LYCOPODIALES

The order lycopodiales includes plants that characteristically have:

(a) slender weak-stem, with small moss-like leaves; without ligules,
(b) club-shaped fruiting bodies or strobilii, which are homosporous,
(c) embedded antheridia, with biflagellate antherozoids.

The order with a single family lycopodiaceae comprises of two living genera *Lycopodium* and *Phylloglossum* and a fossil *Lycopodites*. *Lycopodium* is world-wide in distribution and monotypic *Phylloglossum drummondii* is endemic to Australia and neighbouring islands. The fossil *Lycopodites* resembled present-day *Lycopodium* in many respects.

LYCOPODIUM (Club-Moss)

Lycopodium with about 400 species (Bierhorst, 1971) is world-wide in distribution. A large majority of the species are found in tropics. Plants are slender, herbaceous or shrubby sporophytes with a wide range in habit and habitats. In tropics are mainly the pendulous epiphytes (Fig. 3.1 A), and the temperate ones are prostrate trailing forms (Fig. 3.1 B),

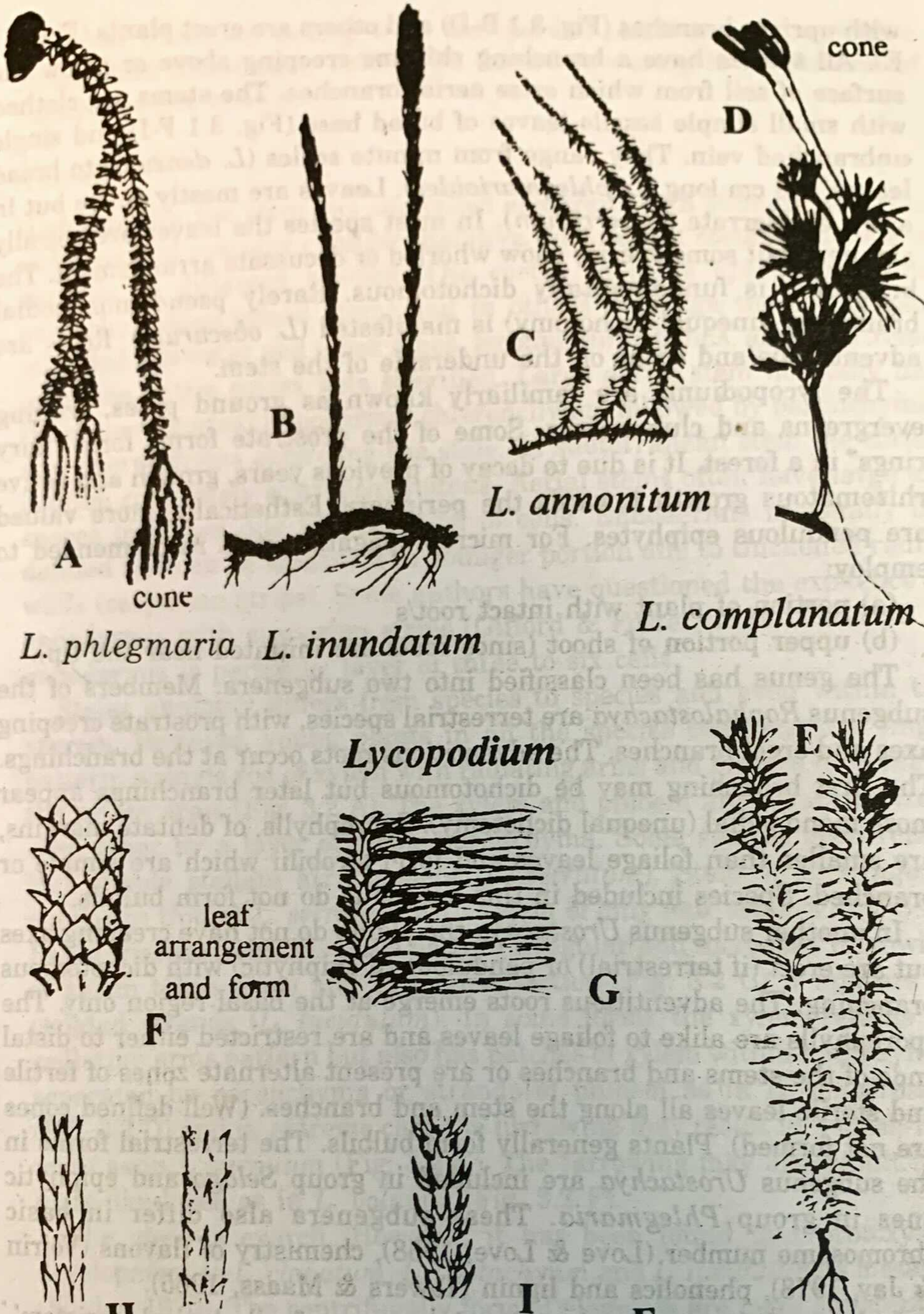

Fig. 3.1 *Lycopodium*, morphology of sporophyte.
A, pendulous plant *L. phlegmaria*. B,C, *L. inundatum* and *L. annonitum*, erect and prostrate axes. D, *L. complanatum* var *flabelliforme*, erect axis. E, *L. lucidulum*. F-I, Leaf form and arrangement. F, *L. rufescence*. G, *L. mandioccanum*. H, *L. complanatum* var *flabelliforme* dorsal and ventral views. I, *L. cernuum*.

with upright branches (Fig. 3.1 B-D) and others are erect plants (Fig. 3.1 E). All species have a branching rhizome creeping above or below the surface of soil from which arise aerial branches. The stems are clothed with small simple sessile leaves of broad base (Fig. 3.1 F-I) and single unbranched vein. They range from minute scales (*L. densum*) to broad leaves, 2-3 cm long (*L. phlegmarioides*). Leaves are mostly entire but in a few are serrate (*L. serratum*). In most species the leaves are spirally arranged but some species show whorled or decussate arrangement. The branching is fundamentally dichotomous. Rarely pseudomonopodial branching (unequal dichotomy) is manifested (*L. obscurum*). Roots are adventitious and occur on the underside of the stem.

The lycopodiums are familiarly known as ground pines, trailing evergreens and club-mosses. Some of the prostrate forms form "fairy rings" in a forest. It is due to decay of previous years, growth and active rhizomatous growth towards the periphery. Esthetically, more valued are pendulous epiphytes. For micropropagation it is recommended to employ:

(a) portion of plant with intact root/s

(b) upper portion of shoot (since roots are initiated near the tip).

The genus has been classified into two subgenera. Members of the subgenus *Rophalostachya* are terrestrial species, with prostrate creeping axes and erect branches. The adventitious roots occur at the branchings. The first branching may be dichotomous but later branchings appear more monopodial (unequal dichotomy). Sporophylls, of dentate margins, are smaller than foliage leaves and form strobilii which are simple or branched. Species included in this subgenus do not form bulbils.

In another subgenus *Urostachya* the plants do not have creeping axes but are erect (if terrestrial) or pendulous (if epiphytic) with dichotomous branching. The adventitious roots emerge at the basal region only. The sporophylls are alike to foliage leaves and are restricted either to distal ends of the stems and branches or are present alternate zones of fertile and sterile leaves all along the stem and branches. (Well-defined cones are not formed). Plants generally form bulbils. The terrestrial forms in the subgenus *Urostachya* are included in group *Selago* and epiphytic ones in group *Phlegmaria*. These subgenera also differ in basic chromosome number (Love & Love, 1958), chemistry of flavons (Voirin & Jay, 1978), phenolics and lignin (Towers & Maass, 1965).

In *Lycopodium* growth takes place by a group of cells, 'apical meristem', (Naugarede & Loiseau, 1963; Freeburg & Wetmore, 1967) rather than a single apical cell, as in stems of most other pteridophytes. In dichotomous branching single centre of meristematic activity gives rise to two. The initiation of two unequal centres is common and results in pseudomonopodial branching (*L. densum* and *L. obscurum*). The most unequal branching results in the formation of condensed axes which become specialized for vegetative propagation and are called "bulbils" or "gemmae". Some species (*L. lucidulum* and *L. selago*) regularly have typical unequal dichotomy and produce condensed branches (bulbils or gemmae) which on falling from the parent plant secure vegetative propagation (Stevenson, 1976). The factors favouring the formation of bulbils are not known.

Anatomy

Histologically, the stem has one-celled epidermis with stomata, a cortex and a central vascular cylinder. Relative thickness of cortex and stele is variable in different species. The cortex in some species remains parenchymatous (small stem) and in others with age the cortex gets sclerified into outer and inner zones, forming three bands, and in extreme cases the entire cortex gets sclerified. Large aerial stem normally has three-zoned cortex; hypodermal chlorenchyma, followed by parenchyma, and sclerenchyma encircling the stele. In subterranean stem the cortex is often completely sclerenchymatous. Aerial stems often have large air spaces in cortex due to disruption of cells. Endodermis is usually ill-defined and can be identified in younger portion due to thickened radial walls (casparian strips). Some authors have questioned the existence of endodermis with casparian strips (Gifford & Foster, 1989). Internal to endodermis is pericycle; layer of three to six cells.

Stelar anatomy differs from species to species and even within the species. However, young plants in all the species conform to a single pattern: a single rod of xylem with radiating arms and phloem in between the xylem arms (Fig. 3.2 A). The xylem and phloem are separated from each other by a layer of stelar parenchyma. Some species even retain this simple stellate arrangement (*L. serratum*). Stele of *L. selago* is similar to that of *L. serratum* with xylem of only four arms (Fig. 3.2 B). In a deviation from this basic pattern irregular and increased furrowing of xylem takes place and in a cross section (Fig. 3.2 C) it appears as isolated strands (*L. lucidulum*). In some forms the xylem retains its radiating arms pattern but also has patches of xylem within main xylem, separated by parenchyma or strands of phloem as in *L. squarrosum* (Fig. 3.2 D) and in extreme case the furrowing may result in a mesh-like mass as in *L. cernuum* (Fig. 3.2 E). The furrowing may also result into plate-like lobes as in *L. volubile* (Fig. 3.2 F).

The stele is exarch. However, it has been found that protoxylem development in *L. clavatum*, *L. tristachyum* and *L. lucidulum* is mesarch (Wilder, 1970). The centrifugally formed elements are more apparent in longisections but often undetectable in cross sections, mesarchy is more pronounced in *L. clavatum*.

The protoxylem elements form a peripheral group of up to 20 cells with few or no intermixed parenchyma cells. This feature separates *Lycopodium* from all other living vascular plants. Their secondary wall thickenings consist of indirectly connected rings (Bierhorst, 1960). Metaxylem tracheids are either scalariform or have circular bordered pits. The sieve cells of the phloem are elongate and pointed. The sieve areas are scattered and are inconspicuous on lateral and end of walls

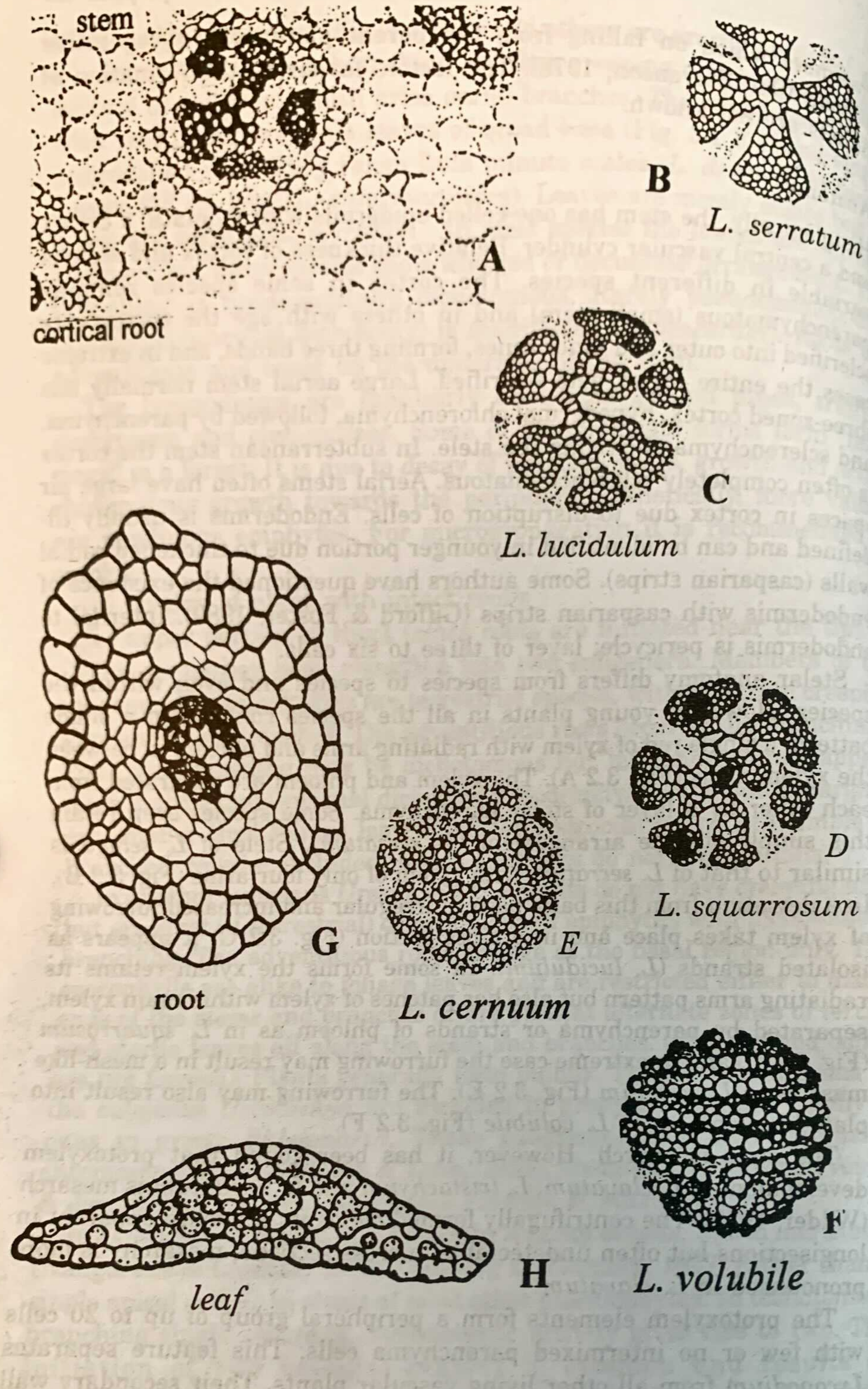

Fig. 3.2 *Lycopodium*, anatomy of sporophyte. A, *L. serratum*, a part of stem showing central stele and two cortical roots. B-F, variations in pattern of stem stele. G, t.s. of root of *L. serratum*. H, leaf in cross section.

(Lamourex, 1961). The sieve areas are not lined with callose (Warmbrodt & Evert, 1974). It is contrary to the situation in vascular plants.

The embryonic root is short-lived, the roots on older plants are adventitious and show equal dichotomous branching. Over the apical meristem of the root is the calyptra and proximal to the apex is a long zone of unicellular hairy extensions, borne in profusion. The cortex in roots with a complete tissue maturation is often completely sclerenchymatous. The xylem is crescent-shaped (C or U) with phloem in concavity (Fig 3.2 G). The roots are often diarch but usually they are not (Pixley, 1964). The two protoxylem points are two poles of U or C-shaped vascular strand but often one or more protoxylem points are also located on the convex side of stele. The former matures earlier than the latter. The roots originate chiefly from pericycle tissue of stem and do not grow out straight through cortex but grow vertically (through the stem cortex) before emerging below. As a result in a transection of stem many roots are seen in the cortex (Fig. 3.2 A) and are oriented in such a way that the open ends of their xylem face towards the outside of stem.

The roots of *Lycopodium* are peculiar in two respects; the lateral ones are not endogenous in origin and root hairs are paired. In some species root stele is very similar to stem stele. Roots of *L. clavatum* have parallel plates of xylem. At the point of attachment with the rhizome the root is polyarch and exarch (Pixley, 1968). Therefore, except for size it becomes difficult to distinguish the two organs.

The leaf trace branches off from the protoxylem point of stem stele and while traversing the cortex centrifugal protoxylem is added to it resulting in mesarchy (Fig. 3.2 H).

Rerproduction

In majority of the species due to gradual transition of vegetative leaves into sporophylls, at the distal ends of the main axes or branches, strobilii or cones are formed. The cones rarely may be borne on long stalks (Fig. 3.1 D) with scale-like leaves (*L. complanatum* var. *flabelliforme*). The sporophylls are smaller than foliage leaves and in some species are chaffy scales with dentate or serrate margins. In pendulous epiphytes the strobilii are often highly branched tassels (Fig. 3.1 A). In strobilii of *L. drumondii* the apex becomes active and forms a vegetative axis with reduced leaves, which in turn matures into a strobilus. In other forms like *L. obscurum* and *L. flabelliforme* the strobilii produce only vegetative extensions. In species (*L. lucidulum*) where cones are not formed, fertile and sterile leaves form alternate zones all along the stem and in some all leaves in a mature plant form sporangia. Such species are considered to be primitive and are included in selago group. These species characteristically have; (a) undifferentiated strobilus; (b) closely similar vegetative leaves and sporophylls, and (c) the entire metaxylem elements consisting of circular bordered pits (*L. lucidulum*, *L. selago*) that are not followed by scalariform pits as in most other species.

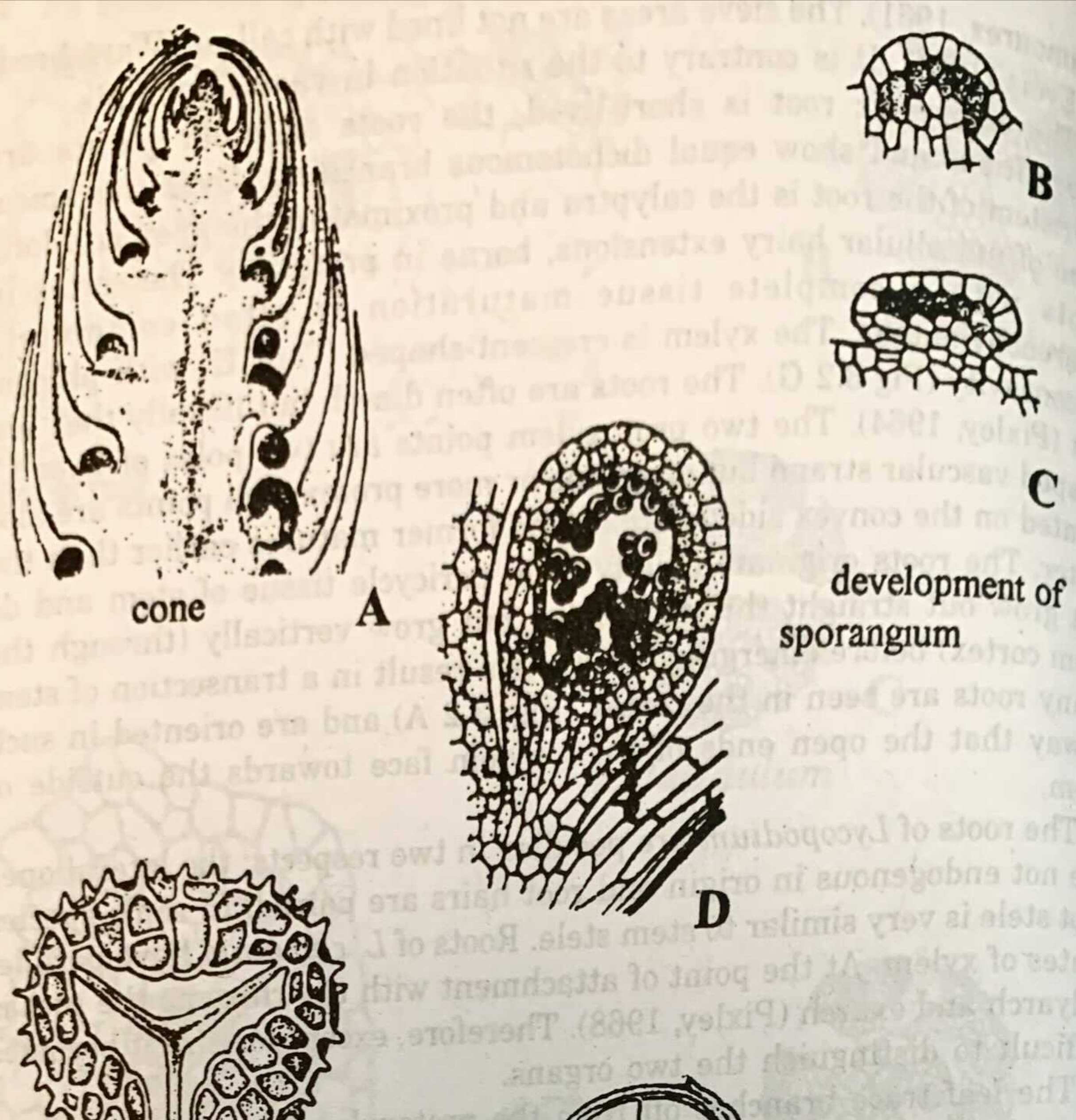

Fig. 3.3 *Lycopodium*, cone structure, development of sporangium and germination of spore.

A, *L. obscurum*, longisection of cone, sporangia in various stages of development. B-D, *L. selago*, stages in development of a sporangium. E,F, *L. complanatum* and *L. lucidulum* spores. G-I, stages in germination of spore and development of a gametophyte.

Each sporophyll produces only one sporangium. The sporangium is borne on upper (adaxial) surface of sporophyll (Fig. 3.3 A) but later may become axillary. The sporangia are 1-2.5 mm in diameter, reniform to subspherical with short stalk or pad-like base. The mature sporangia are yellowish and liberate spores through a slit, of thin cells, in the wall transverse to sporophyll. In many species the sporophylls fold backward exposing the sporangia as they mature.

Sporangial initials differentiate normally on the upper side when sporophyll is still embryonic. Therefore, in a longisection of developing cone all stages can be seen (Fig. 3.3 A). By periclinal divisions, the initials form inner and outer layers of cells (Fig. 3.3 B,C). The inner layer forms sporogenous cells and the outer layer forms the sporangial stalk and wall of the sporangium. This process in which sporangia develop from a group of superficial cells is known as eusporangiate method. After periclinal division due to differential growth i.e. active divisions in sporogenous tissue result in upward bulging and the sporangium assumes a reniform shape. Later, periclinal divisions in surface layer lead to the formatilon of five-celled outer layer. The layer surrounding sporogenous cells stains deeply and acts as tapetum (Fig. 3.3 D) and gets decomposed during maturation of spores. As the sporangia mature the peripheral layers also breakdown and a mature sporangium has only one-cell-thick wall. Due to breakdown of peripheral cell and tapetal layer, spores come to lie in a fluid mass.

The spores which are produced in large quantity are homosporous, small, light with smooth or ornamented wall (Fig. 3.3 E,F), and a triradiate mark (a point of attachment in spore tetrads). They contain oil as reserve food and in some species are chlorophyllous. The large surface area exposed makes them valuable as diluants of pollen samples in plant breeding programmes, as reducing agent in gunpowder, However, their utility as dusting powder in use of surgical gloves and for coating of pills is to be discouraged, because the spores may cause inflammations.

In some species the spores are green and thin-walled. These germinate (Fig. 3.3 G-I) in a few days after dispersal and form small (2-3 cm) surface-living green prothalli. Such prothalli are cylindrical or ovoid with branches or lobes (Fig 3.4 A) and are short-lived, maturing in the same season. In other species the spores are non-green and thick-walled, the germination is delayed by years and in the mean time spores get buried and form subterranean mycorrhizic prothalli which are non-green. To begin with, such prothalli are top-shaped (Fig. 3.4 B) and later become irregular or convoluted (Fig. 3.4 C) and take years to mature. The former type (surface-living and green prothalli) is prevalent in tropical species (*L. cernuum*) and latter (subterranean and non-green) in temperate creeping ones (*L. obscurum*, *L. clavatum*, *L. complanatum*).

The gametophytes very early in their development, 4 or 5-celled stage, come to have mycorrhizal association. The fungus contributes substances essential for the growth of a gametophyte (Bruce, 1976). Growth of a

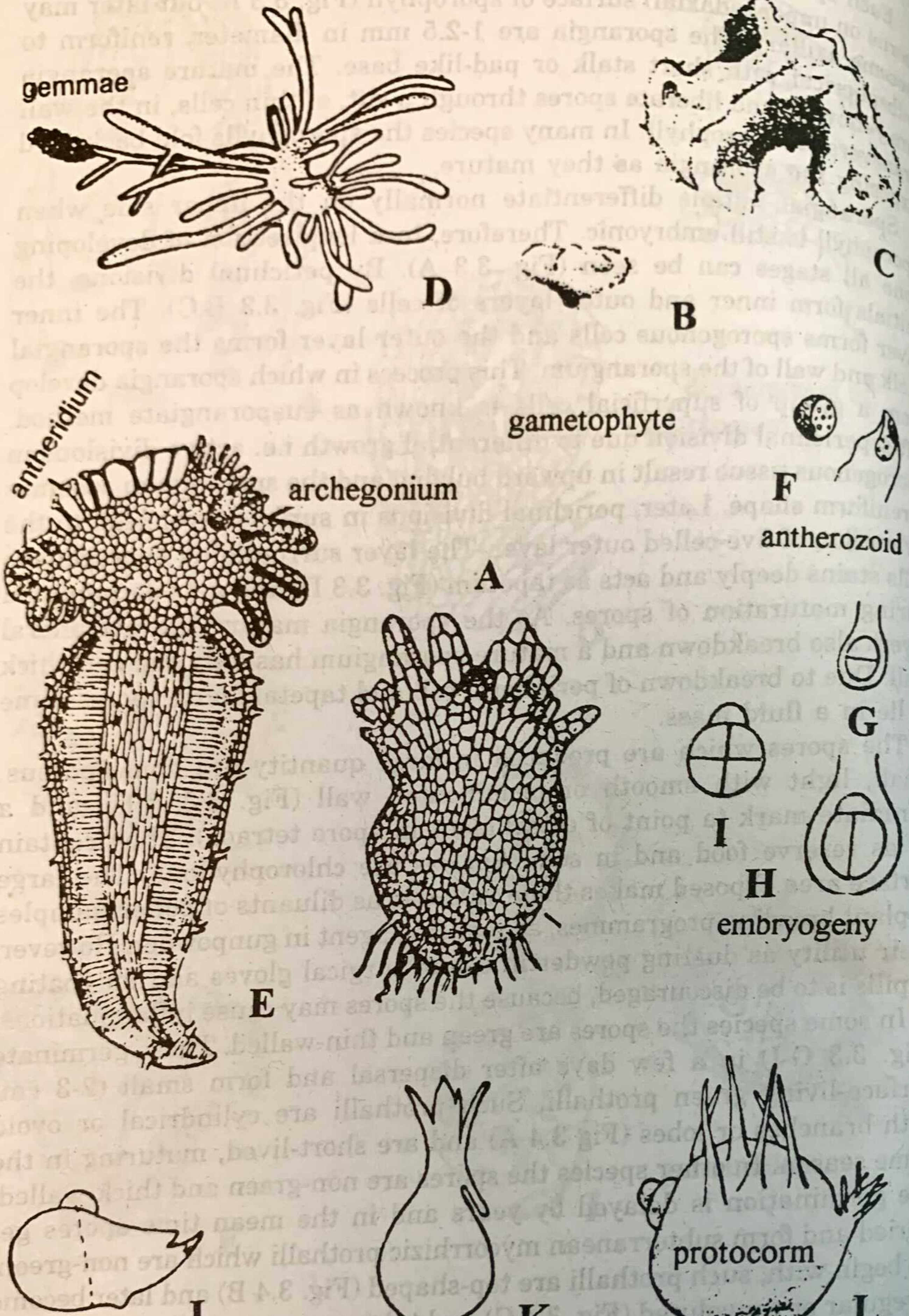

Fig. 3.4 *Lycopodium*, gametophyte, embryogeny and protocorm. A-D, gametophytes of *L. cernuum*, *L. clavatum* and *L. phlegmaria*. E, longisection of gametophyte of *L. complanatum* showing sex orgons. F, antherozoid, G-I, J-K, stages of embryogeny. L, a protocorm.

gametophyte takes place by a group of meristematic cells organized at the apex. Gametophytes in some species are partly subterranean with chlorophyllous aerial portion. In some epiphytic species (*L. phlegmaria*), the prothallus is irregularly fragmented and these fragments form gemmae (Fig. 3.4 D) which secure vegetative propagation of the gametophytic generation.

The prothalli are monoecious and each sex organ originates from a single superficial cell just behind apical meristem. In subterranean types the antheridia and archegonia form distinct patches and cover the entire crown (Fig 3.4 E) or base of its lobe. In elongated types they are present on the central cushion and are intermingled. Antheridia are sunken and produce large number of pear-shaped biflagellate antherozoids (Fig. 3.4 F) which are attracted chemotactically (Doyle, 1970) by the archegonial exudate (citric acid). Archegonia are sunken at the venter and only the necks protrude. Subterranean prothalli have archegonia of long necks (as many as 14 neck canal cells in *L. complanatum*) and surface-living prothalli have short-necked archegonia (sometimes just one neck canal cell in *L.cernuum*).

Although gametophytes of *Lycopodium* are bisexual but in some species selfing is not favoured (Soltis & Soltis, 1988), the reasons for cross fertilization are not known.

First division of fertilized egg is transverse to long axis of archegonium (Fig. 3.4 G). The outer suspensor cell normally does not undergo division or may become three-celled. The inner cell gives rise to two superimposed tiers of four cells each (Fig. 3.4 H,I). The upper tier in some species swells up to form a foot and from the lower tier is derived the embryo proper (Fig. 3.4 J). Two cells facing meristem develop into stem and other two form leaves and primary root (Bruchmann, 1910). Root differentiates laterally (Fig. 3.4 K), at a place where apical region and foot are joined.

In some species (*L. cernuum*) distal tier develops into a massive globose structure -Protocorm- that pushes its way through gametophyte. The protocorm (Fig. 3.4L) bears rhizoids and from its upper surface differentiate leaf-like, avascular structures, protophylls. After the formation of many protophylls on the protocorm is organized a shoot meristem. The first root arises from the base of stem.

Protocorm, in its structural organization apparently intermediate between gametophyte and sporophyte, has been considered by earlier workers as an evolutionary forerunner of a leafy vascular plant (see also chapter 11, for partial gametophyte and sporophyte).

PHYLLOGLOSSUM

Monotypic *Phylloglossum drummondii* is confined to a few sites in Australia, Tasmania and New Zealand. It is a perennial plant and all parts except the underground tuber die at the end of growing season. The entire plant body hardly exceeds ten centimetres in height. From the tuber arises, every year, an aerial axis bearing a cluster of quill-like leaves (Fig. 3.5 A). Extending laterally from the axis are 1-3 unbranched roots and a short leafless branch which terminates into a young tuber. The new tuber lives through dry period and then produces a new plant, securing vegetative multiplication. The tuber-bearing-branch may bear leaves and has the vasculature of a branch.

In a fertile plant the stem apex extends into a long stalk, terminating into a strobilus. The cone (Fig. 3.5 B) comprises a few sporophylls in whorls of three. The structure is essentially lycopodioid. Each sporophyll bears a near-axillary sporangium. The spores are yellow and tetrahedral.

The gametophyte and embryogeny are poorly known. From the available accounts, gametophyte and embryogeny are essentially similar to *Lycopodium* spp. forming surface-living green gametophytes.

The vascular cylinder differs from *Lycopodium*. At the base of stem is amphiphloic siphonostele (Fig. 3.5 C). It fades out in tuber (Fig. 3.5 D) which lacks vascular elements. Higher up, in the cone axis the vascular cylinder breaks up and becomes dictyostelic. The number of bundles gets reduced (Fig. 3.5 E) as the strobilus is approached.

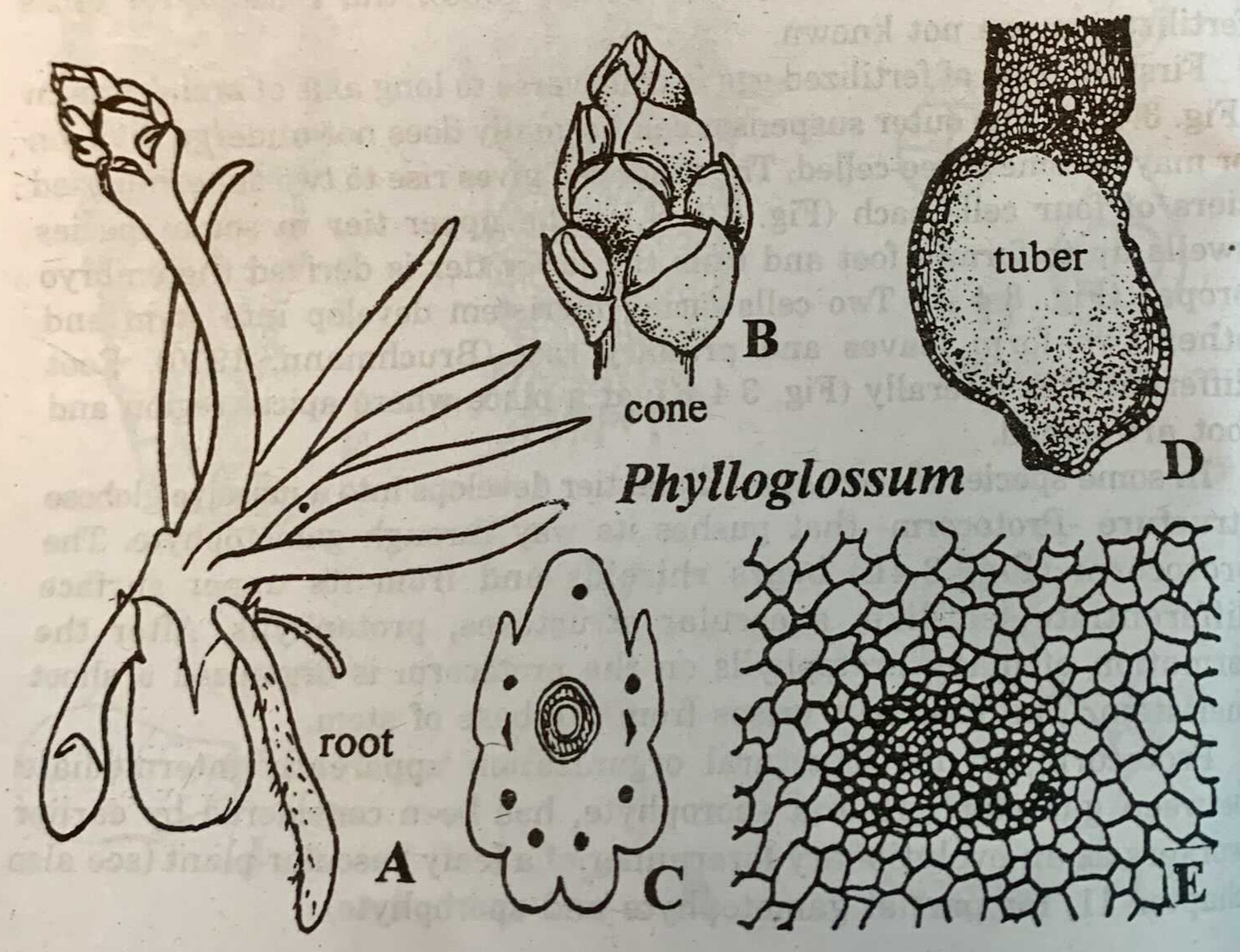

Fig. 3.5 *Phylloglossum*, morphology and anatomy.
A, *P. drummondii*, a sporophyte. B, an enlarged view of the cone.
C, stem in transection. D, longisection of tuber. E, longisection of cone stalk showing two mesarch bundles.