A NEW GENUS OF EARLY LAND PLANTS WITH NOVEL STROBILAR CONSTRUCTION FROM THE LOWER DEVONIAN POSONGCHONG FORMATION, YUNNAN PROVINCE, CHINA

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ABSTRACT. *Adoketophyton subverticillatum* (Li and Cai) comb. nov. is described from the Siegenian of southern Yunnan, China. It consists of dichotomously branching axes, with terminal compact strobili in which lateral units are inserted oppositely and decussately so that they form four vertical rows. Each unit comprises a stalked, fan-shaped, bract-like appendage bearing an adaxial sporangium with dehiscence into two equal valves. Although such reproductive characteristics parallel those of lycophytes, the shape of bract and absence of microphylls indicate that this plant presents a new combination of characters, presumably within the tracheophytes. It is perhaps closest to the Barinophytales, another group of vascular plants of uncertain affinity. Anatomical information, particularly on the cauline xylem and on the vascularization of the bract (if any) is required before assignment to a higher taxon. These Lower Devonian assemblages from Yunnan include cosmopolitan genera such as *Zosterophyllum* and *Drepanophycus*, but they also contain a high proportion of endemic taxa many of which exhibit novel combinations of characters not yet known elsewhere. Their distinctive nature may thus be evidence for provincialism in early land vegetation.

SOME of the most exciting recent discoveries in early Devonian palaeobotany have come from China (Li 1982; Geng 1983, 1985; Hao 1985, 1988, 1989*a*, 1989*b*). This is particularly apposite as the majority of the evidence for the nature of early land vegetation comes from Laurussia (Boucot and Gray 1982; Edwards 1990*a*, 1990*b*; Edwards and Davies 1990) providing somewhat biased analyses on vascular plant phylogeny, global biostratigraphy based on megafossils, and palaeogeography. Lower Devonian assemblages from Yunnan Province are important because they contain large numbers of specimens, are diverse and come from strata whose ages are being critically assessed (e.g. Hao 1989*b*). They contain cosmopolitan genera such as *Zosterophyllum* and *Drepanophycus* (Halle 1936; Hsü 1966; Cai and Schweitzer 1983; Hao 1985) as well as plants with combinations of characters that do not fit nicely into existing classifications (e.g. Geng 1983; Hao 1988). We describe such a plant here. It was originally named *Z. subverticillatum* by Li and Cai (1977), but their analysis was limited by the small number of fragmentary fossils. This reassessment is based on extensive new collections.

LOCATION AND STRATIGRAPHY

Details of the locality are given in Hao (1989*b*) and Text-figure 1. The fossils come from a hillside exposure, near Zhichang village, Wenshan district, Yunnan Province, of the Posongchong Formation from the horizon with *Stachyophyton yunnanense* Geng (1983) some 70 m below that with *Discalis longistipa* Hao (1989*b*), and 30 m above the base of the formation. There is no direct evidence for the age of these continental deposits containing abundant plants and fish. They overlie unconformably the Meitan Formation containing lower Ordovician fossils and are overlain by the Pojiao Formation with corals and brachiopods. The latter is considered equivalent to the lower part of the Yujiang Formation in Guangxi Province occurring above sediments dated as late Siegenian by conodonts. The Pojiao Formation is thus thought to be Lower Emsian and the underlying

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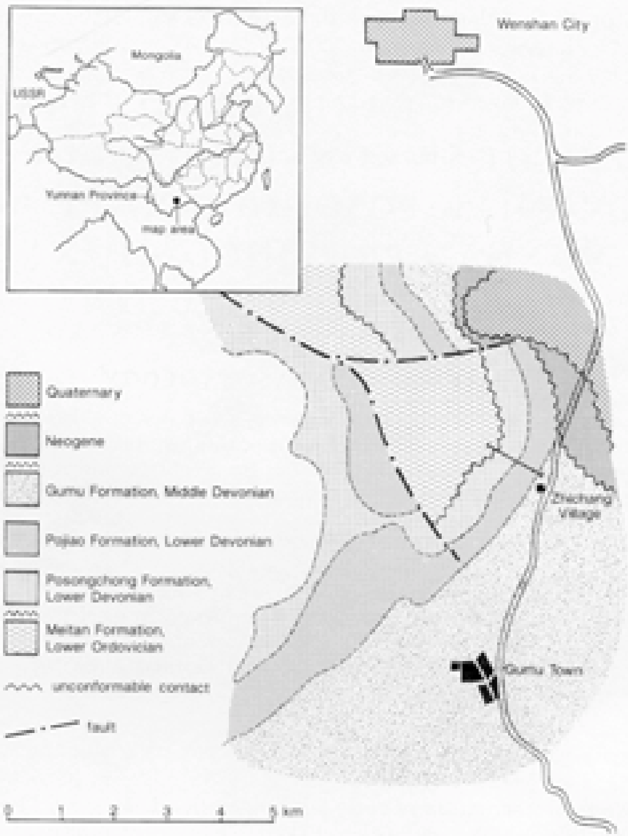

TEXT-FIG. 1. Locality map showing outcrops to south of Wenshan City. Line to north-west of Zhichang village indicates section through Lower Devonian sediments.

Posongchong Formation, late Siegenian in age, although the possibility that it is earliest Emsian cannot be entirely eliminated.

MATERIAL AND METHODS

The matrix is a very fine, slightly micaceous sandstone with rather homogeneous texture and only weak bedding fabric. Depending on the extent of weathering, its colour ranges from cream to buff to yellow-grey, the latter relatively unweathered examples containing fossils with the most coalified material. In most specimens only a coaly dusting remains over an iron-stained impression, whose colour again is variable ranging from pale pink (Pl. 2, fig. 8) to tan to darker brown (Pl. 2, fig. 10). Many strobili retain their three-dimensional form and certain axes and sporangia are infilled with matrix. Casts of spirorbid worms are visible on some fan-shaped appendages (Pl. 1, fig. 5). Permineralizations range from individual cells replaced by limonite or a pink unidentified material, to small areas of replaced axis, to complete strobili replaced by presumed iron oxides (Pl 1, fig. 4). Cellular preservation is rare (Pl. 4, figs 2–4, 7). Permineralized axes with preserved xylem occur in the same matrix, but not attached to a strobilus.

Coalified material removed on film-pulls or oxidized in Schulze's solution failed to yield cuticles, spores or xylem. Morphological detail and three-dimensional relationships were achieved by developing specimens with tungsten needles (dégagement), a technique greatly facilitated by the soft texture of the weathered matrix except that coaly material very readily sloughed off. Relatively small rock specimens and permineralized fragments were dried, mounted on stubs and coated with gold prior to SEM examination using a Cambridge 360 SEM. More completely preserved axes and strobili were embedded in a cold setting resin sectioned, smoothed and polished for investigation by reflected light using an Olympus Vanox (Kenrick *et al.* 1991). The photographic equivalent of serial sections at close intervals (Text-fig. 2) was realized by alternately grinding, polishing and photographing an embedded fragment of a strobilus, 1·5 mm long. Grade 600 followed by 800 carborundum were used and approximately 0·1 mm of fossil and sediment removed at each stage so that sixteen serial photographs were obtained. Specimens CBYn 9002001-9002059 are deposited in the Institute of Botany, Academia Sinica, Beijing, China.

SYSTEMATIC PALAEONTOLOGY

PLANTAE INCERTAE SEDIS

Genus ADOKETOPHYTON gen. nov.

Derivation of name. Greek *adoketos*, unexpected or surprising.

Type species. Adoketophyton subverticillatum (Li and Cai) Li Cheng-Sen and Edwards comb. nov.

Diagnosis. Distal aerial parts of plant with smooth dichotomously branching axes and terminal strobili composed of compound lateral fertile units. Each unit comprises a bract-like flattened appendage and single adaxially inserted sporangium with two valves and distal dehiscence around convex margin.

Adoketophyton subverticillatum comb. nov.

Plates 1–4; Text-fig. 2

Basionym. Zosterophyllum subverticillatum Li and Cai 1977, pp. 24–25, pl. 3, figs 1–3; text-fig. 8.

Type material. Holotype PB 6465 Li and Cai (1977), pl. 3, fig. 2, deposited at the Nanjing Institute of Geology and Palaeontology. As this is a fragmentary specimen, paratype CBYn 9002034*a–b* (Pl. 1, fig. 3; Pl. 3, fig. 1) is selected to demonstrate features of the strobilar characters in the diagnosis (Institute of Botany, Academia Sinica, Beijing, China).

Stratigraphy. All specimens come from the Posongchong Formation, Zhichang locality, Wenshan District, Yunnan Province, Lower Devonian (?Siegenian) age.

Diagnosis. As for genus. Vegetative part of plant at least 9 cm tall with smooth axes 0·85 (−1·57)–2·6 mm in diameter ($n = 31$). Parallel-sided strobili with 4 rows of opposite and decussately inserted fertile units up to 90 mm long, the longest with 54 fertile units. Fan-shaped vertically overlapping lateral appendages, 3·2 (−5·6)–10·0 mm maximum width ($n = 76$) with maximum height 3·6 (−15·7)–8·4 mm ($n = 48$), and rigid decurrent stalks, circular in cross-section near base and 0·5 (−0·84)–1·3 mm in diameter ($n = 54$). Vertical distance between appendage insertion 3·2 (−4·9)–7·0 mm ($n = 47$). Sporangia attached to adaxial surface of stalk of appendage, 0·2–1·8 mm from front of insertion, by short stalk 0·11 (−0·6)–1·4 mm wide ($n = 10$) and 0·05 (−0·31)–0·7 mm high ($n = 7$) and covered by subtending appendage. Sporangia of two ± equal valves, with distal dehiscence along convex margin. Valves sometimes slightly tangentially expanded sot that circular to ± elliptical in face view 1·5 (−2·23)–2·7 mm high ($n = 17$) and 2·0 (−2·7)–3·2 mm wide ($n = 16$) with border 0·08 (−0·2)–0·39 mm wide ($n = 6$). Anatomy unknown.

Description. This is based on almost sixty specimens, the vast majority being fragments of strobili. Attached, subtending axes are smooth and considerably narrower than the strobili. The longest exhibit sparse more or less isotomous branching with wide (*c.* 50–70°) branching angles (Pl. 4, fig. 1), and little change in axis diameter from base to apex. Associated sterile axes are less regularly branched and may represent the basal regions of *Adoketophyton subverticillatum.* Circinate tips (Pl. 1, fig. 1) in close proximity to some strobili may also belong to *Adoketophyton.* Proximal parts of some strobili have been found, but most are incomplete distally. The longest 'fragment' (Pl. 1, fig. 3) is suggestive of a plant of quite substantial height, but its subtending axis is missing. Each strobilus comprises four vertical rows of overlapping fertile units, arranged in opposite and decussate pairs. The most conspicuous features of the strobilus are the more or less fan-shaped lateral appendages, which were originally described as sporangia by Li and Cai (1977). The variously fractured strobili and the greater number of specimens available for study have revealed the presence of sporangia inserted adaxially on the lateral appendages, and completely covered by them. Thus the strobilus is composed of lateral fertile units. We are reluctant to use the admittedly more covenient term 'bract' for the sterile segment as this has the connotation of a reduced leaf for which we have no evidence. The strobili are parallel-sided and show little change in appendage size or spacing from base to apex although there is limited evidence for slight twisting (Pl. 1, fig. 3).

The appearances of the strobili vary due to differing orientation during compression and plane of fracture. Plate 3, figure 2 shows an example where a single row of complete appendages is visible in abaxial view with members of two adjacent rows partly exposed 'on end'. Two rows of overlapping appendages are apparent in Plate 2, figure 1, while fortuitous fracture (Pl. 1, fig. 2) reveals the components of the fertile unit in longitudinal section. In the first two examples sporangia are usually, but not invariably, found on dissecting away the appendage (see Pl. 2, fig. 3). The latter show some variation in ab- or adaxial (face) view but are similar within a single strobilus. The majority are fan-shaped (Pl. 2, figs 1–6) with parallel-sided stalks expanding into triangular 'laminae' with straight sides and rounded or frayed distal regions. Some are more rounded laterally (Pl. 2, fig. 9) while others are slightly concave (Pl. 2, fig. 1). The position of a sporangium is sometimes marked by a shallow concavity (Pl. 2, fig. 2) and this is also seen in the curvature in the profiles of appendages (Pl. 2, fig. 3). However others are almost straight (Pl. 2, fig. 10). The basal regions of the appendages are revealed by development or seen in fortuitous fracture, being normally obscured by overlapping distal regions. The well-defined relief seen in the 'compression' fossils suggests that the stalks were quite rigid decurrent structures (Pl. 1, fig. 6; Pl. 4, fig. 6), circular in cross-section when free. This was confirmed by the serial transverse sections through the strobilus (Pl. 1, fig. 4; Text-fig. 2) where the axis becomes lobed below the more or less simultaneous departure of almost circular (in cross-section) appendage stalks. That the appendages were inserted in opposite pairs is confirmed in longitudinally fractured strobili (Pl. 1, fig. 2) and by strobilar axes lacking complete appendages (Pl. 1, fig. 6), although in the latter the exact position of superficial representatives is obscured by the decurrent bases. Vertical distances apart appear to be more or less constant within a strobilus, with no evidence for distal crowding although slight decrease is recorded in the longer specimens.

Stalks are inserted at 20–40° angles to the vertical, again with little variation within a strobilus. That between strobili may relate to degree of maturation in that it seems likely that the appendages would have moved abaxially, facilitating dehiscence of sporangia and scattering of spores.

Where parallel-sided the stalks range between 0·5 and 1·3 mm in width; their length cannot be so precisely determined ($<$ 2·5 mm) because each stalk gradually flattens and expands into the blade. In cross-section at transitions they appear crescentic (Text-fig. 2J–P).

The blade itself is thin and rigid, seen as a thin straight or slightly curved line when fractured longitudinally

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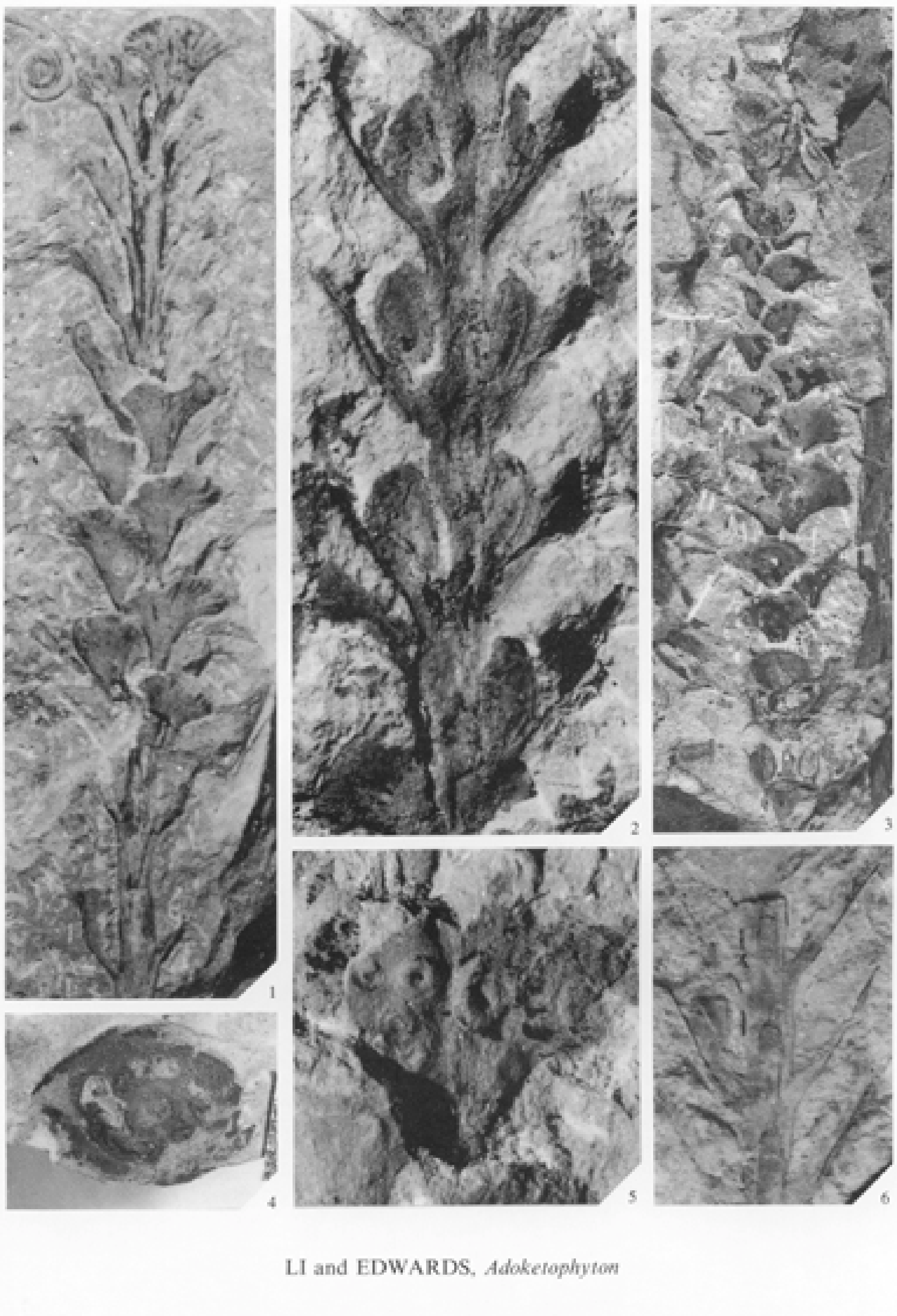
EXPLANATION OF PLATE 1

Fig. 1–6. *Adoketophyton subverticillatum* comb. nov. Posongchong Fm.; S. Yunnan. 1, CBYn 9002001; strobilus showing two rows of appendages and the appearance of that originally described as *Zosterophyllum subverticillatum*; note stalks of 'bracts' only visible at base and isolated circinate axis, × 3. 2, CBYn 9002002; part of fractured strobilus showing sporangia and 'bracts' photographed under unilateral illumination; longitudinal ridges on sporangia on right of axis represent thickening at margin of sporangium valve, × 4. 3, CBYn 9002034*a*; paratype; selected to demonstrate variation in strobilar appearance, × 1·75. 4, CBYn 9002059; transverse section through permineralized axis, representative of that drawn in Text-figure 2; note that at this magnification outlines of organs are masked by staining, × 7·5. 5, CBYn 9002015; impression of abaxial surface of 'bract' photographed in unilateral illumination to show spirorbids, × 10. 6, CBYn 9002031; impression with bases of bracts in relief, × 4.



LI and EDWARDS, *Adoketophyton*

(Pl. 2, figs 8, 10). Its extremities are sometimes irregular, suggestive of the fraying or erosion of less resilient tissues (Pl. 2, figs 2, 4). The slight adaxial curvature of opposing pairs produced a strobilus more or less rounded in transverse section, so that when young it must have superficially resembled an immature *Picea* cone rather than a more sharply angled structure as in a young *Garrya elliptica* inflorescence.

The sporangium is inserted just distal to where the stalk begins to flatten (Text-fig. 2; Pl. 2, fig. 7), up to 1·8 mm from the axis, but the actual junction is not often clearly visible, even when the subtending appendage has been picked away. The sporangial stalk is short and narrow, and often obscureed by the sporangial valves (Pl. 3, figs. 1, 4, 6). In face view the latter range from almost circular to tangentially extended (Pl. 3, figs 1–3, 5–8), but are never wider than the subtending appendage at that level. The more pronounced elliptical examples sometimes result from lateral displacement of the valves of a dehisced sporangium (Pl. 3, figs 5, 7). In side view, sporangia may be strongly flattened as if in section (Pl. 2, fig. 10) or more rounded when folded. The dehiscence line extends around the convex margin (Pl. 2, fig. 7). When sporangia are preserved in side view or are folded, it appears as a slight depression or ridge in the latter (Pl. 1, fig. 2). In certain compressions the margin is characterized by a narrow thicker coalified layer ($< 0·39$ mm). The possibility that the valves were not identical in size comes from dehisced examples where the abaxial valve appears taller than the adaxial (Pl. 2, fig. 10), but this slight asymmetry could well result from differential shrinkage following dehiscence. We have failed to isolate any spores.

Anatomical investigations were a disappointment. Superficial cells of the strobilar axis and appendages, replaced by presumably iron oxides, are elongate and the fact that they are preserved suggests that they were thick walled (Pl. 4, figs 3–4, 7). In the radially orientated somewhat narrower cells of the blade, tapering ends are visible under the dissecting microscope, but when such fragments, and those from axes, were examined under the scanning electron microscope no further detail was observed (Pl. 4, fig. 2). Small 'papillae' on the blade may just reflect irregularities in the entombing matrix.

A partly permineralized stalk contained a block of cylindrical 'thick-walled' cells which under high power incident light microscopy gave the impression of being minutely transversely striated and hence tracheid-like. However, the superficial position of these cells and our failure to see any convincing thickenings under the SEM (Pl. 4, fig. 3) suggest that they were part of a peripheral zone of strengthening tissue, whose presence may account for the regularity in sectional appearance of the stalks.

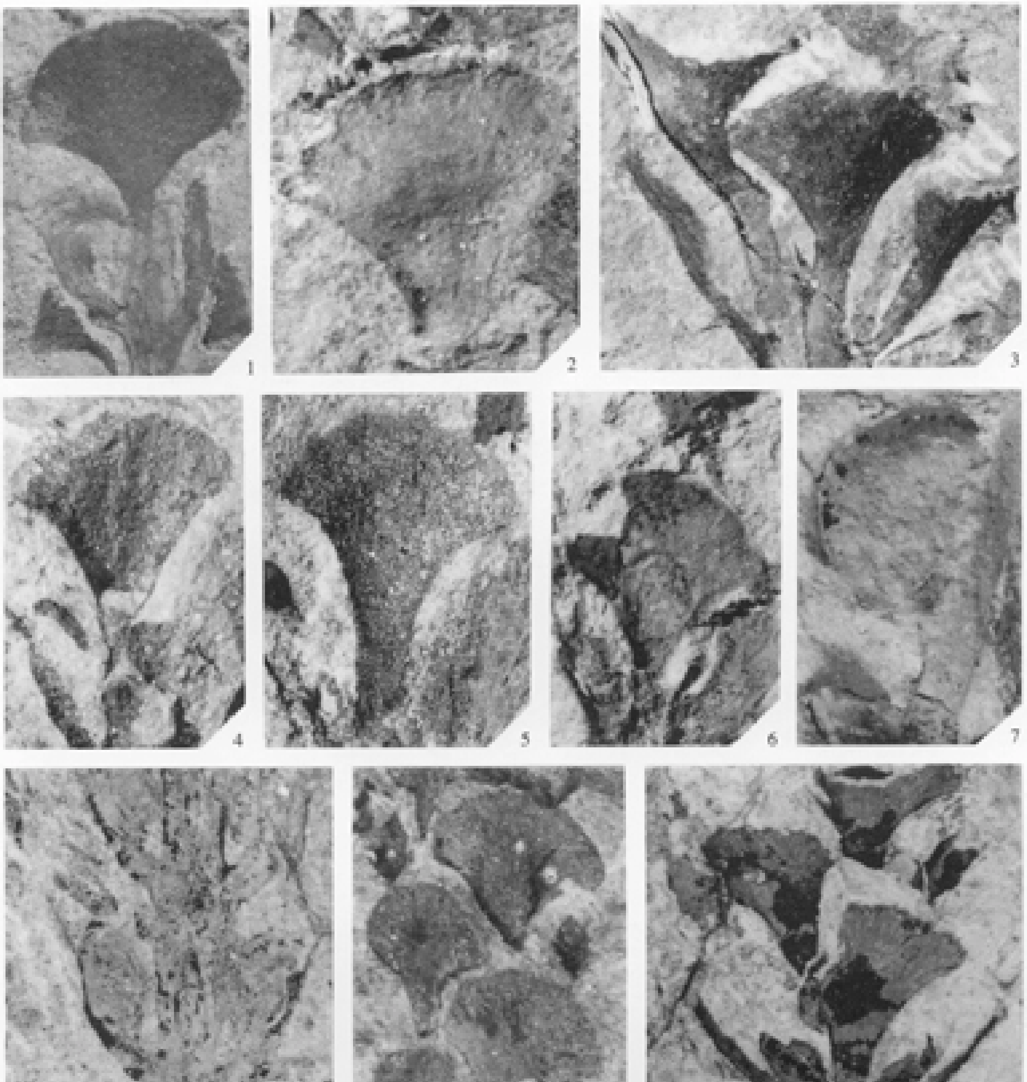
Sections through strobili, while giving important information of relative positions of the fertile parts (Pl. 1, fig. 4; Text-fig. 2) failed to give any extra anatomical detail, except in confirming the existence of thick-walled tissues.

Permineralized axes associated with, but not attached to, the strobili contained centrarch xylem strands, with unusual pitting in the tracheids. We are reluctant to discuss these further here, because we have no unequivocal evidence that they belonged to *Adoketophyton.*

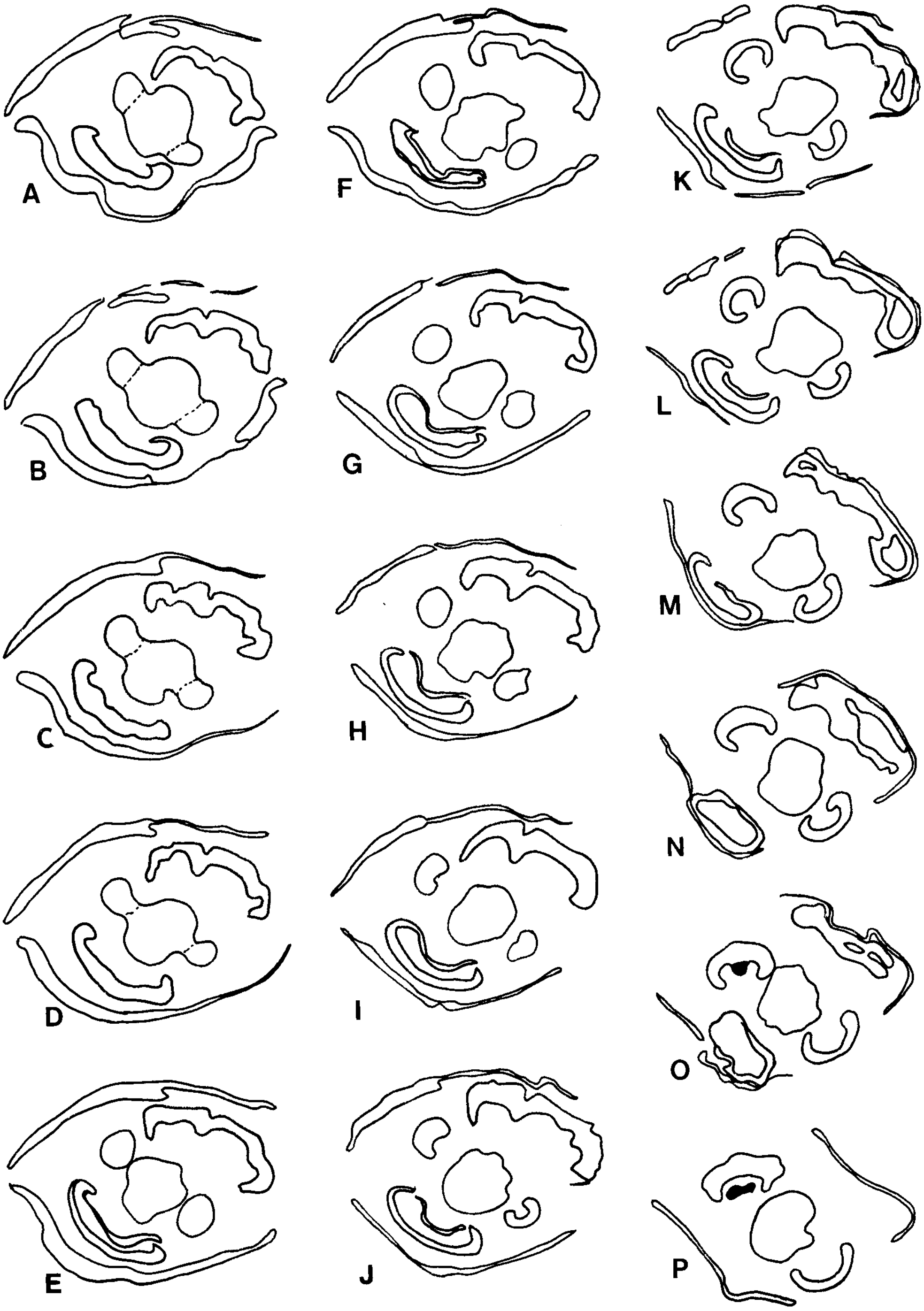
Affinities. Although superficially similar to *Zosterophyllum*, *Adoketophyton* clearly justifies a new genus on the basis of its compound fertile units, a feature not seen in the type genus nor in any other member of the Zosterophyllophytina where sporangia are inserted laterally on the strobilar axis or on aerial branching system, and are not related to any bract-like structures.

EXPLANATION OF PLATE 2

Figs 1–10. *Adoketophyton subverticillatum* comb. nov. Posongchong Fm.; S. Yunnan. 1, CBYn 9002012; abaxial face of exceptionally large 'bract' preserved in fine-grained brown mineral, × 3·75. 2, CBYn 9002048; adaxial face of incomplete 'bract' showing depression originally occupied by sporangium, × 8. 3, CBYn 9002048; bases of 'bracts' in profile and abaxial view, × 6·5. 4, CBYn 9002033; adaxial face of 'bract' showing rock-infilled stalk just below missing sporangium, × 9. 5, CBYn 9002045; abaxial face with bulge marking position of sporangium, × 7·2. 6, CBYn 9002046; adaxial face of 'bract' with remains of sporangium, × 6. 7, CBYn 9002035; impression of sporangium with thickened rims and possible attachment, × 9·1. 8, CBYn 9002004; pale impression with dusting of coaly material showing 'bracts' in vertical section and attached sporangia, × 6·25. 9, CBYn 9002009; small 'bracts' with more rounded outlines, × 5·2. 10, CBYn 9002004; well preserved specimen, with coalified material partly covering orange-brown stained impressions; note the divergent 'bracts'; sporangia towards centre are split into two valves, the abaxial being longer; below there is an uncovered sporangium, × 7·5.



LI and EDWARDS, *Adoketophyton*



TEXT-FIG. 2. A–P, CBYn 9002059; drawings of successive ground surfaces of T.S. strobilus; note the terete outline of the stalk of the fertile appendage when it separates from the strobilar axis; solid black area indicates base of sporangium, × 11.

Intimate association of a leaf and single sporangium, either borne in its axil or on its stalk, is a lycophyte characteristic and in the vast majority of genera such sporophylls are aggregated into strobili. Superficial reading of the description of the fertile parts in the generic diagnosis of *Adoketophyton* would thus seem to indicate lycophyte affinity. However lycophytes are also characterized by the presence of microphylls, i.e. leaves, which are supplied by a single trace from the cauline stele, there being no leaf gaps. The majority of microphylls are undivided and contain a single vein, but some Devonian examples have divided leaves with correspondingly more complex venation (Bonamo *et al.* 1988). In that *Adoketophyton* has smooth axes, and as far as we are aware, no indication of even incipient leaf traces (cf. *Asteroxylon*), it cannot be assigned to the lycophytes. Further the fan-shaped appendage bearing the sporangium is unlike that known for any Devonian lycophyte sporophyll. With this in mind, plus awareness of our almost complete ignorance of the anatomy of *Adoketophyton*, we do not think that the genus is exhibiting heterobathmy – here seen as advanced reproductive features on unmodified smooth axes. This has been suggested by Schweitzer (1980) for *Drepanophycus spinaeformis*, where the reverse is seen and shoots show cauline stelar and foliar characters of lycophytes (Rayner 1984), but there is no consistent association of microphyll and sporangium in the fertile region. Schweitzer regards *D. spinaeformis* as the most derived member of the zosterophylls, but others have united it formally with *Baragwanathia* and *Asteroxylon* in the Drepanophycopsida (Rayner 1984) or informally in the pre-lycophytes (Edwards and Davies 1990; Li C.-S. in press), the phylogenetic connotation being obvious (Niklas and Banks 1990). In the case of *Adoketophyton*, we consider the compound fertile unit an example of convergence, a similar response to selection pressures relating to protection and nutrition of the sporangium, and that this genus is not representative of the ancentral group that gave rise to the lycophytes (see also Niklas and Banks 1990).

A similar association of sporangium and subtending bract was described by Stepanov (1975) in a new genus, *Uksunaiphyton* of uncertain affinity from the early Devonian of the Kuznetsk Basin, Siberia. Strobili, each comprising a single row of appendages, terminate smooth, bifurcating axes, but the distally curving bract is reconstructed as linear. This appearance may well result from longitudinal fracture of a flattened structure, thus strengthening similarities with *Adoketophyton*, but we would like further information on the Siberian specimens before speculating further on affinities.

The Barinophytaceae is a group of Devonian plants of uncertain affinity in which strobili consist of elongate almost linear lateral appendages each with a single large sporangium. Best known is heterosporous *Barinophyton*, where two rows of alternately inserted appendages are recurved abaxially, with each appendage bearing a sporangium on its concave surface, and twisted so that the two rows of sporangia face each other. The xylem in the cone axis is exarch (Brauer 1980). The strobilus of *Protobarinophyton*, which extends into the Lower Devonian in Siberia, is similarly constructed, but is terminal and solitary, whereas those of *Barinophyton* are pinnately arranged (Brauer 1981). These plants differ from *Adoketophyton* in appendage shape and sporangial insertion. Less completely known and hence putative members of the Barinophytaceae are *Krithodeophyton croftii* (Siegenian, S. Wales, Edwards 1968) and the fructification associated with *Enigmophyton superbum* (Frasnian of Spitsbergen, Høeg 1942) where strobili comprise two rows of appendages and sporangia. Sporangia of both taxa are thought to alternate with linear bracts, although their exact relationship could not be determined.

In contrast the strobilus of *Stachyophyton yunnanensis* (Geng 1983), found at the same horizon as *Adoketophyton*, has spirally arranged lateral units, each consisting of a linear appendage which bifurcates terminally and to which a more or less elliptical sporangium is adaxially attached. Such examples illustrate the range of complexity (usually underemphasized) in Devonian strobili which we extend further with this description of *Adoketophyton*. However, we are reluctant to assign the new genus to an existing group and leave it under *Incertae Sedis*.

TABLE 1. Species lists from eastern and southern Yunnan Province, China. Stratigraphy based on Liao *et al.* (1978). For endemic genera, see Li (1982); Geng (1983, 1985); Hao (1988, 1989*a*, 1989*b*); and Hao and Beck (1991*a*, 1991*b*). (? indicates of uncertain taxonomic position; Z, zosterophyll; R, rhyniophyte; T, trimerophyte; * endemic species; † endemic genus).

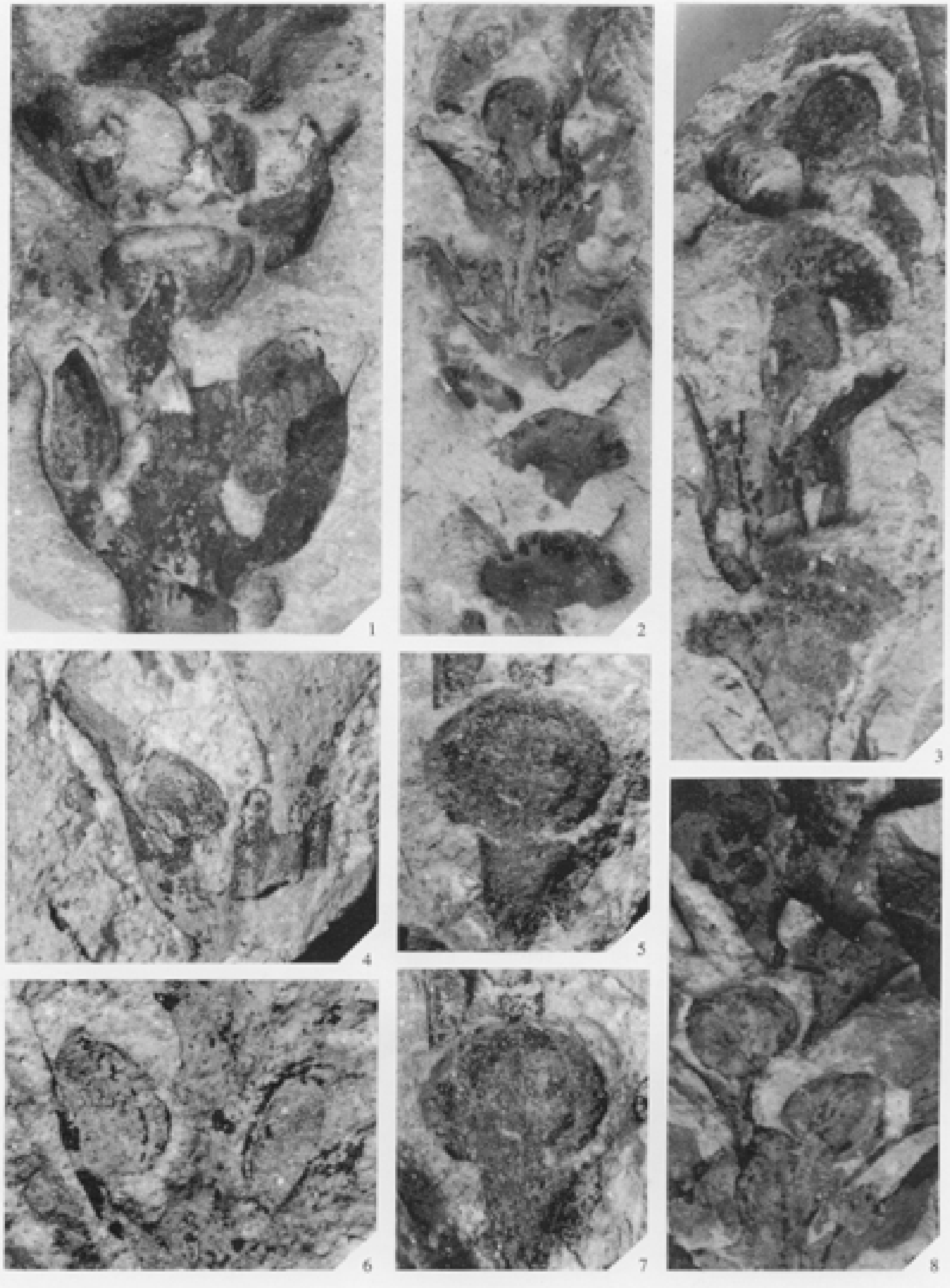
Eastern Yunnan		Southern Yunnan		Europe
Xujiachong Fm.	* *Zosterophyllum yunnanicum* Z * *Z. australianum* Z † *Hsüa robusta* R *Drepanophycus spinaeformis*	Pojiao Fm.		Emsian
Guijiatum Fm.	? *Z. myretonianum* Z	Posongchong Fm.	* *Z. contiguum* Z † *Z.* cf. *australianum* Z † *Discalis longistipa* Z † *Adoketophyton subverticillatum*? † *Huia recurvata*? † *Stachyophyton yunnanense*? † *Gumuia zyzzata* Z † *Eophyllophyton bellum*? † *Catenalis digitata*? † *Yunia dichotoma* T	Siegenian
Xitum Fm.	Various algae *Z.* sp. Z	No deposition in Yunnan		Gedinnian
Xiaxishancun Fm.				
Uppermost Yulongsi Fm.				

DISCUSSION

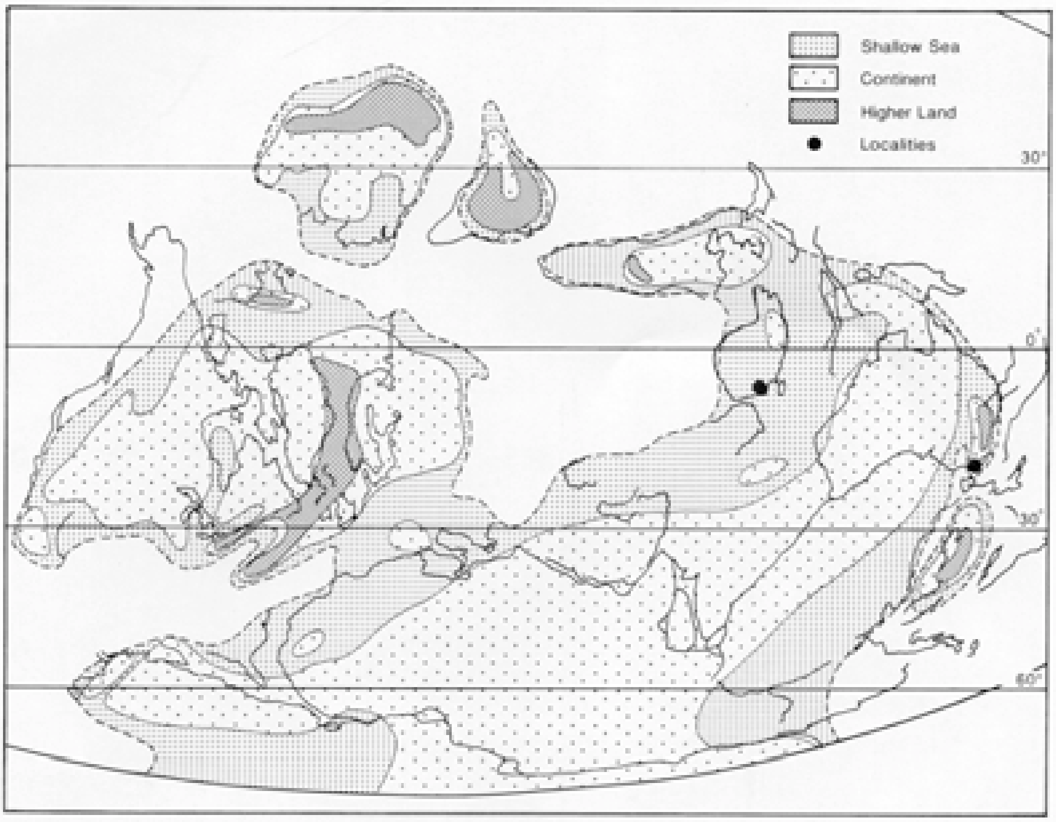
The Lower Devonian species list of higher plants from Yunnan Province given in Table 1 is a remarkable tribute to the recent research activity of Li, Cai, Hao and Geng, and will undoubtedly be extended as extensive collecting continues. Edwards and Davies (1990, fig. 16.3), have recently shown an increase in species in the late Siegenian and early Emsian of Laurussia and inclusion of the Chinese data would accentuate this increase in diversity. When analysed in terms of higher taxa in Laurussia (fig. 16.4) it is seen that rhyniophytes and trimerophytes account for some of the increase, but the major contributors are zosterophylls and taxa which cannot be readily accommodated in the three major subdivisions ('other' in fig. 16.6) or 'pre-lycophytes'. This broadly parallels the affinities of the Chinese species in Table 1. Such proliferation of taxa showing novel combinations of characters would seem to be a botanical example for the increase in disparity

EXPLANATION OF PLATE 3

Figs 1–8. *Adoketophyton subverticillatum* comb. nov. Posonchong Fm.; S. Yunnan. 1, CBYn 9002032*b*; counterpart of base of specimen in Pl. 1, fig. 3; sporangium on lower left is in relief and 'on edge' with dehiscence line visible, × 7.2. 2, CBYn 9002028; part of spike; circular sporangium at top was revealed after removing 'bract'; at bottom is seen typical appearance of entire 'bract' and two rows in profile, × 3·8. 3, CBYn 9002029; part of strobilus with two uncovered sporangia, × 5. 4, 9002037; 'bract' with sporangium. × 8·4. 5, 7, CBYn 9002038; uncovered sporangium; 5 shows attachment and 7, photographed under unilateral illumination, shows overlapping valves, × 8·5. 6, part of spike shown in Pl. 2, fig. 8, × 9·3. 8, CBYn 9002027; two uncovered sporangia near base, and two intact 'bracts' above, × 7·6.



LI and EDWARDS, *Adoketophyton*



TEXT-FIG. 3. Map showing land masses in Lower Devonian times based on Cocks and Scotese (1991) for the earliest Devonian, but modified in that outlines of certain present-day geographical areas are omitted. Localities are in Yunnan and Australia.

that Gould (1989, pp. 49, 207 *et seq.*) thought symptomatic of the initial radiation of a major group, although when compared with the arthropods in Gould's example, the morphological basis for variation in these relatively simple land plants is far more limited.

The record in Laurussia suggests an initial radiation of land plants (e.g. *Cooksonia*) with isotomous branching and terminal sporangia, archetypal features that severely constrained the extent of variation. Change in mode of branching (apical development) seen early in the Devonian of this

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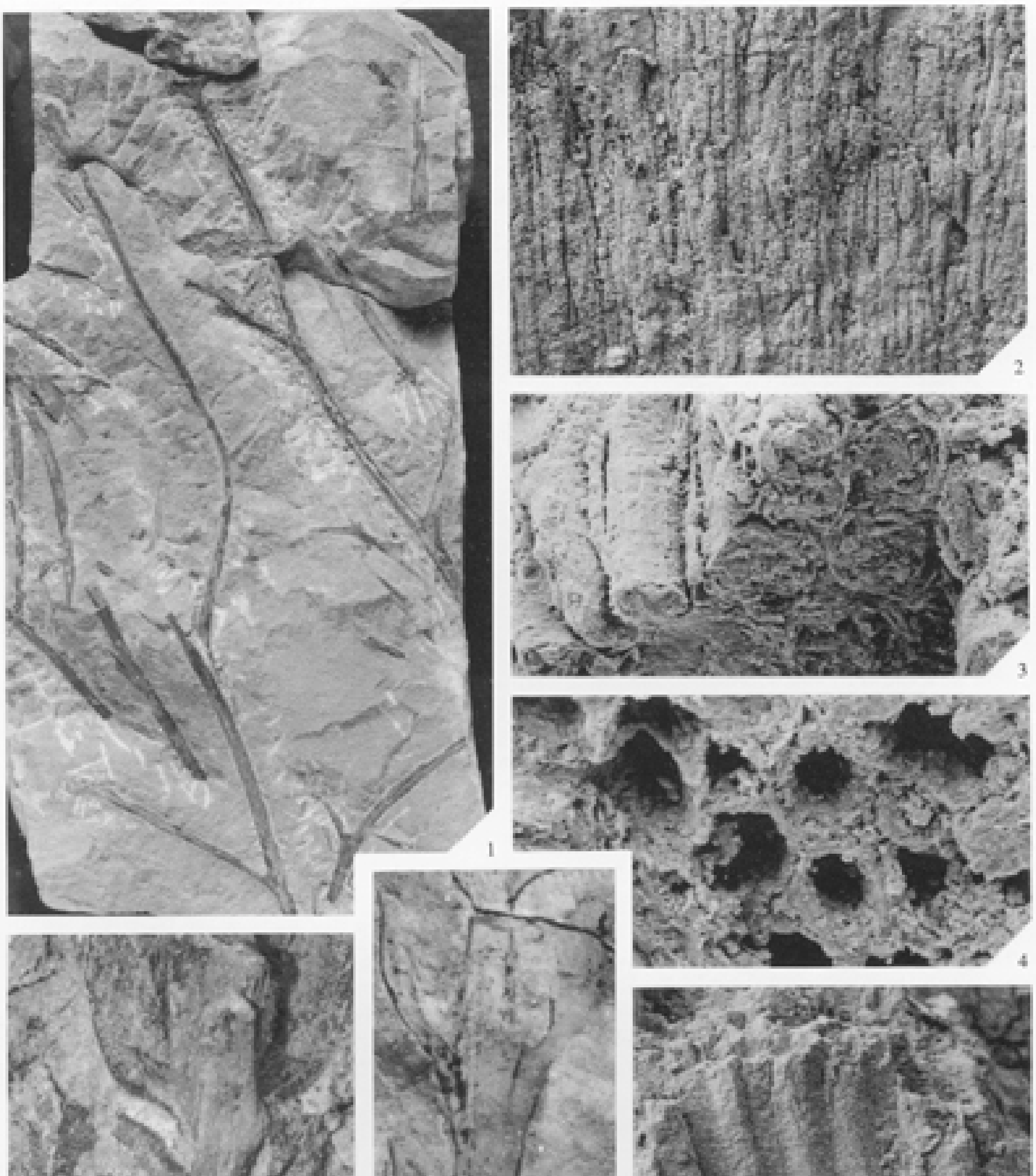
EXPLANATION OF PLATE 4

Figs 1–7. *Adoketophyton subverticillatum* comb. nov. Posongchong Fm.; S. Yunnan. 1, CBYn 9002043; uncovered axes, one of which terminates in a strobilus (arrowed), × 1. 2, CBYn 9002007; permineralized 'bract' showing outlines of superficial cells, × 50. 3, CBYn 9002041; permineralized (? limonite) outer cells of bract stalk; note that the cell surface on the left bears faint horizontal lines, × 500. 4, CBYn 9002041; cells as in 3 but with wall only preserved, × 480. 5, CBYn 9002039*b*; semi-permineralized strobilus, with stalks in relief and sporangia (e.g. that in face view near base) partially preserved in limonite, × 8·2. 6, CBYn 9002030; impression fossil showing the attenuated bases of the stalks in relief, × 5·5. 7, CBYn 9002041; permineralized cells of superficial layers of stalk, × 205.



LI and EDWARDS, *Adoketophyton*

palaeoregion was a release from such archetypal constraints with concomitant increase in disparity. There was also anatomical variation, particularly in the nature of conducting tissues, with plants of similar morphology containing water-conducting tissues characteristic of mosses (*Aglaophyton* (*Rhynia*) *major*, D. S. Edwards 1980), of vascular plants or of unique construction (Hueber 1982; Kenrick *et al.* 1991).

Whether or not such a pattern is repeated on a global scale is conjectural as elsewhere we have only tantalizing glimpses of early land vegetation both temporally and spatially. Later Devonian records from China and Australia broadly correspond in that there are some cosmopolitan plants, but they also contain endemics of uncertain affinity. Anatomical data are sparse, particularly in Australia. A difference is that the Chinese plants appear more complex in organization than coeval Laurussian taxa although to date there are relatively few late Siegenian to early Emsian records in the latter area. A small, but diverse, Pridoli assemblage from north-west China contains a single rhyniophytoid with more complex sporangia than found in Laurussia, but has similarity with Podolia in the presence of a small 'leafy' axis of uncertain affinity (see Edwards 1990*b*, p. 237 for discussion). Palaeogeographically this Xinjiang record is probably on the Kazachstan plate complex, and hence some distance away from both Laurussia and South China localities (Edwards 1990*b*, Chen Xu pers. comm.). In contrast, the Ludlow and early Devonian assemblages from Australia occur in the same geographic region (Victoria). For the most part they differ in composition from the coeval Chinese and Euramerican assemblages, but in the late Silurian again show greater complexity in organization than those for Euramerica. The most surprising element in the Ludlow is the pre-lycophyte *Baragwanathia*, also recorded in the Australian Lower Devonian where it is accompanied by *Zosterophyllum australianum*, *Salopella caespitosa*, *S. gracilis*, *Dawsonites subarcuatus*, *Uskiella* sp., *Yarravia oblonga*, and *Hedeia corymbosa*, an assemblage lacking the disparity of the Chinese one.

Recent palaeogeographical reconstructions for the late Lower Devonian (Text-fig. 3) place South China just south of the equator (*c.* 10° S), somewhat further north than the extensive Laurussian localities (10°–30° S) and Australia (20°–30° S) and close to the latter (Cocks and Scotese 1991). In 1987, Raymond included China and South Laurussia as subunits within a major equatorial–middle latitude phytogeographical unit, in an analysis based on plant traits, such as clustering of sporangia, density of spines. A similar result was achieved by Raymond, Parker and Barrett (1985) on distribution of taxa. Current Chinese investigations emphasize the distinctive nature of the Yunnan assemblages, which certainly cannot be attributed to regional taxonomic practices (Banks 1980; Raymond 1987), but sensible discussion on its phytogeographical and evolutionary significance requires further data, and in addition supporting information on dispersed spore assemblages.

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