ON THE GENERA *CLEPSYDROPSIS* AND *CLADOXYLON* OF UNGER, AND ON A NEW GENUS *AUSTROCLEPSIS*

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(With 1 figure in the text)

In a paper recently published[1] I have briefly expressed the view that the Australian zygopterid generally known under the name *Clepsydropsis australis* is not a *Clepsydropsis*, in spite of its petiolar structure, and should be transferred to a new genus.

The object of the present communication is to state my full reasons for this view.

A review of the genus *Clepsydropsis* Unger

The grounds for creating a new genus for the Australian zygopterid will be best appreciated if we review briefly the history of the genus *Clepsydropsis*. The name *Clepsydropsis* was proposed by Unger[2] for certain fragmentary axes, believed to be fern petioles, of which the distinctive feature was the form of the vascular bundle as seen in transverse section. It is important to emphasise that the genus was an artificial one, no other parts of the plant being known; the affinities were therefore quite uncertain[3].

About the parent stem there has been a good deal of speculation, but nothing is yet definitely known. Prof. Paul Bertrand once suggested that *Clepsydropsis* rachises were borne upon stems of the *Cladoxylon* type[4], with which they were found associated at Saalfeld in large numbers. This view, however, was severely criticised by Solms-Laubach[5] and was subsequently withdrawn[6]. Indeed, Bertrand was able to confirm Solms-Laubach's observation that the petioles of *Cladoxylon* were not of the *Clepsydropsis* type, but were large dorsiventrally constructed organs with a compound leaf-trace: these organs

[1] Sahni (1930), p. 466.
[2] Unger (1856), p. 79.
[3] Unger placed *Clepsydropsis*, like several other "genera" founded on fragments of supposed fern petioles, in an artificial group, the Rhachiopterideae of Corda.
[4] Bertrand (1908); (1911 *a*), p. 250; (1911 *b*).
[5] Solms-Laubach (1910), pp. 540–1; see also Seward (1917), pp. 204–5.
[6] Bertrand (1913), pp. 918–19; (1914).

were found in association with the *Cladoxylons* and were known under the provisional name *Hierogramma*. Organs of the *Hierogramma* type were, in fact, found attached to *Cladoxylon* stems[1]. *Clepsydropsis* was thus again left alone, as a rachis of unknown attribution, and till now no definite clue as to the parent plant has been found.

It is true that the structure of the foliar bundle had already earned for this genus an undisputed place among the Zygopterideae, and this seemed to find support from the recent discovery that in the Australian zygopterid petioles with a *Clepsydropsis*-like bundle were borne upon stems of the well-known *Ankyropteris Grayi* type[2]. This discovery led to the belief that the Thuringian rachises must also have been borne upon stems of the same kind. Indeed, it was thought that the problem as to the stem of *Clepsydropsis* had at last been solved. However, there was no real ground for referring the Australian plant to Unger's genus, for, as I have recently shown, the clepsydroid foliar bundle is by itself no proof of generic identity[3].

In the past, of course, the name *Clepsydropsis*, based on the sole criterion of the foliar bundle, has been employed rather indiscriminately. Stenzel[4] employed it as a sub-genus of Corda's *Asterochlaena*, and he grouped under it such diverse plants as the following:

Names as in Stenzel, 1889	Names now generally adopted	Occurrence	Age	Stem
Asterochlaena (*Clepsydropsis*) *kirgisica* or *Clepsydropsis kirgisica*	*Asterochlaenopsis kirgisica*	W. Siberia	Probably Permian	Known
Asterochlaena (*Clepsydropsis*) *antiqua* or *Clepsydropsis antiqua*	*Clepsydropsis antiqua*	Thuringia	Lower Carboniferous	Unknown
Asterochlaena (*?Clepsydropsis*) *noveboracensis*	*Asteropteris noveboracensis*	Canada	Upper Devonian	Known
Asterochlaena (*Clepsydropsis*) *duplex*	*Metaclepsydropsis duplex*	W. Europe	Carboniferous	Known

More recently I have myself inadvertently referred the Australian zygopterid to *Clepsydropsis*, having been misled by the resemblance in the foliar bundle.

The question is, are we justified in continuing to employ an old generic name, originally applied to imperfectly known fragments of obscure affinity, for more completely known plants from distant regions of the world and of different geological ages, merely because they all possess a clepsydroid bundle in their leaves?

[1] Solms-Laubach (1896), Pl. 2, fig. 13; Pl. 3, fig. 4; *ibid.* Pl. 2, fig. 10. See also Scott (1923), p. 162, Fig. 64.

[2] Osborn (1915); Sahni (1919); Sahni (1928).

[3] Sahni (1930), pp. 465–6.

[4] Stenzel (1889).

Of the several plants referred by Stenzel to *Clepsydropsis*, two (*Asteropteris noveboracensis* and *Metaclepsydropsis duplex*) are now universally recognised as distinct genera. As for the *Asteropteris*, Stenzel was himself doubtful about the reference to Unger's genus; the reference of the other species to *Clepsydropsis* could scarcely have been justified even on the petiolar structure alone, and Paul Bertrand recognised this fact by creating for it the genus *Metaclepsydropsis*.

The Siberian species once referred to *Clepsydropsis* was also recently transferred to a new genus, and full reasons for this were given in my paper already cited. I will now try to show that the use of the name *Clepsydropsis* cannot be justified for the Australian plant any more than for the Siberian.

I have already suggested elsewhere that if we are to avoid confusion the name *Clepsydropsis* should be restricted to the Thuringian rachises and to any clepsydroid rachises of unknown attribution which may be discovered in the future. *Failing this restriction the only logical course would be to place in the same genus both the Siberian and the Australian zygopterids, and in fact all newly discovered plants which may happen to have clepsydroid foliar bundles, regardless of any differences which they may show in their stem and leaf-trace characters.* It seems to me obvious that even with our present imperfect knowledge of the Zygopterideae a grouping so artificial as this should not be tolerated.

There can be no doubt that if we had found only the stem and the proximal part of the leaf-trace, the Australian plant would have been referred to *Ankyropteris*, as Mrs Osborn was actually inclined to do[1]. It is equally certain that if we knew only the higher parts of the rachis, where the foliar bundle shows its definitive form, the plant would be assigned to *Clepsydropsis*, and this has actually been done. But knowing, as we do, that the plant combines an *Ankyropteris*-like stem with *Clepsydropsis*-like petioles, we are on the horns of a dilemma. Should we give prime importance to the stem and leaf-trace structure and call the plant an *Ankyropteris*, or should the fully formed petiolar bundle, on which the classification of the group is so largely based, have precedence? A simple expedient which I once suggested[2] was to combine the two genera, merging *Ankyropteris* in the older genus *Clepsydropsis*; but it has recently become apparent to me that such a course would only have caused further confusion.

[1] See Sahni (1919), pp. 82, 83.
[2] Sahni (1918), pp. 375–6; (1919), p. 84.

In the history of the genus *Clepsydropsis* we thus see an instructive example of the way in which reliance upon an isolated character, namely the Clepsydroid bundle, has again and again led us into difficulties.

The only alternative seems to be to create a new genus, based upon a *synthesis* of the characters. I therefore suggest for the Australian zygopterid a new generic name *Austroclepsis*. The plant would thus be renamed *Austroclepsis australis* (E. M. Osborn) Sahni comb.nov.

Austroclepsis *Sahni gen.nov.*

Diagnosis. Zygopterid ferns combining *Clepsydropsis*-like, *Ankyropteris*-like and *Tempskya*-like characters. The definitive form of the foliar bundle is identical with that in *Clepsydropsis*[1]; the stem stele corresponds almost exactly with that of *Ank. Grayi* or *Ank. scandens*[2]; the leaf-trace, both at its origin and in its course through the stem cortex, also agrees mainly with that of *Ankyropteris*, except that the structure is simpler owing to the absence of an adnate axillary strand[3]; the repeatedly forked leaf-bearing stems are bound together by means of adventitious roots into a *Tempskya*-like false stem[4].

Occurrence. Carboniferous of Australia. The only genus of Zygopterideae so far known from the southern hemisphere, with the possible exception of a *Botrychioxylon*-like axis epiphytic among its adventitious roots[5].

Affinities. The nearest known ally is the Siberian genus *Asterochlaenopsis* Sahni[6]. This genus resembles *Austroclepsis* in having a *Clepsydropsis*-like petiolar bundle and a stem stele differentiated into an outer and an inner zone; but it differs from the new genus in having a simple stem, in the numerous rays of the central part of its stele, in the structure of the leaf-trace both at its origin and during its course through the stem cortex, and in the slightly abaxial points of origin of the pinna-traces which thus approach the condition in *Asterochlaena*[7]. From *Ankyropteris* the new genus differs in its *Tempskya*-like false stem, and especially in the final form of the foliar bundle, which is that of a typical *Clepsydropsis*. *Clepsydropsis* Unger is known only from its rachises. In their individual structure

[1] Sahni (1928), Pl. 4, fig. 19. [2] *Loc. cit.* Pl. 4, fig. 15, etc.
[3] *Loc. cit.* Pl. 3, fig. 10; Pl. 5, figs. 30, 31, 34, 35, etc.
[4] *Loc. cit.* Pl. 1, fig. 1. [5] *Loc. cit.* Pl. 6, figs 50, 51, and text, p. 25.
[6] Sahni (1930).
[7] All these features are fully described and figured in detail in Sahni (1930); see especially Text-fig. 4 and Pl. 50, figs. 6–10; Pl. 51, figs. 15–25.

these rachises agree generally with the primary petiole of *Austroclepsis*; but they vary in diameter from as little as 4 or 5 mm. to as much as 27 mm. If we ignore certain differences which are probably due to the exigencies of preservation[1], the rachises of different sizes, described under several distinct names (*C. composita* Ung., *C. robusta* Ung., *C. antiqua* Ung., *C. antiqua* var. *exigua* P. Bertrand), readily fall under one species as rachises of different orders in a single diffusely branched frond (see Fig. 1). As I have already suggested elsewhere[2], a plant bearing fronds of such a kind must have differed considerably from any known member of the Zygopterideae. The mere presence of a clepsydroid bundle in the leaf need not imply a generic identity of Unger's plant with the Australian zygopterid any more than with the Siberian. These points will be further elaborated in a special part at the end of the paper. The comparison with *Tempskya* refers only to the habit and, of course, implies no affinity with the Cretaceous genus. For the present the *Tempskya*-like false stem may be included as a diagnostic character of the genus; it is for the future to show whether it runs through the whole genus or has only a specific value.

The only known species of the new genus is

Austroclepsis australis (*E. M. Osborn*) *Sahni comb.nov.*

1915. Preliminary observations on an Australian *Zygopteris* E. M. Osborn (1915), p. 727 (no figures).

1917. *Ankyropteris australis* E. M. Osborn *in litt.*, see Sahni (1919), p. 82.

1919. An Australian specimen of *Clepsydropsis*. Sahni (1919).

1928. *Clepsydropsis australis* (E. M. Osborn MS.). Sahni (1928).

SPECULATIONS ON THE HABIT AND AFFINITIES OF *CLEPSYDROPSIS* UNGER

The resemblance of *Austroclepsis* with *Clepsydropsis* Unger, so strikingly shown in the foliar bundle, seems to me to express at most a distant affinity. For reasons presently to be stated, I believe that the habit and mode of branching of Unger's leaves was very different from that of both the Siberian and the Australian zygopterids.

In my paper on *Asterochlaenopsis* I hinted at the possibility "that Unger's *Clepsydropsis* rachises, with their varying diameters, represented branches of a large *Hierogramma* frond, in which case a

[1] See, on this point, the critical observations of Solms-Laubach (1896), pp. 25–7, and of Bertrand (1911), p. 4.

[2] Sahni (1930), p. 466.

Thuringian *Cladoxylon* would still be the parent stem of *Clepsydropsis*"[1].

Soon after that paper was sent to the press I made another European tour and was able to examine some of the other scattered remnants of the Unger Collection, preserved at Breslau, Lille and London, and to re-examine the material at Berlin. The most I can say is that my suspicions on the *Clepsydropsis-Cladoxylon* question were strengthened, especially by an examination of some sections in Prof. Bertrand's laboratory at Lille. If this suspected connection

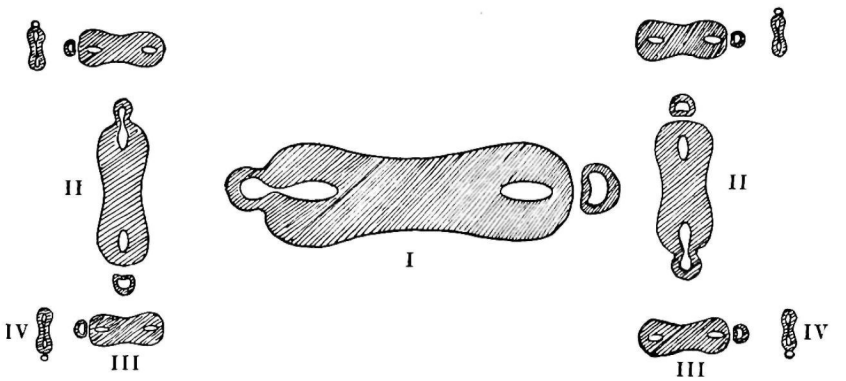

Fig. 1. *Clepsydropsis antiqua* Unger. Ground plan of foliar bundles showing probable mode of branching of the frond, as visualised by Paul Bertrand in his hypothetical form, *Eoclepsydropsis*. The large and small clepsydroid bundles, here shown as belonging to different orders of branching in a single frond, correspond to those of rachises previously described under the names *C. robusta* Ung. (I), *C. antiqua* Ung. (II, III), and *C. exigua* P. Bertrand (IV). If, as suggested in the text, these "species" or "varieties" are only different conditions of *C. antiqua* Ung. the fronds of this plant must have differed widely in habit from those of any zygopterid at present known.

could be established beyond doubt we should have the strongest possible grounds for removing the Australian species from Unger's genus. For the present, however, it must be admitted that this proof is lacking, and until we know better *Clepsydropsis antiqua*[2] must be considered entirely by itself. But even then the great variation in the diameters of these rachises[3], and the little that we know of their

[1] Sahni (1930), p. 466 footnote.

[2] Including *C. robusta* Ung., *C. composita* Ung. and *C. exigua* P.B., which are probably only different conditions of *C. antiqua*. See Solms-Laubach (1896), pp. 25–7; Bertrand (1911), p. 4; Sahni (1919), p. 82.

[3] The diameter varies from as little as 4 or 5 mm. to at least 15 mm., the structure remaining the same. In *C. robusta* Stenzel records a diameter of as much as 27 mm.

mode of branching, suggests a habit distinct from that of *Asterochlaenopsis* and *Austroclepsis*. The Saalfeld rachises seem to have belonged to a large diffusely branched frond with ramifications in two different planes, one perpendicular to the other (see Fig. 1) rather than to a leaf in which a dominant main rachis gave off minute appendages on the two sides. In such a frond, each branch rachis must have been supplied at its base by a ring-like strand which higher up became clepsydroid by tangential flattening and median constriction. This is clearly suggested by the known facts that (*a*) lateral bundles were nipped off as rings from the ends of the peripheral loops, and (*b*) at least in one case (the *C. exigua* of Bertrand) the inner ends of the two peripheral loops have been found connected together by a persisting bridge of small tracheids similar to those lining the loops themselves[1]. Now if we try to visualise the habit of such a frond it will be found that the branches were in two rectangular planes, for each annular strand, as it came off, became flattened in a plane at right angles to that of the parent bundle. If from our knowledge of the behaviour of the strands we were to reconstruct the frond in a ground plan, the reconstruction would agree in a remarkable way with Prof. Bertrand's hypothetical form *Eoclepsydropsis*[2], which he regarded as the *Urform* of the Zygopterideae.

The unusual habit which this mode of branching would impart to the frond is easy to imagine. Thus, quite apart from whether *Clepsydropsis* Unger was the foliage of *Cladoxylon* or not, the available facts seem to support the idea that it was a diffusely branched frond of very peculiar habit, unlike that of any of the other plants which have been referred to *Clepsydropsis*.

It is considerations such as those set forth above that make me hesitate in regarding the Thuringian rachises, without further evidence, as co-generic with any other known plant.

SUMMARY AND CONCLUSIONS

1. Reasons are given for the view that the southern zygopterid generally known as *Clepsydropsis australis* is not a *Clepsydropsis*, in spite of its petiolar structure, but represents a new and distinct genus. For this the name *Austroclepsis* has been proposed.

2. *Austroclepsis* is distinguished from other Zygopterideae by a

[1] Bertrand (1911), Pl. 1, figs. 1–5; Pl. II, fig. 16; (1911 *a*), p. 21, fig. 21; see Sahni (1919), p. 84.

[2] Bertrand (1909), p. 258, Text-fig. 36.

combination of *Clepsydropsis*-like, *Ankyropteris*-like and *Tempskya*-like characters. The petiolar bundle is of the *Clepsydropsis* type, but the stem stele and leaf-trace sequence agree with the corresponding organs in *Ankyropteris Grayi* or *A. scandens*, except that the leaf-trace has no adnate axillary strand. The repeatedly forked leaf-bearing axes are bound together by adventitious roots into a *Tempskya*-like false stem. The only known species is *A. australis* (E. M. Osb.) Sahni comb.nov. With the possible exception of a slender *Botrychioxylon*-like axis epiphytic among its roots, *Austroclepsis* is the only genus of Zygopterideae yet recorded from the southern hemisphere.

3. There is some evidence that in their habit and mode of branching the Thuringian leaves referred to *Clepsydropsis* differed considerably from those of both the Siberian and the Australian zygopterids and, indeed, from any zygopterids at present known.

4. Even if *Clepsydropsis* Unger was a zygopterid (which on present evidence seems uncertain) it should not be accepted without hesitation as co-generic with any other member of that family.

5. To avoid confusion it is desirable that the name *Clepsydropsis* be used in the sense of a form genus, that is, it should be reserved for rachises of unknown attribution containing vascular bundles of that type. The presence of clepsydroid strands in the leaves is not by itself a proof that the plants in which they are found belong to the same *natural* genus.

ACKNOWLEDGMENTS

I wish to express my sincerest thanks to Dr Crookall (London), Prof. Soergel (Breslau), Prof. Gothan (Berlin) and Prof. Paul Bertrand (Lille) for the courteous and liberal manner in which they gave me access to the material. To Prof. Gothan I am further indebted for permission to cut fresh sections from some of Unger's blocks, and for many other kindnesses during my visits to Berlin. Prof. Bertrand laid me under a deep obligation by sacrificing much of his time in detailed discussions, both personally and in correspondence, over the possible attribution of *Clepsydropsis* to *Cladoxylon*. It has also been my privilege, for which I am deeply grateful, to discuss this and other theoretical points with Prof. A. C. Seward, F.R.S., and Dr D. H. Scott, F.R.S.

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