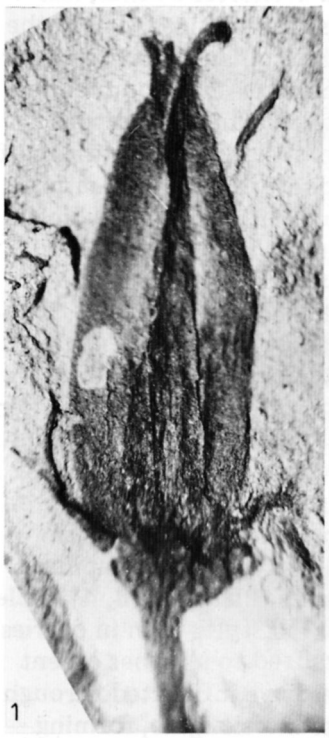
3


4

PLATE V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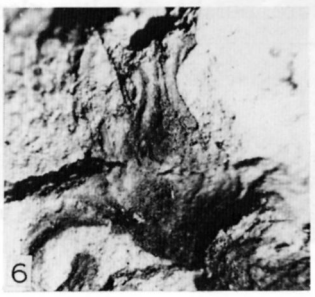
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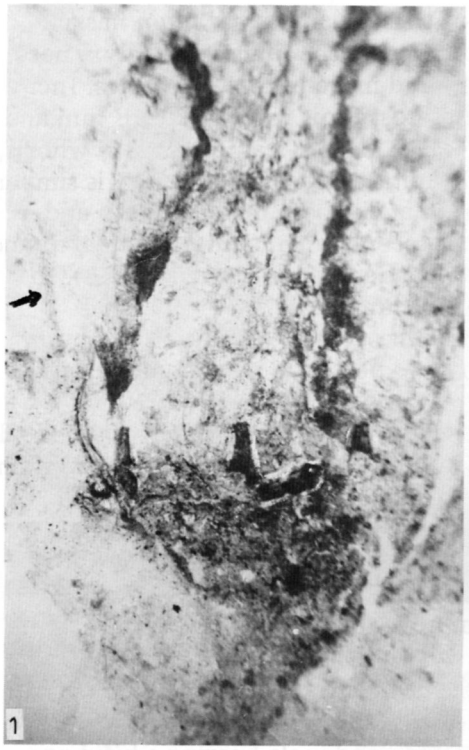
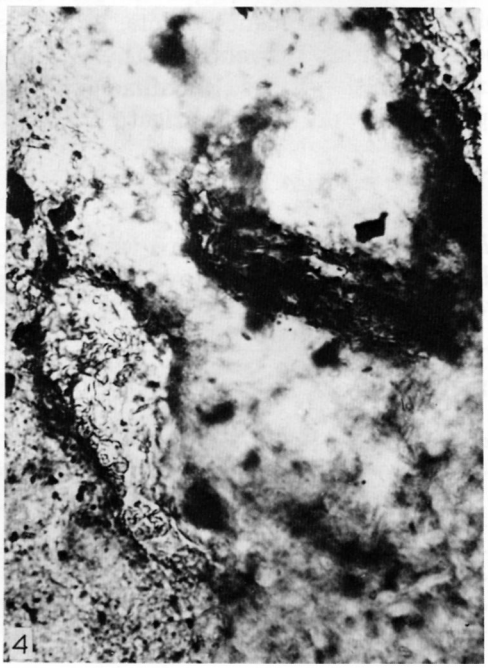
PLATE VI





whorl, syncarpous ovaries of five closed carpels with contracted locules, free styles and capitate stigmas, we singled out *Linum, Oxalis* and *Geranium* of the order Geraniales which share most of these characters. *Linum* has a dichasial inflorescence, actinomorphic flowers with a persistent calyx, nectaries on staminate disk, five-lobed ovary and more or less free styles. Incidentally, in *Linum flavum* L. styles of heterostylous forms are 6—8 mm and 8—11 mm long, much like in *Sarysua. Oxales* has ten stamens in two whorls, free styles which are often glabrous, and capitate stigmas. *Geranium* is similar in having stamens slightly if at all coherent at the base, nectar glands and conspicuously five-lobed ovary, often pubescent, with locules attenuated and sterilized in the upper half of the carpels (Kaden and Lanovaya, 1963). In this genus some stamens can be reduced to staminodia.

The coherence of stamens and appendicular central column in the ovary can be seen as derived characters not to be expected in early representatives of the order.

In polymorphic populations of heterostylous *Linum* and *Oxalis*, individuals with longer and shorter styles cooperate in the highly evolved breeding system (see Weller, 1976). It may be possible that the association of longer and shorter flowers with slightly different style lengths in *Sarysua* point to incipient heterostyly.

Genus *Taldysaja* Krassilov et Shilin, gen. nov.

Name: After the locality of Taldysaj in south-central Kazakhstan.
Type species: Taldysaja medusa Krassilov et Shilin sp. nov.
Diagnosis: Inflorescence fasciculate on a long peduncle bearing a bifid prophyll and inflorescence bracts. Branches of the fascicle spiny, distally sterile, bearing solitary flowers or in the proximal part one- or two-flowered spikelets axillary to the spines. Rachillae of the spikelets spinulate showing long sterile apeces. Flowers with imbricate perianth scales and a flask-shaped gynoecium.

Taldysaja medusa Krassilov et Shilin, sp. nov. (Plate IX, 1—7; Plate X, 1—6)

Name: Medusa — a gorgon with a head of snakes (see Plate IX, 1).
Holotype: N 284/375, now at repository of the Institute of Biology and Pedology, Vladivostok (Plate IX, 1).

PLATE v

Sarysua pomona

1. **Flower split through median plane showing side wings of two carpels and a locule of the third carpel between them, X 10.**
2. **Top of a gynoecium showing free styles, X 15.**
3. **Four exposed styles, arrow on a stump of the fifth one, X 15.**
4. **Gynoecium showing folds between the ovary lobes, X 10.**
5,6. **Flower with shorter gynoecia, X 10.**
7. **Different focus of 1.**

Fig.3. *Sarysua pomona*, arrangement of flowers supposedly representing a dichasial cyme (top) and reconstruction of a flower (bottom), diagramatic cross-section (left) and tangential section (right) of a gynoecium.

PLATE VI

Sarysua pomona

1. Transfer of a flower showing stamens, X 20. Arrow on a stamen not in focus.
2. Left portion of the same transfer, X 100.
3. Hooked appendage (staminode?) and a clavate body (gland?), transfer, X 250.
4. Scar of a gland on the receptacle, X 400.

Locality: Taldysaj on the Sarysu River, south-central Kazakhstan.
Age: Santonian—Campanian.
Description: Inflorescence is a fascicle of about eight branches, 15—20 mm wide, born on a peduncle more than 45 mm long (base lacking). The peduncle is 2 mm wide, longitudinally striated. Scars of two bracts are seen at the base of a fascicle and 8 mm below them there is a bifid bract slightly wider than the peduncle (Plate IX, 5).

The inflorescence branches spread radially and curve upwards, seem fleshy, taper to the apex. They are covered with spines which are born spirally, spreading at acute angle, thickened at decurrent base but thin, recurved and apparently soft above, leaving rounded pits when shed (Plate IX, 6, 7). Distal portions of the branches show nothing but spines and are evidently sterile. Proximally some of them bear rounded scars about 1.2 mm in diameter showing a central depression and slightly elevated margins (Plate IX, 6). The scars are about 1 mm apart, axillary to the spines. They could be left by abscissed flowers of the type seen in Plate X, 5.

Most flowers appear as ovate bodies 4—5 mm long, showing imbricate scales. Occasional planes of cleavage through flowers expose a gynoecium which is flask-shaped, slightly angular, bifid at the apex (Plate X, 1). In Plate X, 2 a longitudinally split gynoecium shows a single seed or internal cast of the locule.

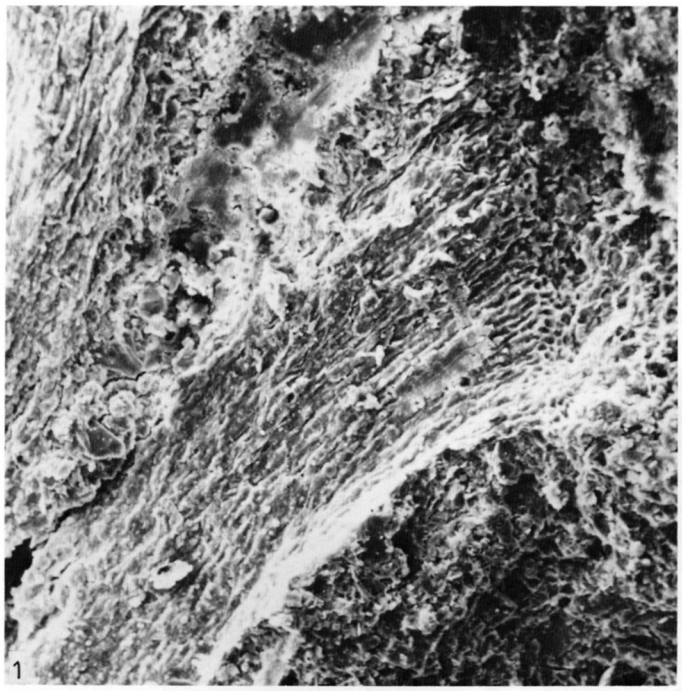
At the base of the branches flowers are so crowded that it is difficult to make out individual structures. However some observations suggest that in this region flowers were born in spikelets. Plate X, 4 shows three spirally arranged appendages the upper of which is a short spinulate branchlet. The lower two are of about the same length but consist of overlapping flowers apparently concealing axis parallel to the upper one. We suggest that two lower appendages are few-flowered spikelets while the upper spinulate branchlet is a rachilla which somehow shed its flowers. In proximal portions of other branches a delicate spinulate axis, 3 mm long — sterile tips of rachillae — arises obliquely over densely packed flowers (Plate X, 2, 3). The rachillae look like miniature branches of the first order.
Remarks: Despite many uncertainties of the above description, there is little doubt that we are dealing with fairly complex inflorescence bearing much reduced pistillate structures — flowers or, as it may be, florets or anthoids (the letter terms are applied to reproductive units of grasses and sedges). In our interpretation, the inflorescence branches are spikes showing proximal-distal gradient of complexity, that is bearing spikelets proximally and solitary flowers distally (Fig.4).

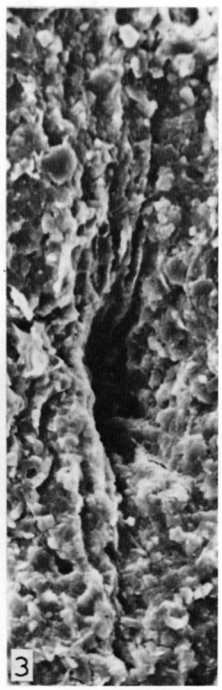
PLATE vn

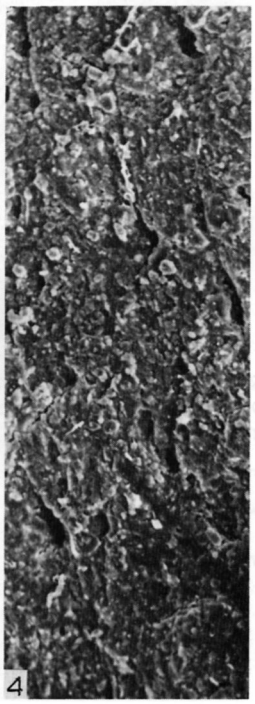
Sarysua pomona

1. SEM of styles showing epidermal cells and near the top some of cortex cells, X 200.
2. Stylar cortex cells, X 1500.
3. Hair base on the ovary, X 600.
4. Distribution of hairs on the ovary, X 150.

PLATE VII







LATE VIII

Description on p. 111.

PLATE X

Description on p. 111.

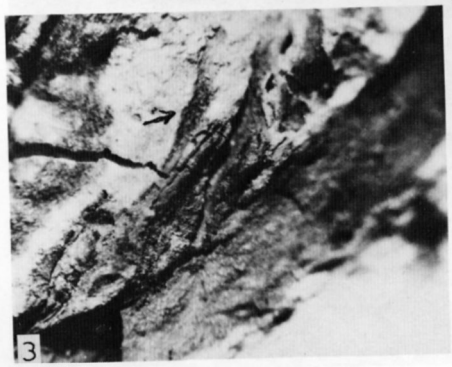
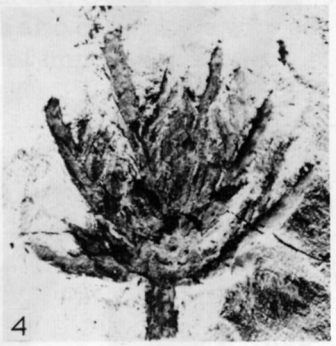
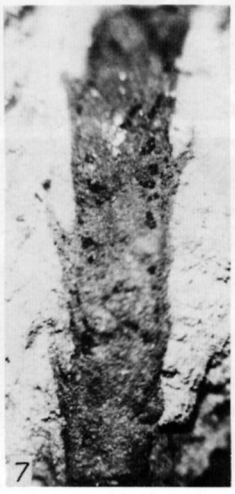


PLATE IX

Description on p. 111.





The peduncular bracts of *Taldysaja* are not unlike in some palms (Uhl, 1972) and the raised scars of flowers on the lateral branches resemble areoles of rattans (see, e.g., Dransfield, 1982). However, the general aspect of the fasciculate inflorescence is rather sedge-like and the flask-shaped bifid pistil also resembles bicarpellate gynoecia of sedges (generally considered as derived from the more common tricarpellate ones). Also in sedges sterile tips of rechillae often project beyond anthoids. The sedge comparison suggests that the spines subtending spikelets and the spinules of the rachillae are glumes (empty in the distal portions of the branches) and glumellae respectively.

DISCUSSION

Both reproductive structures hitherto known from the middle Albian of Kazakhstan — *Caspiocarpus* (Vachrameev and Krassilov, 1979) and *Hyrcantha* gen. nov. — are related to the Ranunculaceae, suggesting that this group was prominent among ancestral angiosperms. *Hyrcantha* also shows some paeoniaceous characters. *Paeonia* was linked to the Ranunculaceae by classical authors, but on the evidence of vascular anatomy it is more similar to the Magnoliaceae, while certain developmental features (though disputed, see Sawada, 1971) indicate affinities with the Dilleniaceae. Our interpretation of *Hyrcantha* seems to support the first view but it is also compatible with an assumption that *Paeonia* is a much modified relic of important ancestral plexus giving rise to a number of angiosperm lineages.

PLATE VIII (p. 108)

Sarysua pomona

1. SEM of split styles showing transmitting tissue, X 200.
2. Top of the left style, X 500.
3. Rounded body (arrested pollen tube?) in the transmitting tissue, X 600.

4. SEM of a stamen, X 300.

PLATE IX (p. 109)

Taldysaja medusa

1—4. Fasciculate inflorescences, X 2.
5. Bifid peduncular bract (prophyll?) and scars of two bracts above, X 10.
6. Inflorescence branch showing two scars of the flowers, X 10.

7. Distal part of a branch showing spines, X 10.

PLATE X (p. 110)

Taldysaja medusa

1. Flask-shaped gynoecium bifid at the apex, X 10.
2,3. Basal portion of a branch bearing spikelets. Note sterile tip of a rachilla (arrow) and a split gynoecium at its base showing seedlike body — a locule cast or ovule, X 15 and 10.
4. Inflorescence branch bearing a rachilla above and two spikelets below, X 10.
5. Inflorescence branch bearing solitary flowers, X 10.
6. Scars of shed flowers on a branch, X 10.

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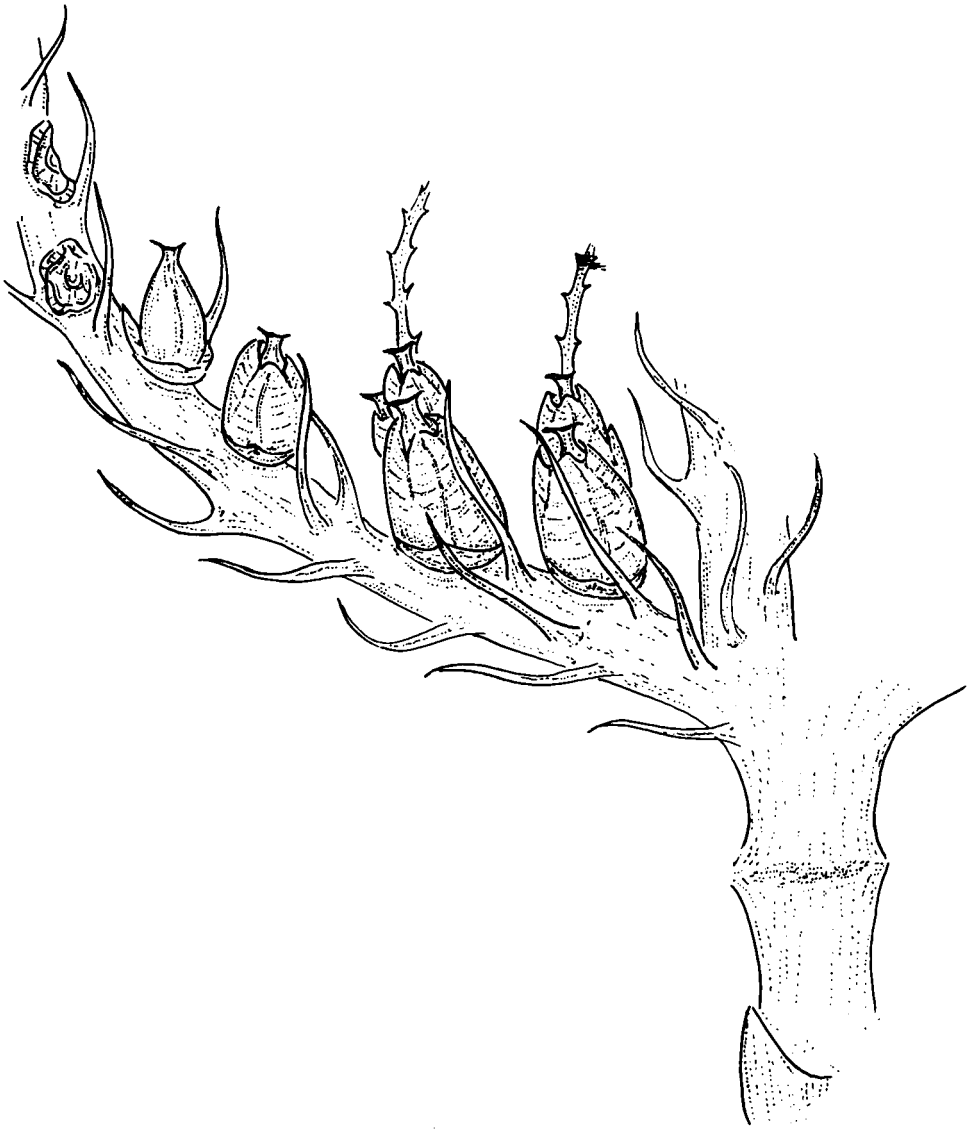

Fig.4. ***Taldysaja medusa*****, reconstruction of an inflorescence branch.**

In the Late Cretaceous diversity of the angiosperm reproductive structures was already considerable. As evidenced by *Taldysaja*, they reached a high level of complexity. *Sarysua* is similar to *Hyrcantha* in persistent calyx and in the shape and dimensions of the carpels. It is conceivable that these syncarpous reproductive structures have descended from the ancestral ranunculoid—paeonioid complex. On the other hand *Taldysaja* represents a separate line of development possibly related to the sedge-like plants from the Lower Cretaceous of the Lake Baikal and Mongolia (Krassilov and Bugdaeva, 1981; Krassilov, 1982).