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Additional observations on *Zosterophyllum yunnanicum* Hsü from the Lower Devonian of Yunnan, China

Dianne Edwards^a, Nan Yang^b, Francis M. Hueber^c, Cheng-Sen Li^b

^a* *School of Earth and Ocean Sciences, Cardiff University, Park Place, Cardiff CF10 3AT, UK*

^b *Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China*

^c *National Museum of Natural History, Smithsonian Institution, Washington D.C. 20560-0121, USA*

* Corresponding author, Tel.: +44 29208742564, Fax.: +44 2920874326

E-mail address: EdwardsD2@cardiff.ac.uk

ABSTRACT

Investigation of unfigured specimens in the original collection of *Zosterophyllum yunnanicum* Hsü 1966 from the Lower Devonian (upper Pragian to basal Emsian) Xujiachong Formation, Qujing District, Yunnan, China has provided further data on both sporangial and stem anatomy. We show that the sporangia dehiscenced into more or less equal valves through a mechanism that involved the development of large thick-walled cells. Furthermore the coalified xylem is composed of tracheids with G-type thickenings (predominantly annular secondary thickenings with small circular to irregular perforations in the intervening wall), confirming the presence of this form of vascular element in the genus *Zosterophyllum*. The species diagnosis is emended. Characterisation of dehiscence mechanisms in fossil sporangia is complicated by their different modes of preservation. A brief critical survey of the marginal features in bivalved sporangia in zosterophylls and other selected species is followed by a

discussion on their putative functional significance. Preservation notwithstanding, we identify clear differences in mechanisms related to the nature of the underlying cellular structure of the dehiscence feature. The distinctive groove present in many species might represent a mechanism for regulating the timing of dehiscence in response to atmospheric conditions.

Keywords: *Zosterophyllum yunnanicum*, sporangial border, dehiscence, Early Devonian, Yunnan Province

1. Introduction

Specimens of *Zosterophyllum*, from the Xujiachong Formation in Yunnan Province, China, were described by the late Prof. J. Hsü in 1966 as a new species, *Z. yunnanicum*, it being the first record of the genus in China. Subsequently, 29 species of *Zosterophyllum* were listed from Southwest China by Li and Cai (1977); seven were new (*Z. bifurcatum*, *Z. contiguum*, *Z. dushanense*, *Z. longhuashanense*, *Z. sinense*, *Z. spathulatum*, *Z. subverticillatum*), three were previously published (the type species *Z. myretonianum*, *Z. yunnanicum* and *Z. australianum*) and 19 of uncertain validity were left as *Z. sp.* and required more detailed evaluation (e.g., Cai and Schweitzer, 1983; Gensel & Andrews, 1984; Wang, 2007). Subsequently, investigation of additional collections in Yunnan Province has allowed re-interpretation of *Z. contiguum* and *Z. subverticillatum* (Li and Cai, 1977) and their assignation to new genera, *Demersatheca* (Li and Edwards, 1996) and *Adoketophyton* (Li and Edwards, 1992) respectively. *Zosterophyllum longhuashanense*, *Z.*

spathulatum and *Z. bifurcatum* were all described from single and very fragmentary specimens and require more characters to establish even their generic identity. *Z. sichuanense* is being restudied and may be transferred to a new genus (work in progress). Better preserved material from various localities in Yunnan has since allowed the erection of a number of endemic species including Pragian *Z. ramosum* (Hao and Wang, 2000), *Z. minifertillum* and *Z. tenerum* (Hao and Xue, 2013), Lochkovian *Z. xishanense* (Hao et al., 2007), *Z. minorstachyum* (Xue, 2009) and *Z. shengfengense* (Hao et al., 2010), and extension of the range of the genus into the Silurian (*Z. qujingense*; Hao et al., 2007). *Zosterophyllum yunnanicum* was revised from new material by Hao (1985), who added data on epidermal features and spores, and Wang (2007), who provided information on branching patterns and strobili.

This paper is based on unfigured material of *Z. yunnanicum* in the Institute of Botany, Chinese Academy of Sciences from the original collection made by Hsü (1966), and presents new data which further characterise the species.

2. Locality data, material and methods

The fossils were collected from the Xujiachong Formation in Qujing District, Yunnan, China. Details of the locality and stratigraphy are given in Hsü (1966) and Hao (1992). The age of the formation was estimated as late Pragian to early Emsian by Wang (2007) and the strata containing the plants described here, which were collected from the upper part of the formation, as early Emsian based on bivalves and comparative fossil plant assemblages (Wang, 2002), a biostratigraphic coefficient

based on plants (Gerrienne and Streel, 1994, Wang, 2007) and spores (Gao, 1981). More recently, Wellman et al. (2012) extracted well-preserved spore assemblages from the *Z. yunnanicum* horizons and placed them in the *polygonalis-emsianensis* Spore Assemblage Biozone (PE-SEB) of Richardson and McGregor (1986) of early Pragian to ?earliest Emsian age, but cautioned against correlation based on stratigraphic sequences alone especially between the distant Euromerica and the Chinese palaeocontinents in the absence of other biostratigraphically useful co-occurring fossils.

The fossils are coalified and preserved in grey to buff mudstones (Plate I). Fifteen specimens were investigated and nine illustrated. Standard palaeobotanical techniques were employed including maceration of fragments in Schulze's solution, and *dégagement* using tungsten steel needles (Leclercq, 1960; Demaret-Fairon et al. 1999). Coalified fragments were mounted on carbon discs on aluminium stubs and sputter coated with gold-palladium before viewing with an FEI (Philips, Eindhoven, The Netherlands) XL30 ESEM FEG scanning electron microscope at 20kV.

3. Descriptions

3.1. Axes and strobili

The fragmentary smooth axes are up to 100 mm long and 0.6 to 1.7 mm wide. Branching is dichotomous or of the H- or K-type (arrowed in Plate I), but lacks the axillary structures noted by Wang (2007). An elongate strand (Plate II, 7,8,9) macerated from an axis contained tracheids, 13-15 μm wide with mainly annular,

sometimes helical, secondary thickenings separated by a wall containing numerous small circular to irregularly shaped perforations (Plate II, 9) —organisation that typifies G-type thickenings (Kenrick and Edwards, 1988; Kenrick and Crane, 1991; Edwards, 2003).

Almost all the axes are fertile with the terminal strobili composed of helically arranged, closely packed sporangia. The more or less parallel alignment of the strobili and their proximity at the same level (Plate 1) in an allochthonous assemblage suggest that all the strobili on this slab might have belonged to the same plant, although there remains the possibility of current alignment.

Strobili are 30 to 50 mm long and 4 to 6 mm wide. Individual strobili sometimes decrease in diameter distally because individual sporangia become smaller (Plate III, 1, 3). Strobilar appearance also varies depending on the preservation of the sporangia; some are folded laterally (Plate III, 1 lower left side; 6 right side) and others are compressed without distortion such that a dorsiventral view is seen (Plate III, 3, 7 middle row). Although superficially the sporangia appear to be attached in four rows (i.e. opposite and decussate; Plate III, 7), careful dissection indicates that individuals are inserted in a very low helix.

3.2. *Sporangia and stalks*

Each sporangium is borne on a short stalk inserted at an acute angle with only slight (Plate IV, 1, 2) or no (Plate III, 1, 5 lower arrow) adaxial curvature, such that the sporangium is held erect and almost parallel to the strobilar axis. The stalk gradually increases in width below the sporangium but there is no well-defined

junction (Plates III, 8, 9; IV, 1, 2, 4) in dorsiventral view, The stalks are 0.8 to 1.2 mm high (n = 12) and 0.4 proximally to 0.8 mm wide distally (n=10).

Each sporangium has two almost equal valves, and in face view, these may be circular or elliptical in outline with a gradual change in shape and often slight decrease in size from base to apex of a single strobilus. The diameter of the circular sporangia which ranges from 1.2 and 2.5mm. These are usually located distally in the strobilus(Plate III, 2, 4). The height of the elliptical sporangia ranges from 1.2 to 2.5 mm, and their width from 1.7 to 3.3 mm. The surface on the outside of a well preserved valve exhibits striations, probably representing epidermal cells, radiating without interruption from near the base of the sporangium to the convex margin (Plate III, 8, 9), and so a well-defined border is not obvious in this type of preservation and aspect. However when fragments of wall are missing its inner limits are marked by a coaly line or ridge which extends around the convex margin confirming the presence of a marginal feature which tapers towards the junction with the stalk (Plate IV, 3). Where the coaly wall is almost completely absent, the outer limit of the sporangium is also marked by a dark line (Plate III, 4) and a groove represents the inner limits of the border. In some specimens the junction between border and presumed sporogeneous area is marked by a gap in the coalified wall (Plate III, 9). The border itself is usually 0.3-0.4 mm wide (maximum width = 0.5 mm, n = 44) (Plate III, 4, 5 upper arrows, 7 arrows).

In sporangia compressed laterally or folded, the border is represented by two extended triangular areas that diverge at angles between 26 and 57 degrees and taper

from a broad base to a point (Plate IV, 7). In all such specimens the border of the abaxial valve is very slightly the longer and often wider at its base (Plate III, 1 arrows, IV, 1 arrow, 2 arrows, 5 arrows, 6-8.). This is confirmed by scanning electron micrographs of fractured fragments of sporangia (Plate II, 1, 2, 3 arrows, 4 arrows) where the base of the abaxial wall is thicker than the adaxial and contains some thick walled cells with rounded triangular lumina (Plate II, 1 arrow, 2 arrows; Text fig. 1e). Where the two borders converge proximally, there is a narrow, apparently non-cellular, flat-topped band, about 25 μm wide (Plate II, 5, 6 arrows), which probably represents the dark ridges noted in light microscopy (Plate IV, 3 arrows). Here it is named the connecting band because it is a region of organic/cellular continuity between the valves. There is no evidence of further fusion between the borders of the two valves.

The sporangia are usually highly compressed dorsiventrally. In some examples the sporangial cavity is filled with a film of sediment on the surface of which, as well as on fragments of macerated sporangial wall, are occasional spores. These have been examined by scanning electron microscopy. They are smooth walled with very poorly preserved trilete marks (Plate II, 5 S-arrow, 10), but curvaturae were not observed. Spore diameter is 24 to 34 μm .

4. Systematic palaeobotany

Subdivision Lycopytina sensu Kenrick and Crane, 1997

Class Zosterophyllopsida Hao and Xue, 2013

Order Zosterophyllales Banks, 1968

Family Zosterophyllaceae Banks, 1968

Genus *Zosterophyllum* Penhallow, 1892

Zosterophyllum yunnanicum Hsü, 1966

Emended diagnosis: As in Wang (2007), new information in bold: Axes naked. Rhizomes K- or H- shaped. Erect axes dichotomous or pseudomonopodial in branching. Epidermal cells elongate, 70-280 μm long and 12-60 μm wide. Fusiform stomata 65-80 μm long and 40-70 μm wide, with two guard cells enclosing a pore. **Central vascular strand with G-type tracheids (predominantly annular secondary wall thickenings; intervening primary wall with small circular to irregular perforations) 13-15 μm diameter.** Fertile axes 0.5-2.7 mm wide, sometimes K- shaped and bearing an axillary axis. **Strobili** consisting of up to 50 lateral sporangia closely and helically arranged. **Bivalved sporangia with circular to elliptical outline in face view; 1.0-3.3 mm high and 1.2-4.8 mm wide. Border up to 0.5 mm wide comprises the free margins of the two valves. In longitudinal section the free margins taper from base to apex; base of abaxial margin wider than adaxial, and composed of large thick-walled cells.** Sporangial stalks, 0.6-3.0 mm long and 0.3-0.9 mm wide, **widen into bases of sporangia.** *Retusotriletes*-type of isospores, 20-55 μm in diameter, smooth, with simple **sutures** extending 1/4-3/4 of spore radius.

Notes. This new information on the nature of tracheidal thickenings and sporangial architecture makes *Zosterophyllum yunnanicum* one of the most completely known species in this cosmopolitan genus. Earlier Hao (1985) had

described epidermal features, including stomata and spores (cf. *Retusotriletes* aff. *triangulatus*), while Wang (2007) gave further data on branching patterns, including the K-type that is seen in the type species. Surprisingly, although tracheids with annular to spiral thickenings have been described in this and other species, this is only the second record of G-type thickenings in the genus *Zosterophyllum* (*Z. divaricatum*; Gensel 1982). Their presence in taxa such as *Gosslingia breconensis* (Kenrick and Edwards, 1988), *Ventarura* (Powell et al., 2000) and *Deheubarthia splendens* (Edwards et al., 1989), all zosterophylls with scattered lateral sporangia, and basal lycophytes, *Asteroxylon mackiei* (Edwards, 2003), *Baragwanathia abitibiensis* (Hueber, 1983) and *Drepanophycus qujingensis* (Li and Edwards, 1995) had led to the inference that such tracheids characterized the basal Lycophytina *sensu* Kenrick and Crane (Edwards, 2003). They are not exclusive to that subdivision being found for example in *Adoketophyton* and *Euphyllophyton*. All these records are based on permineralisations, such that the absence of G-type tracheids in zosterophylls, largely preserved as compressions, may well be a taphonomic effect. In the light of this, the permineralised tracheids of *Z. llanoveranum* (Edwards, 1969a) and *Z. cf. fertile* (Edwards, 1969b) merit revisiting. The H-shaped branch described here was isolated in the matrix, and so its position on the plant, for example on the rhizome cannot be substantiated. The spores illustrated here do not show clear curvaturae, but this may result from their immaturity or poor preservation. The very small discrepancy in length between the valve borders is not considered sufficient to merit removal of the species from the genus *Zosterophyllum* which is characterized by two

equal valves (see below). The significance of the sporangial border will be explored in more detail in the next section.

5. Review of marginal features in zosterophyll and other (selected) bivalved sporangia

An early innovation in the reproductive biology of vascular plants was a sporangium composed of two valves, with circular, reniform or transversely elliptical outlines, which were accompanied by marginal features, often somewhat uncritically named thickened borders, and often assumed to be involved in controlled dehiscence (Fig.1).

Such sporangia were sometimes terminal (eg. *Aberlemnia* (*Cooksonia*) *caledonica* Gonez and Gerrienne 2010 (Edwards1970)), but most widespread in the zosterophyll clade where they occur in sporangia in strobili or distributed over axes. There is a major problem in making valid comparisons on the nature of the margin between taxa because of the different preservation types involved (cf the Scottish impression material (Edwards 1970) and the coalified Brazilian fossils described by Gonez and Gerrienne (2010)). Clearly permineralisations, e.g. silica or iron compounds, give good cellular detail, as do charcoalifications. Coalified compressions are less informative yet form the bulk of our evidence. *Zosterophyllum yunnanicum* provides a rare example where some three-dimensional detail remains in compressions.

We concentrate on taxa in which some cellular detail is known on marginal features and exclude the taxa in which the valves are clearly of unequal size (eg.

Crenaticaulis, Banks and Davis 1969).

5.1. *Sporangia of Zosterophyllum with unequivocally thickened permineralised borders*

Data come from two examples from the Pragian-Emsian Senni Beds from South Wales. The more completely preserved in *Z. llanoveranum* shows that each valve margin is free and composed of large crescentic cells and is united to its counterpart at the base of a groove running around the convex margin via a number of layers of less distinct, thin-walled cells about the same thickness as the remainder of the wall of the valve (Fig. 1c; Edwards, 1969a). A broadly similar organisation but one which is less well defined is present in *Z. cf. fertile*. The strobili in both taxa contain two rows of sporangia and were placed in the sub-genus *Platy-Zosterophyllum* by Croft and Lang (1942).

5.2. *The margins of compression fossils of Zosterophyllum sporangia*

Some taxa such as *Z. yunnanicum* show traces or lack any evidence of a marginal feature in abaxial views of valves preserved as compressions and certainly no evidence of a uniform thickening. The basal thickenings in the border in sporangia in side view (eg. Plate IV, 7) in *Z. yunnanicum* were observed in detail only via scanning electron microscopy (Plate II, 2). There is of course the possibility that the more distal regions of the valves in this taxon were equally wide in life but distally composed of thin-walled cells that were more readily compressed and homogenised

during diagenesis, thus accounting for the tapering. In other species, marginal thickening is more pronounced and of apparent uniform thickness throughout (e.g. Chinese *Z. australianum* Hao and Wang, 2000), but the type species, *Z. myretonianum*, is again typical of those where records of the border depend on preservation. Thus Lang (1927) described a thickened convex margin, while Edwards (1975) failed to find one in essentially impressions, although she described a line interpreted as the inner limit of a thickened margin in rare specimens. In the light of the new information presented here, this might be equivalent of the connecting band. In superb colour illustrations of, *inter alia*, *Zosterophyllum* sporangia, Hao and Xue (2013) included one of *Z. australianum* (Fig. 4.14b) where a ridge is clearly visible, as it is in sporangia of their new species, *Z. tenerum* (Fig. 4.19) and *Z. minifertillum* (Fig. 4.17) as well as a further species in the Pragian Posongchong Formation, *Z. ramosum* (Fig. 4.16: Hao and Wang, 2000). In *Z. tenerum*, sporangia preserved in lateral view show a ‘dehiscence line’ along the middle part of a shallow depression rim with two further parallel lines indicating the edges of the two valves (Hao and Xue, 2013; Fig. 4.19f, g), whilst in *Z. minifertillum* which lacks cellular detail, a distal split explained as the projecting edge of the border in a mature folded sporangium (Hao and Xue 2013, Fig. 4.17c) might represent the free margins and merits closer examination. In all these Chinese taxa the sporangia are helically arranged in strobili and almost all show prominent borders, described as unthickened in *Z. tenerum*. *Zosterophyllum myretonianum* itself was considered a possible member of a third group (R-type; Fig 1j, k), based on *Ramoferris amalia*, where the

border was poorly developed or absent (see below).

5.3. Selected additional records of sporangia with well-defined margins

These are selected not only because they show additional anatomical data on marginal features but also have relevance to dehiscence mechanisms and phylogenetic relationships. Thus a number of taxa assigned to the Zosterophyllales Hao and Xue, 2013, will not be considered further here. They include certain species of the type genus, eg. *Z. rhenanum*, and the Přídolí Canadian Arctic example of *Distichophyton*, where the sporangium is sometimes represented only by the crescentic limiting line, and those in a non-strobilate clade, eg. *Gosslingia*, (Gosslingiaceae *sensu* Hao and Xue, 2013) where only thickened margins are reported.

Considering silicified zosterophylls from the Pragian-?Emsian Rhynie Chert, where distribution of sporangia (strobili v. fertile zones) is less clear. Borders occur in zosterophylls, *Trichopherophyton teuchansii* (Lyon and Edwards, 1991; Fig. 1a) and *Ventarura lyonii* (Powell et al., 2000). In both, the adaxial valve is very slightly smaller and its wall thinner than the abaxial, but both show an increase in thickness at the margins and the poorly preserved tissue uniting the valves occurs at the base of a very well defined groove. In *Trichopherophyton* this tissue is continuous with a similarly coloured zone on the insides of the valve walls. The cells at the limits of the border are also darker, suggestive of an originally different chemistry, but with little evidence for thick cell walls. In *Ventarura*, where the appearance of the groove

and margins is far more variable, some sections show a lining layer of thick cuticle on each side but in others it is replaced by dark rods. The wall cells are elongate and perpendicular to the groove. The wall itself is at least three-layered, the outermost comprising thin-walled cells that lengthen closer to the groove. They overlie a zone of dark, thick-walled crescentic cells somewhat similar in shape and orientation to those in *Z. llanoveranum* and again with long axes perpendicular to the groove. These become lighter towards the inside where continuous with the broken-down cells lining the locule of the sporangium.

The affinities of *Adoketophyton* (Li and Edwards, 1992) remain conjectural. It has been placed in a basal position within the Lycophytina (Kenrick and Crane, 1997) because each sporangium in a closely packed strobilus is subtended by a bract, considered homologous to a sporophyll, although axes lack microphylls and the xylem is centrarch. It was resolved as a sister group to the Zosterophyllopsida in a recent cladistic analysis (Hao and Xue, 2013). Hao et al. (2003) in describing sporangial wall features from fragmentary permineralisations mention two clusters of thick walled cells forming the margins of sporangial valves which appear joined at the base of these areas (Fig. 1f). The remaining parts of the sporangial walls are composed of six to nine layers of thin walled cells.

Sporathylacium was described from isolated charcoalfied sporangia from the Lochkovian Welsh Basin, so that its appearance as a compression is unknown (Edwards et al., 2001). Elliptical to almost circular sporangia comprise two equal valves united at the base of a shallow wide depression extending around the

circumference. The free margins of the valves show little superficial relief and are composed of thick-walled cells, elongate in longitudinal fracture (Fig. 1b, d), and hence somewhat reminiscent of those in *Z. llanoveranum*. At the base of the depression and uniting the valves is a structureless mass with proximal extensions. On fracturing along the depression, a ridge of this homogeneous material, c.20- 25 µm wide and superficially similar to the connecting band of *Z. yunnanicum*, is seen in this region. Its spores, because they lack curvaturae and possess equatorial thickenings, preclude close relationship with the zosterophylls.

Finally, although again known only from charcoaled and not compression material is a Přídolí rhyniophytoid, *Hollandophyton colliculum* (Rogerson et al., 2002) in which single bivalved sporangia terminate smooth isotomously branching axes. The epidermis of the sporangium is composed of colliculate cells that pass without interruption around the free margin and form the walls of a depression (Fig. 1,1). Fusion of the valves at its base is via a superficially flat strip of tissue with vague indications of cell outlines. The depression does not extend around the entire margin, becoming shallower close to the subtending stem.

5.4. Selected sporangia lacking thickened borders in the zosterophyll complex

In *Ramofaris amalia* (Hao and Xue, 2011), a zosterophyll in the Pragian Posongchong flora, sporangia are helically arranged in loose strobili or are more widely spaced. There is no thickened border but bivalve sporangia are said to dehisce around a narrow rim with 'slot inside' for dehiscence, marked by two rows of

short rectangular cells on the valve margins. The authors considered this arrangement sufficiently distinct from the two types of sporangia border they had described for *Zosterophyllum* (see above) that they designated an R-type (Fig. 1j, k). They cited the pear-shaped sporangial outline resulting from the absence of basal lobes at the junction with the stalk as a further sporangial character in this type.

The affinities of *Nothia* from the Rhynie Chert remain uncertain. Although once placed in the rhyniophytes, in Kenrick and Crane's cladistics analysis (1997) it was resolved as a plesiomorphic member of the Lycopytina. Sporangia are lateral on long stalks and are irregularly arranged. Axes lack evidence of tracheidal thickenings. Sporangia have unique marginal features. In contrast to most zosterophylls, there is no marginal thickening where the two valves meet along the convex margin. Instead there is a decrease in wall thickness to a single layer of cells each with cup-shaped wall thickenings whose differential shrinkage led to splitting along a superficial line of slightly elongate cells (Fig. 1g).

6. Sporangial architecture and dehiscence

The separation of spheroidal and dorsiventrally flattened, essentially ellipsoidal sporangia, into two equal or almost equal segments via a split around the convex margin would allow maximum exposure of spores to the atmosphere for efficient dispersal. Surveys of the construction of the sporangia, both morphological and anatomical, indicate that this has been achieved in a number of ways. The mechanisms involving maturation of sporangia ending with dehiscence possibly

influenced by both internal and atmospheric conditions (from inferences based on extant examples) remain conjectural, especially as there are few if any similarly constructed sporangia today, an observation also made by Ligrone et al. (2012). Particularly intriguing are those sporangia where fusion of the two valves occurred at the base of a depression some distance from the atmosphere, with no evidence there was ever fusion over the whole sporangial border. Could this be related to the retention of water in the groove under wet conditions and, only when this had evaporated, would the atmosphere be sufficiently dry to facilitate efficient dispersal? The example in *Sporathylacium* where the homogeneous zone, possibly originally mucilaginous or produced by deliquescence of cells, at the base of the groove, might represent a further stage in this drying-out process. In other examples, it is difficult to postulate from anatomical information how stresses might be set up that would result in dehiscence. Are there structural advantages in having the junction of the valves 'internalised' that outweigh those of direct contact with the atmosphere should there be some kind of controlled dehiscence? Does such organization protect the more delicate tissues (assuming these to be thin-walled cells) involved in dehiscence from damage on exposure?

7. Marginal features in equibivalved sporangia and relationships

In seeking ancestry of the Lycophytina and particularly the zosterophyll clade, plants with *terminal* bivalved sporangia with marginal features deserve some scrutiny (eg Hueber, 1992). These include *Aberlemnia (Cooksonia) caledonica* (Gonez and

Gerrienne, 2010) where circular to reniform sporangia terminate smooth, isotomously branching axes, but the type material comprises only impressions and the border, if present, is marked by a linear depression or ridge and could easily be removed (Edwards, 1970). Fanning et al. (1992) illustrated a row of brick-shaped cells in this region, the only cellular preservation in a compression tentatively named as *C. caledonica*. In other plants similar sporangia terminate unbranched or variously branched lateral axes. An example of the former is a single late Silurian specimen from Arctic Canada, which, although the authors named it *Zosterophyllum* sp, appears to possess elliptical sporangia terminating short lateral axes whose diameters approach that of the main axis (Kotyk et al. 2002, Fig.14). A sporangium preserved in dorsiventral view appears to have a narrow thickened border. Such examples provide little information on the nature of the border, but in *Renalia* Gensel, 1976, frequently cited as a grade intermediate or transitional between rhyniophytes and zosterophylls (Gensel,1976; Kotyk et al., 2002), developmentally or perhaps taxonomically closely related to the *Zosterophyllum* lineage (Niklas and Banks, 1990), a basal zosterophyll (Hueber,1992) or sister to the Lycopytina in some cladograms (Kenrick and Crane,1997; Fig. 4.12), the margins of the valves are not thickened, but the dehiscence line is flanked on each valve by a row of thick-walled rectangular cells (Gensel,1976). A similar arrangement was reported for *Ramoferis amalia* from the Pragian Posongchong flora and based on this feature alone (perhaps unwisely overweighting one character), *Renalia* might be more closely related to *Ramoferis* than to other zosterophylls with well-defined borders. Kenrick and Crane (1997) in

their cladistic analyses chose to treat all marginal features considered as thickenings as homologous, essentially variations on a basic theme (character-state transitions), although they recognised the possibility of convergence as suggested by other authors. Nevertheless they scored the character as absent or present. Hao and Xue (2013) again using the margin as a binary character but as either a thickened border or a limited or no border. In deliberations prior to a cladistics analysis of early vascular plants, Hao and Xue (2013) distinguished a *Z. llanoveranum* type (Zl-type) with swollen thickened border, which included *Z. ramosum*, from a *Z. australianum* type (Za-type) with extended thickened border (Fig. 11-o). The two groups were united, admittedly on less than satisfactory evidence, in that the junction between the two valves is at the base of a groove whose sides correspond to the marginal feature and which extends around the entire free margin of the sporangium. *Zosterophyllum myretonianum* itself was considered a possible member of a third group (R-type; Fig 1j, k), based on *Ramoforis amalia*, where the border was poorly developed or absent (see below).

Our survey suggests that although widespread in the zosterophyll clade, marginal thickenings and depressed dehiscence lines are not exclusive to it, and not all zosterophylls possess a prominent marginal feature. Considering this variation within the zosterophylls, it is noteworthy that the two examples of margins comprising thick-walled cells (in *Z. llanoveranum* and *Z. cf fertile*) have strobili with two rows of sporangia. In describing *Z. llanoveranum*, Croft and Lang cautiously suggested separating it from the type species *Z. myretonianum* with helically arranged sporangia

and the erection of a subgenus *Platy-Zosterophyllum* a hypothesis supported by the basal position of *Z. llanoveranum* in the 2013 cladistic analysis of Hao and Xue. The difference in sporangial construction would seem to strengthen the distinction of a new clade, but information is also needed from permineralisations of other zosterophyllums, as well as other genera with similarly organised strobili (e.g. *Distichophytum* (= *Rebuchia*); Schweitzer, 1979) for which Hueber (1972) suggested that the mucronate tips noted in the folded sporangia represented thickened borders. A similar feature characterises folded sporangia in *Z. llanoveranum* and *Z. fertile*. Such data are unlikely to come from the very extensive zosterophyll assemblages from China, because there are only two records of strobili with two rows of sporangia. The first comprises two small fragments in the Pragian Posongchong Formation, described as *Distichophytum* sp. (Hao and Xue, 2013), and the other is a single, very poorly preserved strobilus in the Emsian Xujiachong Formation named *Zosterophyllum longhuashanense* (Li and Cai, 1977). This is in marked contrast to records from Laurussia, where, for example, the Přídolí assemblage from Arctic Canada is dominated by such forms (Kotyk et al., 2002), and several taxa occur in the Lower Devonian assemblages from the Rhineland (Schweitzer, 1979.). *Zosterophyllum divaricatum* (Gensel, 1982), a Laurussian Emsian representative with a bilaterally symmetrical strobilus, resolved in Kenrick and Crane's, 1997 analysis of the Zosterophyllopsida, showed a sister-group relationship with the Sawdoniales which contains the Gosslingiaceae, another clade with bilateral symmetry and again poorly represented in China. This has led to a suggestion by Hao et al. (2007) that

zosterophylls with helical arrangements of sporangia were dominant in the early Devonian floras of China compared with those with bilateral symmetry as found in Laurussia (Xue, 2012), although there are examples in the genus *Zosterophyllum*, including the type species, with helically arranged sporangia in Laurussia. *Zosterophyllum myretonianum* is recorded in China, e.g. in the Sichuan Lower Devonian assemblage, but these fossils require reinvestigation.

8. Concluding remarks

When Hsü established *Zosterophyllum yunnanicum* in 1966, it was the first record of Lower Devonian vascular plants, excluding *Drepanophycus* (Halle, 1927) from China and since then, it has been reported from further localities in Yunnan, Guizhou, Guangxi, Hunan and Sichuan provinces (Hsü, 1966; Li & Cai, 1977,1978; Hunan Bureau of Geology and Mineral Resources, 1988; Geng, 1992), so much so that it has been cited as the Lower Devonian index fossil in the floristic area named 'The *Zosterophyllum* Flora' covering South China (Li and Cai 1978). In the almost fifty years that have elapsed since then, there has been an extraordinary proliferation of information on new localities especially in Yunnan with new assemblages and new taxa, many of them endemics that reveal combinations of characters that defy conventional classification, but also include plants that heralded the diversification of lineages that were to dominate vegetation in the Mid and even the Late Devonian. This radiation is particularly well encapsulated in the impressive book written by Hao and Xue (2013) on the plants of the Posongchong Formation, although *Z. yunnanicum*

itself is surprisingly absent from the localities in the Wenshan area. The authors see the increasing diversity in the Pragian as a global event, but it is clear that Laurussian assemblages, often dominated by zosterophylls, lack the disparity seen in China, and thus fuel the hypothesis that South China was the probable centre for basal lycophyte radiations (Hao & Gensel, 1998; Hao & Wang, 2000; Wang et al., 2006), while retaining more basal taxa such as *Zosterophyllum*. Indeed the oldest known species comes from Qujing, Yunnan Province (Hao et al. 2007).

Acknowledgements

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Plate legends

Plate I. Slab with aligned strobili of *Zosterophyllum yunnanicum* from the type locality in Qujing District, Yunnan. Arrow indicates H-branching typical of the genus. CBYn0302. Scale bar = 10 mm.

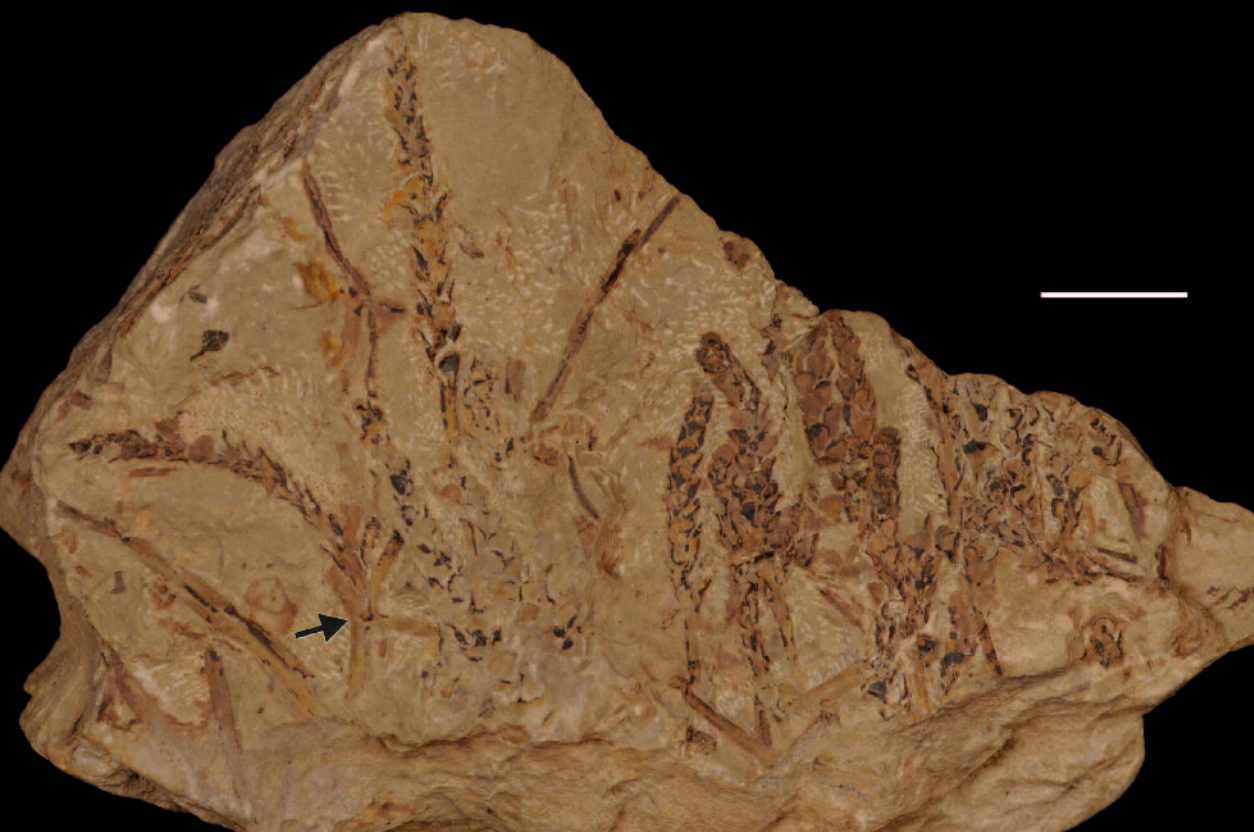


Plate II. Scanning electron micrographs of *Z. yunnanicum*. CBYn 0303.

1. Fragment of distal region of sporangium shows divergence of the margins of the valves (arrow indicates abaxial valve). Scale bar = 100 μm .
2. Enlargement of Fig.1 shows part of the base of the margin of the abaxial valve. Arrows indicate large lumina of three cells. All walls are homogenized. Scale bar = 50 μm .
3. Fragment of edge of sporangium; border of abaxial valve preserved in part. Arrows indicate position of connecting band. Scale bar = 100 μm .
4. Longitudinal fracture of sporangial margin. Border of adaxial wall has broken away (above arrow). Parallel arrows indicate abaxial and adaxial walls of the body of the sporangium, while single lower arrow indicates abaxial wall. Scale bar = 50 μm .
5. Connecting band magnified from 6. S-arrow indicates a spore found attached to sporangial wall. Scale bar = 25 μm .
6. Connecting band (arrows) located between valves. Internal surface of free border to the top of image. Scale bar = 100 μm .
7. Vascular strand recovered on maceration of axis. Scale bar = 500 μm .
8. Longitudinally fractured tracheid with annular thickenings on surface of strand in 7. Scale bar = 20 μm .
9. Fragment of G-type tracheid shows irregular pitting in wall between secondary thickenings. Scale bar = 5 μm .

10. Smooth-walled spore with traces of trilete mark found attached to sporangial wall. Granules are probably contaminants. Scale bar = 10 μm .

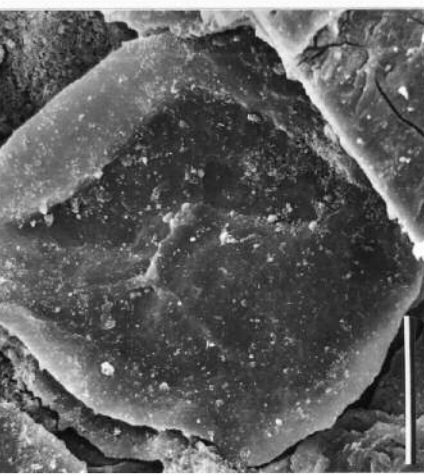
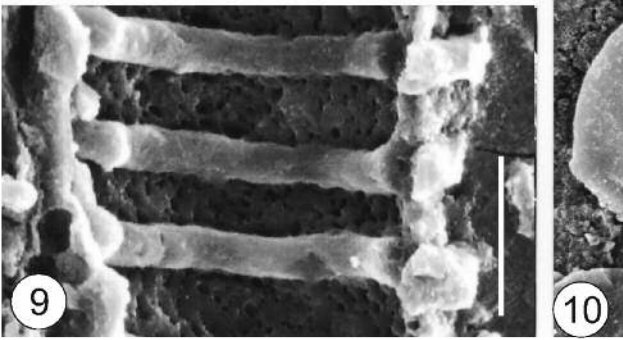
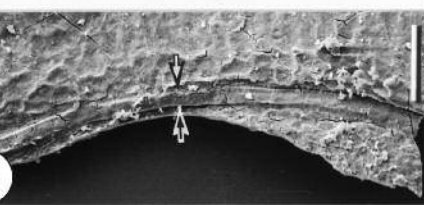
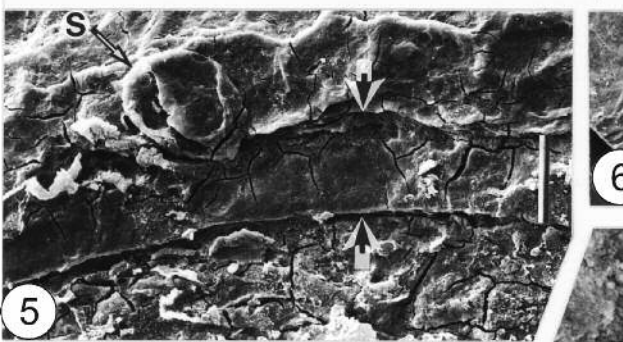
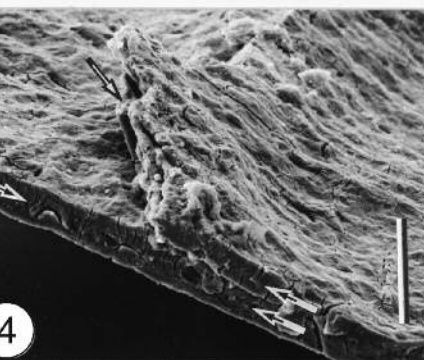
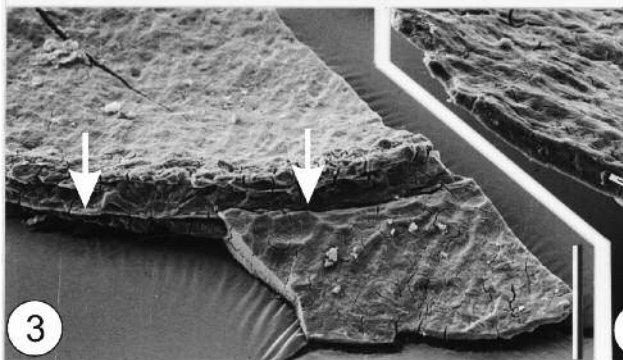
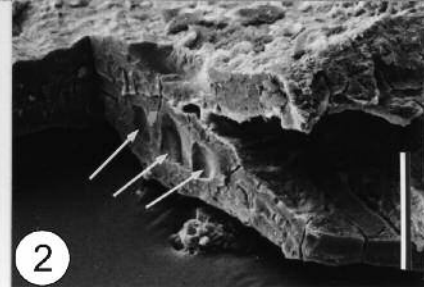
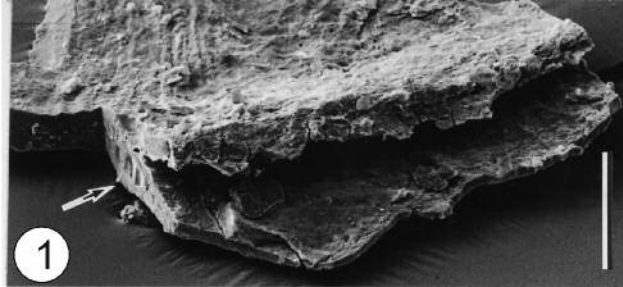


Plate III. Sporangial characters in *Z. yunnanicum*. Scale bars = 1 mm, except in 1.

1. Strobilus enlarged from Plate I with intact base and incomplete tip. Arrows indicate distal separation of valves at convex margins. Scale bar = 5 mm.
2. Irregular longitudinal fracture of part of strobilus exposing adaxial valves of the sporangia further from the observer. Arrow indicates a distal circular sporangia. CBYn 0304.
3. Basal region of strobilus showing lateral attachment of variously folded and compressed sporangia proximally (small arrows) and elliptical valves in face view more distally (black arrow). CBYn 0301.
4. Small sporangium, almost circular in outline. CBYn 0300.
5. Sporangium in face view demonstrating absence of distinction between valve and stalk. Lower arrow indicates attachment. Small black arrows indicate limits of marginal feature. CBYn 0302.
- 6, 7. Two contrasting appearances of strobili (enlarged from Plate I) following longitudinal fracture.
- 8, 9. Exterior appearance of valves with radiating striations representing remains of cells. Note lack of continuity in position of connecting band in 9. CBYn 0302, CBYn 0300.

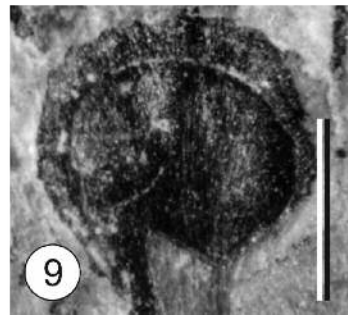
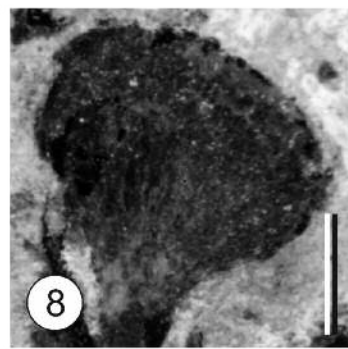
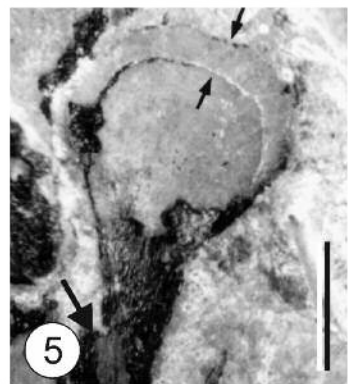
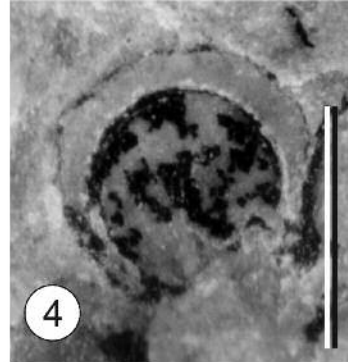
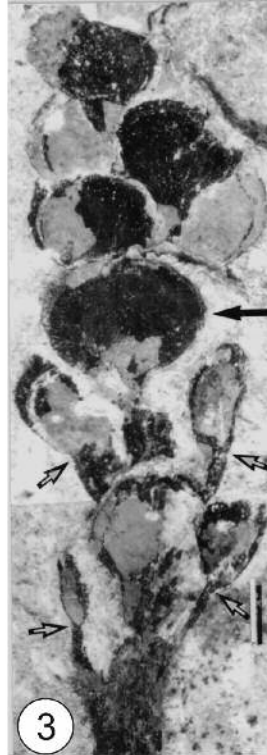
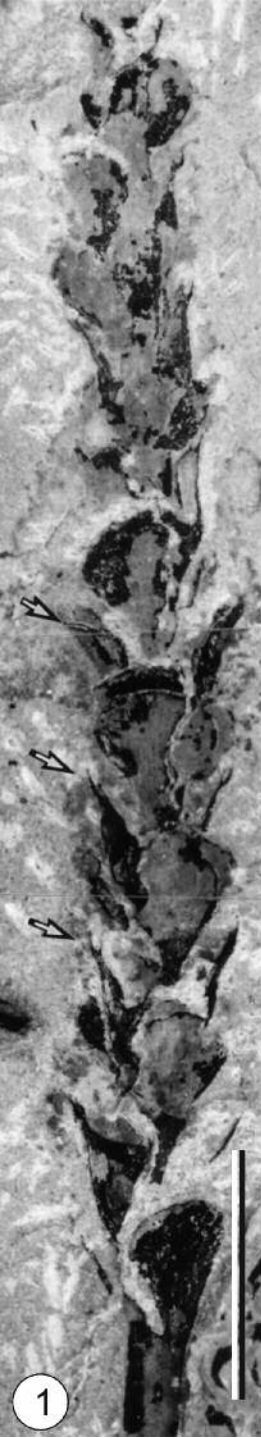


Plate IV. Sporangial characters in *Z. yunnanicum*. Scale bars = 1 mm.

1. Basal part of strobilus. Note folded sporangium (arrowed) showing separation of the border distally but lack of distinctive border on abaxial valve. CBYn 0305.
2. Basal part of strobilus with number of sporangia in profile. Top arrows show diverging border. Lower arrow indicates longitudinal section through valves near the margin. CBYn 0309.
3. Distal parts of four sporangia with conspicuous connecting bands (arrowed) in abaxial valves. CBYn 0307.
4. Almost intact abaxial surface of abaxial valves. CBYn 0305.
- 5-8. Laterally compressed sporangia providing details of the diverging borders (arrowed in 5) in profile. Note increase in thickness close to the sporogeneous area. 5, CBYn 0310; 6, 7, CBYn 0302; 8, CBYn 0307.

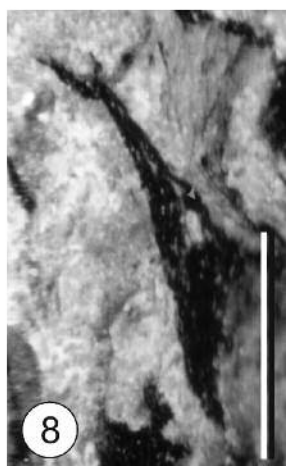
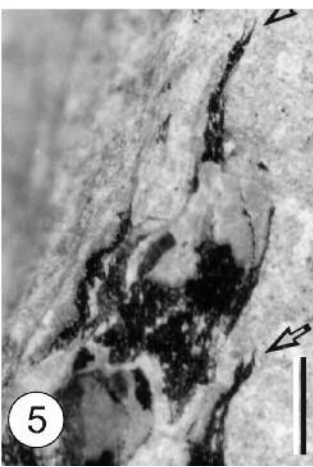
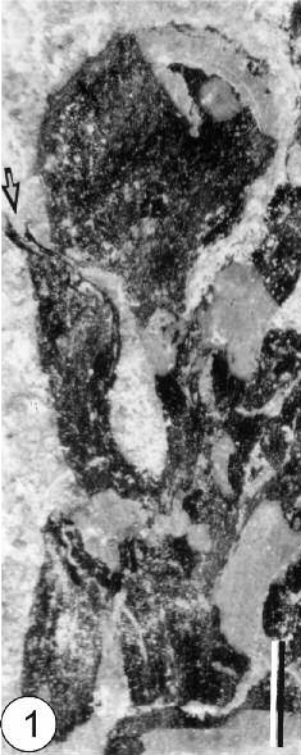


Fig. 1. Line drawings of longitudinal sections through dehiscence of selected sporangia.

a. *Trichopherophyton teuchansii* Redrawn from Edwards *et al.* 2001. Botanical Journal of Linnean Society. Fig. 34, p. 305. Scale bar = 10 μm .

b, d. *Sporothylacium salopense* Redrawn from Fig. 34 as for a. Scale bar = 10 μm .

c. *Zosterophyllum llanoveranum* Fig. 34 As for a, b, d. Scale bar = 50 μm .

e. Idealised reconstruction of longitudinal section through border region of *Z. yunnanicum*.

f. *Adoketophyton subverticillatum* reproduced from Hao and Xue, 2013, Fig. 6.6 with permission. Scale bar = 200 μm .

g. *Nothia aphylla* Redrawn from El-Saadawy and Lacey 1979. Fig. 4, p. 135. Scale bar = 500 μm .

h, h' *Asteroxylon mackiei* (h-immature, h' mature sporangium) Redrawn from Kerp *et al.* 2013. Fig 6D, F, p.301. Scale bar = 100 μm .

i. *Hollandophyton colliculum* Scale bar = 100 μm .

j-o. Reproduced with permission from Hao and Xue 2013, Fig. 6.5, page 223.

Outlines indicate variation in sporangial outlines in zosterophylls. j, k. R-type

represented by *Ramofieris amalia* (convex junction, no thickened border. l, m.

Zl-type represented by *Zosterophyllum llanoveranum* with swollen thickened margin

and faint junction. n, o. Za-type represented by *Z. australianum* with extended

thickened margin and a slightly concave junction.

