Origin and Evolution of Lycopsid members – An overview

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ABSTRACT

The members of the Lycopsida Group possess a long history of origin in the zosterophyll complex and the Lower Devonian is represented by the members of Drepanophycales and the Protolepidodendrales. In the Carboniferous, lycopsids were represented by at least four major orders *viz.*, Lepidodendrales, Isoetales, Lycopodiales and Selaginellales. Recent morphological and gene sequencing analyses suggest the occurrence of an early basal dichotomous segregation of the vascular plants, separating the lycophytes from the rest of the vascular plants. Considerably good amount of data sets have accumulated by this time and the idea of delineation of the lycopsid members into clearly defined taxonomic groups are sometimes getting blurred as the new fossils have been described with unusual combination of characters that are shared by more than one group. Sometimes, the old concept of interrelationships and evolution needs reconsideration by the analysis of information available from new fossil records and the extant members. In view of this, in the present paper an attempt has been made to present an overview of the recent understanding of the Lycopsida Group.

Key-words: Lycopsida, origin, evolution.

REVIEW AND DISCUSSION

Presence of vascular tissues and cryptogamic mode of reproduction, association of these two characters in pteridophytes delineates them from all other groups of plants. Pteridophytes appeared as early as mid-Silurian period as evidenced by the presence of *Cooksonia* in the fossil record (Edwards & Feehan 1980). Though, there are many other reports of the presence of dispersed trilete meiospores (Ghosh & Bose 1949-50; Naumova 1949), cuticles and other plant fragments said to be of vascular plants (Krystofovich 1953) from earlier than Middle Silurian strata, but these could not be taken with certainty (Stewart 1960; Banks 1975; Pratt et al. 1977; Gray & Boucot 1977) as they were not found in organic connection and may equally be parts of non-vascular plants like *Aldanophyton*, *Protosalvinia* and *Nematothallus*.

Lycopsid members are characterised by assemblage of characters such as single axial or adaxial sporangia on the sporophylls, lateral in position in relation to the main stem, exarch xylem and presence of microphyllous leaves. Probable origin of lycopsid members is from the Zosterophyllopsida group of plants of the Lower Devonian period (Banks 1968), as the members of this group already developed lateral sporangia and exarch xylem in number of genera viz., *Zosterophyllum*, *Gosslingia*, *Crenaticaulis*, *Sawdonia* etc. The other lycopsid character i.e., microphyllous leaf is suggested to have evolved by the elaboration of non-vascularised enation like structures present in *Sawdonia*, *Bathurstia*, *Crenaticaulis*, *Kaulangiophyton* and establishment of a vascular trace in them in future course of evolution through the process prescribed in the enation theory (Bower 1935). The origin of leaf trace in microphyllous leaf leaves have no

impact on the cauline vascular cylinder i.e., no leaf gap is produced. *Asteroxylon* with its vascular supply in the leaf up to the leaf base is considered as an intermediate stage in the evolution of microphyllous leaf, as found in *Drepanophycus* and *Lycopodium*. As such, *Asteroxylon* is considered as a transitional member between the Zosterophyllopsida and the Lycopsida groups. Though, initially *Asteroxylon mackiei* was thought to have terminal sporangia (*Nothiaaphylla*), but discovery of lateral sporangia near the axils of microphylls justifies its placement in the Lycopsida group (Lyon 1964).

Origin of the Zosterophyllopsda group, which is considered as an ancestral group of the Lycopsida, might have originated from the rhyniaceous stock through reduction of the fertile telomes as found in *Renalia hueberi* (Gensel 1976) and resulting in lateral sporangia from terminal sporangia. Such a shifting of position of sporangia from terminal to lateral position in relation to the main stem took place as a side line of evolution. In the Zosterophyllopsida, the sporangial arrangement had no definite relationship with the enations as noted in *Sawdonia*, *Crenaticaulis* and *Kaulangiophyton*. But, how the microphylls in the lycopsids got associated with the sporangia in axillary or adaxial position is difficult to explain. There are some hypothetical stages suggested in the enation theory where shifting of the sporangia from cauline to the axillary position of the leaves took place. Only in *Baragwanathia* and *Drepanophycus*, the compression fossils from the Lower Devonian period, there are some associations of sporangia with the microphylls (Lang & Cookson 1935; Edwards et al. 1979; Grierson & Banks 1963; Banks & Grierson 1968).

Smith et al. (2006) with the help of morphological characters and gene sequencing techniques suggested a very early basal dichotomy in the vascular plants segregating the Lycophytes from all other vascular plants - the Euphyllophytes, consisting of two clades, the Spermatophytes and the Monilophytes. The group Monilophytes is comprised of Psilophytes, Sphenophytes and the Filicophytes.

Both morphologically and anatomically Lycopsid plants are of various types. These variations may be due to the acquisition of habitats of diverse types from warm climates to alpine regions and from epiphytic to terrestrial to aquatic/swampy conditions (Sporne 1976). On the basis of morphology, growth forms, habit, nature of spores etc. the lycopsid members are usually grouped into seven orders viz., Drepanophycales, Protolepidodendrales, Lycopodiales, Lepidodendrales, Pleuromeiales, Isoetales, and Selaginellales (Taylor et al. 2009). Variations to this treatment are also noted (Stewart & Rothwell 1993; DiMichele & Bateman 1996) where the rhizomorph bearing lycopsids (Lepidodendrales and Isoetales) are placed under the Isoetalean clade. As research continues with the lycopsids, it is becoming increasingly clear that delineation of major clades is now more difficult to resolve as more and more fossils are being discovered with overlapping characters, which are shared by more than one group (Gensel & Berry 2001).

Drepanophycales has two genera *Drepanophycus* and *Baragwanathia* and they are the most primitive lycopsid members (Banks 1960). In some other treatments, they are considered as prelycopsids or transitional between zosterophylls and the true lycopsids (Schweitzer 1980; Gensel & Andrews 1984). *Drepanophycus* was found in the Lower Devonian and existed up to the Upper Devonian and is represented by several species (Grierson & Banks 1963). While, *Baragwanathia* is known by only two species namely *B. longifolia* having restricted distribution from the Silurian-Devonian rocks of Australia and Lower - Middle Devonian of Canada (Lang & Cookson 1935; Hueber 1983). The other species *B. abitibiensis* is known from the Lower Devonian of Canada (Hueber 1983). The exact age of *Baragwanathia* is still unsettled (Garrett et al. 1984) but may be somewhere around Lower to Upper Devonian (Stewart 1983). Both of these genera were homosporous and herbaceous like the extant members of the Lycopodiales. The microphylls in the Drepanophycales were arranged helically but appeared to be in near-whorled or pseudo-whorled pattern and the sporangia were near axial or borne on the stem, a little above the appendage (Bateman 1996). The stomata present on the stem is paracytic in *D. spinaeformis* and secondary wall thickenings are annular to spiral.

The members of the order Protolepido-dendrales are *Protolepidodendron*, *Leclercqia*, *Colpodexylon*, *Estinophyton*, *Sugambrophyton* and *Spencerites* (Taylor et al. 2009). They differ from each other in the number of forkings at the tips of the leaves and in the number and arrangement of sporangia on the fertile leaves. No organized strobilus is produced in these genera but sporophylls are intermixed with the vegetative leaves. These are small, herbaceous, homosporous plants appeared in the Lower Devonian and gradually declined in the Lower Carboniferous. They are well demarcated from the members of the Drepanophycales in having distally forked or branched leaves and having enlarged leaf bases (leaf cushions). Protolepidodendrids lack the characteristic leaf abscission property of the lepidodendrids. The stalked attachment of the sporangia at the distal end of the leaves of protolepidodendrids aroused considerable interest as its origin was difficult to explain through enation theory. The origin of the protolepidodendrids with three dimensionally oriented leaf segments (Schweitzer 1980; Bonamo & Grierson 1981) is supposed to have taken place from the rhyniaceous type through the process as prescribed in the telome theory of Zimmermann (1952), while the spirally disposed spine like leaves in *Drepanophycus* and *Baragwanathia* (Drepano-phycales) evolved through the zosterophyllopsids. So, it can be said that in the Lower Devonian there were two lines of evolution of microphyllous leaves in the lycopsids (Stewart 1983). In one line, it evolved through elaboration of enations (Drepanophycales, Lycopodiales) and in the other line through the modification of telome trusses (Protolepidodendrales, Lepidodendrales). Transverse dehiscence of the globose sporangia of Drepanophycales suggests its affinity with the Lycopodiales, while, longitudinal dehiscence of sporangia of the Protolepidodendrales relates them with the Lepidodendrales. Protolepidodendrids are eligulate except *Leclercqia*. Discovery of ligule in the homosporous protolepidodendrid *Leclercqia complexa* (Grierson & Bonamo 1979) is very significant since it sheds light on the origin of ligule in the heterosporous lycopsids from such type of plant, as this is the only record of ligulate lycopsid with homospory. It is possible that such type

of herbaceous, homosporous, ligulate protolepidodendrids gave rise to the herbaceous, ligulate, heterosporous forms like members of the Selaginellales in the Upper Carboniferous.

Ligule is an important character found only in the Lycopsida group of the vascular cryptogams and its presence or absence determines taxonomic placement of a lycopsid. The shapes and sizes of ligules vary from species to species in extant members and extinct members were noted earlier (Harvey-Gibson 1896; Maslen 1898; Singh et al. 2010). Some species of *Selaginella* produce two ligules per leaf were noted earlier by Ball (1925) in *S. martensii* and confirmed later by Singh et al. (2010) in *S. panchghaniana*. Various functions have been attributed to this structure, some of which are secretion and accumulation of water, mucilage secretion, enzymes or superficial conduction of water (see Pant et al. 2000). Sigee (1974) made an electron microscopic study on the ligule of *Selaginella* and suggested secretion of mucilage from the ligule was not possible since there was continuous covering of cuticle over the surface devoid of any pores. He suggested that mucilage could come out only after the disorganization of the ligule.

The origin of heterospory took place from the homosporous members in the Middle Devonian period and later on became clear with the appearance of bimodal spore sizes by regression of spores, developing two types of spores; the smaller one microspores producing male gameophytes on germination and the larger one megaspores producing female gametophytes (Srivastava & Srivastava 2001 and the references therein). Origin of heterospory was a major event in the evolution, since it was associated with changes in the pattern of spore germination from exosporic to endosporic type, thus producing extreme reduction in the prothallial tissue of the gametophytes and resulting unisexuality from bisexuality (Mukhopadhyay 2009 and references therein). Occurrence of both microspores and megaspores within the same sporangium (amphisporangiate condition) probably served as an intermediate stage toward evolution of heterospory from homospory and can be traced in the enigmatic fossil members *Barinophyton* and *Protobarinophyton*

(Brauer 1980, 1981). Such a stage of evolution is also noted in the extant lycopsid members like *Isoetes indica* and *Isoetes pantii* (Goswami & Arya 1968, 1970). After attainment of heterospory, there was a tendency to reduce the number of megaspores per megasporangium and ultimately reaching a condition where a single functional megaspore exists. There are examples both in the extinct and extant members of lycopsids where different numbers of megaspores are noted in the megasporangium. This has been achieved following two processes: in the pre-meiotic stage there was a gradual reduction in the number of megaspore mother cells from many to one and further reduction in the number of megaspores from four in a tetrad to only one in the post-meiotic stage. Pre-meiotic reduction of megaspore mother cells is mostly noted in *Isoetes*, while, both pre-meiotic and post-meiotic reductions are noted in different species of *Selaginella* (Duerden 1929). Fossil evidences of reduction of megaspore number are noted in different species of *Flemingites*. In *F. noei* hundreds of megaspores are found within a megasporangium while, in *F. foliaceous* only four megaspores are present. In other species of *Flemingites* intermediate number of megaspores is present. Ultimately, a single functional megaspore is found in *Lepidocarpon*.

Recent discoveries of some fossil specimens Like *Wuxia*, *Chamaedendron*, *Longostachys*, *Protolepidodendropsis* and *Zhenglia* from the Devonian of China indicate that these plants are transitional between Protolepidodendrales and Lepidodendrales in their assemblage of characters and might have served as precursors to the origin of Lepidodendrales (Taylor et al. 2009). Megasporophylls bearing megasporangia have been found in *Wuxia*, *Chamaedendron* and *Longostachys* (Schweitzer & Li 1996; Cai & Chen 1996 and Berry et al. 2003). *Chamaedendron*, *Longostachys* and *Protolepidodendropsis* are arborescent but secondary xylem has been recorded only in *Longostachys*. Aggregation of sporophylls in an area resembling a cone like structure is found in *Zhengliaradiata* (Hao et al. 2006), another late Devonian to Carboniferous representative.

Two extant genera *Lycopodium* and *Phylloglossum* and one extinct genus *Lycopodites* constitute the order Lycopodiales (Gifford & Foster 1989). *Lycopodium* is worldwide in distribution from tropical to temperate to arctic regions (Bierhorst 1971). *Phylloglossum drummondii*, a highly reduced and specialized monotypic plant is restricted to Australia and New Zealand. *Lycopodites* specimens have been known from the rocks of Devonian to Pleistocene (Krausel & Weyland 1937; Harris 1976; Krassilov 1978; Rigby 1978) and they include both isophyllous and anisophyllous forms. *Lycopodites* are mostly found in vegetative conditions and in that case there is the possibility of getting it confused with the young twigs of the lepidodendrids. The distinguishing character ligule, which differentiates the lepidodendrids from *Lycopodites* is not always very clear.

The genus *Lycopodium* as conceived by Linnaeus, was a heterogeneous assemblage, and the genera like *Tmesipteris*, *Psilotum*, *Selaginella* and *Phylloglossum* were isolated from it from time to time by different workers (Bernhardi 1801; Willdenow 1802; Kunze 1843). *Lycopodium* has undergone a long taxonomic vicissitudes. Even after separation of these genera, the remaining *Lycopodium* was not considered homogeneous and various small genera were created from it from time to time (Sen & Sen 1978; Mandal & Sen 1979; Dixit 1984). The basis of creation of these small genera is mainly based on the nature of leaves, bulbils, spore and prothallial morphology, branching pattern etc. However, wide variations exist among the authors in the acceptance of these genera. Pichi Sermolli (1977) considered a single family Lycopodiaceae under Lycopodiales, containing seven genera viz., *Huperzia*, *Phlegmariurus*, *Phylloglossum*, *Diphasium*, *Diphasiastrum*, *Lycopodiella* and *Lycopodium* in his classification. But, Taylor et al. (2009) consider only four genera under Lycopodiaceae [*Huperzia* (439 spp.), *Lycopodiella* (41 spp.), *Lycopodium* (476 spp.) and *Phylloglossum* (1sp.)]. All these members are herbaceous, eligulate, homosporous and devoid of secondary growth. The basic stellar structure in *Lycopodium* is actinostelic (*Huperzia selago*), in one way giving rise to plectostelic forms by schizogenous

splitting (*Lycopodium clavatum, L. volubile*) and in the other way developing mixed protostelic form (*Lycopodiella cernua*) through the formation of extensive phloem islands in the xylem. Other primitive characters of this group are the erect/pendant habit, presence of cortical roots and the vegetative leaves are intermixed with the sporophylls. The advanced features are the creeping habit, absence of cortical roots and development of well-organized strobili. Gametophytes of lycopsids are of varied forms in the same species (*Huperzia selago*) or in different species and are mycotrophic. This mycotrophic property was also noted within the ancestral forms of the lycopsids. In the Devonian rhyniopsids it has been identified as caused by members of Glomeromycota, the *Glomites rhyniensis* (Taylor et al. 1995). 'Mycotrophy in pteridophyte is significant, data linking the past pteridophyte diversity and exploitation of mycotrophy would be valuable, since such relationships would reflect an advantaging strategy for their success in a wide array of habitats throughout geologic time' (Page 2002). The spores of tropical members of *Lycopodium* germinate immediately and develop surface living, photosynthetic gametophytes, while, the temperate members have a prolonged dormancy in spore germination and the resultant gametophytes are subterranean and mycotrophic. However, Freeberg & Wetmore (1957) showed that it is the dormancy which is significant and responsible for different forms of the gametophytes in *Lycopodium*. When dormancy of the spores in different species of *Lycopodium* was broken by scarification and grown on culture media, all the gametophytes were found identical in morphology and photosynthetic. Normally the gametophytes are bisexual but cross fertilization has also been reported (Soltis & Soltis 1988).

Phylloglossum drummondii, a highly specialized living monotypic genus of the Lycopodiaceae shows a unique property that its sporophyte under adverse condition survives as a geophyte in the embryonic stage as a tuber under the soil. With the onset of favourable condition the tuber (protocorm) develops few protophylls, adventitious roots and a strobilus at maturity (neoteny). In *Lycopodiella cernua* also, under unfavourable conditions, the epibasal cell produces a mass of undifferentiated cells (protocorm) bearing protophylls which differentiates ultimately into a sporophyte under favourable condition. Wardlaw (1955) suggested that organization of a shoot apex may be delayed in the embryo and such swelling of the tissues is expected under abnormally high carbon/nitrogen ratio. This trait may be considered a derived condition which is permanently fixed in *Phylloglossum* with evolution and development of high polyploidy.

Members of the Lepidodendrales viz., *Lepidodendron, Diaphorodendron, Lepidophloios, Bothrodendron, Sigillaria* are arborescent, heterosporous, ligulate lycopsids, which were dominant elements of the Carboniferous time and became extinct in the Permian (Taylor et al. 2009). The genus *Lepidodendron* was segregated into a new genus *Diaphorodendron* (DiMichele 1985). Later, *Diaphorodendron* was divided further into *Diaphorodendron* and *Synchysidendron* and were placed under a new family Diaphorodendraceae (DiMichele & Bateman 1992). Their arborescent habit was due to the activity of a unifacial cambium, which contributed only secondary xylem inside. But unlike the woody trees of today, secondary xylem in the lepidodendrids accounts for only a small proportion of the diameter of the stem; rather the extensive periderm is primarily responsible for the massive trunk (Taylor et al. 2009). In *Diaphorodendron* the periderm is bizonate, differentiated into phellem and phelloderm but in *Lepidodendron*, the periderm was homogeneous. As these plants grew in swampy habitats, an aerating channel of tissue (parichnos) is found in these plants for facilitating respiration. Leaf abscission property has developed in this group of plants leaving scar marks on the leaf cushions. This may be a fact that leaf shedding property developed to avoid growth of epiphytes on the plant surface (Page 2002). The shape and disposition of the leaf cushions are very characteristic and help in identifying genera. The different cone genera found in this group show a tendency of evolution of monosporangiate cone (*Lepidocarpon, Achlamydocarpon* and microsporangiate *Lepidostrobus*) from the bisporangiate cone

(*Flemingites* type). Brack-Hanes & Thomas (1983) suggested for the use of the terminology *Lepidostrobus* for the microsporangiate cones in the monosporangiate cone genera, whereas, *Flemingites* for the bisporangiate cone genera. Reduction of megaspore numbers from several hundred (*Flemingites noei*) to only one functional megaspore (*Lepidocarpon*, *Achlamydocarpon*) in the megasporangium and its retention within the megasporangium is a remarkable feature towards the development of seed habit (Brack-Hanes 1978). Another interesting feature found in this group is the development of laminar extension from the stalk of the megasporophyll which surrounds the megasporangium and gives a protective integument like structure (*Lepidocarpon*). Different stages of development of laminar extension were recorded in different species of *Lepidocarpopsis* (Abbott 1963) and *Achlamydocarpon*. The morphological nature of integument of megasporangia of these lepidodendrids was laminar in nature and the micropyle was an elongated slit like structure allowing spermatozoids to enter for fertilization. It is quite unlikely for the seed plants where the integument was a modification of the telome truss, the micropyle was pore like and the ovule was indehiscent. As such, the lepidodendrids bearing integumented megasporangium are called pseudo-spermatophytes. The morphology of the megasporophylls of *Achlamydocarpon* and *Lepidocarpon* were modified into a boat shaped structure and at maturity dropped individually from the cone in the water below and transported to a far distance (Phillips 1979). The wing like extension of the megasporophylls in *Achlamydocarpon* also suggests air borne dispersal (Thomas 1981). Drastic change of climate and tectonic activity might be the cause of mass extinction of this giant lepidodendrids in the Permain (DiMichele & Phillips 1996; Cleal & Thomas 2005).

Giant members of the Lepidodendrales had extensive root system, which is known as Stigmarian root system. This dichotomously divided root structure spreads horizontally for a considerable part and then goes downward. The arrangement and anatomy of spirally arranged stigmarian rootlets had striking similarity with those of *Isoetes* and this resemblance reveals that members of Isoetales are derived from the lepidodendrids by extensive reduction (Magdefrau, 1956). A downgrade series of evolution was proposed starting from *Lepidosigillaria* with *Sigillaria*, *Pleuromeia*, *Nathorstiana* as intermediate forms leading ultimately to *Isoetes*. Stewart (1983) gave an explanation of how this could be achieved anatomically. But, how the lateral disposition of sporangia in *Sigillaria* changed to terminal position in *Pleuromeia* and *Isoetes* could not be explained (Brown 1958). Again, higher stratigraphic sequence of *Nathorstiana* (Cretaceous) than *Isoetites* (Triassic) mentioned by Bock (1962) stood on the way of accepting this path of evolution of *Isoetes* from *Nathorstiana* as proposed by Magdefrau (1956).

Discovery of some miniature arborescent lepidodendrids (*Cyclostigma*, *Valmeyerodendron* and *Lepidosigillaria*) from the Upper Devonian and onwards with lobed cormose rhizomorph opened up a new possibility that this group of plants probably functioned as a common ancestor originating Isoetalean members in one way and the Lepidodendrales on the other line (Jennings 1972; Stewart & Rothwell 1993). These plants were ligulate, heterosporous and a combination of other characteristics which fit well their placement as a common ancestor.

The Isoetales is now recognized as having an extensive fossil history, probably dating from the Devonian (Pigg 2001). *Clevelandodendron ohioensis*, an Upper Devonian lycopsid has been interpreted to have an isoetalean lineage (Chitaley & Pigg 1996), which is 1.25m long and bearing terminally a bisporangiate strobilus like the *Flemingites*. Similarly, another Carboniferous lycopsid with isoetalean affinity is the heterosporous *Chaloneria cormosa*, which is about 2 m long bearing spirally arranged leaves and alternating micro- and megasporophylls (*Polysporia*), cambial growth and periderm. *Chaloneria* resembles the modern *Isoetes* in the lobed rhizomorph-like stem and in the peculiar anatomical details including the presence of few layered thin-walled cells like trabeculae within the sporangial wall (Pigg & Rothwell 1983). Mesozoic representatives of isoetalean lineage include Cretaceous genera *Nathorstiana* and *Nathorstianella*, which

possess root arrangement and stellar morphology like the extant *Isoetes* (Karrfalt 1984, 1986). Several fossils that resemble morphologically with the modern *Isoetes* have been described from the Triassic and placed under the *Isoetites* (Bose & Roy 1964; Pigg 2001) or in the genus *Isoetes* (Srivastava et al. 2004). These findings suggest that the cormose lycopsids did not evolve from the arborescent forms with stigmarian base by reduction, but co-existed at the same time or before, with the lepidodendrids.

Apart from the bulbous cormose base and anatomical similarities, the megaspore morphology of some species of extant *Isoetes* like *I. dixitei, I. gardneriana, I. panamensis, I. melanotheca* exhibit striking similarities in the possession of angular or auriculate extension like those of the Carboniferous megaspore genus *Valvosporites* of *Chaloneria* bearing cone genus *Polysporia*. The pittings of mesosporium of microspores of Permian miospores also have similarities with the *Isoetes*. These findings provide additional support to the relationship of *Isoetes* with *Chaloneria* and *Polysporia* and supports the contention that *Chaloneria* and *Polysporia* served as ancestors of the modern *Isoetes* (Srivastava 2000 and references therein).

The basal part of *Paurodendron fraipontii,* a member of the Lower Carboniferous was thought to be related to *Selaginella* (Phillips & Leisman 1966; Schlanker & Leisman 1969). But, work of Rothwell & Erwin (1985) established that the spiral rooting pattern and anatomy of radial *Paurodendron* with secondary growth and monarch root traces has relationship with the Isoetales and not with the *Selaginella*. Another fossil genus *Oxroadia* described from the Lower Carboniferous, suggests it as a diminutive intermediate structure between *Stigmaria* and *Isoetes* (Alvin 1965; Bateman 1992), which has one to three times dichotomously forked radial root stock with spirally arranged roots and anatomical similarities with *Paurodendron*. They consider stigmarian lepidodendrids as primitive and reduction of the stigmarian root has resulted unbranched rootstock of *Paurodendron* via *Oxroadia*. So, it is found that there

are conflicting views regarding the origin of *Isoetes*. If the lobed corm of *Isoetes* originated from the stigmarian root base, the amount of reduction is insuperable. As such, it is most logical to assume that Isoetalean and Lepidodendralean clades developed from common ancestors like *Lepidosigillaria* and *Cyclstigma* like plants with lobed cormous base like *Protostigmaria* (Jennings 1975). *Protostigmaria, Chaloneria, Paurodendron* served as intermediates towards the evolution of *Isoetes* like plants. Lepidodendrids with Stigmarian type of root stock developed from the lobed rhizomorph in another line via *Oxroadia*.

In the present day, the Isoetales are represented by only two living genera *Isoetes* and *Stylites* under the family Isoetaceae. However, sometimes *Stylites* is also treated as a subgenus of *Isoetes* (Gomez 1980).These genera are ligulate, heterosporous lycopsids. *Isoetes* is represented by about 70 species distributed worldwide and occupy different types of aquatic to terrestrial habitats of tropical to subtropical climates. *Stylites* is represented by only two species and was first discovered from the high mountain of Peru around the margins of a lake (Amstutz 1957). *Stylites* is a variant form of *Isoetes* and derived from *Isoetes* was explained by Bierhorst (1971). The morphology of rhizome is pointed, the axis is dichotomously branched and roots develop from one side of the axis in *Stylites*, which are different from *Isoetes*. Both of these genera are adapted to CAM type of photosynthesis (Keeley 1982). *Stylites* is unusual in having absence of stomata and in its absorption of CO_2 through roots (Kelley et al. 1984). *Isoetes* plants acquired assemblage of several unusual characters which have marked them enigmatic plant. These include abnormal position and function of cambium resulting formation of prismatic tissue inside and secondary cortex outside; replenishment of secondary cortex every year and sloughing off of the old cortex; almost absence of dichotomous branching; extreme reduction of vertical growth; extreme shortening of the stem axis, the vertical part of which gives rise to leaf traces and the squat horizontal part gives rise to root traces in a definite pattern, presence of velum and ligule, sporangia with trabeculae.

Pleuromeia belonging to Pleuromeiales was considered previously as an evolutionary transitioned group between the arborescent lycopsids and the herbaceous cormose forms like *Isoetes*. But this idea has changed due the presence of herbaceous cormose lycopsids as contemporarily with the lepidodendrids. *Pleuromeia* is an exclusive Triassic genus known from a wide variety of habitats from different places of the world (Retallack 1975 and the references therein). This sudden abundance of *Pleuromeia* in the Early Triassic is suggested to be remarkable. Looy et al. (1999) suggested that after the mass extinction of the woody lepidodendrids in the Permian, occurrence of *Pleuromeia* played a key role in repopulating some of the terrestrial ecosystem. It has an unbranched trunk up to 2m tall and a four lobed rhizomorph from which roots arise in a helical manner. Usually, a single bisporangiate strobilus is present at the tip or there may be many small *Cylostrobus* like strobili. These plants have trilete megaspores and monolete microspores. Members of the Pleuromeiales have been included either in the Lepidodendrales or in the Isoetales as they share features of both the groups (Taylor et al. 2009).

Selaginella is the only terrestrial, heterosporous, ligulate, extant lycopsid member belonging to the order Selaginellales, which appeared by the Lower Carboniferous and is represented by *Selaginella fraipontii*. Presently, *Selaginella* is represented by about 750 species throughout the world (Jermy 1990). *Selaginella* is a conserved name as two other names (*Selaginoides* Seguier and *Lycopodioides* Bohemer) have priority over it (Pichi Sermolli 1971). *Selaginella* has undergone many taxonomic changes and there is difference of opinions that whether it should be considered as a natural taxon or a mixture of smaller genera (Dixit 1992; Mukhopadhyay 2001 and the references therein). *Selaginella* is broadly divided into two subgenera, one group named *Homeophyllum* bearing members with isophyllous leaves and the other group called *Heterophyllum* consisting of members with heterophyllous leaves (Hieronymous 1900). All the leaves in *Selaginella* are asymmetric except the axillary leaf. The nature of vegetative leaves and sporophylls play an important role in the taxonomy of *Selaginella*

(Alston 1945). Many botanists tried to determine the morphological nature of the aerial root (rhizophore) and interpreted it variously as a shoot, as a root and as an organ *sui generis* (Van Tieghem 1871; Goebel 1905; Bower 1908; Worsdel 1910; Williams 1937). Webster and Steeves (1963, 1964, 1967) studied in detail the ontogeny of rhizophore in some isophyllous (*S. densa*, *S. wallacei*) and anisophyllous species (*S. kraussiana*, *S. martensii*). They found a thin tissue corresponding to that of a root cap, an apical cell cutting at its four faces in bipolar directions but did not find any tissue demarcating the separation of rhizophore and the root. These attributes firmly established the root nature of the rhizophore. *Gosslingia*, a Lower to Middle Devonian zosterophyllopsid had scar mark at the point of each dichotomous branching to which vascular supply is present. It indicates the presence of some organ like rhizophore of *Selaginella*.

The isophyllous group of *Selaginella* bears vessel elements in the xylem and lacunae in their roots. The heterophyllous members are devoid of vessel elements and lacunae in their roots. The first group is morphologically simple but anatomically specialised and the second group is morphologically specialised but anatomically simple. So, these two groups are cognate to each other and no one group can be the precursor of the other group but diverged much earlier in two different lines from a common ancestor. The probable pathways of evolution of different characters like stellar structure, forking of leaf venation, resupination of strobili, development of laminal flap and reduction in the number of megaspores in *Selaginella* have been shown by Mukhopadhyay and Sen (1986). Mukherjee & Sen (1981) reported for the first time that *Selaginella* possesses microphyllous leaves but in *S. adunca* all the vegetative and sporophylls bear dichotomously forked veins. Subsequently, in some other species like *S. schaffneri*, *S. Noveeneosis* branched veins were reported (Wagner et al. 1982; Gopalakrishnan et al. 1994). Occurrence of laminar flap on the adaxial surface of the larger sporophylls along the mid-vein in the dimorphic sporophyll bearing members of *Selaginella* is another interesting feature (Mukhopadhyay & Sen 1981) and has some role in the evolution of seed habit

that is comparable to *Miadesmia*. This laminal flap increases the photosynthetic surface of the lamina as well as helps in capturing the microspores at the close vicinity of the megaspores, as the margin of this flap possesses long hairs. In *Selaginella noveeneosis* laminal flap has also been reported on the vegetative leaves (Gopalakrishnan et al. 1994). Usually, the microspores are dispersed singly in *Selaginella* except in *S. intermedia* where a group of tetrads are released in a lump like a polyad and might have some role in zoophillous pollination (Mukhopadhyay & Bhandari 1999). This is the only record of dispersal of microspores in lumped or polyad condition in pteridophytes. This type of pollination has some biological advantages. A single act of transport of microspore polyad to the vicinity of megaspore increases the chance of availability of many genetically different male gametes for mating.

Embryogeny in the lycopsid members are of endoscopic in nature. The innermost cell of a two-celled zygote develops the shoot of the embryo. The embryo may bear suspensor as found in *Lycopodium* and *Selaginella* or may be devoid of a suspensor as in *Isoetes*. Presence of suspensor is considered a primitive feature (Bower 1922, 1935). With the loss of suspensor of the embryo, the obligatory endoscopic polarity may be retained or completely changed to an exoscopic condition of polarity (Goebel 1928). On the other hand, there is an equal possibility of derivation of endoscopic condition from the exoscopic condition of polarity, which is met with the bryophytes and the psilopsids. The fossil records of embryos of *Lepidocarpon* and *Bothrodendrostrobus* reveal that they were also devoid of suspensor in their embryos like that of extant *Isoetes* (Phillips 1979; Stubblefield & Rothwell 1981).

It is interesting to note that in the extant homosporous lycopsids, *Huperzia selago* (n= 130) and *Phylloglossum* (n= 255) have very high number of chromosomes while, the heterosporous lycopsids *Selaginella* (x= 7, 8, 9, 10, 12), *Isoetes* and *Stylites* (x= 10, 11) have very low number of chromosomes. This indicates that polyploidy played a major role in the speciation of homosporous lycopsids while, aneuploidy played a vital role in the speciation of the heterosporous lycopsids (Walker 1979).

The high chromosome numbers in homosporous pteridophytes may be derived due to an ancient multiplication of an initial base number, which Chiarugi (1960) termed as palaeopolyploidy. It was previously thought that the homosporous pteridophytes undergo self-fertilization continually and produce homozygous sporophytes and there is least scope for future innovations. But, Klekowski & Baker (1966) argued that polyploidy in homosporous pteridophytes provide a mechanism for allowing genetic variability. Klekowski (1973) further elaborated the idea that high levels of polyploidy was necessary in homosporous pteridophytes to create and maintain genetic variations. Release of genetic variations accumulated in homozygous sporophytes takes place either through hybridization or by homeologous recombination.

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