BISCALITHECA (COENOPTERIDALES) FROM THE UPPER PENNSYLVANIAN OF ILLINOIS

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ABSTRACT. The frond anatomy and sporangial attachments of *Biscalitheca musata* Mamay are described from the Upper Pennsylvanian locality near Berryville, Illinois.

BISCALITHECA MUSATA has been allied with the Zygopteridaceae because of sporangial similarities with *Etapteris lacattei* and species of *Zygopteris*; however, the attachment of these to anatomically identifiable coenopterid genera has not been previously demonstrated. The vegetative parts of *Biscalitheca* and sporangial attachments in stalked soral groups were not known when the genus was established by Mamay (1957).

Materials. Two coal balls (Nos. 1271 and 7051) were collected from the Calhoun Coal near Berryville, Illinois, where the type material was obtained by Mamay (1957). The Calhoun Coal occurs in the Mattoon Formation, McLeansboro group, and is Upper Pennsylvanian in age. Coal ball 7051 contained compact sporangial masses scattered over a length of 8 cm. and a width of about 3 cm. along one edge of the coal ball. Specimen 1271 lacked the massive compaction of sporangial aggregations and included, in section, pinnately arranged soral groups along with three orders of connected frond divisions which extended across about 12 cm. in the widest section of the coal ball and was traced through a length of about 10 cm. Our description is based on specimen 1271 for the most part.

GENERAL MORPHOLOGY

The recovered portion of the frond of *Biscalitheca musata* included three orders of foliar members in a bipinnate arrangement. A stalked soral group, usually of seven sporangia, extended from the trailing edge of the base of each of the ultimate non-laminate divisions. The suggested reconstruction of a frond portion in text-fig. 1 includes a rather broad rachis with two rows of alternating primary pinnae. Soral stalks are attached on the rachis side at the junction of primary and ultimate pinnae; the relative lengths of the soral stalks are slightly exaggerated for clarity. An enlarged restoration of a sorus with a segment of the soral stalk is shown in text-fig. 2. The rachis and primary pinnae are covered by scale-like emergences exclusively and uniformly along upper or adaxial surfaces (Pl. 23, fig. 1), and similar multicellular outgrowths were preserved around the basal one-half of the ultimate divisions (Pl. 24, fig. 5).

The rachis is flattened in the plane of the primary pinnae, but the ultimate or secondary pinnae are directed slightly upward away from the rachis and out of the plane described by previous divisions (Pl. 21, fig. 1). By far the largest frond segment, which we descriptively refer to as the rachis, extended diagonally between adjacent broken edges of the coal ball for a length of only 3·5 cm. (Pl. 21, fig. 2; Pl. 22, fig. 1). Coal-ball sections including the rachis revealed a maximum of 2 primary pinnae on one side and 5 on the

other. In the broadest sectioned part of the frond, excluding the rachis, 10 primary pinnae, apparently from the same side of the rachis, were observed about 8·5 mm. from each other. It is estimated that about 12 cm. of the length of the frond was represented in the coal ball. In transverse section the rachis is broadly ellipsoidal with the lower surface more rounded than the upper. The upper surface appears to have been almost
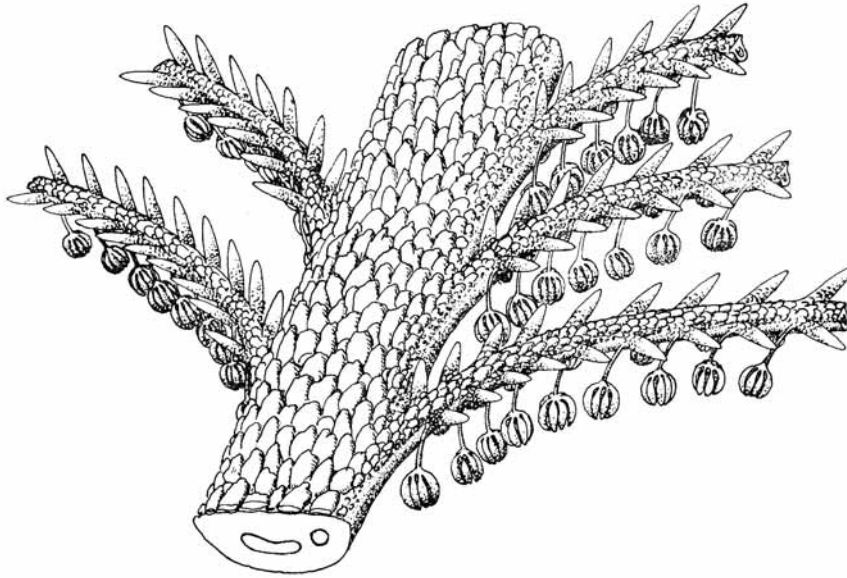
TEXT-FIG. 1. Suggested reconstruction of a portion of the fertile frond of *Biscalitheca musata*. Three orders of foliar divisions are represented with ultimate pinnae extending upward distally out of the plane of previous divisions. The stalked, circular sori occur in two rows.

flat, but this may be somewhat exaggerated, as is the width, because of crushing in the plane of the primary pinnae. The width of the crushed rachis was about 15 mm. with a maximum thickness of 3 mm.; despite inaccuracies in the dimensions attendant on crushing and the proximity of successive pinnae bases, the rachis seems to have been at least 2–3 times wider than thick. Primary pinnae were traced up to lengths of 7·5 cm., and the distance between successive primary pinnae on the same side of the rachis ranged from 7 to 11·5 mm. Measurements from the centres of primary pinnae, however indicated that the distance between pinnae was usually 8·5 mm. Primary pinnae have a maximum diameter of 3 mm. with 1·5–2·0 mm. the most common diameters encountered. Each primary pinna exhibits a striking branching pattern in which opposite to sub-opposite pairs of short cylindrical divisions arise distichously (Pl. 21, fig. 1). The bases of successive pairs of secondary pinnae are 7–8 mm. apart and the distal portions, without emergences, are oriented slightly upward and distinctly toward the end of the primary pinna. The secondary, or ultimate pinnae, are approximately 1·8–2·1 mm. in

basal diameter and tapered distally through a length which preservationally did not
exceed 8 mm. The smoothly cylindrical to slightly angular soral branches are 4–5 mm.
long and 0·5–0·7 mm. in diameter (Pl. 22, fig. 3; Pl. 23, fig. 2). Representative sections
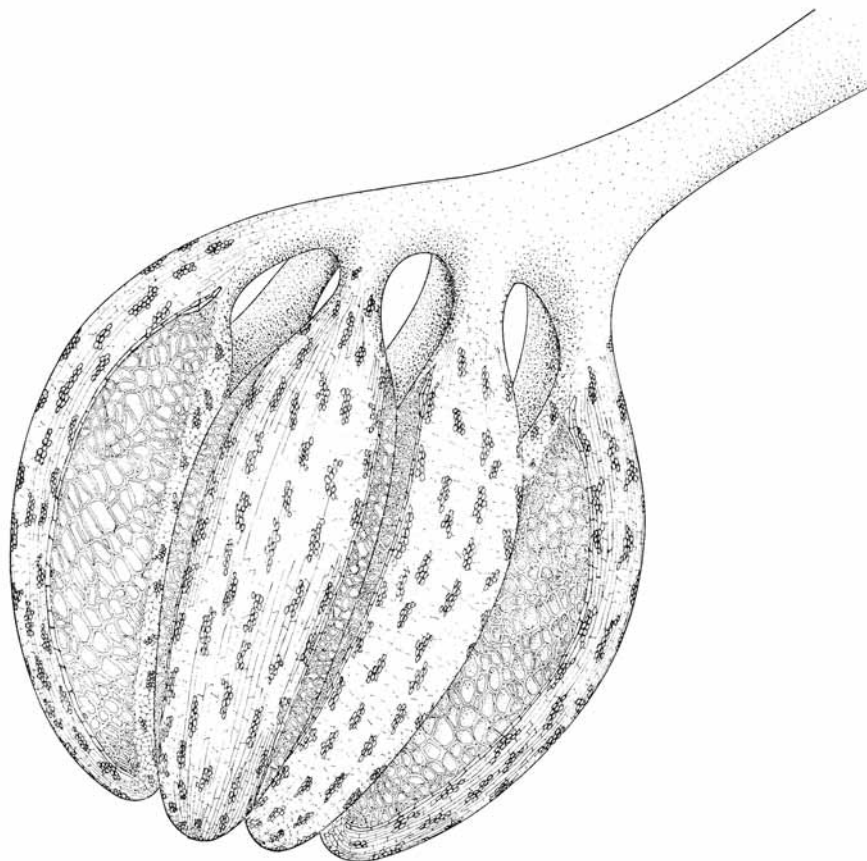
TEXT-FIG. 2. Suggested reconstruction of stalked, circular sorus of *Biscalitheca musata* with apparently
the region of dehiscence of each sporangium facing outward.

through a sorus showing the general arrangement of the soral stalk and attached
sporangia are shown in Pl. 23, figs. 2, 3 and Pl. 24, fig. 3. The banana-shaped sporangia
are 3–4 mm. in length, and spatially, in the coal ball, the two sori from an opposite pair
of ultimate divisions extended toward the rachis to very near the base of the pair of
ultimate divisions next behind. The sori were frequently appressed alongside the primary

pinna, directed toward the rachis; in Plate 22, fig. 6, the soral stalk is shown above, one of the sporangia below, and the junction of primary and ultimate pinnae at the bottom.

FROND ANATOMY

Rachis. The width of the xylem strand of the rachis is about 0·85 mm. with a minimum thickness at the ends of 0·4 mm. prior to prominent trace formation. The somewhat bar-shaped xylem appears to have a slight median, adaxial groove, and the adaxial to slightly lateral trace formation and emission imparts some adaxial curvature to the strand (Pl. 21, fig. 2; Pl. 22, fig. 1). The abaxial side of the strand is relatively flat. In accurate transverse sections, the xylem strand appears to be flattened laterally. Trace formation and emission are marginal, and in cross section, the crescent to semicircular-shaped pinna traces are about twice as wide as thick. Trace formation consists of an increase of tracheids along the adaxial portions with lateral extension beyond the sides of the abaxial portion of the band (Pl. 21, fig. 2); with departure of the pinna trace, the associated portion of the adaxial face is flattened and the other adaxial edge exhibits trace formation (Pl. 22, fig. 1). Distinct adaxial arms are not distinguishable. Tracheid diameters in the rachis xylem range from 20–80 μ. Protoxylem groups are not usually distinct, and tracheids of smallest diameter appear to be limited to the median portion along the adaxial face or immediately beneath the median portion of the adaxial face. One protoxylem group may be observed associated with incipient traces, but during trace emission the protoxylem could not be clearly followed. The vascular strand of the rachis is outlined by a narrow dark band of amorphous material which is separated from the tracheids by an unpreserved zone of about 100 μ in width.

Primary pinnae. Xylary strands of primary pinnae differ somewhat in transverse configuration from that of the rachis and also from those of the ultimate pinnae. The abaxial face, both sides and, at certain stages, even the adaxial face of the xylem is flattened in primary pinnae (Pl. 21, fig. 3; Pl. 22, fig. 2). The xylem strand is about 0·4 mm. thick, and the maximum width, which is attained across the abaxial portion, is slightly less than the thickness. The strand becomes narrower adaxially, and during trace formation and emission two adaxial extensions develop. The xylem strand usually exhibits a slight median adaxial groove which becomes more prominent immediately prior to trace emission (Pl. 24, fig. 4). Extending abaxially from the slight groove, a narrow zone of smaller tracheids frequently gives the appearance that the strand is essentially U-shaped with the arms of the U appressed (Pl. 21, fig. 1; Pl. 22, fig. 2). In well-preserved specimens the continuity of the tracheids along this zone can be seen. Along the adaxial face of the strand, the proximity of the two extended trace portions may temporarily enclose a small non-tracheidal zone between them. The zone between the trace-contributing edges of the xylem strand frequently appears as an unpreserved peripheral loop (Pl. 21, fig. 3). The dimensions of the loop are approximately $50 \times 75 \mu$.

Sori and their attachment. The minute traces from the primary pinnae branch at the base of the ultimate pinnae and a small vascular segment passes into the soral stalk (Pl. 24, fig. 4). The soral stalk consists of a central xylem core, cylindrical to slightly elliptical in cross-section, and there is a zone of ground tissue with scattered secretory

cells along the innermost edge (Pl. 22, fig. 3; Pl. 24, fig. 4). Secretory cells extended throughout the length of the soral stalk into the slightly expanded and branched portion where sporangia are attached (Pl. 23, figs. 2, 3; Pl. 24, fig. 3).

The sporangia are borne in compact clusters of 6–9 with 7 being a quite regular number. Three representative sections through a sorus of 7 sporangia are shown in Plate 23, fig. 4 and Plate 24, figs. 1, 2 with portions of all 7 appearing in Plate 24, fig. 1. The sporangia exhibit a distinct orientation in many sori, and it is suggested that this was probably the initial arrangement with all the sori (text-fig. 2). The distal end of each sporangium arches toward the centre of the sorus. The dorsiventral faces of sporangia are oriented toward and away from the centre of the soral aggregation with annuli directed more or less toward those of laterally adjacent sporangia. The lower surface of the sporangium (according to Mamay's description) with smaller, irregularly shaped and oriented cells, faces toward the inside of the soral group. The orientation of sporangia in the sori, with the outer wall composed of slender cells with the elongate dimension parallel to the sporangial axis, suggests that the outer face constituted a region of dehiscence.

Sporangia and spores. The sporangia and spores have been described in detail by Mamay (1957), and our specimens agree with the type material in the gross morphology of the sporangium and spores. We have calculated that a sporangium 3·6 mm. long and 0·9 mm. diameter contains about 8,000 spores of 65 μ diameter. All the sporangia of a given sorus either exhibited (Pl. 22, fig. 5) or lacked (Pl. 23, fig. 2) dark coloured, endosporal contents.

Non-vascular tissue with moderately thick cell walls occupies the central region of each sporangial pedicel (Pl. 21, fig. 5) and joins the divisions of vascular tissue from the soral stalk. In some sporangia an inner wall layer 1–2 cells in thickness of non-indurated cells is frequently observed (Pl. 22, fig. 5); in particularly well-preserved sporangia the inner wall layer is 4–5 cells in thickness. In longitudinal section these cells measure approximately $30 \times 160 \mu$.

Ultimate pinnae. The xylary strand of the ultimate pinna in cross-section is band-shaped with a slight adaxial curvature. The xylem band is 4–5 cells thick and up to 15 tracheids wide (Pl. 21, fig. 1, upper left), and tissues immediately surrounding it are thin-walled, parenchymatous cells of extremely small diameter (Pl. 24, fig. 5).

Vascular tissue. Tracheids are generally scalariform in all the foliar members and in the soral stalks (Pl. 21, fig. 4; Pl. 22, fig. 4). Along the adaxial and lateral faces of the xylem of the primary pinnae is a rather well-preserved narrow band of up to 4 cells which apparently constituted a phloem zone (Pl. 22, fig. 2); no sieve areas were observed.

EXPLANATION OF PLATE 21

Figs. 1–5. *Biscalitheca musata.* 1, Primary pinna, T.S., with secondary pinnae laterally, oblique. Note soral stalk left of primary pinna, T.S. Slide 1950, ×34. 2, Rachis with vascular strand at incipient stage of trace formation. Multicellular outgrowths on adaxial (upward) surface. Slide 1919, ×34, T.S. 3, Primary pinna with peripheral adaxial loop and departing trace. Slide 1929, ×135, T.S. 4, Scalariform thickenings of xylem of primary pinna. Slide 1943, ×96, L.S. 5, Multistratose annulus wall and pedicel of sporangium. Slide 1948, ×135, T.S.

During pinna trace emission, tissue from this zone accompanied the xylem portion of the trace. The phloem zone was separated from the xylem and, in turn, from cortical tissues by distinct dark lines or narrow bands of apparently crushed parenchyma.

Cortex. The cortical anatomy of the rachis and primary pinnae is essentially the same. The inner cortex is about one-half the width of the outer cortex. The most conspicuous components of the inner cortex are large, moderately thick-walled cells measuring about 150 μ in diameter and 230 μ in length. The large cells are arranged in vertical series end to end, and the lumens of many are filled with a black substance; 2–4 of these secretory chains of cells may be seen along a given radius of the inner cortex. Intermixed among the vertical series of large cells are numerous small, isodiametric parenchyma cells. The inner portion of the outer cortex is composed of larger parenchyma cells, minimally of 85 μ diameter and isodiametric; these centrifugally give way to successively longer parenchyma cells attaining lengths from 150–250 μ with a maximum diameter of 95 μ within a band of some 5–6 cells in thickness. The end walls are transverse. The outer and larger portion of the outer cortex exhibits progressively longer cells with smaller diameters, slightly thicker walls, and tapered end walls. The ground tissue of ultimate pinnae is composed of uniformly parenchymatous cells, usually longer than wide (Pl. 21, fig. 1, right), attaining maximum diameters of 160 μ. Secretory cells observed in the ultimate pinnae were limited to the lower portion and frequently were entirely absent.

Epidermis and emergences. Epidermal cells of the primary pinna are quite small and somewhat rectangular in cross-sections of a pinna; the epidermis is not well preserved in the rachis. Hairs are not present. The adaxial surface of the rachis and primary pinnae and the lower half of the roughly cylindrical ultimate pinnae are covered with emergences which vary from 450–625 μ in width and up to 240 μ in thickness. The emergences are irregular to ellipsoidal in section; they appear to be slightly indented or notched at the tip (Pl. 21, fig. 2). These multicellular outgrowths are composed of uniformly thin-walled cells with a maximum diameter of 85 μ; the outermost cells are slightly smaller and frequently contain dark coloured material. Stomata were not observed.

SYSTEMATIC TREATMENT

Genus BISCALITHECA Mamay 1957

Type species. B. musata Mamay 1957.

Emended diagnosis. Fertile frond bipinnate, non-laminate, rachis up to 15 mm. wide, 12 cm. long; alternate penultimate pinnae, 8·5 mm. (7–11·5 mm.) apart, 3–1·5 mm. wide, up to 7·5 cm. long; opposite to subopposite ultimate pinnae 7–8 mm. apart, 2·1–1·8 mm. in diameter, up to 8 mm. long; ultimate pinnae extend distally out of plane of other frond divisions.

Emergences, scale-like, slightly bifid, uniformly along adaxial surface of rachis and primary pinnae and around proximal one-half of ultimate pinnae.

Xylary strands in transverse section, shallow C-shaped in rachis and ultimate pinnae, and quadrilateral in primary pinnae with broad abaxial face tapering laterally to narrow adaxial face; protoxylem groups adaxial where distinct; tracheidal thickenings scalariform.

Cortex, two-zoned; inner cortex one-half width of outer, composed of large, moderately thick-walled cells ($150 \times 230\,\mu$) with long axes end to end in vertical chains, intermixed small, isodiametric parenchyma cells; outer cortex centrifugally exhibits gradation from isodiametric to elongate parenchyma cells with transverse end walls to narrow, fusiform.

Soral stalk, attachment at trailing edge of junction of primary and ultimate pinnae, 7–8 mm. apart, probably pendant to trailing, terete to slightly angular, 0·5–0·7 mm. diameter, 4–5 mm. long, with terete xylary strand branching into 7 (6–9) divisions near base of as many terminal, sporangial pedicels; scattered secretory cells in inner cortical zone. Sorus, circular, with 7 (6–9) sporangia distally curved toward centre with annuli lateral and region of dehiscence away from centre. Sporangial pedicels terete, to 0·35 mm. in diameter, non-vascularized, attached to divisions of soral stalk.

Sporangia banana-shaped, 3–4 mm. long, 0·9–1·1 mm. in diameter, bilateral, dorsiventral; sporangial wall unistratose to multistratose with a pair of lateral multiseriate, longitudinal annuli, 10–12 cells wide; outer sporangial wall between annuli containing elongate, double-rowed sclerotic nests ($250 \times 80\,\mu$) and elongate-fusiform ($100 \times 20\,\mu$) cells in the region of dehiscence, paralleling sporangial axis on outer face; cells of inner face between annuli, smaller and less regular in shape, intermixed with sclerotic nests less uniformly oriented.

Spores spherical, trilete, usually 58–70 μ in diameter (range 38–100 μ) endosporal contents frequent.

Remarks. Additional details on sporangia and spores are to be found in the original diagnosis by Mamay (1957) and need not be repeated here. This amended diagnosis is based on specimen 1271, slides 1917 through 1950, and peel preparations in the paleobotanical collection (Morrill Hall), Botany Department, University of Illinois, Urbana, Illinois.

Discussion. Biscalitheca presents certain points of close similarity to those of *Etapteris lacattei* (Renault) Bertrand although Mamay (1957) did not regard them as congeneric. We agree with Mamay's treatment, but the sporangia described under these two generic names are so striking in their size, shape, and massive lateral annuli that their close relationship is strongly suggested. Our description of *Biscalitheca musata* affords information on the vegetative parts, and certain features of the vascular anatomy are quite different from the frond parts of *Etapteris lacattei*. In view of the sporangial similarities and anatomical dissimilarities of the fronds of *Biscalitheca* and *E. lacattei*, it seems desirable to summarize the rather confusing nomenclatural history of the sporangia presently referred to *E. lacattei*.

The distinctive features of vascular tissues in the frond axes of *Zygopteris elliptica* and *Z. lacattei* were first described and figured by Renault (1869, pl. 7, figs. 10, 12); Bertrand

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EXPLANATION OF PLATE 22

Figs. 1–6. *Biscalitheca musata.* 1, Trace departure from vascular strand of rachis. Slide 1921, ×34, T.S. 2, Vascular strand of primary pinna; adaxial side on right. Slide 1923, ×135, T.S. 3, Soral stalk. Slide 1936, ×135, T.S. 4, Tracheids of soral stalk with scalariform thickenings. Slide 1918, ×135, L.S. 5, Pedicellate sporangium with multistratose wall sectioned through annulus. Slide 1917, ×34, L.S. 6, Primary pinna, right, oblique L.S., ultimate pinna, lower left, soral stalk, upper left, sporangium from soral stalk, middle left. Slide 1945, ×34.

(1909, 1911) later concluded that *Z. elliptica* was a foliar division of *Z. lacattei*, and he substituted the new combination, *Etapteris lacattei*. The identity of *Zygopteris* and *Etapteris* has been demonstrated by Sahni (1932), and reference may be made to the informative study of stem and frond anatomy of *Zygopteris* by Baxter (1952); it is not necessary to review that point here.

In 1876 Renault described as 'fructifications of *Zygopteris*' terminal clusters of sporangia which are about 2·5 mm. long, banana-shaped, and with a massive, multiseriate annulus running along opposite sides of each sporangium (1876, pl. 1, figs. 1, 2, 2 *bis*, 3). Renault also included a figure of the petiole of *Zygopteris lacattei* (1876, pl. 1, fig. 4), but he did not demonstrate that the sporangia were attached to *Z. lacattei*; Bertrand (1909, 1911) also held the opinion that the sporangia, as originally figured by Renault, were borne by *Etapteris lacattei*, but no evidence of this was presented. The attachment and affinity of this anatomically known, stalked, soral group, therefore, has been inferred.

An additional series of binomials were simultaneously introduced with accompanying illustrations of zygopterid frond compressions by Renault (1876, pl. 1, figs. 12–17), by Grand'Eury (1877) and by Renault and Zeiller (1888, pl. 32, figs. 5–7). Renault (1876, p. 23, text) employs the name *Androstachys* for the fertile frond parts (= *Androphyllum* on his pl. 1, figs. 14, 15) and *Schizopteris pinnata* Grand'Eury for sterile ones. Grand'Eury (1877, p. 201, text) in turn, employed the binomial, *Schizostachys frondosus* (= *Androstachys frondosus* in his pl. 17, fig. 3). Finally, both the sterile and fertile frond parts were figured under the binomial, *Zygopteris pinnata*, by Renault and Zeiller (1888, pl. 32, figs. 5–7).

Certain points seem to be especially critical in clarifying the nature of this group of fossils in which the taxonomy is hardly less complex than the structure of the sporangium wall. The sporangia of the two suites of fossils (petrifactions and compressions) originally figured by Renault (1876) and referred to *Etapteris lacattei* and *Zygopteris pinnata* respectively display the characteristic, massive, lateral annuli suggesting rather strongly that they represent the same genus if not the same species. While the massive annuli are highly distinctive, the lack of details and inconsistencies in subsequent French illustrations render exact comparisons impossible. The sporangia described by Renault on the basis of petrified specimens and compressions are probably closely related to the American *Biscalitheca*; detailed comparisons of sporangial morphology with *Biscalitheca musata* have been previously made by Mamay (1957).

Further comparisons of *Biscalitheca* may be made with the soral aggregation and soral stalk of *Etapteris lacattei* in addition to the fertile frond compressions of *Zygopteris pinnata* and *Monoscalitheca fasciculata* which are not known anatomically. Terminal, stalked clusters of sporangia were borne by all four taxa, ranging in number from 3–8 in *Etapteris lacattei* to 10–16 in *Monoscalitheca fasciculata*; the range of sporangial number per sorus is more restricted in *Biscalitheca*, and seven is the usual number. The sporangia in all four taxa are pedicellate; however, the soral stalks of *Zygopteris pinnata* are quite short compared to those of *Monoscalitheca* and *Biscalitheca*. Soral stalks in the last two genera attained lengths of 4–5 mm. which are approximately comparable to the maximum lengths attained by their sporangia. The soral stalks of *Biscalitheca* are 0·5–0·7 mm. in diameter compared to 1 mm. in *Monoscalitheca*. In *Etapteris lacattei* the sorus was borne on a small cylindrical axis (Renault 1876, pl. 1, fig. 4 *bis*) with a minute

stele of 12–14 small cells, presumably tracheids, and scattered secretory cells are present in the surrounding ground tissue. These anatomical features seem important because they compare closely with the corresponding soral stalk of *Biscalitheca*. The soral stalk of *Etapteris lacattei* was approximately 1·3 × 1·8 mm. in a slightly oblique transverse section based on measurements of Renault's illustration. There is, however, no conclusive evidence that the soral stalk figured by Renault and in other publications cited above was borne on a *Zygopteris* frond. Despite regular soral arrangements in *Biscalitheca* and *Etapteris lacattei*, compact sporangial aggregations of both taxa have been encountered (Mamay 1957; specimen 7051, this study; Renault 1896, fig. 8, pl. 31), and in these specimens attachment of soral stalks to the frond was not established. Although the anatomy of the highest orders of frond divisions of *Zygopteris* is not presently known, the differences in the anatomy of foliar members of *Biscalitheca* and *Zygopteris* or *Etapteris* seem to emphasize the difficulty in relating *Biscalitheca* to any previously described zygopterid or in clarifying the possibility of soral attachment of sporangia referred to *Etapteris lacattei*.

The vascular strands of the frond of *Biscalitheca*, except in the soral stalks, exhibit bilateral symmetry, and the rachis and primary pinnae occur in the same plane. The primary pinnae of *Etapteris lacattei* and *E. scotti*, which are on the order of 4–5 mm. in diameter, also possess bilateral symmetry, and both species give rise to two rows of arc-shaped pinna traces. Subsequent changes of the xylary strands of the secondary pinnae are not known. A pair of antennae are present on one face of the xylary strand of the primary pinna of *E. lacattei*, and traces to secondary pinnae arise from a pair of ridges associated with protoxylem on the opposing face. This is distinct from *Biscalitheca* which exhibits no antennae; the abaxial face of the two trace-bearing orders (i.e. rachis and primary pinnae) is more or less flattened.

The transverse xylary configuration of the primary pinnae of *E. scotti*, as figured diagrammatically by Bertrand (1909, text-fig. 21), bears some resemblance to that of the primary pinnae of *Biscalitheca* (Pl. 21, fig. 3; Pl. 22, fig. 2). Both types of vascular strands are widest along the abaxial face, and a small peripheral loop-like zone is sometimes formed during trace formation in *Biscalitheca*. The median groove of the abaxial portion of the xylem in *E. scotti* is not evident in *Biscalitheca*. Although there appear to be several similarities in primary pinna strands of *E. scotti* and *Biscalitheca* (the range of zygopterid tracheids includes scalariform thickenings), no close relationship can be suggested. There is no evidence at present that the frond portion of *Biscalitheca*, which we have described, originated from a quadriseriate phyllophore as in *Etapteris*.

EXPLANATION OF PLATE 23

Figs. 1–4. *Biscalitheca musata*. 1, Primary pinna with stalk of sorus at left. Common trace to soral stalk and ultimate pinna at right. Multicelluar outgrowths on adaxial (upward) surface. Slide 1944, × 34, T.S. 2, Sorus and stalk. Slide 1937, × 22·5, L.S. 3, Sorus; see also fig. 2 and plate 24, fig. 3. Slide 1939, × 22·5, L.S. 4, Sorus; see also Plate 24, figs. 1, 2. Slide 1927, × 22·5, L.S.

EXPLANATION OF PLATE 24

Figs. 1–5. *Biscalitheca musata*. 1, Sorus with 7 sporangia, Slide 1925, × 22·5, L.S. 2, Sorus; see also fig. 1, and Plate 23, fig. 4. Slide 1926, × 22·5, L.S. 3, Sorus; see Plate 23, figs. 2, 3. Slide 1941, × 22·5, L.S. 4, Primary pinna with attached soral stalk, at right. Slide 1928, × 34 T.S. 5, Ultimate pinna in proximal region. Slide 1945, × 34, T.S.

The foliar anatomy of *Biscalitheca* appears to be distinct from that of previously described coenopterids. It has been previously pointed out (Phillips and Andrews 1966) that the filicoid foliar member illustrated by Mamay (1957, fig. 12) is similar to *Catenopteris simplex*; however, there is presently no further evidence that *Catenopteris* and *Biscalitheca* may be complementary plant parts. A shallow C-shaped vascular strand occurs in the petiole of *Catenopteris*, tracheidal thickenings are scalariform as in *Biscalitheca* and the two genera are presently known only from the Berryville locality. The distinctive anatomy of the inner cortex of the rachis and primary pinnae of *Biscalitheca* has not been observed in the petiolar bases of *Catenopteris*. The ultimate divisions of the frond of *Biscalitheca* also exhibit a narrow band of tracheids forming a shallow C-shape in cross-section (Pl. 21, fig. 1, upper left) and do not exhibit the distinctive inner cortical anatomy of previous divisions. Multicellular scale-like emergences partially cover the ultimate divisions and occur along the adaxial surface of the rachis and primary pinnae. These have not been observed in *Catenopteris*.

The exact order of division represented by the unattached specimens of *Biscalitheca*, *Monoscalitheca*, and *Zygopteris pinnata* are uncertain. It seems quite probable, however, that the largest frond members, which in each genus are markedly broad, are primary pinnae if not rachises and, on the basis of size and location of sori, that we are comparing similar parts of the three taxa. Grand'Eury (1877) described a rachis fragment of *Zygopteris pinnata* (= *Androstachys frondosus*) about 15 cm. long with primary pinnae having a maximum length of 8 cm. The sori are borne for the most part along one side of the primary divisions, but his figures reveal little in the way of significant details. The orientation of the short-stalked sori of *Z. pinnata* appears to be more or less toward the distal end of the primary pinnae which bear them, and the orientation in *Monoscalitheca* is similar. The sori are about 3 mm. apart in *Monoscalitheca*, and one slightly overlaps the base of the next. According to Abbott (1961): 'The sori are borne almost immediately on the acrostichous or lower side of the branch as the branch leaves its larger axis.' The portion of the recovered frond of *Monoscalitheca* was 6–8 cm. in length with primary divisions attaining lengths up to 6 cm. and about 5 mm. apart. At least 12 cm. of the *Biscalitheca* frond was recovered with primary divisions usually 8·5 mm. apart and lengths of 7·5 cm. attained. *Biscalitheca* exhibits one additional order of division, one which projects out of the plane of the remainder of the frond segment. If the ultimate members of the frond of *Biscalitheca* were removed, an arrangement of sori (i.e. linear on the lower to lateral margins of the primary pinnae) somewhat similar to *Monoscalitheca* and *Zygopteris pinnata* would result. The question may be raised concerning the presence of an additional division in these last two taxa which, if not in the same plane as previous divisions, may not be readily apparent in the splitting of compression specimens.

The similarities of frond size, soral arrangement, and, to a certain extent, the number and arrangement of frond divisions further add to the close comparisons of sporangial morphology among *Biscalitheca*, *Monoscalitheca*, and *Zygopteris pinnata*.

The high degree of specialization evident in well-preserved sporangia of *Biscalitheca* and *Monoscalitheca* is unparalleled among ferns outside of those attributed to the zygopterid group. The sporangia are much more complex than any living free sporangiate types. Although the evidence is indirect, the bulk of information available suggests that the sporangium of *Biscalitheca* developed in a eusporangiate manner; this includes

the massive size of the sporangium, large spore output (8,000 per sporangium), extensive annulus development and the preservation of a wall more than one cell in thickness. The development of an extensive annulus or annuli is exhibited by *Botryopteris globosa*, *Anachoropteris involuta*, and a number of other coenopterids of the late Paleozoic, but none compare closely with the extent and precise annulus orientation of *Biscalitheca* and the presumed sporangia of zygopterid ferns.

ADDENDUM

Sometime after this study was completed and submitted for publication a new species of the genus, *Biscalitheca kansana*, was described by Cridland (1966). His fossil is a compression specimen and was collected from the Lawrence shale in the Upper Pennsylvanian of eastern Kansas. This horizon is only slightly above the Calhoun coal from which *B. musata* was obtained (Cridland, Morris, and Baxter 1963, p. 63).

The sporangia of *B. kansana* lack the small nests of minute sclerotic cells in their wall; otherwise they appear to be identical with those of *B. musata*. If we are dealing with two species it is evident that they are very closely related. Cridland, of course, receives full credit for discovering the frond, or frond fragment, on which these unique sporangia were borne. It seems interesting and significant that his restorations of a portion of the frond, and the individual sporangial aggregates, are very close to ours, since his study was based on a compression and ours on a coal ball petrifaction. It is convincing evidence that modern techniques enable us to reach essentially identical conclusions when dealing with a fossil that is preserved in two very different ways. That the two species are closely related is obvious but beyond this our studies have yielded almost wholly different kinds of information. Our study of *B. musata* has been concerned primarily with anatomical features and these in turn have enabled us to deal with certain previously described fossils. Since this in no way duplicates Cridland's contribution it has not seemed necessary to alter our manuscript.
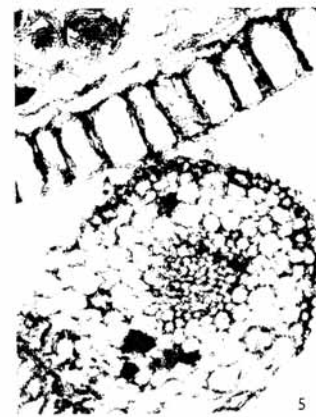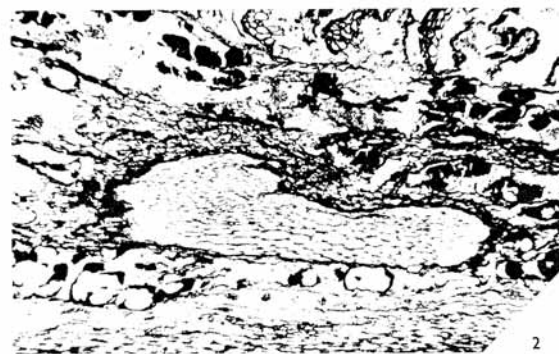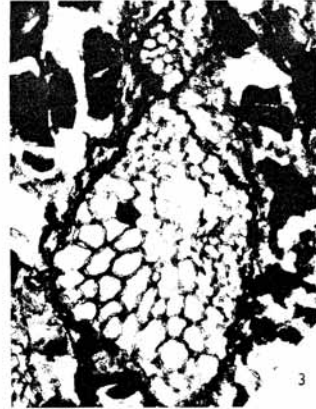
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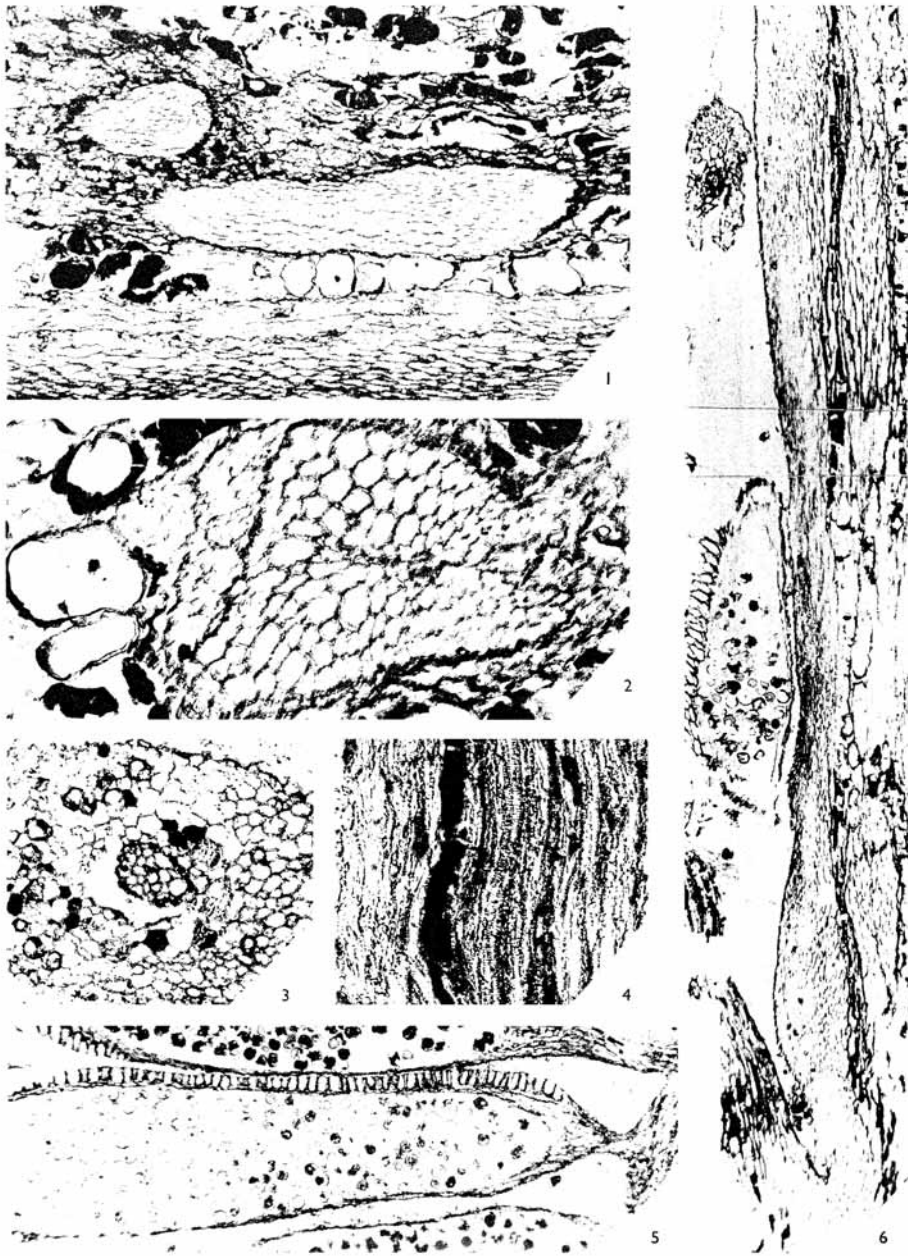
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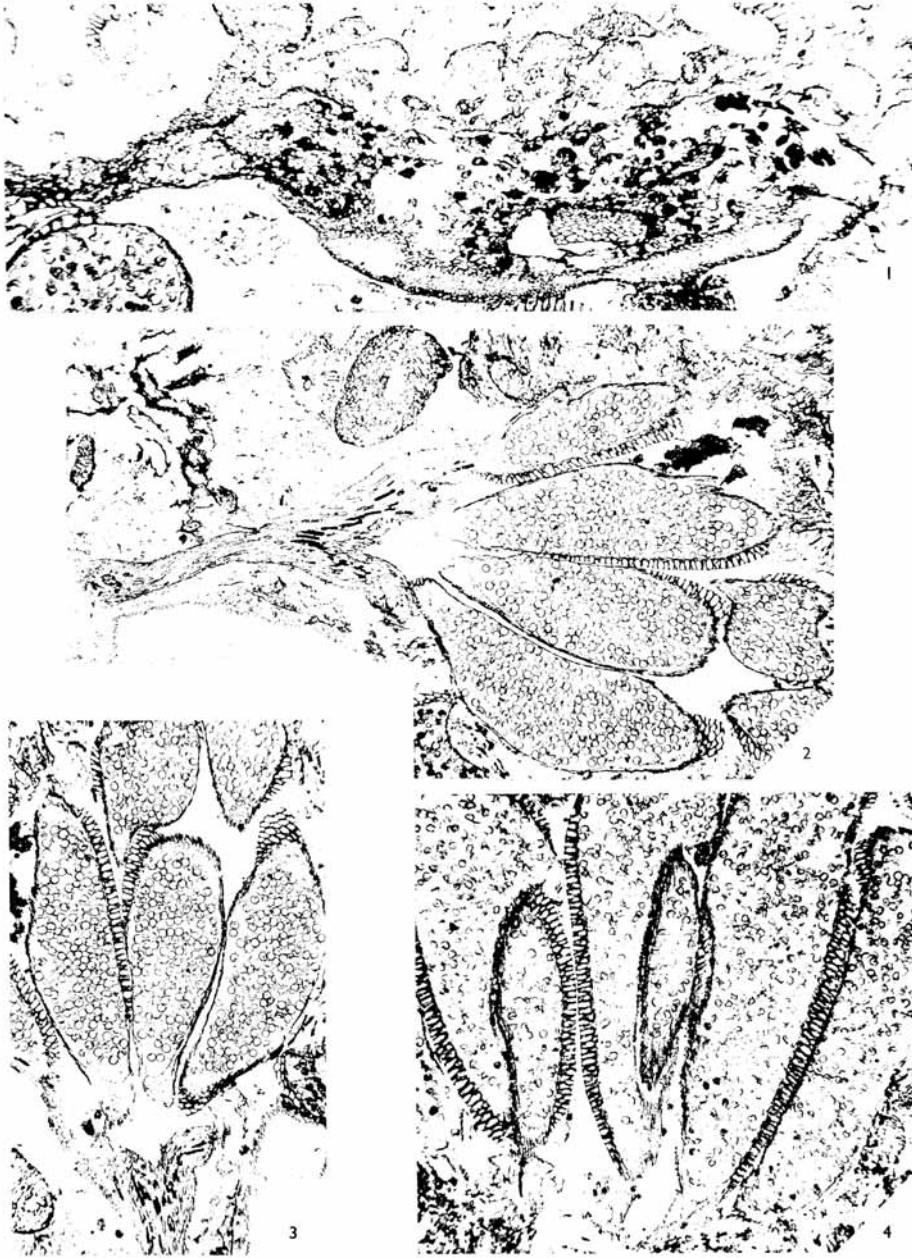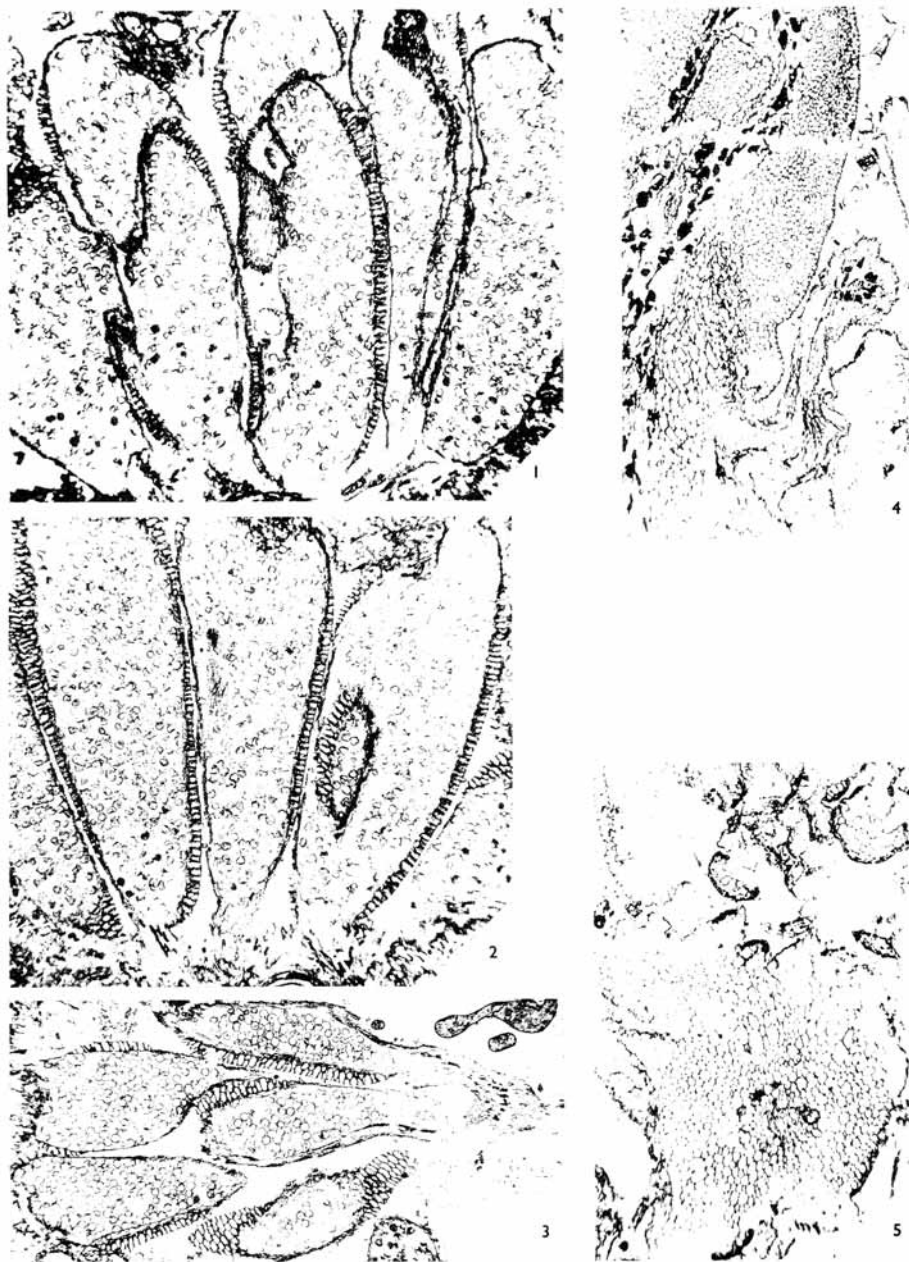Storrs, Connecticut 06268,
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