EARLIEST TRIASSIC ORIGIN OF *ISOETES* AND QUILLWORT EVOLUTIONARY RADIATION

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ABSTRACT—*Isoetes beestonii* new species is the most ancient known species of this living genus. In earliest Triassic shales of the Sydney and Bowen Basins of Australia it is locally abundant as circlets of transversely wrinkled leaves. It was heterosporous with megaspores of *Maiturisporites rewanensis* and microspores of *Lundbladispora* sp. cf. *L. springsurensis.*

Isoetes thus predates *Pleuromeia* from which it has been thought to have evolved. Australian *Pleuromeia*-like subarborescent lycopsids are here reviewed as whole plants, with names based on fertile structures, and include *Cylostrobus sydneyensis* Helby and Martin from the Sydney Basin, *Pleuromeia dubia* (Seward) Retallack from the Sydney and Canning Basins, and *Cylostrobus indicus* (Lele) new combination and *Pleuromeia sternbergii* (Münster) Corda for Germar, newly recorded from the Canning Basin.

There are in addition an array of cormose lycopsids that formed compact conelike plants when fertile, intermediate in stature between *Isoetes* and *Pleuromeia.* One of these is *Tomiostrobus australis* (Ash) Sadovnikov, formerly regarded as a cone, but here reinterpreted as a small pioneering plant of oligotrophic lakes and ponds, like *Isoetes.* Its megaspores are *Horstisporites* and its microspores are the stratigraphically important *Aratrisporites tenuispinosus.* Other similar forms are *Tomiostrobus polaris* (Lundblad) new combination from the early Triassic of Greenland, *T. mirabilis* (Snigirevskaya) new combination from the early Triassic of the Tunguska Basin of Siberia, *T. taimyrica* (Sadovnikov) new combination from the Early Triassic of the Taimyr region of Siberia, *Lepacyclotes ermayinensis* (Wang) new combination from the middle Triassic of China, *L. convexus* (Brik) new combination from the middle-late Triassic of Kazakhstan, and *L. zeilleri* (Fliche) new combination from the middle Triassic of France and Germany.

The diversity of isoetaleans in early Triassic floras and the weak vascular system of permineralized *Tomiostrobus* and *Pleuromeia* contradict the traditional view that *Isoetes* evolved by reduction in size from *Pleuromeia* and that its opportunistic life style allowed it to avoid plant competition. It is now more likely that Isoetaceae were weedy survivors of Permian-Triassic extinctions. The adaptive radiation and decline of Triassic quillworts matches the recovery from near-extinction, then decline of therapsid reptiles, for which these plants may have been an important food.

INTRODUCTION

OVER THE past two decades early Triassic lycopsids have been discovered to be widespread and diverse. My interest has been primarily in early Triassic lycopsids from southeastern Australia. Two of these fossil species are now envisaged as small plants that may have filled an ecological role comparable to bunch grasses and rosette weeds of lowland meadows and ponds. These fossils are suprisingly similar to the living quillwort *Isoetes* for plants of such geological antiquity. The systematic and paleoecological study of these fossils have suggested extensive revision of other Triassic lycopsids from around the world. The confusing array of names applied to Triassic lycopsids are here brought to order using as a working principle the idea that they should be named as whole plants after their reproductive structures (Sadovnikov, 1982a; Dobruskina, 1985; Wang, 1991). This approach is more useful for early Triassic lycopsids than other kinds of fossil plants, because of the common occurrence of these modestly sized plant fossils in monospecific assemblages of entire plants in growth position. It may not in all cases prove possible to identify isolated leaves or immature specimens of these fossil plants, but the sporophylls show impressive regularity of size and form. The plan view of the sporophyll is particularly diagnostic (Figure 1).

MATERIALS AND METHODS

The primary concern of this research was early Triassic lycopsids of the sea cliff exposures north of Sydney, Australia (Figure 2). Initial studies showed that these cosmopolitan plant fossils warranted extensive international comparison (Retallack, 1975), which has now been pursued in the field and in museums in North America, South Africa and Russia. Specimens are housed in a variety of public collections: the Australian Museum in Sydney N.S.W. (AMF-); Geology Department, University of New England, N.S.W. (UNEF-); Sydney University, N.S.W. (SUGD-); Geological Survey of Queensland, Brisbane, Queensland (GSQF-); Geology Department, University of Tasmania, Hobart, Tasmania (UT-); División Paleobotánica, Facultad de Ciencias Naturales y Museo de La Plata, Argentina (LPPB-); Solms-Laubach collection at the Université Louis Pasteur, Strasbourg, France (SL-); Eigil Nielsen collection University of Copenhagen, Denmark (EN-); Tianjian Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, Tianjian, China (TG-); Geological Institute of the Russian Academy of Sciences, Moscow (GI-); Komarov Botanical Institute, Leningrad, Russia (KB-), Birbal Sahni Institute of Palaeobotany, Lucknow, India (BSIP-); South African Museum, Capetown (SAM-), Department of Paleobiology, Smithsonian Institution, Washington, DC (USNM-). Detailed information on University of New England fossil localities (UNEL-) are on file in the Geology Department in Armidale, NSW.

A cladistic analysis was also attempted using the computer program PAUP version 2.4.1 (Swofford, 1985). The shortest, most consistent tree was chosen from among a variety of runs using only those taxa for which no more than nine character states were unknown.

All of the species of lycopsids of this research have been named, illustrated, and described previously. The following systematic outline is by way of a review, and aims to clarify the taxonomy of this confusing group with new emendations, emended diagnoses, synonymies and cataloguing of holotypes. Fuller descriptions of many of these plants, and particularly of their spores, can be found in the articles cited. The taxonomic revision offered below is a basis for the ensuing account of their ecology and evolution.
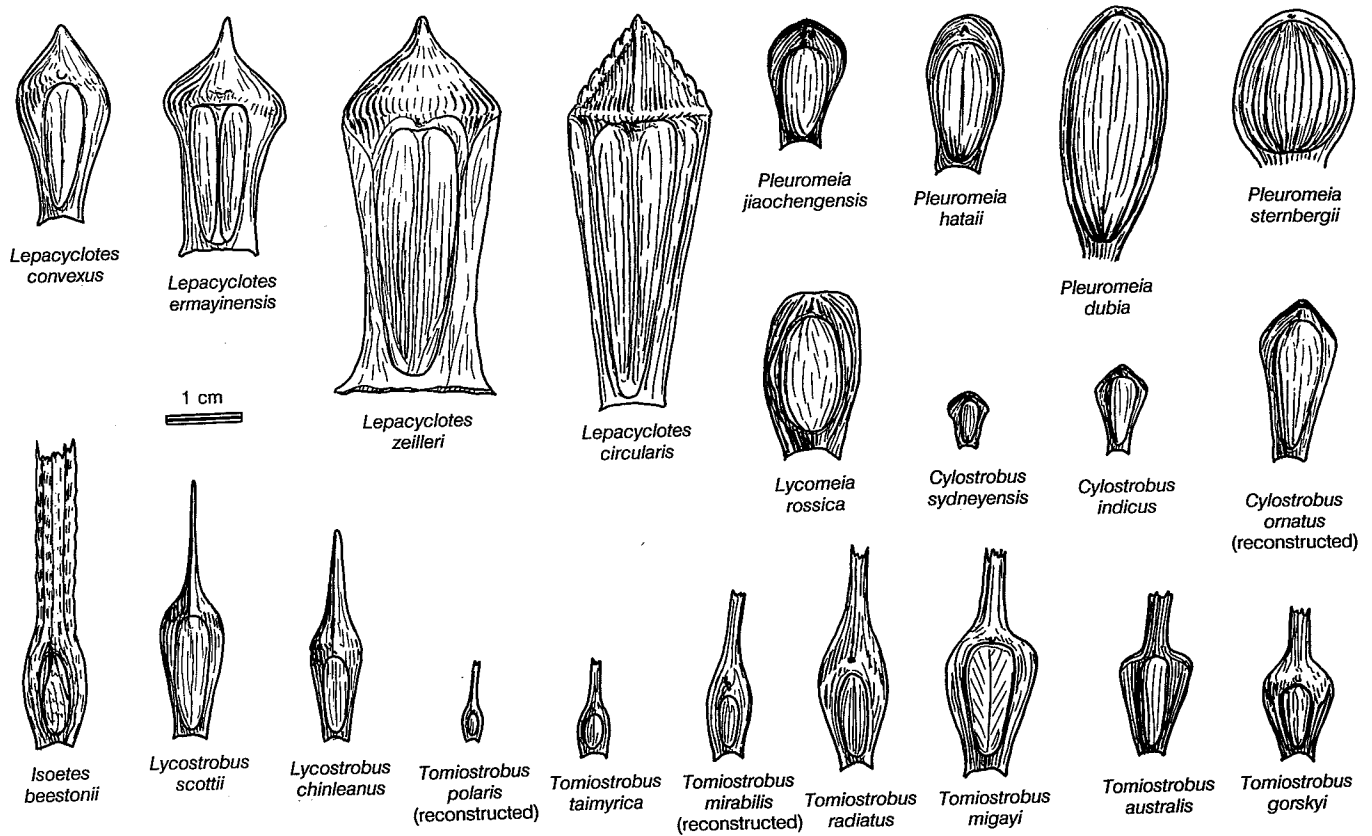
FIGURE 1—Comparison of Triassic lycopsid sporophylls, all drawn to same scale. These are the most diagnostic remains for recognizing species of these plants.
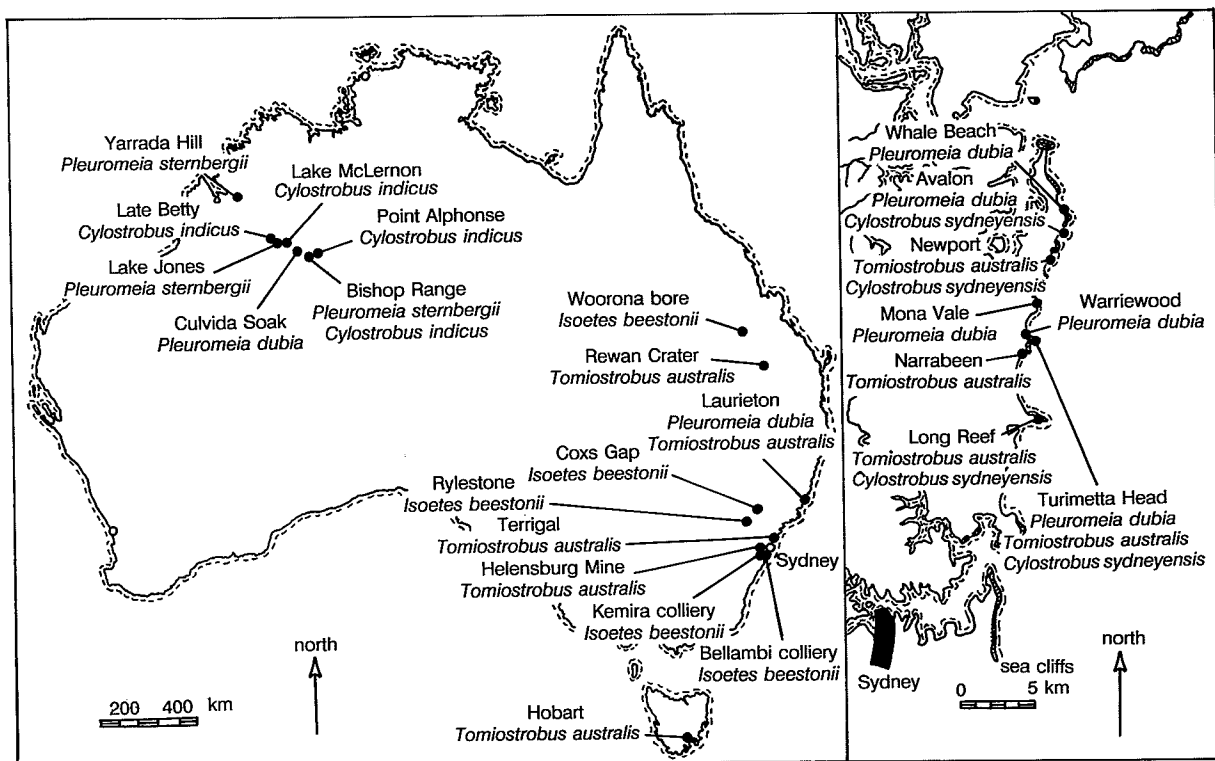

FIGURE 2—Localities for Triassic lycopsids in Australia (left), with more detailed map for the area north of Sydney (right).
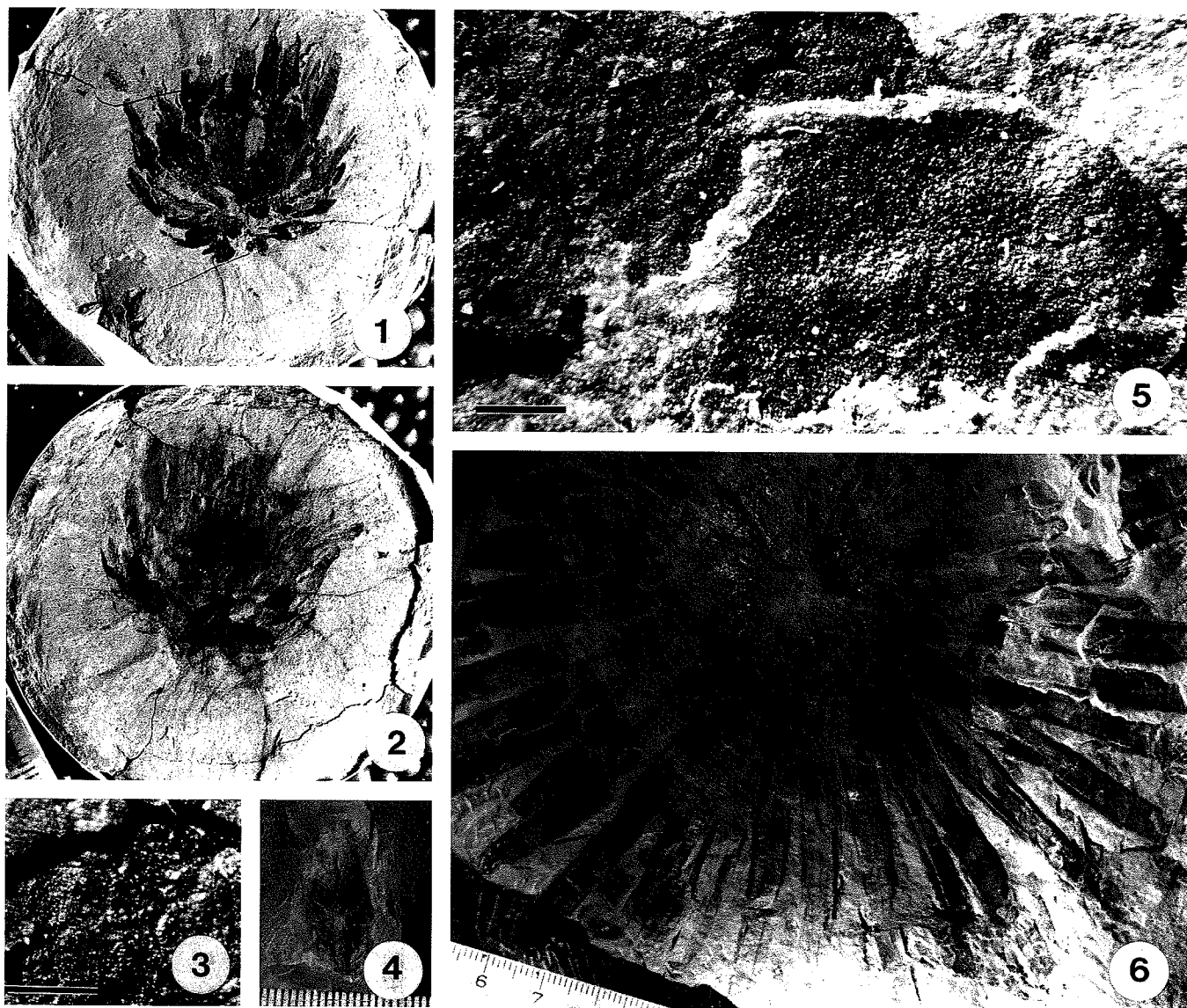
FIGURE 3—*Isoetes beestonii* new species, *1, 2*, fertile plant, part and counterpart (holotype GSQF12953); *3*, detail of megaspores (GSQF12953); *4*, leaf base (AMF91460); *5*, megasporangium (above) and microsporangium (below; GSQF12953); *6*, leaf circlet of sterile plant (AMF58791). Localities and formations include basal Rewan Group south of Blackwater, Queensland (*1–3, 5*) and Coal Cliff Sandstone in Bellambi Colliery (*6*), and Widdin Brook Conglomerate at Coxs Gap (*4*), both in N.S.W., all earliest Triassic. Scales in mm (*1, 2, 4, 6*) and 1 cm long (*3, 5*).

SYSTEMATIC PALEONTOLOGY

Class LYCOPSIDA

Order ISOETALES

Family ISOETACEAE Underwood, 1882

Genus ISOETES Linnaeus, 1753

ISOETES BEESTONII new species

Figure 3

Cylomeia undulata (Burges, 1935). WHITE, 1981, p. 723, figs. 1–3, 5; WHITE, 1986, p. 138, figs. 193, 195, 201, 205.

Skilliostrobus sp. cf. *S. australis* (Ash, 1979). WOOD AND BEESTON, 1986, p. 42, figs. 3–9.

Cylomeia PIGG, 1992, p. 599, fig. 5.

Holotype.—Fertile plant compression (Figure 3.1–3.3, 3.5; GSQ12953).

Diagnosis.—Plant with leaves 5 mm broad and up to 90 mm

long; leaves with widely spaced stomatal furrows and common transverse undulations between and outside the furrows; leaf bases flaring to cordate; corm rounded to crudely tetragonal; rootlets fine (1–2 mm) occasionally bifurcating; sporangia on unmodified leaves, with transverse trabeculae at 1 mm intervals; base of ligule flaring into a sunken glossopodium; apex of sporangium partially covered with velum; heterosporous, with megasporangia near base and microsporangia near apex. Megaspores trilete, tetrahedral to biconvex with subtriangular to subcircular amb, 280–450 μm in equatorial diameter; laesurae extending to 3/4 of spore radius, slightly sinuous with conspicuously raised lips 25–40 μm high at the trijunction, and tapering toward prominent arcuate ridges which delimit a rounded triangular contact area; exine cavate, with robust (7–10 μm thick) sexine and thin nexine; sexine reticulate with fine punctae; muri of reticulum broadest at their bases and tapering to form undulose crests with

fine baculose projections (1–2 μm); meshes of reticulum rounded polygonal (10–23 μm across) in equatorial and distal regions, but reduced to 5–12 μm in proximal areas; reticulum extends onto laesurae. Microspores trilete, subtriangular, cavate, 34–50 μm in equatorial diameter; cingulate; with finely scabrate sexine bearing slender spinae.

Type locality.—At 157.17 m in Queensland Geological Survey exploration bore Woorona NS34, south of Blackwater, Queensland, Australia (Figure 2); basal Rewan Group (Wood and Beeston, 1986), now thought to be of earliest Triassic age (Morante et al., 1994).

Additional specimens and localities.—Coal Cliff Sandstone in roof shales of Bellambi (AMF58791, 60882, see White, 1981, figure 3; 1986, figures 193–195, 201, 205), and Kemira Collieries (MMF16456) and Widdin Brook Conglomerate in the western coalfield at the eastern end of Coxs Gap Railway tunnel (MMF13643–6, 13648–52, 13666, AMF91460) and near Rylestone (AMF39862, see White, 1981, figure 5), all in the Sydney Basin of New South Wales, Australia (Figure 2) and earliest Triassic palynozone of *Protohaploxypinus microcorpus* (Morante et al., 1994).

Comparisons.—Spores of *Isoetes beestonii* new species include megaspores of *Maiturisporites rewanensis* Wood and Beeston (1986) and microspores of *Lundbladispora* sp. cf. *L. springsurensis* de Jersey (1979). The similar genus *Isoetites* is regarded as a *nomen vanum* (Chaloner, 1967). Sporangia at the base of otherwise unmodified leaves in *Isoetes beestonii* are distinct from the conelike reproductive regions of other Triassic quillworts (Figure 1; Table 1). The various species of fossils referred to *Isoetes* and *Isoetites* have been reviewed by Hill (1987), Banerji (1989), Skog et al. (1992), Skog and Hill (1992), and Pigg (1992). None of these have transverse undulations of the leaves comparable to those of *I. beestonii* new species. Transverse undulation due to compaction of a fleshy leaf is also found in *Lepacyclotes ermayinensis* (Wang) new combination, *Pleuromeia sternbergii* (Mader, 1990) and *P. dubia* (Seward) Retallack (1995b).

Genus Tomiostrobus (Neuburg) new emendation

Type species.—*Tomiostrobus radiatus* Neuburg 1936.

Emended diagnosis.—Lycopsid with rounded basal corm and short conical stem; roots narrow and parallel sided; root scars small and circular; leaves helically arranged in a single terminal cluster, linear, elongate, apices frayed, bases dilated, ligulate, with twin abaxial stomatal furrows and central vascular strand, commonly wrinkled transversely; leaf scars rhomboidal, wider than long, with central vascular scar; most of apex bearing sporophylls when fertile, heterosporous, with megasporophylls near base and microsporophylls near apex; sporophylls with short frayed leaf remnant distal of obovate base, bearing adaxial obovate sporangium; megaspores trilete, round to subtriangular and cavate; microspores monolete or trilete, spherical to oval, cavate.

Comparison.—*Tomiostrobus* would have appeared very similar to living *Isoetes* when sterile, but differed from *Isoetes* in its more massive development of secondary tissue and unlobed corms. The sporophylls of *Tomiostrobus* with their frayed distal limb and projecting lateral lobes were distinct from the fertile leaves of *Isoetes* (Pigg, 1992), and sporophylls of other Triassic lycopsids (Figure 1; Table 1).

Tomiostrobus australis (Ash) Sadovnikov, 1982a Figure 4

Skilliostrobus australis Ash, 1979, p. 73, figs. 4–11; Holmes and Ash, 1979, p. 50, figs. 3.1 and 2; White, 1986, fig. 208.

Cylomeia capillamentum White, 1981, p. 731, figs. 9–10; White, 1986, figs. 202–203.
Tomiostrobus australis (Ash, 1979) Sadovnikov, 1982a, p. 103, fig. 3h.
lycopsid rhizophore Turner, 1984, p. 90, fig. 1.
Cidarophyton rewanense Chaloner and Turner, 1987, p. 51, fig. 1, pl. 1, figs. 1–4 only.

Holotype.—Compressed fertile specimen (AMF58856).

Emended diagnosis.—Stem tear shaped, 2–6 cm high, 2–3 cm in diameter; rootlets fine (0.1–0.3 mm); leaves long (up to 103 mm) and narrow (3–4 mm), with a wider base (3–7 mm); sporophylls strongly imbricate, cuneate, expanding from a narrow base (1–2 mm wide) to an outer edge (up to 22 mm wide) forming prominent lobes on either side of a narrow (2–4 mm) parallel-sided limb extending beyond the lobes for 7–20 mm to a frayed end; sporangia cuneate 2 mm wide and 10 mm long. Megasporangia with 64 megaspores, microsporangia with several thousand microspores. Megaspores trilete, cavate, spherical, with proximal surface pyramidal and distal surface rounded; amb rounded to subtriangular, 0.8–1.1 mm diameter, with transverse width 10–20 percent less than vertical height; laesurae straight to end of contact area, with membranous lips elevated 32–46 μm high; nexine delicate, about 1 μm thick, granular; sexine robust, 9–12 μm thick, forming outer layer of exine and lips of laesurae and showing tiny round pits (punctae) 1 μm diameter and larger angular pits 4 μm diameter; larger scale sexine reticulum weaker on contact areas and lips of laesurae than distal face, with meshes polygonal, 20–88 μm diameter; walls (muri) of reticulum up to 18 μm high, broadest near base, 0.5–3.8 μm wide, tapering toward crest to form sharp spinose or rounded projections; hemispherical warts 5.4–9 μm diameter and 1 μm high near center of meshes near proximal pole; contact face marked by irregular arcuate ridge about 10 μm wide. Microspores monolete, bilateral, broadly elliptical to circular, 27–38 × 36–40 μm; laesurae straight to slightly curving, with low membranous lips, extending along major axis; exine cavate with nexine less than 1 μm thick and sexine 1–2 μm thick; inner body of nexine 18–25 × 27–31 μm, loosely enclosed within sexine, proximally attached; sexine finely granulate.

Type locality.—Sea cliffs 100 m south of the Skillion, near Terrigal, New South Wales (UNEL1691): Gosford Formation, late Early to early Late Triassic (Scythian-Anisian: Ash, 1979).

Additional specimens and localities.—Other localities include the Camden Haven Formation near Laurieton, N.S.W. (Holmes and Ash, 1979), Knocklofty Sandstone 16 km north of Hobart, Tasmania (Ash, 1979), and the Arcadia Formation in Rewan Crater, Queensland (Turner, 1984; Chaloner and Turner, 1987). The list of additional specimens following does not include those mentioned or figured by Ash (1979), Turner (1984), or Chaloner and Turner (1987): Gosford Formation near Terrigal, N.S.W. (AMF91455, 914566a,b, from UNEL1691); Newport Formation north of Narrabeen (UNEF13824–6, 13831 from UNEL1457), "Narrabeen" (probably Turimetta Head, SUGD4013), Turimetta Head (UNEF13829 from UNEL1436), north of Newport (SUGD2058), Helensburg Mine (MMF17471), all in N.S.W. (Figure 2) and late Early to early Middle Triassic.

Remarks.—Megaspores of *Tomiostrobus australis* would be referred to *Horstisporites* if found dispersed and the microspores to *Aratrisporites* (Ash, 1979). I agree with Skog and Hill (1992) that *Cidarophyton* (Turner, 1984; Chaloner and Turner, 1987) is a natural cast of a decorticated and abraded basal stele of *T. australis*. By analogy with permineralized *Tomiostrobus mirabilis* (Snigirevskaya, 1980, 1981), this would have lost much of the apical lacunar tissue and pith. This woody basal part of the plant would have resisted decay longer than fleshy leaves and cortex, and may have been transported with wood chips and bone into the sandy conglomerate lag deposits of an ancient

TABLE 1—Comparison of Triassic Isoetaceae.

Taxon	"Cone"	Sporophyll	Megaspore	Microspore	Locality	Age
Isoetes beestonii sp. nov.	Squat conical, most leaves fertile, bisexual	Like sterile leaf	*Maiturisporites rewanensis* Wood and Beeston 1986	*Lundbladispora* sp. cf. *L. springsurensis* de Jersey 1979	Rewan Fm, Queensland, Coal Cliff Sandstone, N.S.W., Australia	earliest Triassic
"*Isoetites*" *sagittatus* Wang and Wang 1990a	Most leaves fertile, bisexual	Spindle-shaped?	Trilete, with reticulate sexine	Unknown	Heshankou Formation, China	late Early Triassic
Tomiostrobus radiatus Neuburg 1936: generitype	Partial circlets of sporophylls known, bisexual	Fusiform with mucronate tip	*Horstisporites*	*Aratrisporites*	Maririninskaya, Kayalakhskaya, Nezhdelinskaya, Fad'yukudinskaya, Ostashkino Suites, Siberia	late Early Triassic
Tomiostrobus australis (Ash) Sadovnikov 1982a	Beehive shaped, bisexual	Triangular, with long frayed distal limb	*Horstisporites*	*Aratrisporites*	Newport Fm, N.S.W., Arcadia Fm, Queensland, Knocklofty Sandstone, Tasmania	late Early to early Middle Triassic
Tomiostrobus olenekensis (Krassilov) Mader 1990	Unknown	Sporangium oval	*Horstisporites*	Unknown	Olenekian Beds, Siberia	late Early Triassic
Tomiostrobus gorskyi (Vladimirovich) Sadovikov 1982a	Partial circlets of sporangia known	Wide subrhomboid, mucronate	Unknown	Unknown	Byzovskaya Suite, Siberia	late Early Triassic
Tomiostrobus migayi (Schvedov) Sadovnikov 1982a	Unknown	Subtriangular with rounded shoulders and slender limb	Unknown	Unknown	Maririninskaya, Fad'yukudinskaya, Kayalakhskaya, Nedzhelinskaya Suites, Siberia	late Early Triassic
Tomiostrobus polaris (Lundblad) comb. nov.	Cylindrical, bisexual	Keeled, with long slender limb	"*Banksisporites*" *pinguis* Dettman 1961	*Densoisporites playfordi* (Balme) Balme 1970	Wordie Creek Fm, East Greenland	late Early Triassic
Tomisstrobus mirabilis (Snigirevskaya) comb. nov.	Squat, conical	Fusiform with long limb	*Horstisporites*	Unknown	Tutonchanskaya Suite, Siberia	Early Triassic
Tomiostrobus taimyrica (Sadovnikov) comb. n.	Cylindrical	Fusiform with elongate limbs	Unknown	Unknown	Fad'yukudinskaya Suite, Siberia	late Early Triassic
Lepacyclotes circularis Emmons 1856: generitype	Beehive shaped, bisexual	Triangular, with bluntly pointed tip	trilete	*Aratrisporites* (abundantly associated, not in situ)	Chinle Fm, Arizona; Tuckahoe Fm, Virginia; Pekin Fm, North Carolina, U.S.A.	early Late Triassic
Lepacyclotes convexus (Brik) comb. nov.	Unknown	Narrow subrhomboid, mucronate	Unknown	Unknown	Kurashasaiskaya Suite, Kazhachstan	Middle to Late Triassic
Lepacyclotes ermayinensis (Wang) comb. nov.	Bisexual	Triangular with mucronate tip	*Djikstraisporites*	*Aratrisporites*	Ermaying Formation, China	early Middle Triassic
Lepacyclotes zeilleri (Fliche) comb. nov.	Known only from partial circlets, bisexual	Triangular with mucronate tip	*Tenellisporites marcinkiewiczae* Reinhardt and Fricke 1969	*Aratrisporites minimus* Schultz 1967	Lettenkohle and Schilfsandstein, Germany, France	late Middle to early Late Triassic
Lycostrobus scottii (Nathorst) Nathorst 1908: generitype	Ellipsoidal, elongate, bisexual	Keeled, with slender distal limb	*Nathorstisporites hopliticus* Jung 1958	*Aratrisporites*	Helsingborg, Sweden	latest Late Triassic
Lycostrobus chinleanus Daugherty 1941	Ellipsoidal, elongate	Keeled, with slender distal limb	Unknown	Unknown	Chinle Fm, Arizona	early Late Triassic
Lycostrobus petiolatus Wang and Wang 1990b	Cylindrical	Keeled, mucronate	cf. *Echitriletes*	Unknown	Ermaying Fm, China	early Middle Triassic
Pleuromeia sternbergii (Munster) Corda for Germar 1852; generitype	Elongate, unisexual	Oval to rounded forming rim to sporangium	*Pusulosporites populosus* Fuglewicz 1973	*Densoisporites nejburgii* (Schultz) Balme 1970	Buntsandstein, Germany, Austria, France, Spain, Italy and Poland; Bogdinskoy, Taralinskoy to Khozbulakskoy Suites, Kazachstan; Olenekian Beds, Primorie; Alikagarskoy, Yokun'shskoy Suites, Tadjikistan; Heshankou Fm, China; Erskine Sandstone, Western Australia	
Pleuromeia jiaochengensis Wang and Wang 1982	Ellipsoidal, unisexual	Oval, bluntly pointed	trilete	Unknown	Liujiakou Fm, China	early Early Triassic
Pleuromeia dubia (Seward) Retallack 1995b	Unknown	Oval, forming rim to sporangium	Unknown	Unknown	Newport Fm., N.S.W.; Culvida Sandstone, W. Australia; Burgersdorp Fm, South Africa	late Early to early Middle Triassic

TABLE 1—Continued.

Taxon	"Cone"	Sporophyll	Megaspore	Microspore	Locality	Age
Pleuromeia hataii Kon'no 1973	Cylindrical, unisexual?	Keeled with rounded tip	trilete	not known	Osawa Fm, Japan	late Early Triassic
Lycomeia rossica (Neuburg) Dobruskina 1985: generitype	Oval, bisexual	Oval, forming rim to sporangium	trilete	Densoisporites nejburgii (Schultz) Balme 1970	Rybinsk Suite, Russia	late Early Triassic
Cyclostrobus sydneyensis (Walkom) Helby and Martin 1965: generitype	Oval, bisexual	Triangular, keeled, obtusely pointed tip	"Banksisporites" viriosus Scott and Playford 1985	Aratrisporites tenuispinosus Playford 1965	Newport Fm, N.S.W., Australia	late Early to early Middle Triassic
Cylostrobus indicus (Lele) comb. nov.	Unknown	Subtriangular, mucronate	Unknown	Unknown	Parsora Beds, India; Blina shale, Western Australia	late Early Triassic
Cylostrobus ornatus (Morbelli and Petriella) Retallack 1975	Oval, bisexual	Triangular, keeled, obtusely pointed	Banksisporites	Aratrisporites	El Tranquilo Fm, Argentina	Late Triassic

Note: Pleuromeia obrutschewii, P. jokunzhica, and P. patriformis are regarded as indistinguishable from P. sternbergii (Wang and Wang, 1989; Krassilov and Zakharov, 1975; Dobruskina, 1985; Mader, 1990) and the cone P. altinis is probably an ecotype of P. jiaochengensis (Z.-Q. Wang pers. comm., 1995). "Annalepis" chengdeensis is included within Lepacyclotes ermayinensis and both P. epicharis and Lycomeia sinensis within L. rossica (Wang and Wang, 1989; Mader, 1990). Tomiostrobus bulbosus, T. beloserovii and T. fusiformis are all taken as junior synonyms of T. radiatus by Dobruskina (1985). Lepacyclotes circularis is a senior synonym of species regarded as identical by Brown (1958: L. ellipticus) and by Cornet and Olsen (1990: Leptocyclotes americana). Metalepidodendron (Mader, 1990) is a misspelling of Mesolepidodendron (Wang and Wang, 1990a). "Pleuromeia" oculina (Mader, 1980), P. labiata, P. longchuanensis, P. wuziwanensis (Huang and Zhou, 1980), Ferganodendron (Dobruskina, 1974), Isoetodendron (Bock, 1969), Pleuromeiopsis (Dobruskina, 1974), Bedheimia (Schuster, 1933; Mader, 1990), Mesolepidodendron (Wang and Wang, 1990a), Grammaephloios (Harris, 1935), and Chinlea (Miller, 1968) are known only from stems, so not included in this account. I know of no illustrated accounts of Pleuromeia marginulata, P. sanxiaensis, Annalepis sangzhiensis, or A. latiloba of Meng (1995), and provisionally regard them as nomina nuda. Dispersed spores of "Spencerites" could be allied to Lycostrobus chinleanus (Daugherty, 1941), but remain inadequately documented.

stream. Conelike fossils referred by White (1981) to "Cylomeia capillamentum" are here interpreted as fertile individuals of Tomiostriobus australis in growth position with abundant fine radiating roots.

TOMIOSTROBUS MIRABILIS (Snigirevskaya)
new combination

Takhtajanodoxa mirabilis SNIGIREVSKAYA, 1980, p. 95, fig. 1; SNIGIREVSKAYA, 1981, p. 45, pls. 1–6.

Holotype.—Permineralized fertile corm specimen KB39 (collection 866).

Diagnosis.—Plant herbaceous, perennial, 3–40 cm high, 3–20 cm in diameter, including wide radially symmetrical stele, sometimes dichotomously branched, densely covered with helically arranged sporophylls; sporophylls, numerous, entire, with single vein, strongly swollen basally and linear, planar, sometimes frayed distally; ligule with a histologically differentiated glossopodium; stele with xylem divided by network of sheetlike lacunae; large mixed pith reaching 0.5 cm diameter and including secondary xylem; wide cortex complexly differentiated, in transitional zone from stem toward the rhizomorph, the pith, sheeted lacunae and exarch protostele gradually disappear, passing downward into secondary xylem in the area of the rhizomorph and increasing to 1.8 cm in diameter; rhizomorph with helically arranged rootlets, conical at base, with xylem there and in leaves of scalariform tracheids with fimbrils. Numerous megaspores 300–450 μm in diameter, with trilete branching tetrad ribs, narrow equatorial rim and reticulate surface; microspores not found [translated with emendations from Snigirevskaya (1980)].

Type locality.—On the right bank of the lower Tunguska River, 2 km below Kislokan, eastern Siberia; Tutonchanskaya Suite, Tunguska Basin. This fossil has been regarded as latest Permian in age (Sadovnikov, 1982a, 1995), but I follow Snigirevskaya (1980, 1981), Dobruskina (1982) and Mogutcheva (1995) in a middle Early Triassic age.

Remarks.—It may seem bold to transfer a complete permineralized plant, the epitome of fossil plant preservation, to a genus established for compressions of sporophylls. However a comparable reassignment of permineralized cones of Austrostrobus (Morbelli and Petriella, 1973) to the compression genus Cylostrobus (Retallack, 1975) was accepted (Sadovnikov, 1982a; Dobruskina, 1985; Skog and Hill, 1992). In the present case, new interpretation of Tomiostrobus australis leaves little to separate "Takhtajanodoxa" from that genus. Tomiostrobus mirabilis differs from other species of the genus in its fusiform sporophylls with a long distal limb (Figure 1). The ligule and glossopodium of T. mirabilis are remarkably well preserved, but similar to the broad swollen base of the ligule in impressions of sporophylls of other species of Tomiostrobus (Sadovnikov, 1982a).

TOMIOSTROBUS POLARIS (Lundblad)
new combination

Selaginellites polaris LUNDBLAD, 1948, p. 352, figs. 1–11.

Holotype.—Fertile plant (EN9/8-1946; Lundblad, 1968).
Diagnosis.—See Lundblad (1968, p. 352).
Type locality.—Northern slope of Mt Steensby, 10 m below the Anodontophora fraasi zone; Wordie Creek Formation, late Early Triassic (Birkelund and Perch-Nielsen, 1976).

Remarks.—The megaspores of this genus have been identified as Banksisporites pinguis (by Chaloner, 1967), and the microspores as Densiosporites playfordii (Balme, 1970). The trilete microspores differentiate this species from other species of Tomiostrobus whose microspores are known (Table 1). This is a
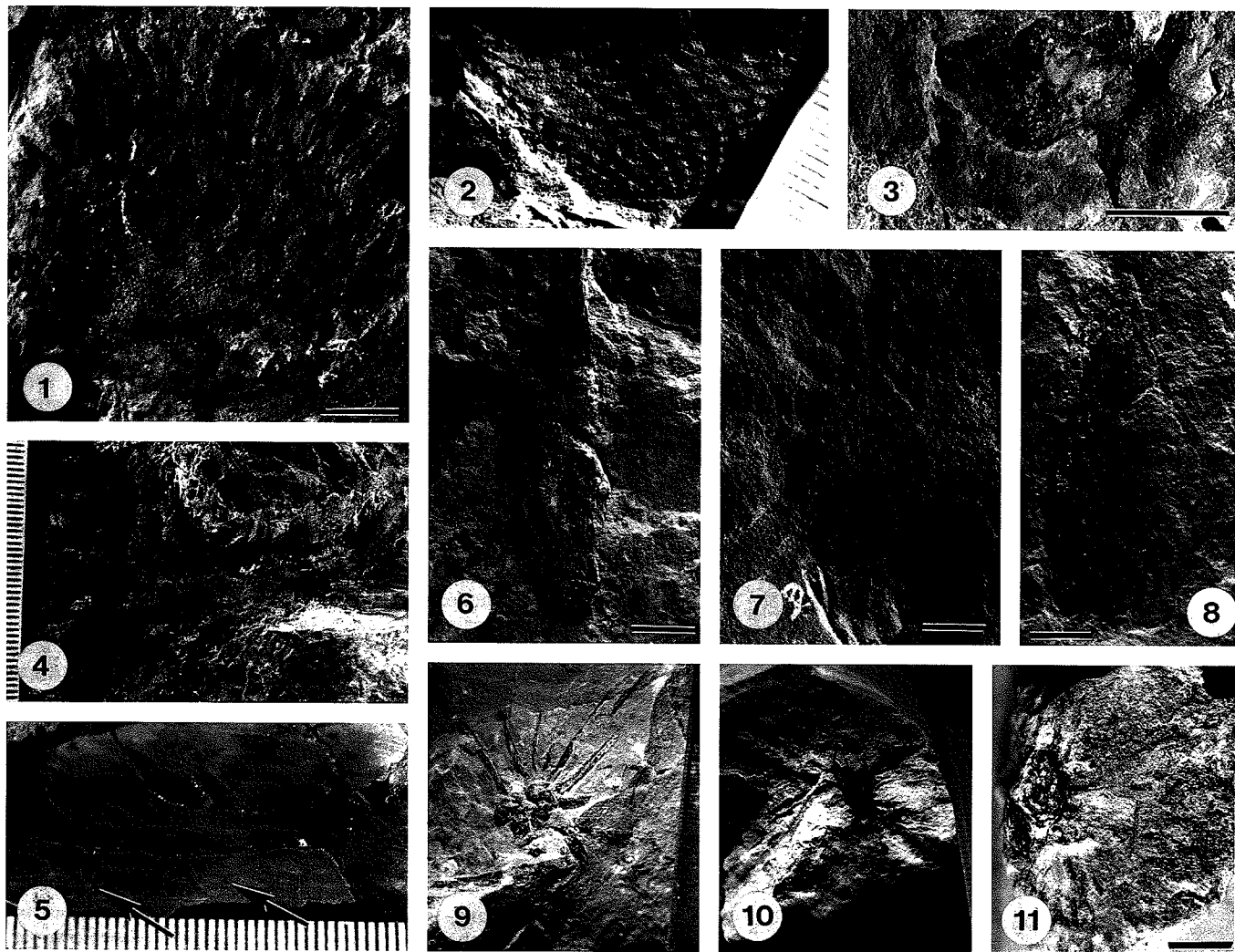
FIGURE *4—Tomiostrobus australis* (Ash) Sadovnikov 1982a; *1*, fertile specimen (UT52901) in growth position with basal corm, root scars and rootlets; *2*, corm of fertile specimen (UT52929); *3*, corm with leaf bases above (AMF91455); *4*, leaves attached to stem (to left) and washed together to create appearance of peduncle of fertile specimen (UT52885); *5*, cross-section in sawn slab of fertile specimen (wide curved crack, AMF91456a, b) in growth position with rootlets (at arrows); *6–8*, corms and short conical stems with infertile leaf remnants attached (UNEF13831, SUGD2058, UNEF13829 respectively); *9*, leaf circlet of infertile specimen (UNEF13824 = AMF78283); *10*, short stem of infertile specimen in growth position (UNEF13826); *11*, cross section of stem of infertile specimens (UNEF13827 = AMF78285). Formations and localities include Knocklofty Formation near Hobart (*1, 2, 4*), Gosford Formation near Terrigal (*3–5*, UNEL1691), and Newport Formation near Turimetta Head (*8*, UNEL1436), North Newport (*7*), and North Narrabeen (*6, 9–11*, UNEL1457), all late Early to early Middle Triassic.

larger and more fleshy fossil with much more elongate sporophyll limbs than found in *Selaginella* or *Selaginellites* (Chaloner, 1967). Bifurcating axes on the same slab (Lundblad, 1948) are interpreted here as rootlets.

TOMIOSTROBUS TAIMYRICA (Sadovnikov) new combination

Pleuromeia taimyrica SADOVNIKOV, 1982b, p. 706, fig. 1.

Holotype.—Cone (GI4561/1223-1; Sadovnikov, 1982b).

Diagnosis.—Stem erect, unbranched; stem diameter generally 3–6 mm (reaching 15 mm in the lower part); bark without leaf cushions, with narrow, irregularly sinuous, longitudinal cracks in lower part; spirally arranged transversely lenticular leaf scars are as high (measured along the stem) as 0.6–0.8 mm and as wide as about 1 mm and distant from neighboring scars some 2.5–3 mm measured along the stem and 3 mm across the width

of the stem; the length of the leaf scar divided into two by a leaf trace that is on the adaxial side of the leaf; leaves deciduous, narrow (0.2–0.3 mm), almost needle shaped, well spaced, individually dilated at the base; strobilus terminal, cylindrical, reaching a length of 40–70 mm and a width of 10–25 mm; axis of the strobilus slighty broadened; sporophylls deciduous, their scars low (up to 1 mm) and very wide (4–8 mm) depressions bent into the form of a wide letter "V"; sporophylls oval, as wide as 5–11 mm and as long as 9–13 mm, not counting the limb, which extends to the apex of the sporophyll; limb more than 7 mm long and generally 2–5 mm wide; oval sporangium is 6–8 mm long and 3.5–5 mm wide; sporangia with trabecular material (translated and edited from less formal description of Sadovnikov, 1982b).

Type locality.—In gray-green siltstones among variegated beds on the right bank of the Chernokhrebetnaya River, 3 km above the mouth of the Ostantsova River, eastern Taimyr region, Si-

beria: upper Fad'yukudinskaya Suite; late Early Triassic (Sadovnikov, 1982a).

Remarks.—This is a species of *Tomiostrobus* very similar to, but larger than *T. polaris* (Figure 1). Although Dobruskina (1985) questions the identity of bark fragments referred to *T. taimyrica*, even the fertile portions of *T. polaris* and *T. taimyrica* are more elongate than usual for *Tomiostrobus*. These species may be ancestral to *Cylostrobus* and *Pleuromeia*, which lack their prominent elongate limbs to the sporophylls. Sadovnikov (1982a) used the lack of a keeled base of the sporophyll to justify inclusion of *T. taimyrica* in *Pleuromeia* rather than *Tomiostrobus*, but I agree with Dobruskina (1985), who discussed variation in quality of keel preservation and difficulties in botanical interpretation of the keel.

Genus LEPACYCLOTES (Emmons)
new emendation

Type species.—*Lepacyclotes circularis* Emmons, 1856.

Emended diagnosis.—Lycopsid with leaves attached to short lobed to rounded corm, with round rootlet scars and fine rootlets; leaves ligulate, elongate, helically arranged in terminal cluster; most of apex covered by sporophylls; velum covers sunken sporangium in elongate, triangular basal part of sporophyll; outer tip of sporophyll acuminate to bluntly pointed; heterosporous, with megasporophylls near base and microsporophylls near apex; megaspores trilete, round to subtriangular, cavate; microspores monolete, spherical to oval, cavate.

Comparison.—Like *Tomiostrobus*, *Lepacyclotes* was a cone-like fossil and an *Isoetes*-like plant, as shown by Brown (1958), Bock (1969) and Wang (1991) for different species here referred to *Lepacyclotes*. Unlike *Tomiostrobus*, *Lepacyclotes* lacks a long distal limb to the sporophyll, and has bluntly pointed to mucronate sporophylls (Figure 1) of the kind formerly referred to "*Annalepis*" (Fliche, 1910a). Separation of *Annalepis* from *Lepacyclotes* can no longer be supported, considering that the latter probably also has microspores of *Aratrisporites* (Cornet and Olsen, 1990).

LEPACYCLOTES CIRCULARIS Emmons, 1856

Lepacyclotes circularis EMMONS, 1856, p. 332, pl. 3, fig. 4; EMMONS, 1857, p. 130, pl. 3, fig. 4; FONTAINE, 1883, p. 119, pl. 49, fig. 8; FONTAINE, 1900, p. 311, pl. 47, fig. 4; DAUGHERTY, 1941, p. 81, pl. 15, figs. 1, 2; BOCK, 1969, p. 45, figs. 92–95.
Lepacyclotes ellipticus EMMONS, 1856, p. 332, pl. 3, fig. 6; EMMONS, 1857, p. 129, pl. 3, fig. 6; FONTAINE, 1883, p. 118, pl. 52, fig. 4, 4a; FONTAINE, 1900, p. 311, pl. 47, fig. 5.
Araucarites carolinensis FONTAINE, 1883, pl. 49, fig. 8.
Isoetites circularis (Emmons, 1856) BROWN, 1958, p. 359, figs. 5, 8, 9, 11, 13.
Leptocyclotes americana BOCK, 1969, p. 48, fig. 96; CORNET AND OLSEN, 1990, p. 52, pl. 2.
Lepacyclothes americana (Bock, 1969) ASH AND PIGG, 1991, p. 1639.

Holotype.—The leaf circlet of Emmons (1856) was transferred to the U.S. National Museum according to Brown (1958), but he published no specimen numbers. The holotype is probably USNM8248, and hypotypes, USNM8249–8252.

Emended diagnosis.—Plant large (4–15 cm diameter), with small rounded corm, short stem and few foliage leaves: most of apex covered by sporophylls with sclerified, weakly serrated and bluntly pointed tip directed axially from the long triangular sporophyll base; sporophylls 20–60 mm long, 5–9 mm wide at outer angulation of tip; sporangia oval; heterosporous; megaspores trilete and about 400 μm in diameter; microspores not found in place, but associated microspores are monolete, oval to spherical.

Type locality.—Along the Deep River, 8 km southwest of

Jones Falls, North Carolina; Pekin Formation, Deep River Coalfield, Late Triassic (Carnian: Cornet and Olsen, 1990; Ash and Pigg, 1991).

Additional specimens and localities.—This species also is known from the Productive Coal Measures Member of the Tuckahoe Formation of Virginia (Cornet and Olsen, 1990) and the Chinle Formation of Arizona (Daugherty, 1941), both of early Late Triassic (Carnian) age.

Remarks.—I agree with Cornet and Olsen (1990) after seeing most of these fossils that they all represent a single species, and this should be *L. circularis* by virtue of earlier listing by Emmons (1856). Fragments of the corm in the type material convinced Brown (1958) that it was an *Isoetes*-like plant. The high relief of the specimens from the Chinle Formation (Daugherty, 1941) also indicate a substantial corm rooted to the shaley matrix. Bock (1969) illustrated an especially convincing corm on a plant with immature infertile leaves.

LEPACYCLOTES CONVEXUS (Brik)
new combination

Araucarites convexus BRIK, 1952, p. 44, pl. 9, fig. 9.
Tomiostrobus convexus (Brik, 1952) SADOVNIKOV, 1982a, p. 105, fig. 1e.

Holotype.—Sporophyll GI330 (Brik, 1952, pl. 9., fig. 9).

Emended diagnosis.—Sporophyll subrhomboid in outline, broadly wedge shaped in the basal part, broadly triangular in the upper part, which ends as an obtusely pointed tooth; greatest breadth of the sporophyll is 12 mm, length of the basal part 15 mm and length of the upper part 7 mm; centrally placed oval-elongate sporangium is above a narrow abaxial keel that is preserved as a ridge on the compression; outer end of the sporangium rounded and 5 mm wide, narrowing to 3 mm at the base; edge of the sporophyll flanking the sporangium broadly concave; ligule pit visible beyond upper part of sporangium; compact and woody in appearance [translated with emendation from Brik (1952)].

Type locality.—Bank of Kurasha Stream near junction with Ilek River, western Kazakhstan, Kurashasaiskaya Suite; Middle to Late Triassic (Dobruskina, 1982).

Remarks.—Although referred to *Tomiostrobus* by Sadovnikov (1982a), sporophylls of this species lack the characteristic distal limb of that genus, and have instead the mucronate to pointed apex of *Lepacyclotes* (Figure 1).

LEPACYCLOTES ERMAYINENSIS (Wang)
new combination

Isoetes ermayinensis WANG, 1991, p. 5, text-figs. 2–10, pls. 1–10.

Lectotype.—Of the numerous syntypes of Wang (1991), the most diagnostic is one of the sporophylls (TG8313a), designated herein.

Diagnosis.—See Wang (1991, p. 13).

Type locality.—Near Wubuxian, Shanxi, China; basal Ermaying Formation, early Middle Triassic (Anisian).

Remarks.—This species was reconstructed from isolated sporophylls and leaves (by Wang, 1991), but more complete circlets are now known (Z. Q. Wang, personal commun., 1996). The sporophylls are mucronate and unlikely to have borne the wider undulose leaf fragments on their tips as in *Isoetes* (Figure 1). *Lepacyclotes ermayinensis* has less elongate triangular sporophylls than either *L. circularis* or *L. zeilleri* (Fliche) new combination, and this latter species also differs in having less ornate megaspores. The megaspore morphology of *Lepacyclotes ermayinensis* is quite variable, embracing forms comparable to *Duosporites*, *Membranisporites*, *Horstisporites*, *Echitriletes*,

Baculitriletes, Singhisporites, Nathorstisporites and *Djikstrais-porites*, with the last named genus best for well preserved mature spores (Wang, 1991).

LEPACYCLOTES ZEILLERI (Fliche)
new combination

Voltzia coburgensis SCHÖNLEIN, 1865, pro parte, p. 19, pl. 1, fig. 6.
Annalepis zeilleri FLICHE, 1910a, p. 272, pl. 27, figs. 3–5; FLICHE, 1910b, p. 272, pl. 27, figs. 3–5; GRAUVOGEL-STAMM AND DURINGER, 1983, p. 38; fig. 2, pls. 1–6; MADER, 1990, p. 1175, pl. 96, figs. 3–5; KELBER, 1990, p. 38, figs. 57–59.
Cylostrobophyllum giganteum GRAUVOGEL-STAMM AND DURINGER, 1982, p. 53.

Holotype.—Specimen figured by Fliche (1910a, pl. 27, figs. 3–5): this could not be found in the Faculté des Sciences, École Nationale des Eaux et Forêts, Nancy (L. Grauvogel-Stamm, personal commun., 1995).

Diagnosis.—See Grauvogel-Stamm and Duringer (1983, p. 38).

Type locality.—Near Chauffontaine, Meurthe et Moselle, France; lower Lettenkohle, late Middle Triassic (Ladinian: Grauvogel-Stamm and Duringer, 1983).

Additional localities and specimens.—This species is also known from near Sainte-Anne, Gare de Blainville, Suriauville, Vittel, Noiroy, Rivières-le-Bois and Wasselonne, France in the Lettenkohle (Grauvogel-Stamm and Duringer, 1983) and from Schleerieth and Ochsenfurt, Germany, in the Lettenkohle and Schilfsandstein (Kelber, 1990; Mader, 1990), all of late Middle Triassic (Ladinian) age.

Remarks.—This species is only known from isolated disarticulated sporophylls with megaspores of *Tennellisporites* and microspores of *Aratrisporites* (Grauvogel-Stamm and Duringer, 1983). It can be distinguished from *Lepacyclotes circularis* and *L. ermayinensis* by its mucronate sporophylls with less sclerified tips and its more parallel sided, less triangular sporophylls (Figure 1).

Genus CYLOSTROBUS Helby and Martin, 1965

Type species.—*Cylostrobus sydneyensis* (Walkom) Helby and Martin, 1965.

Diagnosis.—See Helby and Martin (1965, p. 391).

Remarks.—Only three species of this genus are currently recognized because several species were included within the type species by Retallack (1975). Considered as a whole plant reconstruction, *Cylostrobus sydneyensis* should also include "*Pleuromeia*" *longicaulis* (Burges) Retallack (1975). The other two species are *Cylostrobus ornatus* (Morbelli and Petriella) Retallack (1975) from the Late Triassic of Argentina and *C. indicus* (Dobruskina) new combination, from the Early Triassic of India and Western Australia.

The microspores of *Cylostrobus* are *Aratrisporites* and the megaspores are *Banksisporites* (Helby and Martin, 1965; Scott and Playford, 1985). There is such a difference between the ultrastructure of megaspores of "*Banksisporites*" *viriosus* from *Cylostrobus* and the type species of *Banksisporites*, *B. pinguis*, found in place within *Selaginella hallei* (Hemsley and Scott, 1989), that the megaspores of *Cylostrobus* may be better referred to other genera such as *Talchirella* or *Bokarosporites*.

Cones of *Cylostrobus sydneyensis* are closely associated with stems and corms similar in general form to *Pleuromeia* (Retallack, 1975, 1980; White, 1981), and are here taken as part of the same plant. *Cylostrobus* is distinguished by its rounded compact cones with keeled sporangia, intermediate between elongate distal limbs and rounded sporophyll tips of other Triassic lycopsids (Figure 1).

Much of the material included in "*Cylomeia*" by White (1981)

is referred to *Cylostrobus*, which serves her purpose of distinguishing the Australian and Argentine species from allied plants of the northern hemisphere. The type specimen of "*Cylomeia undulata*", which is the presumed generitype, has been referred to *Pleuromeia dubia* (Seward) Retallack (1995b).

CYLOSTROBUS SYDNEYENSIS (Walkom)
Helby and Martin, 1965
Figure 5

Araucarites sydneyensis WALKOM, 1925, p. 221, pl. 31, figs. 2, 7; BURGES, 1935, p. 262, figs. 10, 11.
Lycostrobus longicaulis BURGES, 1935, p. 259, text-fig. 1.
Caulopteris sp. BURGES, 1935, p. 260, text-figs. 3, 4, 5; HELBY AND MARTIN, 1965, fig. 5.
Cylostrobus sydneyensis (Walkom, 1925). HELBY AND MARTIN, 1965, p. 395, fig. 3, pl. 1, figs. 3, 5–7, pl. 2 figs. 10, 11, 18, pl. 3, figs. 22–27; WHITE, 1986, fig. 206.
Cylostrobus major HELBY AND MARTIN, 1965, p. 396, pl. 1, figs. 2, 4, 8, 9, pl. 2, figs. 12, 13, 19.
Cylostrobus grandis HELBY AND MARTIN, 1965, p. 397, pl. 1, fig. 1, pl. 2, figs. 14, 15, 17, 20, 21.
Pleuromeia longicaulis (Burges, 1935). RETALLACK, 1975, p. 17, figs. 1, 8–11.
Cylomeia longicaulis (Burges, 1935). WHITE, 1981, p. 731, figs. 7, 8.
Cylomeia sp. WHITE, 1986, figs. 191–192.

Holotype.—Cone (SUGD16016).
Diagnosis.—See Retallack (1975).
Type locality.—Shales of lower Newport Formation, Turimetta Head, north of Narrabeen, N.S.W. (UNEL1441), late Early to early Late Triassic (Retallack, 1980).
Additional localities.—See Retallack (1975).

Remarks.—The megaspores of this species include "*Banksisporites*" *viriosus* Scott and Playford (1985; see also Hemsley and Scott, 1989) and the microspores are the stratigraphically important *Aratrisporites tenuispinosus* Playford (1965).

CYLOSTROBUS INDICUS (Lele)
new combination

cf. *Araucarites* CARPENTIER, 1935, p. 19, pl. 1, figs. 8, 9.
"feuilles de conifère" CARPENTIER, 1935, p. 17, pl. 1, fig. 10.
Araucarites sp. WHITE, 1961, p. 300, pl. 2, fig. 1; WHITE AND YEATES, 1976, p. 19, pl. 7, fig. 26.
Araucarites cutchensis (Feistmantel, 1876). WHITE, 1961, p. 300, pl. 2, fig. 4.
Araucarites indica LELE, 1962, p. 79, pl. 4, text-fig. 9, figs. 33–37.
Conites sp. LELE, 1962, p. 81, pl. 4, figs. 48, 49.
Lycopodiopsis pedroanus (Carruthers, 1869). WHITE AND YEATES, 1976, p. 17, pl. 6, figs. 18, 19, 21.
fructification WHITE AND YEATES, 1976, p. 21, pl. 8, figs. 24, 25, 27, pl. 10, figs. 35, 36.
ovulate cone WHITE AND YEATES, 1976, p. 22, pl. 9, fig. 32.
Pleuromeia indica (Lele, 1962). DOBRUSKINA, 1985, p. 75.

Holotype.—Sporophyll (BSIP8987).
Emended diagnosis.—Subarborescent lycopsid with stems 12–14 mm in diameter and more than 10 cm long; corm bulbous, 25 mm wide, with four irregular rounded lobes; leaf scar vertically elongate, with single vascular trace and narrow lateral parichnos regions; leaves, elongate, triangular, acutely pointed, with twin stomatal furrows, 20 mm long and 9 mm wide at base; sporophylls subtriangular, 8–12 mm long and 5–6 mm wide at distal end; distal tip of sporophyll sclerified, rounded to very bluntly pointed, directed apically; sporangia elongate oval, sunken into sporophyll.
Type locality.—Near Beli, South Rewa Basin, India: Parsora Beds; Early Triassic (Lele, 1962).
Additional localities and specimens.—This species is also found in monospecific assemblages in the Blina Shale at Point Al-
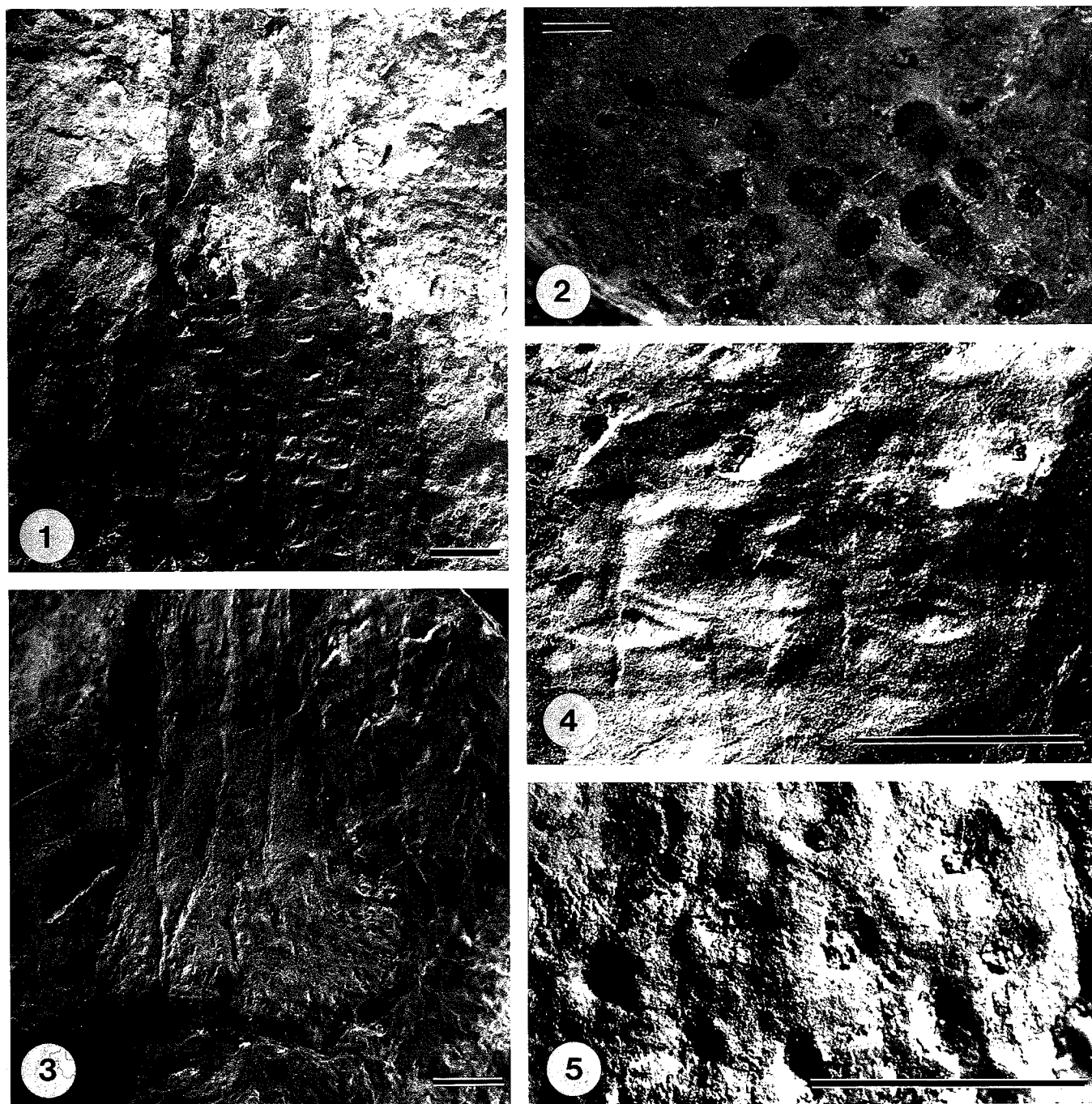
FIGURE 5—*Cylostrobus sydneyensis* (Walkom) Helby and Martin 1965: *1*, stem apex with leaves (SUGD2003); *2*, cones (UNEF13803 = AMF75269); *3*, rhizomorph on stem base (UNEF13805 = AMF75268); *4*, leaf scars on stem (UNEF13809); *5*, root scar (UNEF13811); from north Avalon (*1*, *3*, *5*), Bilgola (*4*) and Turimetta Head (*2*) all in the Newport Formation of late Early to early Middle Triassic age. Scale bars are 1 cm.

phonse, Bishop Range, Lake McLernon and Lake Betty in the Canning Basin of Western Australia (White and Yeates, 1976; Retallack, 1995b) and in bed 3 of the Sakamena Group near Tambohokazo, Madagascar (Carpentier, 1935).

Remarks.—Lycopsid affinities for the fossils from India were first discussed by Bose (1974) and later supported by Dobruskina (1985). The diagnosis of this species can now be emended to include information on corms and decorticated stems from the Canning Basin, Western Australia (White and Yeates, 1976). This species is most similar to *Pleuromeia jiaochengensis* of China (Wang and Wang, 1982), which is smaller with rounded and unlobed corm.

Genus PLEUROMEIA Corda in Germar, 1852
PLEUROMEIA STERNBERGII (Münster)
Corda in Germar, 1852
(partial synonymy—newly referred Australian material only)

Lepidodendron sp. KIDSTON for Foord 1890, p. 102, pl. 4, figs. 4, 4a.
Stigmaria sp. KIDSTON for Foord 1890, p. 103, pl. 4, fig. 5.
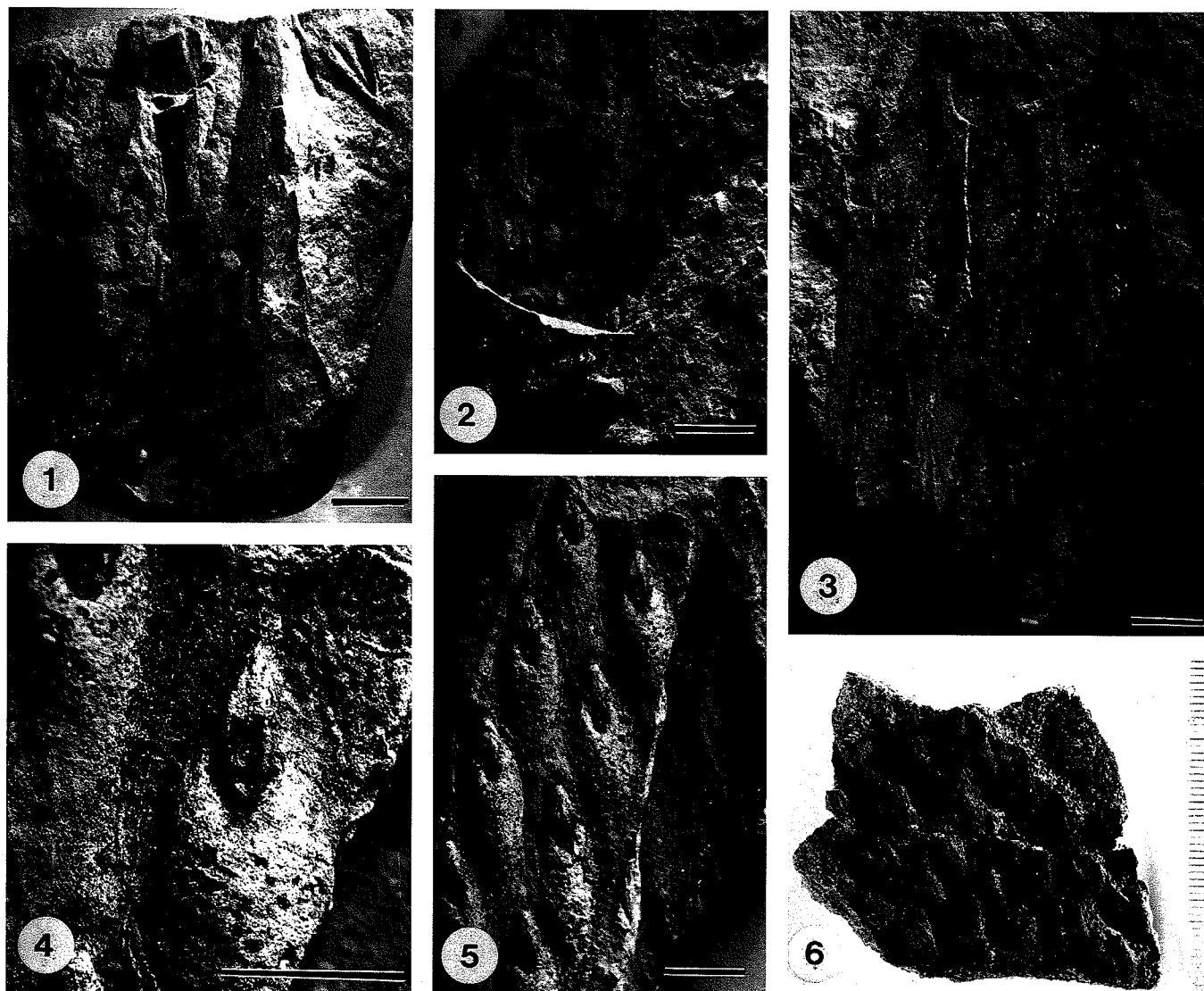*Cyperites* sp. KIDSTON for Foord 1890, p. 103, pl. 4, figs. 7–8.

FIGURE 6—*Pleuromeia dubia* (Seward) Retallack 1995b; *1*, stem, with attached leaves (UNEF13820 = AMF78281); *2*, stem with cortex (UNEF13823); *3*, counterpart of decorticated stem (UNEF13819); *4, 5*, partially decorticated stem with vascular strands (UNEF13818); *6*, deeply decorticated stem (SUGD10045). Formations and localities are Newport Formation from Careel Head near Whale Beach (*1, 2*, UNEL1465), north of Mona Vale (*3–5*, UNEL1421), and south Warriewood (*6*), all late Early to early Middle Triassic. Scale bars 1 cm (*1–5*) or graduated in mm (6).

?*Isoetites elegans* (Walkom, 1941). TEICHERT, 1950, p. 1792.
cycad pith casts WHITE, 1961, p. 300, pl. 2, fig. 3.
Lycopodiopsis pedroanus (Carruthers, 1869). WHITE AND YEATES, 1976, p. 24, pl. 12, figs. 42, 45.
seeds WHITE AND YEATES, 1976, p. 24, pl. 12, figs. 43, 44.

Lectotype.—Corm (SL193: Grauvogel-Stamm, 1993)

Description.—See Mägdefrau (1931), Mader (1990), Grauvogel-Stamm (1993).

Type locality.—Bernberg, Saale, Germany: Hardegsen Folge, Middle Buntsandstein; late Early Triassic (Mader, 1990).

Remarks.—*Pleuromeia sternbergii* is the type species of the genus (Mader, 1990). The synonymy of this well known cosmopolitan species given above includes only newly recognized synonyms from the early Triassic Erskine Sandstone at Bishop Range, Yarrada Hill, Lake Jones and possibly also the Derby town bore in the Canning Basin of Western Australia (Brunnschweiler, 1954). The large round sporophylls of this species are unmistakable (Figure 1).

PLEUROMEIA DUBIA (Seward) Retallack, 1995b
Figure 6

Stigmatodendron dubium SEWARD, 1908 p. 100, pl. 3, fig. 3.
?*Williamsonia* sp. WALKOM, 1925, p. 220, pl. xx, figs 1, 2.
?*Taeniopteris undulata* BURGES, 1935, p. 261, pl. x, fig. 1.
Equisetalean cone WHITE AND YEATES, 1976, p. 26, pl. 13, figs. 47–48.
Lycopod stem b HOLMES AND ASH, 1979, p. 51, fig. 3.3.
Cylomeia undulata WHITE, 1981, pro parte p. 723, fig. 4 only; WHITE, 1986, fig. 207.
Gregicaulis dubius (Seward, 1908) ANDERSON AND ANDERSON, 1985, p. 152, pl. 171–174.
Pleuromeia dubia (Seward, 1908) RETALLACK, 1995b, figs. 2D, 4A.

Holotype.—Stem cast (SAM13727).

Diagnosis.—See Anderson and Anderson (1985).

Type locality.—Alcocks Quarry near Aliwal North, South Africa: Burgersdorp Formation; early Triassic (Anderson and Anderson, 1985).

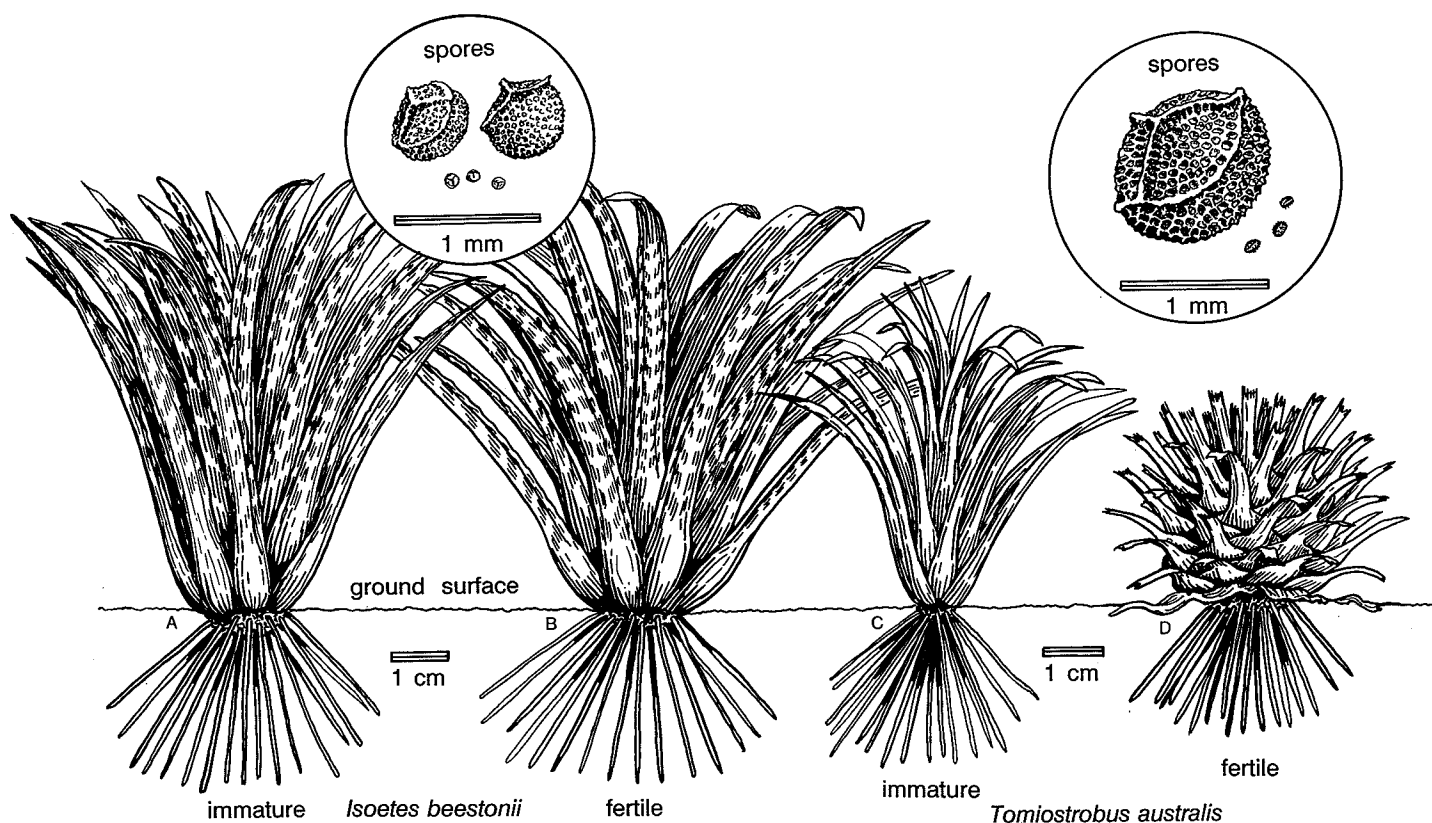*Additional localities and material.*—Newport Formation at

FIGURE 7—Reconstructions of *Isoetes beestonii* sp. nov. from the earliest Triassic of Queensland and New South Wales (left) and of *Tomiostrobus australis* (Ash) Sadovnikov (1982a) from the late Early to early Middle Triassic of New South Wales and Tasmania (right).

Careel Head south of Whale Beach, in shale lens at its western end by the track (UNEL1465 for UNEF13820–1,3), littoral talus north of Mona Vale (UNEL1421 for UNEF13818,9), rock platform south of Warriewood (for SUGD10045), "Narrabeen" (probably Turimetta Head, for SUGD2005, AMF30046), Avalon (AMF59987, see White, 1981, figure 4), all near Sydney, New South Wales, Australia; Camden Haven Claystone near Laurieton, New South Wales (Holmes and Ash, 1979); Culvida Sandstone at Culvida Soak, Canning Desert, Western Australia (Figure 2; Retallack, 1995b), and Burgersdorp Formation in excavations for the reservoir near Aliwal North, South Africa (Anderson and Anderson, 1985), all of late Early to early Middle Triassic age.

Remarks.—Eastern Australian material of *Pleuromeia dubia* is preserved in gray shale and better preserved than the sandstone casts from South Africa, but does not differ in any significant detail. The same array of smooth to deeply decorticated specimens is found in Australia and South Africa, and in neither place have branching stems or attached rhizomorphs been found. Associated large sporangia in South Africa are oval (Figure 1), and more elongate than the circular sporophylls of *Pleuromeia sternbergii*.

Undulose leaves of "*Cylomeia undulata*" have been found attached to *Pleuromeia dubia* in both Australia (Figure 6.1) and South Africa (Anderson and Anderson, 1985, pl. 174, figure 1). White (1981) did not specify a type for "*Cylomeia*" *undulata* (Turner, 1984; Scott and Playford, 1986), but the type specimen is the name-bearer, and this is the isolated leaf of Burges (1935). This specimen has stomatal furrows close to the midrib, and undulations of the margin outside them, unlike *Isoetes beestonii*, specimens of which were also included in "*Cylomeia*" *undulata*

by White (1981). *Pleuromeia sternbergii* also includes rare leaves with short wavelength transverse undulations that may be due to compaction of a succulent leaf (Mader, 1990).

THE ANTIQUITY OF *ISOETES*

Fossils similar to the living quillwort *Isoetes* have been known for some time from the Sydney Basin of Australia in the roof to the Bulli Coal of the southern coalfield of New South Wales (Figures 3, 7) and above the last coal near Blackwater, Queensland (Figures 1, 2). These fossils of *Isoetes beestonii* new species have transverse undulations to the leaves, both between and outside the stomatal furrows. The undulations characteristic of this species bulge against the stomatal furrows in a way suggestive of an originally succulent leaf.

The holotype is a complete fertile plant with sporophylls obscuring the corm, but several, fine, dichotomously branched rootlets radiate from the base (Figure 3.1, 3.2). Fine rootlets also have been found in association with partly disarticulated specimens (White, 1986, figure 195) and other specimens show circular root scars on the carbonized corm remnant (Figure 3.6). In specimens preserved as flattened leaf circlets the corm is an area of strong carbonization and relief due to a siltstone cast in a more or less quadrangular form (Figure 3.6), that may reflect weak lobing. Hence, *Isoetes beestonii* was probably rooted in the shale within which it has been preserved, rather than floating as suggested for comparable plants by Mader (1990).

Like living *Isoetes*, all the leaves of *I. beestonii* were fertile, with megasporophylls near the base and microsporophylls near the apex of the plant (Figure 3.1–3.3, 3.5). Also like living *Isoetes*, the fossil sporophylls have a ligule with a broadly inset base (probably a glossopodium), an obscured sporangial apex

(probably a velum), sporangia embedded in the sporophyll and sporangia have transverse trabeculae (Figure 3.4). Indications of glossopodium and velum especially ally it with the extant genus *Isoetes*. The megaspores extracted from *I. beestonii* have been referred to *Maiturisporites rewanensis* Wood and Beeston (1986) and the microspores to *Lundbladispora* sp. cf. *L. springsurensis* de Jersey (1979). Undifferentiated leaf blades extend beyond the sporangium as in living *Isoetes* (Figure 3.1, 3.2), and unlike the other Triassic lycopsid genera *Tomiostrobus*, *Pleuromeia*, *Lycomeia*, *Cylostrobus* or *Lepacyclotes* (Figure 1).

The earliest Triassic age of *Isoetes beestonii* makes it the geologically oldest known species of the genus. These fossils have been found in the basal 50 cm of the Coal Cliff Sandstone in the roof of collieries mining the latest Permian Bulli Coal in New South Wales (Retallack, 1980, 1995a) and within the basal Rewan Formation 5.8 m above the uppermost Permian coal of the Rangal Coal Measures in Queensland (Wood and Beeston, 1986). Both localities are within the *Protohaploxypinus microcorpus* palynozone, traditionally regarded as latest Permian in age (de Jersey, 1979; Retallack, 1980). However, several new lines of evidence suggest that this palynozone is earliest Triassic. One indication is new radiometric dating of the Permian-Triassic boundary in the likely stratotype sections of China (Claoue-Long et al., 1991), Siberian Traps of Russia (Renne et al., 1995), Permian coal measures of New South Wales (Veevers et al., 1994) and Triassic volcanics of New South Wales and New Zealand (Retallack et al., 1993), which constrains the age of the Permian-Triassic boundary and the last coal in the Sydney Basin to about 250 Ma. A second indication is stable isotopic studies of kerogen in the Sydney, Bowen and other Australian basins studied by Morante et al. (1994), who found that a dramatic lightening of $\delta^{13}C$ in kerogen, characteristic of Permian-Triassic boundary sections worldwide, also is present immediately above the last coals of the Sydney-Bowen Basins. Finally the upper sandstones of the Chhidru Formation in the Salt Range of Pakistan, which have yielded several important species of the *Protohaploxypinus microcorpus* palynozone (Balme, 1970; de Jersey, 1979), are now known to be earliest Triassic because they are above the $\delta^{13}C$ shift (Baud et al., 1989) and have the first appearance of basal Triassic conodonts (Sweet, 1992). Thus, *Isoetes beestonii* lived at the very beginning of the Triassic.

The sedimentary context of the Queensland specimen of *Isoetes beestonii* is difficult to judge because it was found in a drill core (Wood and Beeston, 1986). The fossil is a carbonized compression of a fertile plant in gray shale (Figure 3.1, 3.2). This is a similar style of preservation and matrix to abundant material from roof shales of extensive collieries of New South Wales (Retallack, 1980; White, 1981). There, leaf circlets are found evenly spaced within single bedding planes of finely interlaminated siltstone and shale. The matrix is weakly carbonaceous and includes few other plant remains. Each locality or slab has remains of a comparable stage of development, which varies between localities from infertile leaf circlets (White, 1981, figures 1, 2, 3, 5; White, 1986, figure 193) to fertile more carbonized circlets (White, 1986, figure 201), and disaggregated sporophylls (White, 1986, figure 195). The parallel creases in the leaves of *Isoetes beestonii* are similar to stomatal furrows of lycopsids. Stomata in living *Isoetes* are found in emergent to fully exposed, rather than submerged species, although this generalization is not without exceptions (Pfeiffer, 1922). These observations are suggestive of even-aged, monospecific stands of *Isoetes beestonii* in growth position in and around oligotrophic lakes or ponds.

Ecologically this earliest Triassic *Isoetes* was similar to fleshy-leaved living species of *Isoetes* (Figure 7). The herbaceous body of *Isoetes* with every leaf fertile also is an example of an r-selected or progenetic plant in which reproduction is accelerated over bodily growth (Gould, 1977). *Isoetes* can thus be regarded as both r-selected (ruderal) and tolerant in the terminology of Grime (1979). The growth form and geological context of *Isoetes beestonii* indicates that the genus was ruderal and tolerant from its origin at the beginning of the Triassic.

TOMIOSTROBUS AUSTRALIS AS A CONELIKE QUILLWORT

The early Triassic fossil *Tomiostrobus australis* (Ash) Sadovnikov (1982a) was formerly interpreted as the cone of an arborescent lycopsid by Ash (1979). Reinterpretation as an *Isoetes*-like plant is supported by discovery of its rootlets, immediately below the sporophylls (Figure 4.1, 4.5, 4.10). My search for roots was stimulated by observations of the consistent orientation of most of the specimens at the type locality near Terrigal, N.S.W., as well as near Hobart, Tasmania. Their apex is usually directed more or less upwards (Ash, 1979). Although this could reflect the stable orientation of a lozenge-shaped plant, there was also the possibility that individual plant fossils were rooted in the shale. Growth position was confirmed by cutting several specimens vertical to bedding with a diamond saw, revealing fine carbonaceous roots penetrating the underlying shale (Figure 4.5). A subsequent search of the type locality yielded a specimen compressed laterally to reveal the fan-shaped array of sporophylls above a rounded corm with small round scars of roots (Figure 4.3). Comparable specimens showing basal corms also are known among Tasmanian specimens (Figure 4.1, 4.2).

One difficulty with this interpretation is the structure called a "peduncle" by Ash (1979). This was not a stout attachment organ to a woody plant. Careful examination revealed that the "peduncle" was really composed of sterile leaves with flared bases. In some cases the leaves diverge (Figure 4.4) rather than forming a solid fruiting stalk. Some of these structures figured by Ash (1979, fig. 6F) are exceptionally long for a peduncle and curl back on themselves. Others (Ash, 1979, figs. 6B, E) are twisted over on themselves more like laminar than tubular structures. All lack leaf or root scars and are thin and weakly cutinized like lycopsid leaves, rather than woody stems (as interpreted by Ash, 1979) or long corms (as interpreted by Wang, 1991).

This evidence from the original localities for *Tomiostrobus australis* stimulated reassessment of a variety of other lycopsid fossils. Several teardrop-shaped stems with linear leaves at one end and a rounded root base at the other have turned up in loose blocks of littoral talus at Turimetta Head over the years (Figure 4.7, 4.8). These can be interpreted as uprooted plants of *Tomiostrobus* that were not yet fertile, as they lack spores and the distinctive shouldered sporophylls of specimens from Terrigal and Hobart. Another similar specimen (Figure 4.6) was found in the sea cliffs behind North Narrabeen Surf Life Saving Club in association with other remains (Figure 4.9–4.11) that are in growth position so that leaf circlets radiate within the bedding planes at a stratigraphic level immediately above the fine rootlets. All the plants at Narrabeen are sterile, just as all the plants at Hobart and Terrigal are fertile. In all three cases the fossils represent a monospecific, even-aged stand of herbaceous plants in growth position, as detailed in the following account of their known localities (Figure 8).

The type locality for *Tomiostrobus australis* is in sea cliffs south of the Skillion, near Terrigal, New South Wales (Figure 2), within the early-middle Triassic Gosford Formation (Ash, 1979). The fossils are found within a gray shale (Figure 8.1; UNEL1691) that lies between two paleosols of the Avalon and Warriewood pedotypes (as defined by Retallack, 1977, with pedotype terminology after Retallack, 1994). They were part of the floodplain shale on which the fossil soil later developed. Other nearby localities (UNEL1466, 1690) are dominated by
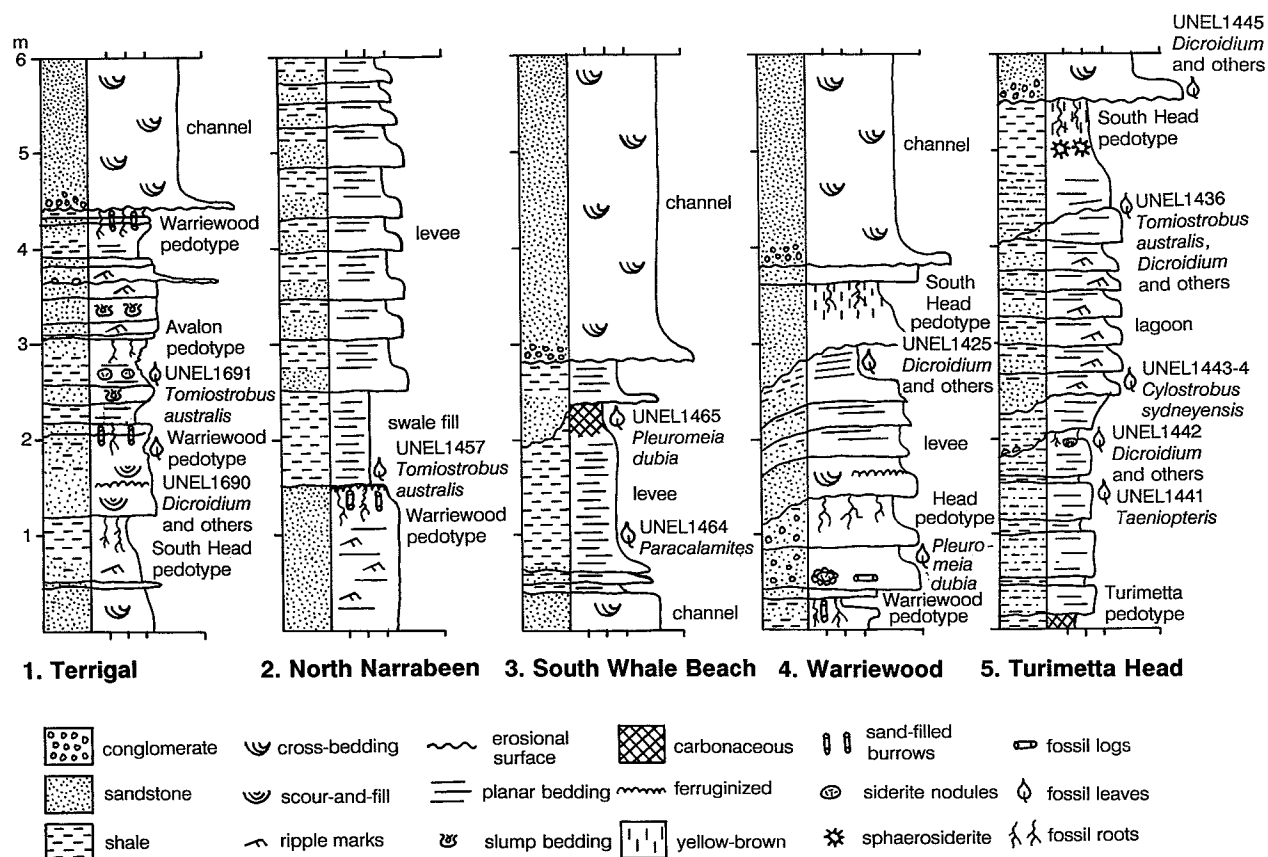
FIGURE 8—Interpreted stratigraphic columns at selected late Early to early Middle Triassic localities for *Tomiostrobus australis* (*1, 2, 5*), *Pleuromeia dubia* (*3, 4*) and *Cylostrobus sydneyensis* (*5*): *1*, Terrigal (grid reference 557974 on sheet 9131-II-S); *2*, North Narrabeen (432693 on 9130-I-S); *3*, South Whale Beach (457787 on 9130-I-S); *4*, Warriewood (433705 on 9130-I-S); *5*, Turimetta Head (436701 on 9130-I-S).

Dicroidium, with *Lepidopteris, Cladophlebis* and indeterminate equisetalean and conifer remains (Ash, 1979), but only *Tomiostrobus australis* has been found in the gray shale (L1691). The fossils appear to be in a single bedding plane and are generally well spaced. All the plants are at a comparable stage of development with mature megaspores whose nexine is close up against the sexine, and with frayed distal limbs of the closely packed sporophylls (Ash, 1979).

Behind North Narrabeen Surf Life Saving Club, 1.5 m above the base of the sea cliff, a single parting in the shale has yielded abundant remains here referred to *Tomiostrobus australis* (Figure 8.2). The shale is evenly laminated and can be interpreted as a pond fill within the levee of a meandering stream, whose channel is exposed to the north at Turimetta Head (Retallack, 1980). There is a paleosol of the Warriewood pedotype underlying this shale unit, but this contains stout woody root traces unlike those from the base of these fossil plants. Again, the fossils are the only species found in growth position within a single bedding plane of a lacustrine shale, but all the plants are immature.

Teardrop-shaped sterile plants now referred to *Tomiostrobus australis* have been found at Turimetta Head north of Narrabeen but in littoral talus whose provenance must be reconstructed (Figure 8.5). The specimen I found (Figure 4.8) was in a matrix similar to a dark shale lens yielding abundant remains of *Dicroidium* and other plants, stratigraphically above the siltstones here that yield the lycopsid cones *Cylostrobus sydneyensis* (Retallack, 1975). Thus this decorticated and drifted specimen of *Tomiostrobus australis* may have come from the levee-swale

complex of a deltaic distributary, rather than lagoonal siltstones with *Cylostrobus*.

Specimens from Long Reef called "*Cylomeia capillamentum*" by White (1981) are here referred to *Tomiostrobus australis* and like that species are preserved within a single bedding plane, in a monospecific stand of regularly spaced individuals. The structures White regarded as hairlike leaves are here interpreted as rootlets. Long Reef has *Cylostrobus* siltstones overlain by shales with *Dicroidium* similar to the sequence exposed at Turimetta Head. The slab with *Tomiostrobus australis* is a finely interbedded shale and siltstone that lacks specimens of the usually abundant *Cylostrobus sydneyensis*. It probably came from a separate stratigraphic level comparable to that for Turimetta Head.

The Tasmanian fossils of *Tomiostrobus australis* came from the Knocklofty Sandstone in a road cut near the well-known Old Beach vertebrate fossil locality, in a carbonaceous shale overlain and underlain by siltstone. This 20 m-thick siltstone is cut out by thick channel sandstones along strike (Banks and Clarke, 1973). The fossils are abundant in a laminated shale, and oriented upright or obliquely. The only fossils other than *Tomiostrobus australis* are scattered equisetalean fragments. All these specimens of *T. australis* are fertile.

Although very abundant when found, *Tomiostrobus australis* did not grow on trees. It was not the cone of an arborescent lycopsid, but a complete plant comparable to living quillworts such as *Isoetes* (Figure 6). A variety of different kinds of fossils can now be seen as different phases in its life cycle. Circlets of linear leaves with flaring bases found in bedding planes represent young plants in growth position. Teardrop-shaped stems with
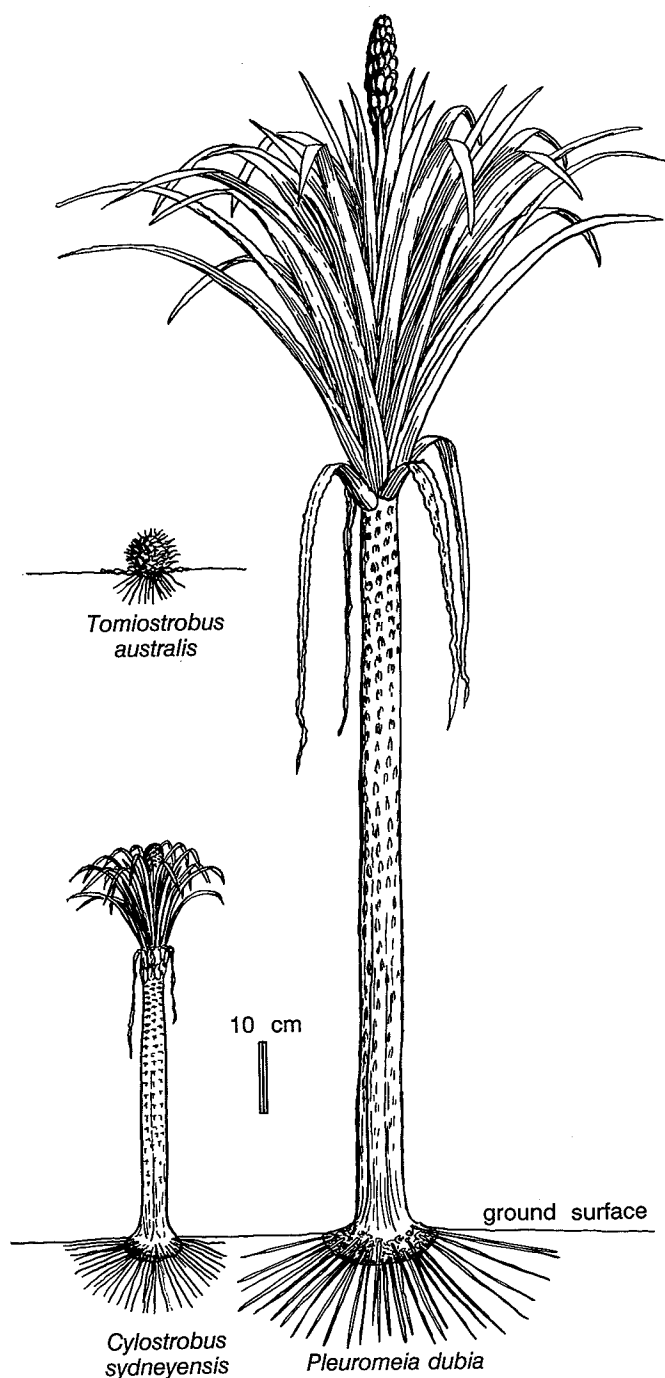
FIGURE 9—Reconstructed habit of three coexisting lycopsids of the late Early to early Middle Triassic Newport Formation near Sydney, Australia: pond colonizing *Tomiostrobus australis*, floodplain meadow *Pleuromeia dubia*, and coastal lagoon margin *Cylostrobus sydneyensis*.

basal pockmarks and upper leaf scars or leaf remnants represent uprooted immature plants. Also common are isolated leaf fragments with a broad central midrib and two sharply defined parallel flanking stomatal furrows. These furrows and their mechanical stiffness are responsible for the forked appearance of withered sporophyll limbs (Ash, 1979). The furrows can be used to argue for a nonsubmerged habitat for *Tomiostrobus australis*, by analogy with the distribution of stomata in living *Isoetes*

(Pfeiffer, 1922). Nonaquatic habitat also is indicated by the scalelike sporophylls of *T. australis*. Living *Isoetes* with scalelike sporophylls can live on dry land (Scott and Hill, 1900) and soil pockets on bare rocks (Lamotte, 1937; Taylor and Hickey, 1992). Fertile plants have the stout and substantial appearance of a tiny pineapple, because the sporophylls have wedge-shaped, closely packed bases with only a short remnant of the withered leaf projecting from the shoulders of the sporophylls. Megaspores of *Horstisporites* were produced at the base of the plant and microspores of *Aratrisporites* near the apex. Dispersal of the spores may have been aided by decay and dismemberment of the plant, because isolated sporophylls are common. The occurrence of *Tomiostrobus australis* in even-aged stands within lacustrine shales is an indication that it was a colonizing species in and around lakes and ponds. It has been found in gray to mildly carbonaceous shales, but not black shales or peats, and so was a plant of oligotrophic waters.

OTHER EASTERN AUSTRALIAN EARLY TRIASSIC LYCOPSIDS

Two other lycopsid plants of late Early to early Middle Triassic age are known from the Newport and Gosford Formations of the Sydney Basin, but these were more substantial plants than *Isoetes beestonii* or *Tomiostrobus australis*. These do not include the branching stem figured by Helby and Martin (1965, plate 1, figure 6) which Wang and Wang (1982) interpret as a lycopsid. I have examined this specimen and it is gymnosperm wood with monopodial branching and a rhombic pattern from coal cleat. In contrast, the two subarborescent lycopsids were similar to *Pleuromeia* with fleshy stems that have never been found to branch. Suitable names for these other lycopsids based on reproductive structures are *Cylostrobus sydneyensis* (Walkom) Helby and Martin (1965) and *Pleuromeia dubia* (Seward) Retallack (1995b; Figure 9).

Cylostrobus sydneyensis has compact cones (Figure 5.2) whose sporophylls are obtusely pointed and keeled, unlike the narrow frayed distal limb of sporophylls of *Tomiostrobus australis* or the rounded termination of sporophylls of *Pleuromeia dubia*. The teardrop-shaped stem of *Tomiostrobus australis* is unmistakable, and the other stems also are distinctive because *Cylostrobus sydneyensis* has leaf scars elongated horizontally (Figure 5.1, 5.4) and *Pleuromeia dubia* has them elongated vertically (Figure 6.1–6.5). These differences are even more striking when the vascular supply and associated tissues are revealed by decortication below the outer cortex (levels explained histologically by Pigg and Rothwell, 1985; for these fossils, compare Retallack, 1975, figure 9D, with this paper Figure 6.3–6.5). Stems attributed to *Cylostrobus sydneyensis* are 3–4 cm in diameter, with an observed length of 22 cm. Overall height of the plant was probably not much more than 50 cm (Retallack, 1975). Stems attributed to *Pleuromeia dubia* have been seen up to 12 cm wide and 117 cm long (in rock platform south of Warriewood, Figure 8.4) and the South African specimens of this species have been found up to 34 cm long. *Pleuromeia dubia* may have reached 2 m high.

These three coexisting lycopsids of the Newport Formation were distinct in their paleoecology and geological distribution. *Cylostrobus sydneyensis* is abundant within a restricted interval of about a meter of interbedded shale and siltstone at the base of the Newport Formation at many localities in the sea cliffs from Avalon south to Long Reef. The stems attributed to this plant form a carbonaceous shale in a thin paleosol near Avalon, and occasionally are found as uprooted fragments further south. The ripple-marked finely interbedded shales and siltstones containing *Cylostrobus sydneyensis* were interpreted as deposits of

a coastal lagoon (Retallack, 1975), and marine influence has been confirmed by subsequent discovery of mytilid bivalves (Grant-Mackie et al., 1985) and trace fossils such as *Rhizocorallium* (Naing, 1993). *Cylostrobus sydneyensis* formed monodominant stands around interdistributary bays of a delta building out into a coastal lagoon or lake. *Pleuromeia dubia* and *Tomiostrobus australis* are not restricted to a single horizon or to the same beds as *Cylostrobus sydneyensis*. They both are found at various stratigraphic levels within the Newport Formation, in shale lenses rather than associated with paleosols that have yielded leaf litters dominated by the seed fern *Dicroidium* and the conifer *Voltziopsis* (Retallack, 1977, 1980). *Pleuromeia dubia* has been found in more carbonaceous shales than *Tomiostrobus australis*, and may have been a marsh plant that aided in the eutrophication and fill of floodplain ponds. At Warriewood (Figure 8.4), *Pleuromeia dubia* is associated with mytilid bivalves (Grant-Mackie et al., 1985), but the logs are in a sandy conglomeratic layer of clay clasts and siderite nodules and appear well removed from growth position. In the Sydney Basin, *Cylostrobus sydneyensis* appears to have been a lagoonal marsh plant closest to marine influence, with *Pleuromeia dubia* a pond-margin plant and *Tomiostrobus australis* an aquatic to emergent pioneering plant of more inland parts of the coastal plain.

Such an interpretation of these plants tallies well with their known occurrence elsewhere. *Tomiostrobus* is widespread in eastern Australia from Tasmania through the Sydney Basin of New South Wales to the Bowen Basin of Queensland (Ash, 1979; Chaloner and Turner, 1987), as well as throughout Siberia (Sadovnikov, 1982a). *Pleuromeia* in the strict sense of plants with rounded sporophyll tips is now best known from deposits of inland ephemeral ponds in Germany (Fuchs et al., 1991). *Cylostrobus indicus* is known from the marine Blina Shale of Western Australia (Gorter, 1978).

Arguments continue to be advanced for a limited ecological role of Triassic lycopsids (Skog and Hill, 1992), but that view is contradicted by niche partitioning between coexisting species within the Newport Formation and by the great diversity of Triassic lycopsids now known. The early Triassic evolutionary radiation of isoetaleans came to include a variety of life styles such as salt marsh, mangrove, desert succulent, colonizers of river banks and lagoon margins, ephemeral plants of floodplain meadows, and submerged aquatic plants of oligotrophic lakes and ponds. This array of niches shows some overlap with, but also important differences from the Paleozoic evolutionary radiation of rhizomorphic lycopsids, which include scrambling and fully arborescent plants not represented in the Triassic radiation (Bateman et al., 1992; Pigg, 1992).

CLADISTIC ANALYSIS OF TRIASSIC LYCOPSIDS

All the Triassic lycopsids known as whole plants (Table 1) were assessed for 21 characters. Those with no more than nine of these character states unknown (Table 2) were subjected to cladistic analysis using PAUP (Swofford, 1985). *Chaloneria cormosa*, a Pennsylvanian plausible ancestor (Pigg and Rothwell, 1983a, b), was used as an outgroup (Figure 10).

Sporophyll shape (Figure 1) and spore type proved to be the most important determinants of overall clade arrangement. The eight well-characterized genera were grouped by the program according to sporophyll shape as follows: undifferentiated (*Chaloneria, Isoetes*), with wide distal limb (*Tomiostrobus*), with narrow distal limb (*Lycostrobus*), with pointed sporophyll tip (*Lepacyclotes*), with keeled and bluntly pointed sporophyll tip (*Cylostrobus*) and with rounded sporophyll tip (*Pleuromeia, Lycomeia*). Trilete microspores are ancestral and are found within

TABLE 2—PAUP data table for cladistic analysis of selected Triassic lycopsids.

```
!Triassic lycopsids
PARAM NOTU = 19 NCHAR = 21 MISSING = 0;
Data (A5,A1,21I1);
chalc    211122221211221222121
isoeb    211122221212212211121
tomir    222112221222212120000
tomia    222122211222212122121
tomip    222122211211222120000
tomim    222122211200002120001
lepac    222121222222002210001
lepee    222112222222112210000
lepez    222112222222112210000
lycos    222122111222111220000
lycoc    222122111200001220000
pleus    122222222111221221112
pleuj    122122222100221222111
pleud    002122222100001222120
pleuh    122122221100221222122
lycor    222122222111221222002
cylos    222121221222221222121
cyloo    222121221222220000000
cyloi    002121221200001222120
```

Note: Characters in order (left to right) are: 1, cone unisexual (1) or bisexual (2); 2, cone undifferentiated (1) or differentiated (2); 3, sporophyll leaflike (1) or modified (2); 4, sporophyll elongate (1) or circular (2); 5, sporophyll tip mucronate (1) or not (2); 6, sporophyll tip bluntly pointed (1) or not (2); 7, sporophyll tip with narrow limb (1) or not (2); 8, sporophyll tip with wide limb (1) or not (2); 9, sporophyll tip keeled (1) or not (2); 10, sporophyll tip rounded (1) or not (2); 11, microscpore trilete (1) or monolete (2); 12, microspore smooth (1) or spinose (2); 13, megaspore spinose (1) or not (2); 14, megaspore with reticulum (1) or smooth (2); 15, stem elongate (1) or not (2); 16, stem tear-shaped (1) or not (2); 17, stem very reduced (1) or not (2); 18, leaves undulose (1) or not (2); 19, leaves elongate (1) or not (2); 20, leaves triangular (1) or not (2); 21, corm rounded (1) or lobed (2).

Chaloneria, Isoetes, Pleuromeia and *Lycomeia*. There is also a clade with monolete microspores represented by *Tomiostrobus, Lepacyclotes, Lycostrobus* and *Cylostrobus*. This emphasis on reproductive features de-emphasizes elongate stems and subarborescent stature, which in most cladograms arose independently in *Cylostrobus* and *Pleuromeia*.

This analysis also calls into question the taxonomic status of two taxa. *Tomiostrobus polaris* with its trilete microspores is distinct from other species of the genus. However a new genus for this species is premature given only a single specimen known (Lundblad, 1948). On the other hand, *Lycomeia rossica* can be distinguished from the senior genus *Pleuromeia*, but is not so different that it needs to be regarded as a separate genus. This question is best deferred until more is known about Chinese fossils referred to *Lycomeia* (Wang and Wang, 1989).

Cladistic analysis is an exercise in pattern recognition that cannot be taken very seriously with so much relevant data unknown. Nevertheless it is a falsifiable scheme. For example, the cladogram (Figure 10) predicts that microspores when found will be monolete for *Cylostrobus indicus* and *Lycostrobus chinleanus* and trilete for *Pleuromeia jiaochengensis, P. dubia* and *P. hataii*.

EVOLUTIONARY RADIATION OF TRIASSIC LYCOPSIDS

The idea of an evolutionary radiation of herbaceous isoetacean lycopsids in the Triassic is not new (Brown, 1958; Wang, 1991), but its basal Triassic age and better understanding of the most ancient herbaceous forms encourages re-evaluation of a variety of other Triassic lycopsids. For example, it now seems more likely that subarborescent Triassic lycopsids evolved from herbaceous *Isoetes* (Figure 11), and these from subarborescent
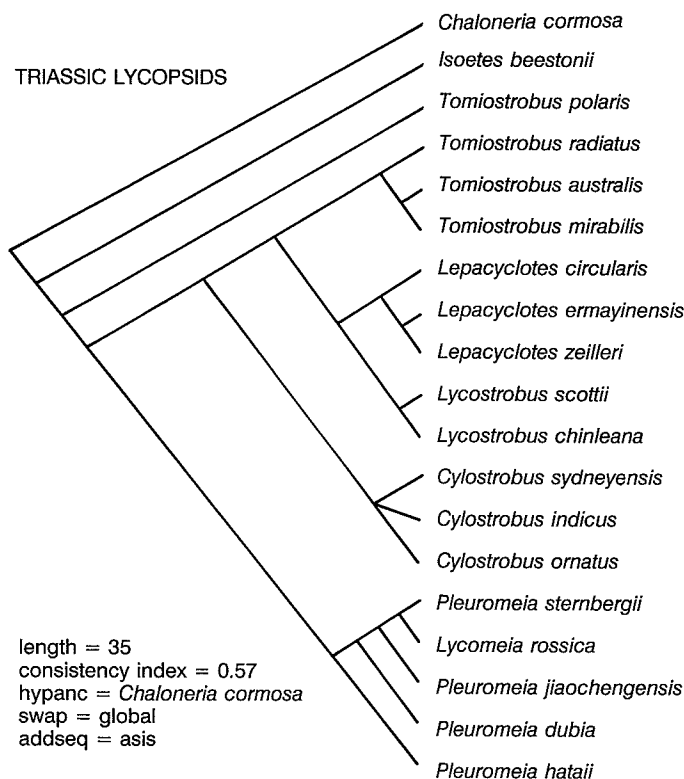
TRIASSIC LYCOPSIDS

Chaloneria cormosa
Isoetes beestonii
Tomiostrobus polaris
Tomiostrobus radiatus
Tomiostrobus australis
Tomiostrobus mirabilis
Lepacyclotes circularis
Lepacyclotes ermayinensis
Lepacyclotes zeilleri
Lycostrobus scottii
Lycostrobus chinleana
Cylostrobus sydneyensis
Cylostrobus indicus
Cylostrobus ornatus
Pleuromeia sternbergii
Lycomeia rossica
Pleuromeia jiaochengensis
Pleuromeia dubia
Pleuromeia hataii

length = 35
consistency index = 0.57
hypanc = Chaloneria cormosa
swap = global
addseq = asis

FIGURE *10*—Cladogram for selected Triassic lycopsids, using PAUP computer program from data of Table 2.

Paleozoic lycopsids such as *Chaloneria* (Pigg and Rothwell, 1983a, b), rather than from arborescent Paleozoic lycopsids such as *Sigillaria* (Mägdefrau, 1931), *Viatcheslavia* or *Signacularia* (Meyen, 1987). Other cladistic analyses also show that arborescent Paleozoic lycopsids evolved from, rather than into, cormose isoetaleans (Bateman et al., 1992; Bateman, 1994).

Further evidence in support of this idea comes from studies of permineralized stems of *Pleuromeia sternbergii* (Snigirevskaya and Srebrodolskaya, 1986), which like some sandstone casts of this species (Mader, 1990) with only a narrow hollow representing the protostele within the trunk, are more like that of an herbaceous than arborescent lycopsid. In addition, permineralized specimens of *Tomiostrobus mirabilis* (Snigirevskaya) new combination also have a protostele, medullated by parenchyma and a lacunar pith of tracheids and parenchyma (Snigirevskaya, 1981). Both *T. mirabilis* and *P. sternbergii* have a more massive vascular system in the corm than higher in the plant (Snigirevskaya, 1981; Roselt, 1992). *Tomiostrobus mirabilis* had ligules with a sunken glossopodium, more like that of *Isoetes* than any comparably preserved Paleozoic lycopsid (Pigg and Rothwell, 1983a; Pigg, 1992). In addition, the lobed rhizomorph of *Pleuromeia* shows a pattern of root production more like that of *Isoetes* than that of Paleozoic tree lycopsids (Karrfalt and Eggert, 1977; Grauvogel-Stamm, 1993).

The stratigraphic sequence of the earliest Triassic herbaceous forms with leafy sporophylls, followed by later Early Triassic subarborescent lycopsids with rounded sporophylls is not only found in southeastern Australia. In China the short (3 cm) herbaceous *Pleuromeia jiaochengensis* with round to bluntly pointed sporophylls in the Liujiakou Formation predates stouter stemmed forms with rounded sporophylls such as *Pleuromeia sternbergii* and *Lycomeia rossica* of the Heshankou Formation

(Wang and Wang, 1982, 1989, 1990a; Mader, 1990). Similarly in the Canning Basin of Western Australia, the small species *Cylostrobus indicus* with bluntly pointed sporophylls in the Blina Shale is followed by larger *Pleuromeia sternbergii* with rounded sporophylls in the Erskine Sandstone and *P. dubia* in the Culvida Sandstone (Retallack, 1995b). The well-known species *P. sternbergii* was thus a cladistic dead end, not a transitional form.

Subarborescent lycopsids persisted at least to the end of the Triassic (Harris, 1935). Subarborescent Triassic lycopsids include *Ferganodendron* (Dobruskina, 1974), *Bedheimia* (Schuster, 1933; Eisenhut, 1966; Mader, 1990), *Isoetodendron* (Bock, 1969), *Mesolepidodendron* (Mader, 1990), *Chinlea* (Miller, 1968) and *Grammaephloios* (Harris, 1935). The last three genera may have been the same species as the cones *Lycostrobus petiolatus* (Wang and Wang, 1990b), *L. chinleanus* (Daugherty, 1941; Miller, 1968) and *L. scottii* (Nathorst, 1908) respectively, but the other subarborescent lycopsids remain poorly known.

Conelike forms such as *Tomiostrobus* include a variety of Siberian species in addition to *T. australis* (Sadovnikov, 1982a). The genotypic species *T. radiatus* also has been found as small plants with a basal corm (Neuberg, 1936; additional material from the Tom River section shown to me by I. A. Dobruskina in 1984). The holotype has also yielded microspores of *Aratrisporites* and megaspores comparable to *Horstisporites* (S. V. Meyen, personal commun., 1985). The genus is expanded here to include *Tomiostrobus polaris* (Lundblad) new combination the Early Triassic of Greenland and *T. taimyrica* (Sadovnikov) new combination from the Early Triassic of Siberia.

There also are Middle and Late Triassic lycopsids with short corms and compact conelike fertile structures. Unlike *Tomiostrobus* these have bluntly pointed to mucronate sporophyll tips and have been widely referred to "*Annalepis*" (Fliche, 1910a). However, *Lepacyclotes* Emmons (1856) has clear priority and also is associated with microspores of *Aratrisporites* (Cornet and Olsen, 1990). These conelike fossils do not comfortably fit within the living genus *Isoetes*. Nor should they be placed in the fossil genus *Isoetites* (Brown, 1958), which is based on a poorly preserved holotype that cannot be distinguished from *Isoetes* and is unidentifiable (Chaloner, 1967). The conelike quillworts include four Middle and Late Triassic species *Lepacyclotes ermayinensis* (Wang) new combination, *L. convexus* (Brik) new combination, *L. zeilleri* (Fliche) new combination and *L. circularis* Emmons (1856). Also among the cormose lycopsids are the short stemmed Cretaceous genera *Nathorstiana* and *Nathorstianella*, long touted as intermediates between *Pleuromeia* and *Isoetes* (Mägdefrau, 1931). An unnamed *Nathorstiana*-like lycopsid from Devet Krizu in the Czech Republic has been thought to be of early Triassic age (Mader, 1990), but its kaolinitic sandstones are much more mineralogically mature than underlying early Triassic rocks. It is more likely early Cretaceous in age, because the fossils are only a few meters below conformable mid-Cretaceous (Cenomanian) marine rocks. The Late Triassic *Lepidanthium sporiferum* of Argentina (Frenguelli, 1943) and *L. microrhombeum* of Germany (Schuster, 1933) are little known lycopsids also comparable with *Nathorstiana*. Conelike quillworts may have persisted into the Paleocene (Brown, 1958; Skog and Hill, 1992).

Herbaceous lycopsids in the Middle and Late Triassic presumably included *Isoetes*, because the genus has a later Mesozoic and Tertiary fossil record and lives still (Walkom, 1941; Drinnan and Chambers, 1986; Banerji, 1989; Ash and Pigg, 1991; Skog et al., 1992). "*Isoetites*" *sagittatus* Wang and Wang (1990b) should not have been referred to that genus, which is a *nomen vanum* because of its indeterminate type species (Chaloner, 1967). Nevertheless, I hesitate to assign these Chinese specimens to *Isoetes*, because of a number of peculiarities. Their elongate

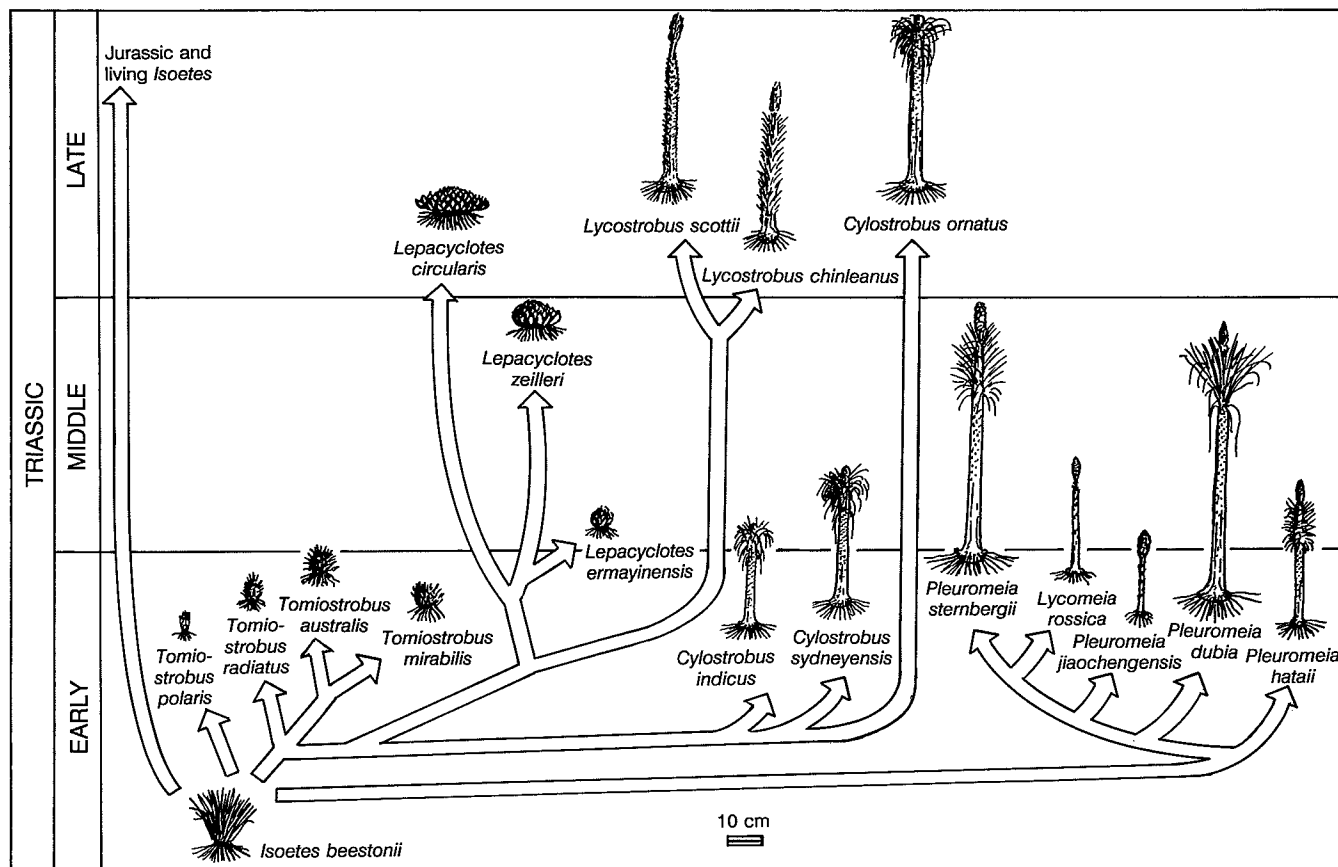## TRIASSIC ADAPTIVE RADIATION OF QUILLWORTS

FIGURE 11—Adaptive radiation of Triassic quillworts, based on cladogram (Figure 10). All are drawn to the same scale (lower center) and are no larger than shrubs.

sporangia are more than their own length above the base of the sporophyll, which is poorly preserved, but appears spindle shaped. More informative material may make it possible to delimit a new genus, but general affinities with *Isoetes* are likely. The fossil record of *Isoetes* no longer includes Late Triassic "*Isoetes gramineoides*" from Pennsylvania, U.S.A. (Bock, 1962, 1969), because Skog and Hill (1992) found it to be a stem and petiole of an osmundaceous fern. The unique Middle Triassic cone *Bustia ludovicii* Grauvogel-Stamm (1991) may have been an herbaceous lycopod, but is eligulate and more lax than *Isoetes* or any of the other Triassic lycopsids. This leaves no clear Triassic fossil *Isoetes*, other than *I. beestonii*.

QUILLWORTS AS THERAPSID FODDER

Within the early Triassic adaptive radiation of Isoetaceae there are two distinct adaptive tendencies: one toward arborescence and another toward compact, sclerified conelike fructifications. Numerous hypotheses have been advanced for the origin of trees in the Devonian (Beerbower, 1985), and can also be considered here for the evolution of subarborescence in quillworts: shade advantage, phytotoxin broadcasting, scattering of spores and deterrence of herbivory. Many of these hypotheses make little sense for plants that were highly gregarious and formed even-aged, monospecific stands no more than 2 m or so high in disturbed, oligotrophic, and desert environments (Retallack, 1975, 1980, 1995a). Coexisting conifer and seed fern trees would have been much larger and effective in providing shade, phytotoxins, and propagule scattering (Retallack, 1977,

1980; Retallack and Dilcher, 1988; Mader, 1990). Deterrence of herbivory however, remains a selective pressure in disturbed, oligotrophic, and desert habitats (Grime, 1979). Subarborescent lycopsids may have kept cones out of the way of earliest Triassic therapsids some 80 cm long and 20 cm high (Retallack, in press), but such weak stemmed plants would have been pushed down easily by geologically later and larger therapsids (King, 1990). The unique masticatory system of therapsids, using horny beaks and paired tusks in a propalinal grinding action (Crompton and Hotton, 1967) would have been well suited for such fleshy leaved, cormose to succulent plants. A case has been made that horsetails were fodder for Permian therapsids (Rayner, 1992). These could have remained an important item of diet into Triassic times, but lycopsids with their more copious spore production, succulent tissues and nonhollow pith, are likely to have been more nutritious. In early Triassic megafossil assemblages of my experience, lycopsids are more common overall than horsetails, and their spores dominate Early Triassic palynoassemblages worldwide (Helby and Martin, 1965; Balme, 1970; de Jersey, 1979).

Browsing pressure may also explain the evolutionary sequence from undifferentiated leafy sporophylls of earliest Triassic *Isoetes*, to the organized conelike sporophylls of *Tomiostrobus* and finally the imbricate sclerified scales of Late Triassic *Lepacyclotes* (Figure 11). Hardening of the fructification in this way has parallels in the increased silicification of anthoecia in a several clades of grasses during the late Miocene under the selective pressure of increasingly hard hoofed and hypsodont

mammalian grazers (Thomasson, 1985). Another possibility is that sclerified scales were adaptations for resisting desiccation in exposed (nonaquatic) habitats, as suggested by Hickey (1986) for nonaquatic living quillworts. These interpretations are not mutually exclusive because therapsid browsing pressure may have been more intense on dry land than in shallow water.

The Triassic quillworts were pioneering plants of disturbed and waterlogged habitats, and in some cases provided good ground cover (Retallack, 1975), analogous to grasses in today's ecosystems. Like many living quillworts, these Triassic plants may have formed bottomland meadows. Isoetacean plants however, never evolved the tillers, rhizomes and extended adventitious roots found in sod-forming grasslands and would only have been ephemeral plants within dry open plains where modern grasslands flourish today (Taylor and Hickey, 1992). The rise and decline of subarborescent and conelike quillworts parallels the early Triassic recovery and late Triassic decline of low browsing herbivorous dicynodonts (King, 1990). Therapsids and quillworts can be viewed as a distinctive early Triassic association, arising from destruction of the Permian-Triassic life crisis and supplanted by rhynchosaur-pteridosperm and dinosaur-conifer associations of the Late Triassic (Retallack, 1995a, 1996).

EARLY TRIASSIC COSMOPOLITAN LYCOPSIDS

The four distinct lineages of cosmopolitan lycopsids *Isoetes, Tomiostrobus, Cylostrobus* and *Pleuromeia* in the Narrabeen Group of the Sydney Basin can be contrasted with the associated fossil flora of Gondwanan endemic plants dominated by the seed fern *Dicroidium*. Similarly, *Pleuromeia sternbergii* was one of the most widespread species of all time, ranging across Eurasia from Germany to Kazachstan and Siberia, and into the Chinese and Australian cratons. One explanation for their geographic indifference may be their opportunistic ecology. Extant *Isoetes* (including *Stylites*; Karrfalt, 1984) show a wide ecological range as pioneering species of oligotrophic lake bottoms, partly emergent lakeside marshes or floodplain meadows, or even sandy or rocky exposed sites (Scott and Hill, 1900; Pfeiffer, 1922; de Vol, 1972; Croft, 1980; Taylor and Hickey, 1992). A pond margin habitat is compatible with the geological occurrence of *Isoetes beestonii, Tomiostrobus australis* and *Lepacyclotes circularis*. Other fossil species such as *Lepacyclotes zeilleri* have never been found articulated or with corms despite local abundance and wide distribution (Grauvogel-Stamm and Duringer, 1983). These species may have lived on dry land a short distance beyond the lacustrine to intertidal settings that favored preservation of their disarticulated sporophylls. Stems attributed to *Cylostrobus sydneyensis* are found as monospecific assemblages in growth position within a carbonaceous paleosol with a leached sandy surface horizon indicating periodic drying of this lagoon margin soil (Retallack, 1975). Early Cretaceous *Nathorstiana* from Quedlinburg, Germany and a comparable plant from Devet Krizu in the Czech Republic, are found in place within sandstone, and interpreted as coastal dune binding plants (Mader, 1990). Comparable dune binding and streamside marsh habitats are also likely for monospecific stands of *Pleuromeia sternbergii* preserved in growth position (Mader, 1990). Thus tolerance of low nutrients and waterlogging was also part of the ecology of these weedy plants, which evolved during the Early Triassic to occupy a variety of niches in addition to colonizing sites disturbed by sedimentation.

Another explanation for the cosmopolitan spread of lycopsids is their tolerance of saline conditions as intertidal plants (Retallack, 1975). They were anatomically herbaceous like salt marsh, rather than woody like mangal (Snigirevskaya and Srebrodolskaya, 1986). A coastal sedimentary context has been

documented for *Lepacyclotes zeilleri* (Grauvogel-Stamm and Duringer, 1983), *Pleuromeia hataii* (Kon'no, 1973), *Cylostrobus sydneyensis* (Retallack, 1975), *C. indicus* (White and Yeates, 1976; Gorter, 1978), and *Tomiostrobus olenekensis* (Krassilov) Mader (1990; Krassilov and Zakharov, 1975). However, there is little indication of marine influence for other species of *Isoetes, Pleuromeia, Lepacyclotes, Tomiostrobus* and its microspore *Aratrisporites* which are widely distributed in inland basins (Fuchs et al. 1991; Sadovnikov, 1982a; de Jersey, 1979). Their Early Triassic adaptive radiation included a variety of habitats in addition to muddy sea shores protected from waves.

Another explanation for the worldwide spread of these lycopsids is that they were among the survivors of a major extinction in the history of life (Retallack, 1995a). Although proposed some time ago (Retallack, 1975), this view did not fare well because profound extinctions affecting marine organisms at the Permian-Triassic boundary (Erwin, 1994) were not initially apparent from fossil plants (Knoll, 1984). Recent radiometric dating and stable isotopic studies have shown that extinctions were equally catastrophic on land and sea. Abrupt latest Permian decimation of the *Glossopteris* flora of Gondwana and the cordaite flora of Angara was followed by a low diversity cosmopolitan flora of lycopsids and conifers and then replaced by Middle Triassic time with diverse pteridosperm floras dominated by *Dicroidium* and *Scytophyllum* (Retallack, 1995a). The low diversity early Triassic flora of lycopsids *Isoetes* and *Tomiostrobus* and conifers *Voltzia* and *Voltziopsis* can also be seen in palynofloras globally dominated by *Lundbladispora, Densiosporites* and *Lunatisporites* (Balme, 1970). Early Triassic megafossil floras are low in diversity with monocultures common, and in addition show a variety of adaptations to difficult conditions including herbaceous habit, succulence, heterophylly, sclerophylly, recurving leaves, and reduced branching (Mader, 1990). Such paleobotanical indications of early Triassic oligotrophic vegetation on land and sea are supported by exceedingly isotopically light carbon in kerogen in numerous sequences throughout the world (Morante et al., 1994), as well as by the global lack of early Triassic coal (Retallack et al., 1996) and coral reefs (Flügel, 1994) and unusually abundant stromatolites on land and sea (Mader, 1990; Schubert and Bottjer, 1992). The world of the early Triassic was recovering from one of the greatest traumas in the history of life, and the isoetacean lycopsids found opportunity in crisis.

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