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AN UPPER DEVONIAN ZYGOPTERID SHOWING CLEPSYDROPSOID AND ETAPTEROID FEATURES[1]

Suzanne Leclercq

ALTHOUGH CONSIDERABLE PROGRESS in research has been made, our knowledge of Zygopteroideae remains incomplete because the material available consists chiefly of isolated plant fragments preserved in various states which are not readily assessed by comparative methods.

Our most valuable source of information is found in petrifications, which generally contain remains of main leaf stalks (phyllophores). The structure of the phyllophore is fairly well known, though the branching system to which it gives rise and the stems from which the phyllophores orginate are seldom to be found. Only a small number of fructifications have been discovered. Furthermore, with few exceptions, nothing is known which relates impression material to petrifications, so the problem of the morphology of the fronds and of the growth habit of these plants remains to be solved.

It is a moot point whether such uncoordinated data supply sufficient information for the discussion of affinities within the Zygopteroideae as a whole. In my opinion, until complementary data become available, it would be better to restrict the discussion to relationship within the genera and families only.

In a few cases, however, the discovery of good material has afforded an opportunity for making detailed studies of the morphology and anatomy of a more or less complete plant. For example, it was my good fortune to collect relatively complete specimens of *Rhacophyton* in the Upper Devonian (Lower Famennian) of Belgium. These remains were deposited in situ and proved to be of large size, showing stem, adventitious roots, fertile and vegetative fronds—all in organic connection. The anatomical structure of these remains was further enhanced by the fact that some portions had been impregnated with iron hydroxyde so that the vascular structure was preserved and could be studied according to the technic given by Leclercq and Discry (1950).

In the full account of the structure of *Rhacophyton* (Leclercq, 1951) a figure showing the growth habit of the plant was made accompanied by an analysis of the vascular supply of the main organs. This detailed study provides a basis for the circumscription of the genus and shows it to include at least three species: *Rhacophyton condrusorum* Crepin (1874), *R. mirabile* (Nathorst) Leclercq (1951), and *R. zygopteroides* Leclercq (1951).

Fragmentary impressions of vegetative and fertile fronds of *Rhacophyton* commonly occur in upper Devonian rocks. They have been recorded in Belgium, Germany (Rheinland), France (bassin de la Loire), Russia (basin of North Sossva), Bear Island, and North America (West Virginia and New York).

MORHOLOGY.—*Rhacophyton zygopteroides* consists of a more or less flexuous, upright, radially symmetrical shoot bearing numerous vegetative fronds which are spirally disposed. Owing to the abundance of the fronds and the comparative slimness of the stem, it seems probable that the plant supported itself by means of strong unbranched adventitious roots which are attached among the bases of the fronds.

The vegetative fronds bear pinnae in two rows, alternating with one another on each side of the rachis. The pinnules are small, 8–10 mm. long, and they are divided into 16 linear segments. There is a bilaterally symmetrical catadromic pinnule inserted at the base of each pinna.

The vigorous fertile frond gives the plant its striking appearance. Here the pinnae are in four

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rows. The pairs of pinnae are broadly united and are alternately inserted. There are sterile and fertile pairs, the latter being situated on the upper part of the frond. Each pair of pinnae bears alternately arranged secondary pinnae on which reduced pinnules were probably inserted. On the lower portion of each pair of pinnae are three pinnules. The basal one is catadromic and is modified into a fructiferous organ on the fertile pairs.

The pendant fructification consists of a dichotomously branched system of slender, flexuous, incurved branches, bearing, in the concavity, short projecting branchlets which may have undergone further subdivision. The sporangia are borne at the tips of these. They are spindle-shaped, about 2 mm. long, exannulate and very numerous. Unfortunately, spores are not present.

The most striking feature of the morphology is the four-rowed arrangement of branches on the fertile frond which strongly supports a relation with the Zygopteroideae. For this reason, the specific name *R. zygopteroides* was proposed.

This distinctive feature is of generic value for it is characteristic of two other species, e.g., *R. condrusorum* Crepin and *R. mirabile* (Nathorst) Leclercq.

ANATOMY.—The investigation of the petrified material confirms the relationship of *R. zygopteroides* with the Zygopteroideae as already indicated by the study of compression material.

The stem is traversed by a single vascular strand which has the configuration of a five-rayed star as seen in cross-section. The xylem is made up of two zones; an outer zone of 4–5 layers of large scalariform tracheids and an extensive central zone of delicate badly preserved tissue. It appears that the tissue occupying the center of the stem stele is prolonged into the prominent arms formed by the wood. The "arm" of wood is a bulged portion which represents the point of initiation of a leaf trace, the latter becoming free at a somewhat higher level. In spite of missing stages representing the departure of the bundle, the leaf trace sequence could be reconstructed. At its base, the free petiolar bundle is a more or less rectangular xylem mass with truncated ends and two small areas of narrow tracheids symmetrically placed, one on each end. The bundle shows two planes of symmetry. Fifty mm. higher, the ends of the bundle are expanded and have a small peripheral loop. The fully formed petiolar strand assumes a clepsydroid form, with a strong median constriction and two loops which usually are circular.

In the formation of the pinna trace, the outer border of the loop becomes detached, giving a crescentic strand with two protoxylem groups. For a while the loop remains open, then is bridged by several layers of tracheids. When passing out into the pinna, the crescentic strand becomes more compact and finally consists of a thin, tangentially elongated band, slightly curved with the concavity facing the parent bundle.

In transverse section, the two ends of the free pinna trace are dissimilar, because each is at a different stage in the formation of the alternately arranged pinnule traces. The pinnule trace consists of a tiny c-shaped bundle with an adaxial curvature.

Figure 1 is a diagram illustrating the sequence of departure of pinna and pinnule traces. It is obvious that the petiolar bundle bears pinnnae in two rows, one on each side. No other lateral organs or emergences of any kind were observed.

The first stages of the emission of the leaf trace of the fertile frond are unknown, but the similarity that exists between the petiolar strand of the vegetative and fertile fronds suggests that both leaf traces leave the stele in the same manner. To avoid repetition, only the features peculiar to the final form of the fertile petiolar bundle will be given.

The clepsydropsoid shape is retained, but the bundle is somewhat greater in length. The xylem shows a more regular arrangement of scalariform tracheids which is interpreted as an indication of cambial activity. In the lower portion of the frond, the bundle shows a narrow split running from one loop to the other, which disappears higher up. The split is thought to indicate the former presence of a connecting bridge of parenchyma or narrow tracheids between the two loops. The main point of distinction with the vegetative frond is the emission of a pair of pinna bundles instead of a

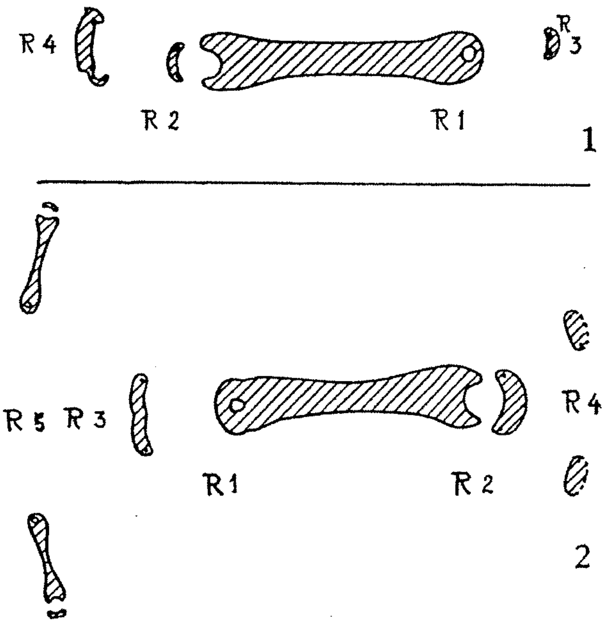

Fig. 1–2.—Fig. 1. Diagram of *Rhacophyton zygopteroides* showing the bundle of a vegetative frond and successive stages in emission of pinna (on two rows) and pinnule traces.—Fig. 2. Diagram of *R. zygopteroides* showing the leaf trace of the fertile frond and the successive stages in emission of a pair of pinna traces. Note the clepsydropsoid structure duplicated in the secondary pinna.

single one. This is in conformity with the external morphology of the fertile frond which bears, as we know, pairs of alternately disposed pinnae.

The process of the emission of a pair of pinna bundles is fairly well known. At the level where a pinna bar has been given off, the peripheral loop of the petiolar bundle is broadly opened. It gradually becomes closed by the development of several layers of tracheids, which represent the first elements of the next pinna bar above. At the same time, the loop is filled with a delicate tissue (probably protoxylem and parenchyma cells mixed together) which ruptures as the size of the loop increases and the xylem elements of the outer border develop. The curved band of the xylem of the pinna bar is soon detached and forms an elongated band, slightly constricted in the middle, which, at a slightly higher level, divides into two strands. At this level the exact shape of each strand is conjectural, although it appears to be elliptical in cross-section, with two lateral protoxylem groups, one on each side.

The pair of pinna traces enters the common base of the double pinna, which then divides into the two branches. Thus, the quadriseriate zygopterid mode of branching is reflected in the internal anatomy as well as in the external form.

It is important to note that the fully formed bundle in each pinna of a pair, has a clepsydropsoid shape. Although the bundle has decreased in size, the general form persists, i.e., the median constriction, the two swollen ends, and the two circular loops are present. Moreover, each pinna trace is oriented at right angles to the parent vascular strand.

The process of the emission of a secondary pinna trace duplicates the stages already described for the vegetative frond, i.e., the loops open out alternately on opposite sides of the pinna trace, each giving off a single narrow crescentic strand with two protoxylems, one on each side. So far, nothing is known of the final form of the free secondary pinna bundle.

A diagram illustrating the successive stages of the emission of a pair of pinna traces is represented by fig. 2.

Discussion.—The investigation of *Rhacophyton zygopteroides* has yielded several unexpected results whose discussion is limited to the anatomical details. An extensive comparative examination of the external form based on impression material has been presented in monographic form (Leclercq, 1951).

The new facts brought forward reveal the following features (1) The plant combines two modes of branching: pinnae in two rows on the vegetative frond and pinnae in four rows on the fertile frond. (2) A clepsydroid vascular strand is maintained in the vegetative as well as in the fertile fronds, even though the process of emission of the pinna traces reflects a dissimilarity for the two types of ramification, i.e., the vegetative petiolar bundle gives off two rows of crescentic strands, while the fertile petiolar bundle gives off four rows of clepsydroid strands (fig. 1, 2). (3) Though the bundles have a clepsydroid shape, there is no indication of the permanent loop from which are cut off pinna traces in the form of closed rings, as in *Clepsydropsis antiqua* Unger (1856; P. Bertrand, 1911), *Asterochlaenopsis kirgisica* Stenzel (1859; Sahni, 1930), *Austroclepsis australis* (E. M. Osborn) Sahni (1928). In fact, the process of the emission of the pinna bar is more like that of *Dineuron* (fig. 3) and *Metaclepsydropsis* (fig. 4, 5), where the loop is temporary and gives off four rows of crescentic strands. (4) It has been ascertained beyond doubt that *R. zygopteroides* combines clepsydropsoid petiolar bundles with temporary loops, crescentic and clepsydroid pinna traces, plus pinnae disposed in two and four rows. These fundamental characteristics raise the question of relationship within the Zygopteroideae. It is generally admitted that the Zygopteroideae divide into two families, namely Clepsydraceae and Etapteridaceae, both known in the Lower Carboniferous and the Permian. The main distinctive features lie in the mode of branching and the behaviour of the loops.

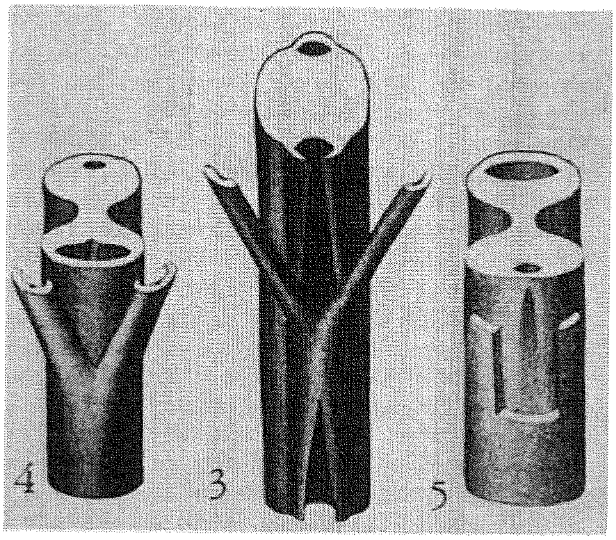

Fig. 3–5.—Fig. 3. Restoration of the vascular supply of *Dineuron* (from Posthumus, 1924).—Fig. 4–5. Restoration of the vascular supply of *Metaclepsydropsis* (from Posthumus, 1924).

The four genera included in the Clepsydraceae (*Clepsydropsis, Ankyropteris, Asterochlaena, Austroclepsydropsis*) bear two rows of pinnae, one on each side; have a permanent loop and pinna bundles cut off as closed rings. Moreover, three of the genera have a clepsydropsoid bundle in the primary rachis (phyllophore).

The genera belonging to the Etapteridaceae (*Dineuron, Metaclepsydropsis, Diplolabis, Zygopteris, Etapteris, Asteropteris*[1]) bear four rows of pinnae, one pair on each side; have a temporary loop which gives off crescentic pinnae bundles, and the branches arising from the primary rachis lie in a plane at right angles to that of the frond.

Though close affinities are indicated here, no definite lines of descent can be established, for our knowledge of the Carboniferous and Permian Zygopteroideae is too defective to make a useful comparison with *R. zygopteroides. Dineuron* and *Metaclepsydropsis* are perhaps the most nearly related genera (fig. 3–6).

In this connection, it is worth while noting observations made by Gordon (1911) on *Metaclepsydropsis duplex* Williamson. He states (cf. page 178) "In some cases, however, the incurved ends (of a primary pinna trace) unite, and the arc then becomes a closed ring (cf. Pl. IV, fig. 43). Such a closed trace is very interesting and probably indicates an ancestral character . . . . In one secondary pinna trace, a similar character was noted and here the emission of the tertiary pinna trace is exactly comparable with the emission of the secondary pinna trace from the primary in *Clepsydropsis antiqua*."

In contrast with *M. duplex*, the species *paradoxa* Unger, reinvestigated by P. Bertrand (1909, p. 205), shows a crescentic pinna bar, which apparently does not divide into two crescentic strands. Thus, in the latter species, the primary rachis would have borne two rows of pinnae instead of the normal four. Unfortunately, the pinna bar could not be followed far enough to see if it divides.

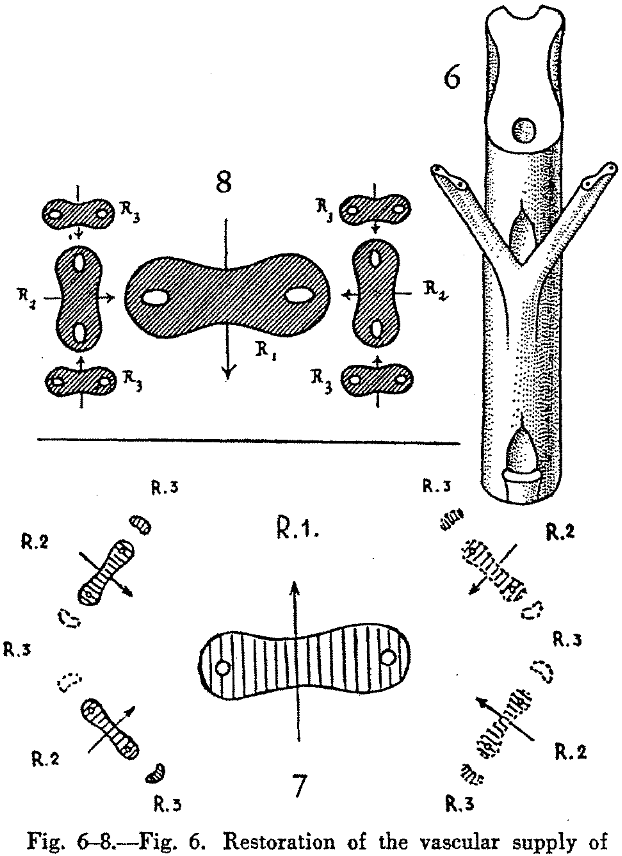

Fig. 6–8.—Fig. 6. Restoration of the vascular supply of the fertile frond of *R. zygopteroides.* Compare the structure of the pinna traces with fig. 3–4.—Fig. 7. Diagram showing the permanent clepsydropsoid bundle in the secondary order of branching and the orientation of the vascular supply at right angles to the parent bundles.—Fig. 8. *Eoclepsydropsis* (from Bertrand, 1909).

In supplement, we may add that in the highly specialized genus *Etapteris,* cases of temporary peripheral loops were observed in *E. tubicaulis* (P. Bertrand, 1909, p. 44), *E. bertrandi* Scott (Posthumus, 1924), *E. renieri* (Leclercq, 1929, 1931, 1932b), *E. scotti* (Leclercq, 1932a) and that K. G. Stenzel (1889) observed (c.f. Pl. IV, fig. 38) a primary rachis of *Clepsydropsis kirgisica* Stenzel, giving off a pair of pinna strands localized on one side. In his text, pp. 21–22, he points out that the two modes of branching occasionally occur though the biserial condition is the most usual.

These abnormal cases explain, in part, the unexpected dimorphism of the branching of *R. zygopteroides* while, on the other hand, the mode of branching of *R. zygopteroides* serves to explain the apparent anomalies mentioned above. (5) *R. zygopteroides* presents two great peculiarities: (A) The strand of the secondary order of branching of the fertile frond (pair of pinnae) duplicates the structure of the primary rachis (petiolar frond), whereas in all other zygopterids, excepting *Stauropteris,* they are quite different. The clepsydroid structure is not repeated in the tertiary order of branching (fig. 2, 6, 7). Moreover, the ramifications of the vascular strand of the fertile frond are orientated at right angles to the parent bundles (fig. 7). This behaviour suggests Bertrand's hypothetical form *Eoclepsydropsis* (1909, cf. p. 258, text fig. 36). In that "Urform," the vascular supply of the branches belonging to different orders, presents a gradually smaller but permanent clepsydropsoid bundle. The whole ramification is in two different planes, one perpendicular to the other (fig. 8). (B) The quadriseriate and biseriate ramifications were found in connection on one plant. These two modes of branching give fresh support to a concept originated by Sahni (1918, 1923) who considers that: "the quadriseriate condition is fundamentally biseriate and must be regarded as derived."

As interpreted by Sahni, the embedded pinna-bar that is given off from a primary rachis bundle and soon after divides into two strands supplying the higher order of branching, *"is a secondary rachis which has not become free."* Consequently, the products of the precocious dichotomy are free, tertiary rachises while—"in the biseriate forms the secondary rachises themselves are free and do not fork" (Sahni, 1918, p. 375).

The vascular system of *R. zygopteroides* answers the question as to how this organism changes from one mode of branching to the other. Facts of this kind tend to cast doubt on the value of subdividing the Zygopteroideae on the ground of the biseriate or quadriseriate branching. On the contrary, the distinction based upon the temporary or permanent loop with emission of crescentic strands or bundles as closed rings appears to be fundamental and, in spite of a few abnormal cases, a more constant feature, for purposes of classification. That these are characters of fundamental importance is well illustrated by *R. zygopteroides* where the process of pinna emission is very similar in vegetative and fertile fronds at the very earliest stages and where the temporary loop is a constant feature for both types of fronds (vegetative and fertile) even though there is a difference in the mode of branching.

We are not inclined to consider the new species as primitive, but as a probable ancestral form of the Etapteridaceae.

SUMMARY

This is a study of relatively complete specimens of *Rhacophyton zygopteroides* from the upper Devonian of Belgium. The results indicate that *R. zygopteroides* combines features of Etapteridaceae and Clepsydraceae. The clepsydropsoid features are revealed by the biseriate branching of the sterile fronds and the presence of clepsydropsoid vascular strands; the etapteroid character is found in the quadriseriate branching of the fertile fronds which, however, like the branches of the sterile fronds, contain clepsydropsoid bundles. Doubt is cast on the validity of separating the Etapteridaceae and Clepsydraceae on the basis of the mode of branching; instead, the primary distinction for these two families is to be found in the peculiar organization of the vascular supply of the fronds. *R. zygopteroides* is probably ancestral to the Etapteridaceae.

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