The classification of early land plants—revisited*

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Three suprageneric categories applied to early land plants—Rhyniophytina, Zosterophyllophytina, Trimerophytina—proposed by Banks in 1968 are reviewed and found to have still some usefulness. Additions to each are noted, some deletions are made, and some early plants that display features of more than one category are set aside as Aberrant Genera.

Key-words—Early land-plants, Rhyniophytina, Zosterophyllophytina, Trimerophytina, Evolution.

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साराँश

प्रारम्भिक स्थली पौधों का वर्गीकरण–पुर्नअध्ययन

हारलॅन पी० बैंक्स

1968 में बैंक्स द्वारा प्रस्तावित प्रारम्भिक स्थली पौधों के तीन महाप्रजातीय समूहों–राइनिओफ़ाइटीना, जोस्टेरोफ़िल्लोफ़ाइटीना एवं ट्राइमेरोफाइटीना, की पुनः समीक्षा की गई है। यह समीक्षा अत्यन्त महत्वपूर्ण सिद्ध हुई है। प्रत्येक समूह में और वर्गक प्रस्तावित किये गये हैं। किन्हीं में से कुछ वर्गक हटा दिये गये हैं तथा कुछ प्रारम्भिक पौधे जो एक से अधिक समूह के लक्षण प्रदर्शित करते हैं भ्रान्तिमान प्रजातियों के अन्तर्गत् रखे गये हैं।

FIRST, may I express my gratitude to the Palaeobotanical Society for the honour it has done me in awarding its International Medal for 1988-89. May I offer the Society sincere thanks for their consideration.

Secondly, may I join in celebrating the work and the influence of Professor Birbal Sahni. The one time I met him was at a meeting where he was displaying enthusiastically an angiosperm flower embedded in a translucent matrix that he had collected recently. All of us were captivated by his infectious personality and concern for palaeobotany. As a young man, I spent considerable time seeking copies of his publications through book dealers. Without question, he made a profound impact on world palaeobotany.

Almost a quarter century ago I suggested a reclassification of some Devonian taxa (Banks, 1968) particularly because Psilophytales had become a catchall group for obviously unrelated organisms and for indeterminable fragmentary fossils. That was at the 100th anniversary of the founding of Peabody Museum, Yale University. It seems appropriate at another 100th anniversary, of the birth of Birbal Sahni, to survey briefly the fate of that reclassification. Several caveats are necessary. I recall discussing an intractable problem with the late great James M. Schopf. His advice could help many aspiring young workers—"Survey what you have and write up that which you understand. The rest will gradually fall into line." That is precisely what I did in 1968.

I sought major trends among the so-called Psilophytales that anyone could see and left aside all the peripheral genera that for one reason or another did not fit. Perhaps they lacked fertile parts or conducting cells or details of branching. Perhaps they were only short-lived geologically. Perhaps they illustrated aberrant body plans in which characteristics had been assembled evolutionarily in unexpected ways producing organisms that were new to our biases. They were no more than dead-end variations related to no other organisms. Edwards and Edwards (1986) expressed my thinking precisely when they wrote (p. 216) "We find it neither necessary nor desirable to fit every species into a lineage." If we can see characteristics so

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assembled as to produce plants that illustrate major trends or lineages leading to subsequent younger floras, then we certainly can visualize the possibility of so assembling characteristics as to produce ephemeral organisms outside the major trends. Such a scenario might parallel that in the Cambrian Burgess shale where animals thought to be arthropods proved to be constructed on body plans different enough to constitute new phyla. But of all the variations only four survived the Cambrian and persisted as the four lineages now seen in Arthropoda. Similarly, none of the most aberrant plants of the early flora appear to have survived Devonian time. Just as examples of such plants, I think of *Germanophyton, Enigmophyton, Platyphyllum, Barrandeina,* and *Duisbergia.*

I see no reason now to depart from Schopf's advice nor to change my approach from a search for major trends. So this talk is but a quick overview of changes since 1968 and my revision thereof (Banks, 1975).

Many papers are omitted for lack of time or space and my own unfamiliarity with the organisms. I emphasize suprageneric categories and minimize generic descriptions of early land plants. The citations will lead one to full descriptions of genera, species, and the dynamic aspects of the early flora. The latter include the physiological requirements of the move to land, the life history strategies involved, the ecological conditions under which the transmigrants had to survive, the evidence for life on land as early as Ordovician time, the stories told by microfossils (spores, bits of cuticle, elongate tubes), the phytogeography of Siluro-Devonian time all of which are being developed rapidly. Papers such as Gray (1984), Selden and Edwards (1989), Edwards (1982, 1986), Edwards and Fanning (1985), Raymond, Parker and Barrett (1985), Raymond (1987) and references therein will quickly introduce a reader to some of these significant and intriguing approaches to early land plant evolution.

RHYNIOPHYTINA

I proposed (1968) this subdivision of Tracheophyta for plants with naked axes bearing fusiform or globose sporangia and with centrarch xylem strands.

Dianne Edwards and collaborators, using a multifaceted approach, have greatly expanded our knowledge of the earliest land plants. She and David Edwards (1986) summarized the taxonomic conclusions and their paper is basic to my review. They broadened the concept of Rhyniophytina to include naked axes that branch isotomously, anisotomously, pseudomonopodially or adventitiously, bore terminal sporangia on main axes or on laterals of limited growth, and probably had centrarch xylem strands.

Edwards and Edwards (1986) excluded plants with overtopping and pseudomonopodial branching from *Cooksonia* (p. 202) and suggested (p. 203) that the change from dichotomous to pseudomonopodial branching was a major change in development. I am convinced that this change in the activity at the apex of the stem is sufficiently important to distinguish rhyniophytes with predominantly dichotomous branching from other groups. Hence, I prefer to omit from Rhyniophytina plants with obvious pseudomonopodial growth. For example, Edwards and Edwards (1986) suggested that *Cooksonia pertonii* and *C. hemisphaerica* in Ananiev and Stepanov (1969) be excluded from *Cooksonia* because they branch pseudomonopodially. They would erect a new genus for the two plants. I agree but would go one step farther and exclude them from Rhyniophytina, restricting the latter to simple dichotomous branching.

Edwards and Edwards (1986) also pointed to the number of genera of rhyniophytes for which neither true tracheids nor intact vascular strands have been found in fertile specimens. Though willing to consider these plants as members of Rhyniophytina, they suggested grouping them informally under the heading "rhyniophytoid", a term apparently coined by Pratt *et al.* (1978). The group so designated includes genera that clearly look like rhyniophytes and even a genus, *Cooksonia*, that has come to be regarded as the oldest vascular plant.

Table 1 is a comparison of my (1975) assignments to Rhyniophytina, those of Edwards and Edwards (1986) and my present thinking. Comments on the listing follow.

Rhynia gwynne-vaughanii (Text-figure 1A) as revised by David Edwards (1980) still is a relatively simple, dichotomizing rhyniophyte despite Edwards' demonstration of the abscission of its sporangia, its adventitious branching, and the resulting tendency toward overtopping.

Uskiella spargens Shute and Edwards (1989) branches isotomously and bears terminal, elliptical sporangia with complex walls, has no dehiscence, and has a conducting system of tracheids. This recent addition (Text-figure 1B) to the rhyniophytes becomes the most typical proven member of the group if nearly all others fall into the rhyniophytoid category.

I omit *Hostinella* and *Aphyllopteris* because they are form genera for vegetative dichotomizing or

Table 1—Taxa included in Rhyniophytina by Banks (1975), Edwards and Edwards (1986), and the present paper (for some omitted genera see Table 2)

Banks 1975	Edwards and Edwards 1986	This paper
Rhyniophytina	Rhyniophytina	Rhyniophytina
Rhyniaceae	Rhyniaceae	Rhyniaceae
Rhynia	*Rhynia gwynne-vaughanii*	*Rhynia gwynne-vaughanii* Kidston & Lang 1917
Horneophyton	*Taeniocrada (T. decheniana)*	*Uskiella spargens* Shute & Edwards 1989
Cooksonia	*Renalia (pro parte)*	
Steganotheca	*Hostinella (pro parte)*	Rhyniophytoids
Salopella	*Aphyllopteris (pro parte)*	*Cooksonia* Lang 1937
Dutoitea		*Eogaspesiea* Daber 1960
Eogaspesiea	Rhyniophytoids	*Steganotheca* Edwards 1970
	Eogaspesiea	*Salopella* Edwards & Richardson 1974
Questionable Rhyniophytina	*Cooksonia*	*Eorhynia* Ishchenko, 1975
Taeniocrada	*Steganotheca*	*Hedeia* Cookson 1935
Hicklingia	*Salopella/Eorhynia*	*Yarravia* Lang & Cookson 1935
Nothia	*Hedeia/Yarravia*	*Caia* Fanning, Edwards & Richardson 1990
Yarravia		*Dutoitea pulchra* Hφeg 1930
Hedeia	Questionable Rhyniophytina	
	Dutoitea	
	Hsüa	
	Horneophyton	
	Excluded Genera	
	Nothia	
	Rhynia major (Aglaophyton)	
	Hicklingia	

pseudomonopodial axes that might be derived from a wide range of plants, not necessarily rhyniophytes. *Taeniocrada* and *Renalia* are discussed below.

Rhyniophytoids

Cooksonia Lang 1937, if it proves to be vascular, would be the oldest vascular land plant and also the simplest when rhyniophytes are restricted to dichotomously branching axes with terminal short, broad or fusiform sporaniga (Text-figure 1C, D). Edwards, Fanning and Richardson (1986) demonstrated its stomata and sterome. Other details appeared in Edwards and Fanning (1985) and Edwards (1990). Edwards, Feehan and Smith (1983) described some of the earliest cooksonias. Fanning, Richardson and Edwards (1988) discussed various kinds of spores extracted from *Cooksonia*. Certainly *Cooksonia* is the most studied of the early land plants and one can only hope that the search for its vascular structure will ultimately be successful.

Dutoitea pulchra Hφeg 1930 is poorly known but does seem to have a dichotomized axis terminated by *Cooksonia*-like sporangia. The axis apparently has tiny projections, unlike most other rhyniophytes.

Eogaspesiea Daber 1960 (Text-figure 1E) is based on clusters of slender axes terminated by ellipsoidal sporangia. Tracheids were reported only from unattached, presumed rhizomes.

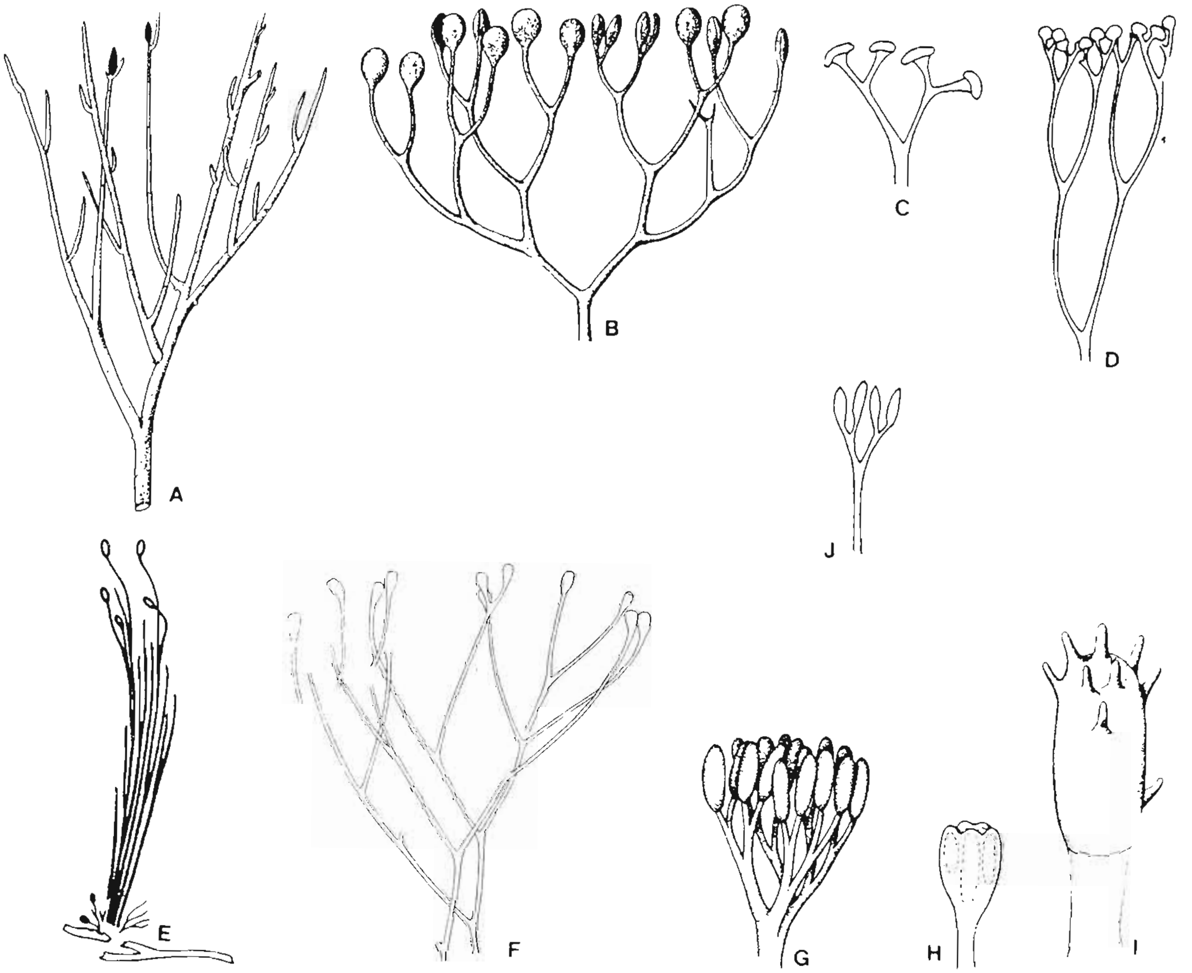
Steganotheca Edwards 1970a (Text-figure 1F)—This plant consists of several times dichotomized axes terminated by elongated sporangia with tapering bases and truncated apices. The central, coalified strand yielded no tracheids.

Salopella Edwards & Richardson 1974 (Text-figure 1J).

Eorhynia Ishchenko 1975—These two plants may be congeneric (Edwards & Edwards, 1986). They are preserved as compressions and are characterized by elongate, fusiform sporangia borne terminally on dichotomizing axes. If petrified, they would probably belong to *Rhynia*.

Caia langii Fanning, Edwards & Richardson 1990 (Text-figure 1I)—Axes dichotomize and bear elongate sporangia with parallel sides and rounded apices. Sporangia bear spinous appendages and occasionally branch. To date, *Horneophyton* is the only early plant to show repeatedly branched sporangia and it is likely that all sporangia of that genus were branched (El Saadawy & Lacey, 1979b).

Hedeia Cookson 1935 (Text-figure 1G) and *Yarravia* Lang & Cookson 1935 (Text-figure 1H)—Hueber (1983) considers *Yarravia* to be a preservational form of *Hedeia*. In *Hedeia* the dichotomizing axes terminate in elongate sporangia borne in corymb-like fashion. Possibly the crushing of some of these sporangia could produce the



Text-figure 1A-J—Rhyniophytina. **A.** *Rhynia gwynne-vaughanii* from David Edwards, 1980; **B.** *Uskiella* from Shute & Edwards, 1989; **C.** *Cooksonia pertonii*; **D.** *C. caledonica* both from Edwards, 1990; **E.** *Eogaspesiea* from Daber, 1960; **F.** *Steganotheca* from Edwards, 1970; **G.** *Hedeia*; **H.** *Yarravia* both from Andrews, 1961; **I.** *Caia* from Fanning *et al.*, 1990; **J.** *Salopella* from Edwards, 1990.

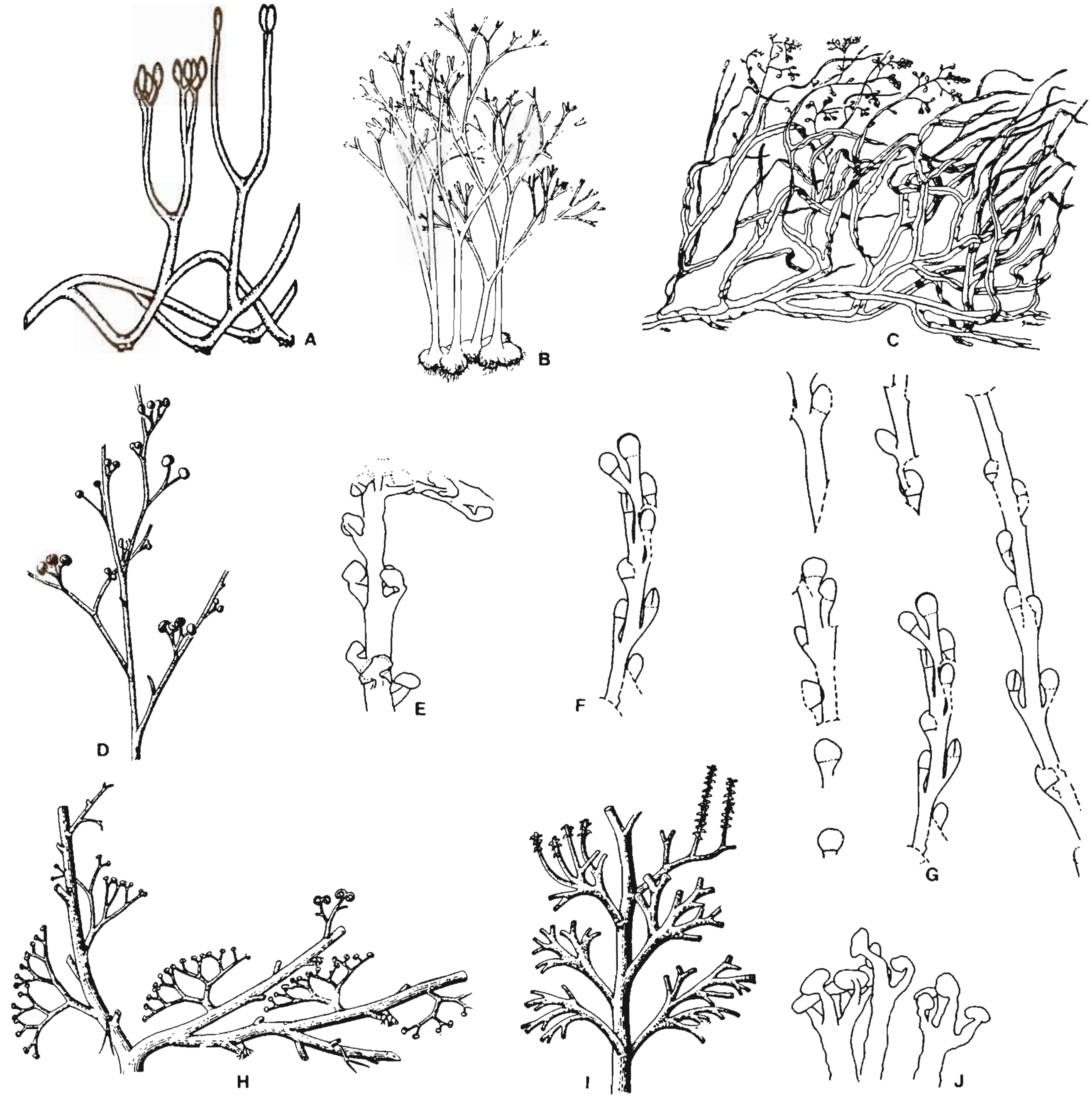
synangiate-like condition seen in *Yarravia*.

The above rhyniophytoids clearly lack only vascular tissue to be designated as proven members of Rhyniophytina from which category they may be excluded only if and when they are shown conclusively to be non-vascular.

Aberrant plants

A strict definition of Rhyniophytina to include only mostly dichotomously branching plants with single, terminal sporangia and centrarch vascular strands immediately eliminates a number of genera previously included in Rhyniophytina (Table 2). These genera display combinations of characters that differ from those of each of the three subdivisions. They seem to be telling us that during Siluro-Devonian time a number of features existed that could be assembled in various ways. When we find several genera whose characters allow us group them as closely related, we have a subdivision or a major trend. Those genera that evolved other combinations stand as isolated organisms that failed to contribute to any major trend. These are the taxa that authors refer to as "possible intermediates" or as "genera difficult to fit into the present classification" (the three subdivisions). In the future, they might become better understood and come to fit the present group or they might be joined with presently unknown forms to suggest other major trends. I now think of them as illustrative of the rapid evolutionary changes that were going on during Siluro-Devonian time. I do not presently consider them to be intermediates between any subdivisions and choose to refer to them as Aberrant Genera.

Aglaophyton (Rhynia) major (Kidston & Lang) Edwards 1986 (Text-figure 2A)—This genus was a cornerstone of my original Rhyniophytina. Edwards



Text-figure 2A-J—Aberrant Plants. **A.** *Aglaophyton* from David Edwards, 1986; **B.** *Horneophyton* from Eggert, 1974; **C.** *Taeniocrada decheniana* from Kräusel & Weyland, 1930; **D.** *Renalia hueberii* from Gensel, 1976; **E, F, J.** *Nothia* from El Saadawy & Lacey, 1979; **G.** Seven sketches of *Hicklingia* from Edwards, 1976; **H.** *Hsüa* from Li, 1982; **I.** *Stachyophyton* from Geng, 1983.

(1986) has since demonstrated that its centrarch strand was not composed of tracheids but rather of cells more like the hydroids in some mosses. It must be removed from a list of early vascular plants but it does not fit any other currently recognized category. Aberrant it is, at least until we reach a better understanding of its conducting cells.

Horneophyton (Text-figure 2B)—This genus is a vascular plant with centrarchy, dichotomy and terminal sporangia. However, apparently all of its sporangia are up to five times lobed, and its columellae are similarly branched (El Saadawy & Lacey, 1979b; Eggert, 1974). The sporogenous cavity is continuous throughout. One other genus, *Caia* (Fanning, Edwards & Richardson, 1990), has been reported to have some lobed sporangia. The repeated branching of the columellate sporangium sets *Horneophyton* aside from rhyniophytes where single, terminal sporangia are the rule. Its corm-like rhizome and peculiar sporangia combine to establish *Horneophyton* as a second aberrant taxon.

Taeniocrada decheniana (Text-figure 2C) as reconstructed by Kräusel and Weyland (1930) branches dichotomously in the vegetative region but its fertile branches divide laterally (pseudomonopodially) to produce somewhat paniculate clusters of elongate, terminal sporangia one side of which is fused to the stalk to which it is attached. I exclude this plant from Rhyniophytina because its fertile branching pattern is more complex, its sporangia tend to be clustered, and each is fused laterally to its stalk. Tracheids are known but maturation of its vascular strand is not.

Renalia hueberii Gensel 1976 (Text-figure 2D)—*R. hueberii* produces main axes that branch pseudomonopodially. The laterals branch dichotomously and terminate in sporangia that are round to reniform. Sporangia dehisce distally along a specialized suture into two equal valves. Its tracheids are known but not its vascular strand. *Renalia* stands apart from rhyniophytes in its advanced, pseudomonopodial branching pattern and clustered sporangia that recall trimerophytes. But the morphology of its sporangia parallels that of zosterophylls. In my opinion, it represents one more evolutionary pattern that neither fits one taxonomic category nor presages another. Gensel (1976) remarked that "intermediates such as *R. hueberii* are difficult to fit into the concept of 'rhyniophytes' or 'zosterophylls' as presently established". El Saadawy and Lacey (1979a) made similar comments about *Nothia*, suggesting that the "two genera should perhaps be classified under yet further subdivisions". Their comments reinforce my feeling that they are better grouped with other unusual forms as Aberrant Plants and that we are not yet ready for additional subdivisions.

Nothia aphylla Lyon ex Hφeg 1976 (Text-figure 2E, F, J)—The main axis of *Nothia* is more or less rhyniophyte-like. It dichotomizes and is characterized by a centrarch conducting strand composed of elongate cells with no thickening nor pitting. These cells can not be called tracheids hence the plant is not a vascular plant. This is the same problem we saw in *Aglaophyton*. Neither plant can now be regarded as vascular. Sporangia of *Nothia* are borne laterally on short, adaxially recurved stalks that are supplied by traces branched from the main axis. Traces end in the base of the stalk. Sporangia that terminate the stalks are more or less reniform and dehisce by a transverse (distal) slit. Sporangia may be borne singly and spirally, in pairs, in whorls, or in terminal clusters. A fertile axis, as a result, resembles a spike. *Nothia* is an ideal example of an aberrant plant with its rhyniophyte-like dichotomies and centrarch strand, its zosterophyll-like "spike" of lateral, reniform sporangia that dehisce by a transverse slit and its conducting elements that are not found in vascular plants. The arrangement of sporangia in *Nothia* is so variable that El Saadawy and Lacey (1979a) think of it as a "morphologically unstable condition from which, theoretically, some of the more constant arrangements characteristic of other groups of Tracheophyta could be derived" and further, "this might be an indication that the process of evolution or development of a whorled arrangement from a spiral one was still proceeding". I agree fully and suggest that this continuing process has produced still another aberrant plant that will fit no rigid classification.

Hicklingia Kidston & Lang 1923 (Text-figure 2G)—Edward's (1976) re-examination of the type specimen of *Hicklingia* and two additional fertile specimens has demonstrated that its globose to hemispherical sporangia are borne laterally on short stalks. They are aggregated into loose spikes. It is instructive to compare the "spikes" of *Nothia, Hicklingia* and the next species, *Huia recurvata*. I have no intent to suggest that these three genera are related but do emphasize that all three evolved a comparable mode of bearing sporangia even if it evolved from different origins. The anatomy of *Hicklingia* is completely unknown, hence we can not even be sure that it is a vascular plant. Edwards, on the basis of its spikes of sporangia that dehisce into two valves, assigned the genus tentatively to the zosterophylls. Its naked, dichotomizing axes are consistent with rhyniophytes. Until its anatomy is known, I retain *Hicklingia* among those early genera that I call aberrant forms.

Huia Geng 1985—Stems of *Huia* branch pseudomonopodially and dichotomously and bear terminal spikes of ovate sporangia whose stalks are recurved adaxially and arranged spirally. Its xylem strand is centrarch and composed of scalariform tracheids. In terms of the size of its axis, *Huia* looks robust. Its stems are up to 1.4 cm in diameter. The stems of *Hsüa* and *Taeniocrada* are closely similar in size but the other so-called aberrant plants range from 1.0 mm to, at most, 6.0 mm in diameter. *Huia* resembles *Nothia* and *Hicklingia* in the spike-like arrangement of its sporangia. This character also suggests affiliation with zosterophylls but the centrarch xylem strand recalls rhyniophytes. The more robust axes that branch pseudomonopodially relate to trimerophytes or, at least, deny a connection to rhyniophytes. Obviously, *Huia* does not fit our present classification. It does, however, illustrate still another combination of characters assembled by the ongoing evolutionary process that we have been reviewing.

Hsüa (Li & Cai) Li 1982 (Text-figure 2H)—Axes of *Hsüa* (Li, 1982) branch pseudomonopodially. Laterals divide dichotomously. Some lateral branches divide isotomously up to 4 times and all tips bear single, round to reniform sporangia that dehisce distally into two valves. Other laterals branch several times and terminate in tips that may be recurved or even circinate. Short, several times dichotomized, branches are considered to be root-like in nature. A centrarch protostele is composed of tracheids. *Hsüa* might be regarded as a highly advanced rhyniophyte except that its branching is much more complex than the dichotomous branching of rhyniophytes and, although its sporangia are single and terminal, the branching axis that bears them produces a sizeable group of up to 16. Both characteristics suggest a simple trimerophyte. However, the round to reniform sporangia that dehisce distally are not characteristic of trimerophytes. Hence, *Hsüa* is retained as an aberrant form.

Stachyophyton Geng 1983 (Text-figure 2I)—This Siegenian plant combines characteristics of several subdivisions. Its profuse pseudomonopodial branching followed by dichotomous laterals suggests trimerophytes. Its fertile branches, called strobili by Geng, recall zosterophylls in general aspect. But on the strobilus, forked sporophylls are attached helically and bear adaxially elliptic to pyriform sporangia with longitudinal dehiscence. Anatomy is unknown. Sporophylls and sporangia suggest lycopods but the absence of leaves (microphylls) on main or lateral axes denies that relationship. Geng suggested a possible relationship to *Krithodeophyton* and *Enigmophyton* two plants whose phylogenetic position is unknown. I agree with Geng that the position of *Stachyophyton* is uncertain. But I see *Stachyophyton* as a demonstration that microphylls could evolve and in close association with sporangia as well. It provides one more demonstration of evolution in action and, like other aberrant forms, it took another direction from the main stream.

Table 2—Aberrant plants that combine features of major suprageneric groups in various ways that defy classification

Aglaophyton—rhyniophyte except for its non-tracheidal conducting cells.

Horneophyton—a rhyniophyte except for its repeatedly dichotomized, columellate sporangia.

Taeniocrada decheniana—a rhyniophyte except for the more complex branching of its fertile branches producing a paniculate appearance.

Renalia hueberii—pseudomonopodial branching and groups of sporangia terminating dichotomizing laterals suggest trimerophytes but sporangial morphology suggests zosterophylls.

Nothia—not a vascular plant, no tracheids. Its axis is rhyniophyte-like and its conducting strand is centrarch though non-vascular. Its sporangia are variously arranged on spikes and recall zosterophylls.

Hicklingia—Axes recall rhyniophytes. No anatomy known. Sporangia borne laterally in spikes recall zosterophylls.

Huia—like *Nothia* and *Hicklingia* sporangia appear to be arranged in spikes as in zosterophylls but the illustrations seem to be less zosterophylloid than the other two genera. Centrarch xylem recalls both rhyniophytes and trimerophytes but pseudomonopodial branching of the robust axes favours trimerophytes.

Hsüa—pseudomonopodial branching of robust axes, centrarch xylem strands, and freely dichotomizing laterals terminated by sporangia suggest trimerophytes. Round to reniform sporangia recall zosterophylls.

Stachyophyton—pseudomonopodial axes with dichotomizing laterals suggest trimerophytes. Strobili recall zosterophylls. Forked sporophylls with adaxial sporangia recall lycophytes but absence of any other microphylls denies that relationship. No anatomy is known.

ZOSTEROPHYLLOPHYTINA

I proposed this subdivision (Banks, 1968) for plants with lateral sporangia that were globose to reniform in shape and that dehisced along the distal margin. The xylem strand, where known, was elliptical in transverse section and its maturation was exarch. In 1968, there were only six genera included and some of these were still unpublished or required name changes. By 1975, two of the name changes and two completely new taxa had been published, yielding six good genera, four of which had preserved anatomical structure. Table 3 lists the taxa known in 1975 and the sixteen genera that are now included in the subdivision.

Plants assignable to Zosterophyllophytina are both abundant and highly variable yet they fit unequivocally into the subdivision. Gensel and Andrews (1984) provided a detailed descriptive survey of the zosterophylls that I shall not repeat here. Reconstructions included here (Text-figures 3A-G, 4A-K) provide a partial understanding of the

Table 3—Zosterophyllophytina as proposed in Banks (1975) and as it stands at the time of writing this paper modified from Niklas and Banks (1990)

Banks 1975	Present Paper	
Zosterophyllophytina Zosterophyllaceae	Zosterophyllophytina Zosterophyllaceae	
	Terminate	Non-terminate, bilateral
Zosterophyllum	*Zosterophyllum* Penhallow 1892 10 species	*Gosslingia* Heard 1927 (see Edwards, 1970b)
Gosslingia		*Crenaticaulis* Banks & Davis 1969
Crenaticaulis	*Rebuchia* Hueber 1970	*Sawdonia* Hueber 1971
Sawdonia	*Gumuia* Hao 1989	*Bathurstia* Hueber 1972
Rebuchia		*Serrulacaulis* Hueber & Banks 1979
Bathurstia		*Margophyton* Zakharova 1981
		Konioria Zdebska 1982
		Oricilla Gensel 1982
		Tarella Edwards & Kenrick 1986
		Anisophyton Remy, Schultka & Hass 1986
		Thrinkophyton Kenrick & Edwards 1988
		Discalis Hao 1989
		Deheubarthia Edwards, Kenrick & Carluccio 1989

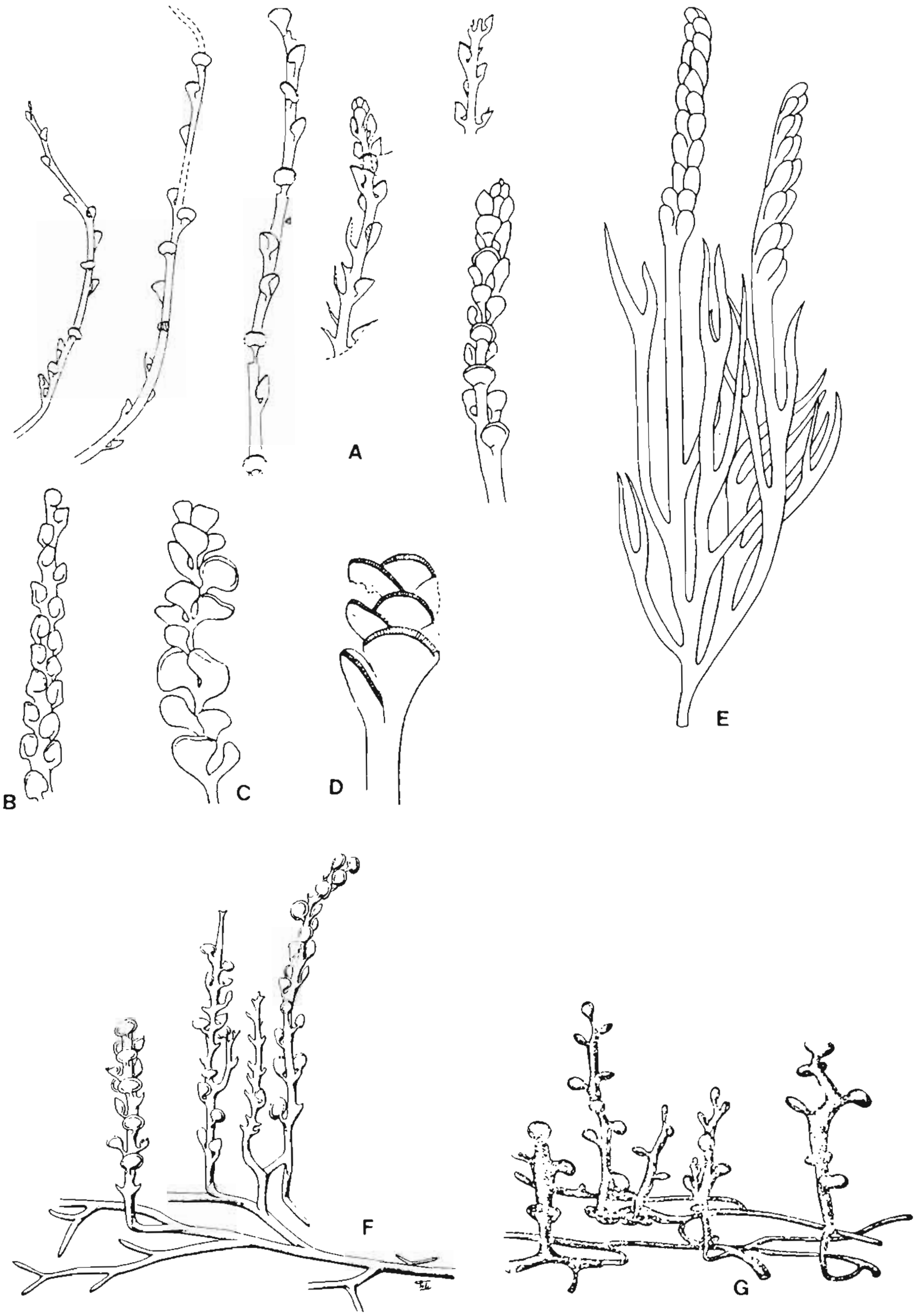
plants in the group and two recent papers give some additional details of the genera. Edwards, Kenrick and Carluccio (1989) provide in tabular form a valuable comparison of the many genera on the basis of a broad spectrum of characteristics. The paper also includes a useful section on the taphonomy and mineralogy of cellularly preserved axes. It is essential reading for an understanding of many aspects of the subdivision.

A second paper (Niklas & Banks, 1990) examined the literature on zosterophylls to review variability in the group and to see what light they could shed on the origin of Lycophytina. Two types of development were recognized. In one, the fertile shoot was terminated by a sporangium (Terminate, Text-figure 3A-G). In the other, fertile shoots were not terminated by a sporangium (Nonterminate, Text-figure 4A-K). Terminate axes usually bore sporangia radially. Nonterminate axes had bilaterally arranged sporangia. Nonterminate axes had enations and often circinate apices. Terminate axes had neither. Enations were borne either radially or bilaterally and their morphology varied from spines to various forms and arrangements of teeth.

Niklas and Banks (1990) suggested that the two conditions of the apex (terminate or not) reflected fundamental differences in the activity of the apical meristem. The terminate group (Table 3) may have arisen as a series of dichotomies in which one axis of each pair produced a sporangium. At the last dichotomy both apices were converted into sporangia, effectively halting further growth. In such a fertile axis each sporangium was a converted apical meristem and each sporangial stalk was homologous with an axis. El Saadawy and Lacey (1979a) postulated precisely this hypothesis to explain the sporangial axes of *Nothia* where sporangia were borne spirally, in opposite pairs, in whorls, in mixtures of whorled and spiral, in terminal groups, or occasionally in fused pairs. They started with a dichotomously branched axis and hypothesized that by "unequal branching, overtopping, three-dimensional branching, condensation and fusion" all the varied sporangial positions in *Nothia* could be derived. *Nothia* is mentioned here to demonstrate plasticity in the morphology of some early land plants not as a taxon in a phylogenetic series leading to zosterophylls. *Nothia* is, rather, one of several aberrrant genera whose suite of characters is unique and therefore fits no currently recognized higher category.

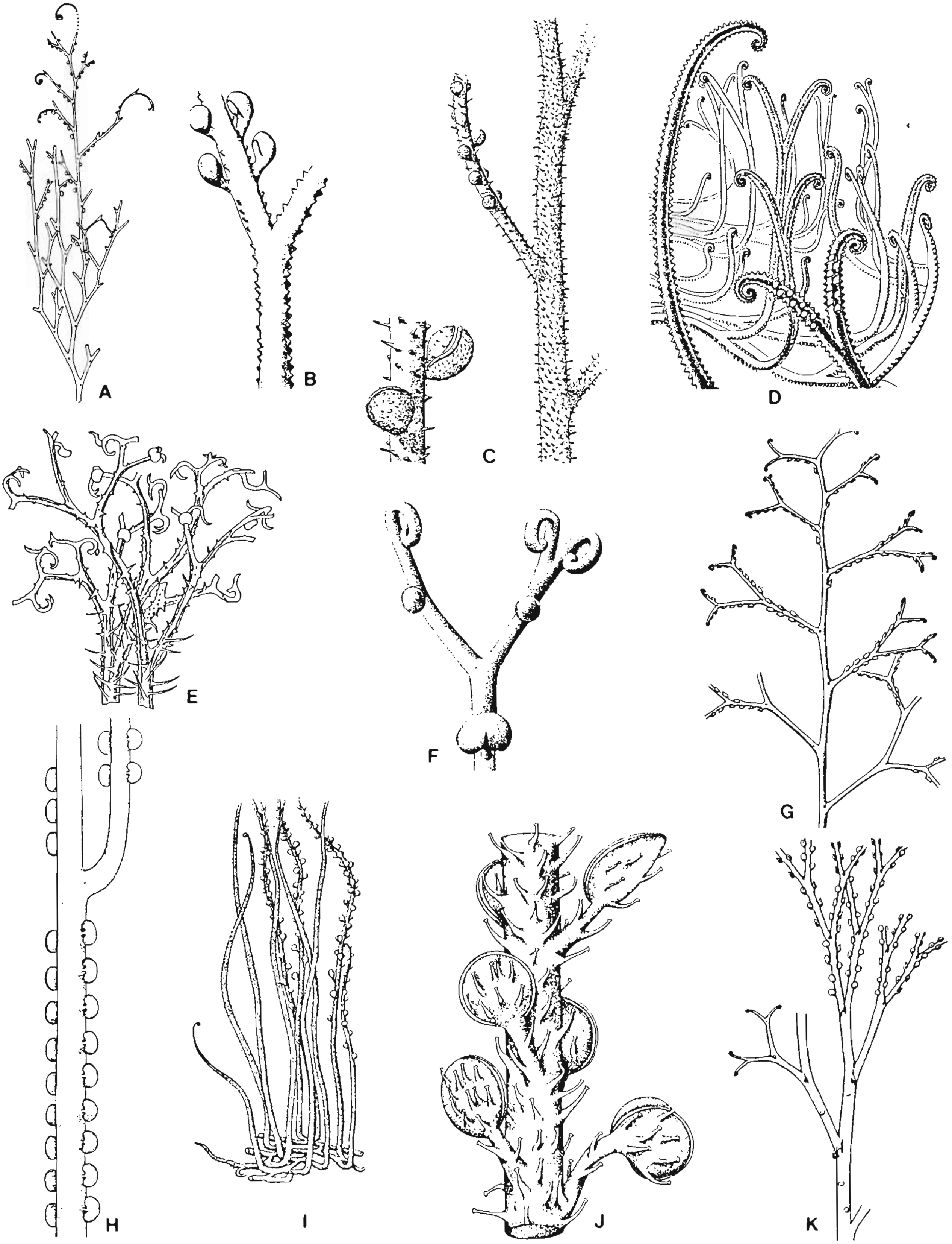
The second group of zosterophylls is the nonterminate category (Table 3). Niklas and Banks (1990) speculated that these genera had apical meristems theoretically capable of continuous growth and of cutting off lateral initials. Some of the intials produced enations, others produced sporangia. These sporangia were not converted apical meristems and the sporangial stalks were not homologous to axes thus differing markedly from the terminate forms. The significant point is that the nonterminate genera evolved the ability to cut off lateral meristems. This was an important morphological change yet it may have been a relatively simple developmental innovation. It seems that genetic changes at the growing apex of early land plants have been underplayed and deserve more emphasis.

The enations in nonterminate genera were usually bilaterally arranged but could be radially arranged as in *Sawdonia* (Text-figure 4C, Table 4). Similarly, sporangia were usually bilaterally arranged but could be radially arranged, as we interpret them in *Discalis* (Text-figure 4J; Table 4). Sporangia in the terminate group were usually radially arranged but could be bilateral as in *Rebuchia* (Text-figure 3E; Table 4). Niklas and Banks (1990) hypothesized that ancestral zosterophylls could produce both terminate and nonterminate axes (Table 4). Subsequent developmental changes evolved the two major groups, those with fertile axes capable of



Text-figure 3A-G—Terminate Zosterophyllophytina. **A.** *Zosterophyllum myretonianum* five sketches from Edwards, 1975, one from Edwards, 1990. **B.** *Z. fertile* from Edwards, 1990; **C.** *Z. rhenanum* and **D.** *Z. australianum* both from Edwards, 1975; **E.** *Rebuchia* from Hueber, 1972; **F.** *Zosterophyllum deciduum* from Gerrienne, 1988; **G.** *Gumuia* Hao, 1990.

continuing growth (nonterminate) and those that ceased growth at some point (terminate). They further speculated that within each of these two groups some fertile axes were radially and others were bilaterally symmetrical. Of the resulting four categories, only one appears to be similar to a potential ancestral lycophyte, the nonterminate, radially symmetrical group that is represented by *Discalis*. Those lycopods that are closest to this category of zosterophyll are *Asteroxylon, Baragwanathia* and *Drepanophycus spinaeformis*. The other three categories appear to be evolutionary deadends. Note that this hypothesis holds that one group of zosterophylls illustrates characteristics that one might expect in an ancestral lycophyte. It does not state that lycophytes arose from zosterophylls



Text-figure 4A-K—Nonterminate Zosterophyllophytina. **A.** *Gosslingia* from Edwards, 1970; **B.** *Crenaticaulis* and **C.** *Sawdonia* both from Gensel, Andrews & Forbes, 1975. **D.** *Serrulacaulis* from Hueber & Banks, 1979; **E.** *Konioria* from Zdebska, 1982; **F.** *Anisophyton* from Remy, Schultka & Hass, 1986; **G.** *Thrinkophyton* from Kenrick & Edwards, 1988; **H.** *Oricilla* from Gensel, 1982; **I, J.** *Discalis* from Hao, 1989; **K.** *Deheubarthia* from Edwards, Kenrick & Carluccio, 1989.

Table 4—Four patterns among zosterophylls hypothesized by Niklas and Banks (1990). This Table is much simplified from that paper

Terminate		Nonterminate	
Radial	Bilateral	Radial	Bilateral
Zosterophyllum spp.	*Rebuchia*	Enations and sporangia radially arranged *Discalis*	Enations and sporangia bilaterally arranged, e.g., *Serrulacaulis* Enations radial, sporangia bilateral, e.g., *Sawdonia*
Early Forms Symmetry in transition *Zosterophyllum llanoveranum* *Z. myretonianum*			

although it is abundantly clear that the two groups have more in common than either one has to any other group. Of course, these ancestral-like forms still lacked microphylls. However, because apical meristems capable of cutting off lateral meristems had evolved and the lateral meristems were potential sporangia or enations, it is possible to visualize the evolution of lateral meristems with greater biochemical potential developing into microphylls. This would simply be a third category of lateral meristems. Such a development has now been seen in the strobili of *Stachyophyton* (Text-figure 2 I), a plant I include among the Aberrant Genera. Additional evidence for this degree of versatility at the apex of early zosterophylls is provided by the branches that are produced in axillary or subaxillary positions on the stem. Once called axillary tubercles, these branches are seen, for example, in *Gosslingia, Crenaticaulis, Anisophyton, Thrinkophyton, Deheubarthia.* It seems abundantly clear that developmental changes in apical meristems were frequent and that plasticity characterized morphology in the early land plants.

In summary, without going into all the details and reciting the caveats required in the Niklas and Banks (1990) theorizing, it is reasonable to postulate that small developmental changes in the apical meristem resulted in the evolution of a wide variety of zosterophylls from some unknown ancestor and that Lycophytina required relatively few additional changes to be evolved from an ancestor that shared many features with terminate, radially symmetrical zosterophylls.

TRIMEROPHYTINA

When I proposed this subdivision in 1968 few data were available (Table 5). Hueber and Banks (1967) had just selected a neotype for *Psilophyton princeps* (Text-figure 5A) but Hueber's revision of the species was only in press (Hueber, 1968). Hence only *Dawsonites*, Halle's name for paired terminal sporangia borne on naked, dichotomizing axes, and *Trimerophyton* (Text-figure 5E), Hopping's (1956) name for certain specimens of Dawson's *Psilophyton robustius*, were clearly indicative of a new group of plants. From that small beginning, the group was expanded (Banks, 1975) particularly by the addition of *Pertica* (Text-figure 5 I) by Kasper and Andrews (1972). *Hostinella*, a form genus for dichotomizing

Table 5—Trimerophytina as proposed by Banks (1968), revised by Banks (1975) and as visualized in the present paper. *Species for which anatomy is known

Banks 1968	Banks 1975	Banks, this paper
Trimerophytina	*Trimerophytina*	*Trimerophytina*
Trimerophyton	*Trimerophyton*	*Trimerophyton robustius* Hopping 1956
Dawsonites	*Pertica*	*Psilophyton kräuseli* Obrhel 1959
	Dawsonites	*_P princeps_ (Dawson) Hueber 1968
	Hostinella	*_P. forbesii_ (Andrews, Kasper & Mencher) Gensel 1979
	Psilodendrion	*P. dapsile* Kasper, Andrews & Forbes 1974
	Psilophytites	*P. microspinosum* Kasper, Andrews & Forbes 1974
		*_P. dawsonii_ Banks, Leclercq & Hueber 1975
		*_P. charientos_ Gensel 1979
		*_P. crenulatum_ Doran 1980
		*_P. coniculum_ Trant & Gensel 1985
		P. szaferi Zdebska 1986
		Hostinella (in part)
		Dawsonites
		Pertica quadrifaria Kasper & Andrews 1972
		P. varia Granoff, Gensel & Andrews 1976
		P. dalhousii Doran, Gensel & Andrews 1978
		Likely Trimerophytina
		*_Yunia dichotoma_ Hao & Beck 1991
		Perhaps advanced beyond Trimerophytina
		Oocampsa catheta Andrews, Gensel & Kasper 1975
		*_Gothanophyton zimmermanii_ Remy & Hass 1981
		Tursuidea paniculata Schweitzer 1987

Text-figure 5A-J—Trimerophytina. **A.** *Psilophyton princeps* from Hueber, 1968; **B.** *P. forbesii* from Gensel, 1979; **C.** *P. dapsile* and **D.** *P. microspinosum* both from Andrews *et al.*, 1977; **E.** *Trimerophyton* from Hopping, 1956; **F.** *Psilophyton dawsonii* from Banks, Leclercq & Hueber, 1975; **G.** *P. charientos* from Gensel, 1979; **H.** *P. crenulatum* from Doran, 1980; **I.** *Pertica quadrifaria*, the dark circles are clusters of sporangia, from Andrews *et al.*, 1977; **J.** *Pertica dalhousii* from Doran *et al.*, 1978.

axes, was added because Banks (1967) found a specimen with a vascular strand like that observed in a specimen of *Dawsonites*, a form genus. The particular specimen proved later to be a piece of *Psilophyton dawsonii*. Two other form genera, *Psilodendrion and Psilophytites* were added as well. Because both are sterile axes never associated with masses of terminal sporangia nor with anatomy, they should probably be removed. In the past decade and a half a number of new species of *Psilophyton* (Table 5; Text-figure 5B-D, F-H), two new species of *Pertica* (Text-figure 5J) and, perhaps, a new genus, *Yunia*, have been added. Andrews, Gensel and Kasper (1975) consider that the laterals of their genus *Oocampsa* (Table 5) branch in more complex fashion than do laterals of trimerophytes hence that *Oocampsa* had evolved beyond trimerophytes and foreshadowed progymnosperms. I suspect that Schweitzer's (1987) *Tursuidea* (Table 5) may be similarly more advanced than trimerophytes. The ridged xylem strands of *Gothanophyton* (Table 5) are more complex than anything yet described for trimerophytes and Remy and Hass (1986) exclude it from that group. No fertile branches are known. However, on the basis of undescribed, cellularly preserved axes that I have collected at *Psilophyton* localities, I suggest that we may find trimerophyte anatomy to be more complex than presently known.

The original characterization of trimerophytes included plants with pseudomonopodial main axes bearing dichotomizing or trichotomizing laterals some of which were terminated by paired, fusiform sporangia. Sporangia were clustered into groups of 16 to 256 where the number depended on the number of dichotomies. The vascular strand was a large, round to elliptic, centrarch protostele. Plants added to the group have modified the description only slightly. For example, main axes of *Psilophyton dapsile* (Text-figure 5C) were mostly dichotomous to weakly pseudomonopodial. In contrast *P. crenulatum* (Text-figure 5H) was shown by Doran (1980) to have a complex branching pattern that foreshadowed the branching in Carboniferous ferns, especially *Psalixochlaena cylindrica*. Trant and Gensel (1985) expressed similar feelings about their species *P. coniculum*. Doran, Gensel and Andrews (1978) suggested that variation in branching in trimerophytes indicates evolution toward aneurophytes by way of *Oocampsa* and also toward certain ferns. Andrews, Gensel and Kasper (1975) discussed and elaborated similar points. All these reports reinforce the original suggestion (Banks, 1968) that trimerophytes "seem a natural outgrowth of Rhyniophytina and Simultaneously foreshadow the more complex branching pattern found among Cladoxylopsida, Coenopteridopsida, and Progymnospermopsida". Stewart (1983, chapter 12, pp. 192-193) and Holmes (1989) derive all, or several, major groups of ferns from Trimerophytina. Hao and Beck (1991) place *Yunia* tentatively in Trimerophytina because of its dichotomous branching, its centrarch protostele, its scalariform tracheids with pit-like perforations in the wall between the bars, and the associated fertile axes that may bear paired terminal sporangia. The sporangia are elliptic rather than fusiform and the center of the xylem strand has considerable parenchyma around the protoxylem. If *Yunia* remains in Trimerophytina, it broadens the concept a little more and permits Hao and Beck (1991) to comment on the use of branching patterns and stelar morphology to relate trimerophytes to Carboniferous ferns.

Psilophyton appears to be the least complex genus with *P. dapsile* as the simplest and possibly *P. crenulatum* as the most complex species. Members of the genus may reach a meter and a half in height. *Pertica* is perhaps the most complex genus and some of its members may reach two meters or more in height.

SUMMARY

A review of three subdivisions (or phyla) of early land plants since they were proposed in 1968 reveals some deletions, numerous additions, and various modifications. David Edwards' (1986) demonstration that *Rhynia major* had no typical tracheids was a major change in Rhyniophytina and led to the establishment of a group here called Aberrant Genera. His redescription (1986) of *R. gwynne-vaughanii* was a striking modification but left *Rhyniophytina* with one genus possessing vascular tissue. To this Shute and Edwards (1989) added *Uskiella*. The continued failure to demonstrate vascular tissue in any other rhyniophytes led Edwards and Edwards (1986, Table 1) to set up an informal group amongst presumed rhyniophytes, the rhyniophytoids which one hopes will ultimately be shown to be vascular. For the present, Rhyniophytina stand as an early group of land plants with no obvious ancestors nor clear cut descendants although one presumes they had the potential to evolve in the direction of trimerophytes.

Zosterophyllophytina has been expanded remarkably. Ten new genera have been added and several new species have been described under *Zosterophyllum*. The additions have confirmed the major features of the group-lateral sporangia with distal dehiscence and, wherever known, exarch vascular strands. Niklas and Banks (1990) have identified four basic patterns in the group. They are those with terminate fertile axes accompanied by either radial or bilateral symmetry and those with nonterminate fertile axes accompanied by either radial or bilateral symmetry. The authors hypothesized that those forms that were nonterminate with radial symmetry most resembled ancestral lycopods, or that they demonstrated the potential for shoot apices to evolve in the direction of lycopods. The aberrant genus *Stachyophyton* further demonstrated the ability of apices to produce microphylls, at least in the form of sporophylls. Remy, Schultka and Hass (1986) described branches of *Anisophyton* that originated near the major branchings and called them angular organs. They are comparable to, but more complex than, the axillary tubercles found, for example, in *Gosslingia* (Edwards, 1970b) and *Crenaticaulis* (Banks & Davis, 1969). They suggested that the type of branching could be used as an additional means of distinguishing among various zosterophylls.

Trimerophytina has been modified by the addition of new species of *Psilophyton* some of which have the characteristic large (in comparison to *Rhynia gwynne-vaughanii*) centrarch xylem strand and masses of terminal sporangia that dehisce longitudinally. Axes branched much more profusely than Rhyniophytina, pseudomonopodially on the main axes and dichotomously on the laterals. New finds, such as *Yunia*, may broaden the scope of the group. Other new forms such as *Oocampsa, Tursuidea* and *Gothanophyton* will ultimately further broaden the group or form the nucleus of intermediate forms between trimerophytes and ferns or other higher forms.

Finally, one encounters those forms that do not fit readily into the three subdivisions but that have combined the characteristics of more than one subdivision. These forms that, for me, demonstrate the rapid evolutionary changes that were in progress in Siluro-Devonian time, I have here referred to as

Aberrant Genera. Only continued search will determine their ultimate fate.

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ADDENDUM

Two reports appearing while this paper was in press bear directly on the thesis presented in the paper. I have treated *Cooksonia* as a rhyniophytoid included in Rhyniophytina, but excluded from Rhyniaceae pending the demonstration of tracheids in its fertile axes. Edwards, Davies and Axe in *Nature* 357 : 683-685 have now published that demonstration and *Cooksonia* on my Table 1 must be moved back to its place as the first of the genera in Rhyniaceae where it has long been thought to belong. Additional evidence that Aberrant Plants were a frequent component of early land floras is provided by a new plant, *Adoketophyton subverticillatum* (Li & Cai) Li & Edwards, published in *Paleontology* 35(2) : 257-272, 1992. This plant, from Yunnan Province, China has fructifications that suggest zosterophylls but its sporangia are borne adaxially on bracts thus recalling lycopods. Vegetative axes, however, lack microphylls or other outgrowth. Hence the plant fits no rigid classification and must be added to the growing list of enigmatic Aberrant Plants listed on Table 2.