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Novel branching structures from the Lower Devonian and a note of caution

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ABSTRACT. Plant fossils from the Devonian Period present evidence for the earliest diversification of the terrestrial flora and include the first examples of many evolutionary important botanical innovations. Here we describe a new kind of plant from the Lower Devonian of Guangxi Autonomous Region in China which is morphologically distinct from other currently recognised plants leading us to erect a new genus, *Changwuia schweitzeri* gen. et sp. nov. *Changwuia* comprises a central axis from which lateral branching systems are borne helically and at short distances from one another. Lateral branching systems have a diagnostic morphology which have the initial appearance of either synangia or cupules, and terminate in numerous long and slender lobes. However, spores have not been found in any of the preparations. In comparison to similarly aged plants *Changwuia* has a comparatively advanced organisation although several important features of the new specimens are unknown restricting a comprehensive understanding of this enigmatic plant. Detailed study of these fossils has important implications on the nature and affinities of certain other early land plant fossils and leads us to present a note of caution with regard to the possible over interpretation of other similarly aged materials.

KEY WORDS: Tracheophyta, *Changwuia*, Siegenian, Lower Devonian, China

INTRODUCTION

Recent investigations on a plant fossil assemblage from the middle part of the Lower Devonian (D_1^2 in the Chinese succession) from Guangxi Autonomous Region in China have identified specimens of a new and unusual kind of plant. The fossils occur in the Shiqiao Group which has been previously reported as containing a plant macrofossil assemblage restricted to *Taeniocrada*, *Zosterophyllum* and *Drepanophycus* (Li & Cai, 1977, Guiquzhuong working group 1978, Cai and Wang 1995). Despite repeated visits to the field locality, only two fragmentary specimens of this plant have been identified although they are sufficiently distinct from the other plants present in this assemblage to discount any affinities with them.

On initial inspection the new fossils appear to be fertile with a synangium-like or cupule-like construction, with several of these structures organised laterally and helically from a central axis. However, numerous other studies on fossil plants have identified these kinds of reproductive organisations to be features of comparatively advanced vascular plants (e.g. Stewart & Rothwell 1993, Taylor & Taylor 1993). In now well known sequences of plant evolution, comparable gross organisations are not observed until at least the Latest Devonian based on existing evidence (e.g. Kenrick & Crane, 1997). The purpose of this present paper is therefore to describe the new fossils in as much detail as the specimens permit and to subsequently consider them in relation to other early land plants. In particular, if these specimens are in fact either synangiate or cupulate, they would represent the earliest occurrence of these novel forms of reproductive organisation.

GEOLOGICAL INFORMATION AND TECHNIQUES

Specimens were collected from the predominantly continental sediments of the Shiqiao Group located near the town of Shiqiao, Changwu county, in the Guangxi Autonomous Region of southern China. These sediments are of middle Lower Devonian (Siegenian) age, equivalent to D_1^2 in the Chinese lithological succession, for which precise biostratigraphic dating is presently unavailable. The fossils are part of a typical Lower Devonian plant macrofossil assemblage that includes *Taeniocrada decheniana*, *Zosterophyllum sinense* and *Drepanophycus* sp. (Li & Cai 1977, Guiquzhoung working group 1978, Cai & Wang 1995).

Two isolated and incomplete specimens have been identified (specimen numbers CBG9805001a, b and CBG9805002, a, b) preserved in a pale yellow fine grained sandstone. Both specimens occur as adpressions from which attempts to reveal anatomical details have proven unsuccessful. The three dimensional arrangement of the plant organs have been determined by the technique of serial degagement (Fairon-Demaret et al. 1999). All of the removed parts of the plant were studied under SEM from which attempts to reveal anatomical details have proven unsuccessful. Of the two specimens identified one has proven to be considerably more informative than the other although, in each case the second specimen does not contradict any of these observations. The following account describes both specimens although we only illustrate the more informative of the two.

SYSTEMATIC PALAEOBOTANY

Tracheophyta, Incertae Sedis

Changwuia gen. nov.

Diagnosis. Axis bearing helically arranged dichotomous branching systems comprising closely spaced initial dichotomies forming four terminal units. Terminal units with closely spaced basal dichotomies producing numerous long, slender terminal lobes.

Etymology. Referring to the Changwu county from which the fossils were collected.

Type species. *Changwuia schweitzeri* sp. nov.

Changwuia schweitzeri sp. nov.

Holotype. CBG9805001, a (part) and b (counterpart) (Fig. 1, Pl. 1 figs 1–6).

Repository. National Museum of Plant Evolution of China, Institute of Botany, Chinese Academy of Sciences. Xiangshan, Beijing 100093. P.R. China.

Type Locality. Shiqiao town, Changwu county, Guangxi, China.

Type Strata. Shiqiao Group.

Stratigraphic Age. middle Lower Devonian (D_1^2), Siegenian.

Etymology. In recognition of the achievements of H.J. Schweitzer on early land plants.

Diagnosis. Axis approximately 2.1–3.3 mm wide, bearing helically arranged lateral branching systems c. 3.2–5.5 mm apart. Lateral branching systems dichotomous with two closely spaced initial dichotomies within approximately 3 mm of the lateral branch departure, forming four more or less equal terminal units. Terminal units with 3 closely spaced dichotomies forming 8 long, slender terminal lobes approximately 3.5–6.2 mm long and 0.3–0.45 mm wide.

DESCRIPTION

In gross morphology each specimen consists of a central axis bearing helically several closely spaced lateral branching systems (points 1–4 in Fig 1; Plate 1, figs 1–4). The morphology of the lateral branching system is at first unclear but several dichotomies as well as numerous elongate ultimate lobes are visible in each. It is these features of the lateral branching systems which give them a synangium-like or cupule-like appearance.

Both specimens are proximally and distally incomplete, with the primary axes being longer than the maximum 33 mm observed and ranging from 2.1–3.3 mm wide. Lateral branching systems depart from the primary axis at intervals of between 3.2 and 5.5 mm, although towards the end of one specimen no additional branching was observed (Fig. 1, Pl. 1 fig. 1). Several of the lateral branching systems are preserved in different orientations within the sediment permitting the identification of features relating to their overall organisation. This variation is shown best in Fig. 1

Fig. 1. Camera lucida diagram of the holotype of *Changwuia schweitzeri* gen. et sp. nov. (CBG9805001) with helical positions of the branching departures from the main axes numbered 1–4 respectively. See description for further details of the lateral branching systems

and Plate 1 figs 5–6 with the uppermost lateral branching system (4 in Fig. 1) being orientated near vertically, the one below it being partially oblique (3 in Fig. 1) while the lowermost two are approximately parallel to the exposed sedimentary surface (1–2 in Fig. 1). Individual lateral branching systems dichotomise twice in close succession to produce four more or less equal parts after approximately 3 mm (Fig. 1; points d in Pl. 1 figs 5–6). Each of these four resultant branches then produces what are here termed terminal units, each ranging from 5.3–6.9 mm long and 2.5–3.1 mm wide and with a prominent broad, flattened base (Fig. 1; c in Pl. 1 fig. 6). This branching is essentially synchronous producing an arrangement which places all four ultimate units side by side and at approximately the same height, wrapped around one side of the primary axis. Terminal units comprise up to four closely spaced synchronous dichotomies forming up to 16 long, slender, terminal lobes which are shown exposed in oblique compressional view at point B in Plate 1 fig. 5. The broad, flattened base of the terminal units marks the position of the dichotomies forming the ultimate lobes. Each ultimate lobe ranges from 3.5–6.2 mm long and 0.3–0.45 mm wide, is terete in cross section, tapers distally and has a bluntly rounded apex (Fig. 1, Pl. 1 figs 5–6). An individual lateral branching system departing from the primary axis would thus comprise four terminal units with collectively up to 64 ultimate lobes. Anatomical or histological features of *Changwuia* are unknown.

COMPARISONS TO OTHER PLANT TAXA

The materials studied here are distinct from the organs of the other 3 plant genera from the same assemblage (i.e. *Taeniocrada*, *Zosterophyllum* and *Drepanophycus*) making affinities with any of these plant unlikely. Each of these plants is relatively well known and none posses axes which bearing in a helical organisation complex lateral branching systems such as these. These specimens are also distinct from the organs of all other currently identified early land plants leading us to create a new genus and species, *Changwuia schweitzeri* gen. et. sp. nov. The distinction of *Changwuia* with other early land plants makes conclusions about its nature and affinity problematic, especially considering the fact that the most comparable fossil taxa are often poorly known themselves. Our comparison will focus on the morphologically most similar taxa namely; *Yarravia* Lang and Cookson 1935, *Hedeia* Cookson 1935 and members of the traditionally viewed Trimerophytes such as *Psilophyton* (Dawson) Hueber and Banks, 1967.

Yarravia from the Lower Devonian of Australia is distinct from *Changwuia* in several ways indicating that the two are different taxonomic entities. *Yarravia* has only 5–6 ultimate lobes which have been interpreted by several researchers as sporangia (e.g. Lang & Cookson 1935, Stewart & Rothwell 1993). However, these structures have not been demonstrated to contain spores so this fertile na-

ture is by no means assured. Here we will consider these structures to be synangium-like as the possibility exists that the lobes may not be sporangia. The synangium like-structure in *Yarravia* is terminal whereas in *Changwuia* they are lateral and helically arranged from a parent axis. Most importantly, *Yarravia* lacks the numerous dichotomies characteristic of *Changwuia* and as a consequence, the synangium-like structures in *Yarravia* have far fewer lobes (typically 5–6). Furthermore, these lobes are fused to one another for the majority of their length unlike the free terminal lobes of *Changwuia* (Lang & Cookson 1935).

The genus *Hedeia* is known from the Lower Devonian of Australia (Cookson 1935, 1949) and has more recently been reported from China (Hao & Gensel 1998). In no case has the presence of spores been demonstrated for this genus. The dichotomous branching system of *Hedeia* produces terminal 'sporangia' at more or less the same level as observed in *Changwuia* although these are distinct, being fusiform in shape with some specimens possessing acuminate tips (e.g. Hao & Gensel 1998). The main distinction between these taxa is the helical organisation of the lateral branching systems in *Changwuia* with each of these comprising four distinct units possessing a greater numbers of ultimate lobes than the number of 'sporangia' in *Hedeia*. The 'sporangia' of *Hedeia* terminate a dichotomous branching system typical of members of the Trimerophytes (Hao & Gensel 1998). Further distinction between the taxa comes through the close spacing and the repeatedly synchronous nature of the dichotomies in *Changwuia*.

Changwuia has superficial resemblance to the fertile branches of traditionally identified members of the Trimerophytes such as *Psilophyton*. However, these terminate dichotomous branching systems and do not occur helically from a single axis as observed in *Changwuia*. *Psilophyton* is further distinct from *Changwuia* in possesses fusiform sporangia with longitudinal dehiscence, each terminally on a short stalk and is known to bear spores (e.g. Banks *et al.* 1975). In addition the fertile branches of *Psilophyton* are much longer than comparable structures observed in *Changwuia*. Additional morphological and anatomical data are needed to allow a more detailed comparison of *Changwuia* with *Psilophyton* and other traditionally viewed Trimerophytes.

DISCUSSION

Despite the superficial similarity of the specimens described here to synangia with numerous basally fused sporangia, our investigation has shown that this feature is only an apparent one. The synangium-like appearance actually relates to the presence of several closely spaced and often difficult to distinguish dichotomies (e.g. point c in Pl. 1 fig. 6). These specimens are therefore 'synangium-like' rather than synangia. More significantly, in the present study spores have been observed in any of the preparations. Considering this it seems inappropriate to consider *Changwuia* as fertile based on the currently available evidence. While it is appreciated that not all sporangia contain spores throughout their ontogeny, it is here considered unjustified to consider previously unknown structures such as *Changwuia* as fertile until sufficient evidence of a fertile nature has been identified. On the other hand, if stratigraphically comparable plants with a similar morphology had been previously found to be fertile, then it might be appropriate to consider these specimens as fertile also. For this reason and because other contemporaneous plants are known to posses fusiform sporangia similar to those of *Hedeia*, it is highly probable that the structures in this genus are sporangia as interpreted by several researchers (Cookson 1935, 1949, Hao & Gensel 1998). The absence of spores in *Hedeia* does not challenge existing evolutionary theories and it is an obvious progression of logic to assume that its terminal units are sporangia. However, we can not be so confident about either *Changwuia* and *Yarravia*, both of which are dissimilar from other unequivocally known contemporaneous plant reproductive organs. It is clear that further information about both of these enigmatic plants is warranted before either can be considered unquestionably fertile.

At present we have no additional information concerning the rest of the whole-plant morphology of *Changwuia*. Further speculation about the nature of this plant is therefore entirely problematic although, these specimens could equally well represent a vegetative or fertile branching system. During this earliest phase of land plant radiation it is extremely likely that either evolutionary convergence or derivation of one kind of branching structure from the other, the two kinds could

be virtually indistinguishable from each other in some plants. Further evidence is warranted to evaluate these possibilities although at the moment, we prefer to simply consider *Changwuia* an unusual and comparatively complicated kind of branching system. The function of the structures described here are therefore unknown.

Due to the fragmentary nature of the specimens examined here, it has not been possible to conclusively determine if the branching systems of *Changwuia* were pendulous or erect in life position. The pendulous orientation chosen in the illustrations (Fig. 1, Pl. 1 figs 1–6) relates to the presence of a long branch length at one apex of the primary axis, which is here interpreted as proximal. In this orientation, the spacing between the successive lateral branching systems becomes closer towards the distal apex, as often observed in other early land plants (Kenrick & Crane 1997).

CONCLUSIONS

The novel branching structures described differ significantly from comparable organs in other early land plants. At present insufficient details of the whole plant morphology are known restricting conclusions on the nature and affinity of these fossils although, it is considered highly unlikely that *Changwuia* is either the fertile or vegetative parts of any of the plants in the same assemblage (*Taeniocrada decheniana*, *Zosterophyllum sinense* and *Drepanophycus* sp.). Despite having the appearance of a synangial aggregation, no evidence of spores, sporangia nor fused sporangia has been identified in the specimens examined; the synangium-like appearance relates to the presence of several closely spaced dichotomies within a single lateral branching system. For future studies focusing on the early radiation of the land plants our note of caution is simple; just because a plant organ looks fertile does not necessarily mean that it is.

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PLATE

Plate 1

Holotype of *Changwuia schweitzeri* gen. et sp. nov. from the Lower Devonian of China

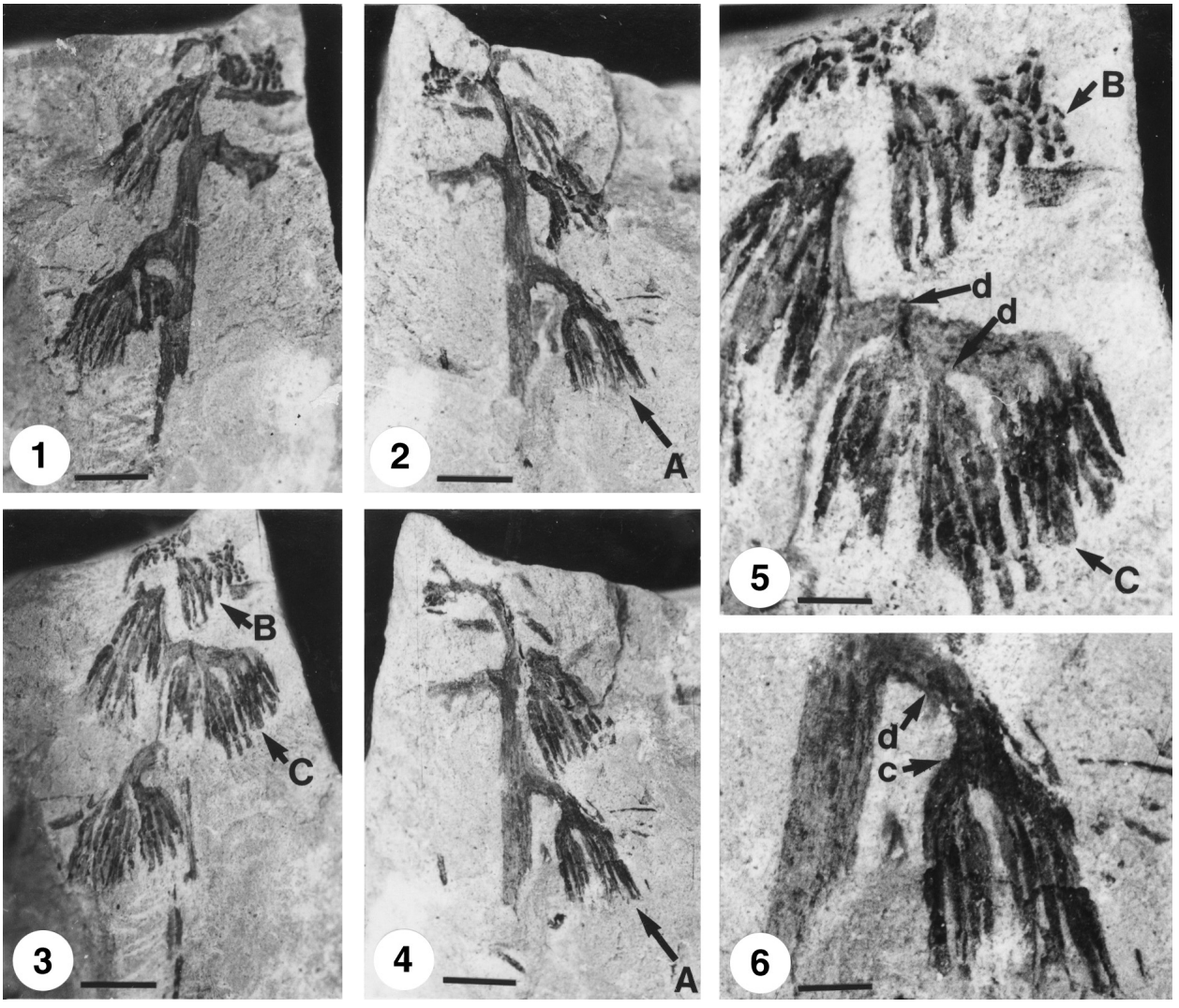
1–2. part and counterpart of a the axis helically bearing lateral branching systems

3–4. same specimens as 1–2 after dégagement to revealing additional features of the lateral branching systems

5. Enlargement of lateral branching systems B and C from 3

6. Enlargement of an ultimate unit of lateral branch A illustrated in 2 and 4

Scale bars = 5 mm except 5–6 = 2 mm. For further details refer to specimen description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