

LYCOPOD SPORES, I. General Spore Patterns and the Generic Segregates of *Lycopodium*¹

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The material presented here is part of an investigation undertaken to test the taxonomic validity of *Diphasium* Presl, a generic segregate of *Lycopodium* L. that seems to be winning increasing acceptance, particularly among European botanists. It was hoped that part of the answer to the *Diphasium* question might lie in the morphology of its spores. Prior to the development of scanning electron microscopy (SEM), lycopod spores had already been found taxonomically useful at several possible levels (Wilson, 1934; Knox, 1950; Harris, 1955; Wilce, 1965). Use of SEM could be expected to increase greatly the available data on *Lycopodium* spore surface patterns. By including in the study spores of a large, representative sample of lycopod species, I hoped to be able to evaluate the other generic segregates of *Lycopodium* as well as to help settle the status of *Diphasium*.

The extensive literature regarding generic segregates of *Lycopodium* has been reviewed regularly and need not be repeated here (Pritzel, 1900; Rothmaler, 1944; Boivin, 1950; Löve & Löve, 1958; Wilce, 1965.) The large number of different taxonomic treatments given to *Lycopodium* reflects the differing perspectives with which systematists have approached the group, coupled with their sometimes rather divergent philosophic views of the proper goals of biological systems of classification.

Past studies of *Lycopodium* spores, except for Knox's (1950) extensive survey, have been limited in scope, dealing either with a single group of species (Wilce, 1965) or with specific floras. The present study includes nearly half of the species Herter (1950) includes in *Lycopodium s. str.* but only about 12% (48 taxa) of those he lists under *Urostachys* (the proper name for which is *Huperzia* Bernh.). Knox (1950) reports on 33 additional species in the latter group and five in *Lycopodium s. str.* not represented in this study.

Spores of many lycopod taxa remain unexamined. Future study of these spores will probably aid in determining relationships between taxa in cases where affinities may otherwise be obscured. It seems doubtful, however, that additional spore types will be found within the group. This survey, while giving a much better view of the spores than earlier methods permitted, has turned up no new major spore patterns, with the exception of the scabrate type found in *Lycopodium casuarinoides*. Certainly for purposes of lycopod systematics above the species level ample information is at hand.

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MATERIALS AND METHODS

The 161 spore samples studied and photographed in this SEM study represent a tentative 89 species and several varieties (the synonymy of certain taxa is not yet clear). Names assigned to taxa with which I have little personal experience are tentative; in such cases (particularly within the *Huperzia* element) I have had to rely on the determination from the specimen label.

Samples were collected from specimens housed in the herbaria of the following institutions: Gray Herbarium (GH), Smithsonian (US), Institute of Jamaica (IJ), and the Universities of California (UC) and Massachusetts (MASS). Specimens were selected giving preference to those collections with widest distribution and most recent date. Specimens chosen were morphologically representative of the taxa to the best of my knowledge. Spores were first examined under the light microscope, and samples with excessive abortion were eliminated from the study.

Samples were mounted on SEM specimen stubs with "Scotch" double-sided tape and coated with a thin layer of carbon followed by gold paladium. Specimens were examined using the A M R Scanning Electron Microscope, normally working at 20 kv and an angle of 45°. Both 100 μ and 200 μ apertures were used with good results. Photographs were taken using "Polaroid" 55 P/N film.

Photographs were taken mainly at magnifications of 2,000 \times and 10,000 \times , although additional observations and photographs were made at various other magnifications ranging up to 24,000 \times . Greater photographic coverage was given to species within *Lycopodium s. str.* (usually 7 to 9 photographs per species) than for those representing *Huperzia* (averaging 4 photographs per species). Samples were observed carefully before photographing to make sure representative spores were selected.

Studies of certain species were extensive, involving population sampling and a comparison of acetylated and air-dried material. The study of *Lycopodium clavatum* included 40 photographs; that of *L. complanatum* 68 photographs. Most such studies, however, included between 18 and 36 photographs.

PRELIMINARY SURVEY

The descriptive terminology in the following paragraphs follows that used by Faegri and Iverson (1950) and Harris (1955).

A preliminary survey was made of spores of well known taxa in the various sections of the genus, which showed spore form to be quite consistent within a sample and between samples of the same taxon from widely separated localities. A certain amount of variation was noted between individual spores, but that variation did not change the general aspect. The spores of some species seemed nearly indistinguishable, whereas others were readily distinguished. Age did not appear to affect the spore surfaces significantly.

In addition, samples of 20 species were acetylated and compared with air-dried spores from the same specimen. In some cases the acetylated spores showed surface detail at high magnifications somewhat more clearly than did air-dried spores, but at the expense of spore shape. The acetylated spores of numerous species collapsed

as they dried on the specimen stub, the proximal spore wall sinking into the spore cavity.

Because major surface features are plainly seen and in most cases high magnification work is satisfactory in air-dried material, for the remainder of the study spores were not acetylated. For comparisons of spores at the species level, however, examination of both air-dried and acetylated material of each sample obviously will yield the best results.

In the main survey, only one major new spore type has been found. A certain amount of interesting variation was noticed between some species within groups, but it is not my purpose at this time to describe the spores of each species studied; the focus here is on the broader differences that characterize the spore types and on the taxonomic implications of these types. Ornamentation patterns of the spore wall in *Lycopodium* fall into five broad classes noted below.

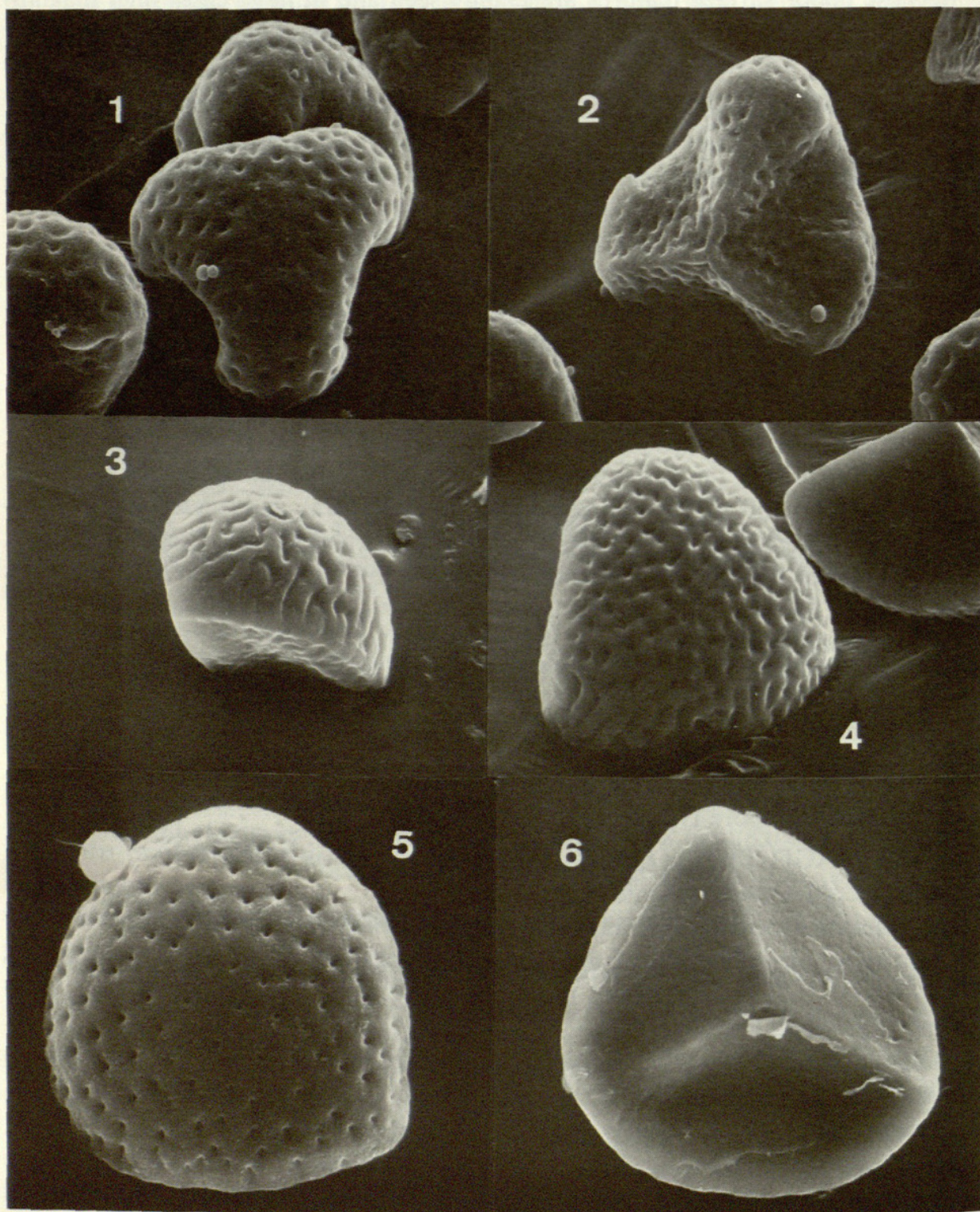
THE FOVEOLATE-FOSSULATE GROUP

The spores of all species examined that belong to the *Huperzia* element of *Lycopodium* fall into the foveolate-fossulate group. These spores can be described generally as free, anisopolar, radiosymmetrical, tetrahedral, and trilete, with laesurae extending to or nearly to the margin. Ornamentation ranges from pitted (foveolate), through a series of intermediate stages in which the pits have sloping walls, to a coalescing of the pits into grooves (fossulate). Surface texture ranges from very smooth to finely pebbled.

Two distinct, although apparently related spore types can be recognized within this broad group, primarily based upon spore outline (contour as seen in polar view), but correlated with other differences as well. No special status is implied for the well-known species from which are taken the names of these or any subsequently described spore types.

THE SELAGO TYPE (Figs. 1-2).—Spore outline is modified from triangular by concave sides and truncate angles. Laesurae are more or less prominent as ridges. Pits or grooves occur on both proximal and distal surfaces. Species may differ in spore size, degree of concavity of the sides, depth, diameter, and spacing of pits on the distal surface, and the prominence of the proximal pitting. Species studied with spores of this type are: *Lycopodium lucidulum*, *L. quasipolytrichoides*, *L. selago*, *L. serratum*, and *L. squarrosum*. To this list may be added *L. celanicum*, *L. miniatum*, *L. fontinaloides* (Knox, 1950), and *L. australianum* (Harris, 1955).

THE PHLEGMARIA TYPE (Figs. 3-6).—Spores are subtriangular in outline, with the sides straight to somewhat convex and the angles rounded. Laesurae range from a relatively prominent ridge to (more commonly) hardly more than corners where the three contact faces meet. Species may differ in spore size and ornamentation, although spores of many seemed nearly indistinguishable. Distal ornamentation ranges from foveolate (Fig. 5) in some species to strongly fossulate (Fig. 3) in others; still others show various intermediate conditions (Fig. 4). Knox separated the fossulate from foveolate types into two different groups; the number of intermediate types seems to discourage this distinction. Proximal surfaces are un-



Lycopodium spores. Fig. 1. Distal view of *L. lucidulum*, $\times 1400$ (Leverett, Mass., 13 Nov 1969, Wilce, MASS). Fig. 2. Same, proximal view, $\times 1400$. Fig. 3. Equatorial view of *L. dichotomum*, $\times 1400$ (Oaxaca, Mexico, Mexia 9141a, GH). Fig. 4. Intermediate fossulate-foveolate condition of *L. reflexum*, $\times 1400$ (Macchu Picchu, Peru, 19 May 1970, Wilce, MASS). Fig. 5. Distal view of *L. billardieri*, $\times 1400$ (New Zealand, Chapman in 1944, GH). Fig. 6. Same, proximal view, $\times 1400$.

ornamented (Fig. 6) in nearly all species; in several there were suggestions of very shallow pits.

Species studies with this spore type are too numerous to list here. They will be discussed in greater detail and listed in a later paper. *Lycopodium casuarinoides* was placed in this group by Knox (1950), but does not belong here. Possibly the error resulted from a confusion of samples, since the plant itself is quite recognizable.

THE RUGULATE GROUP

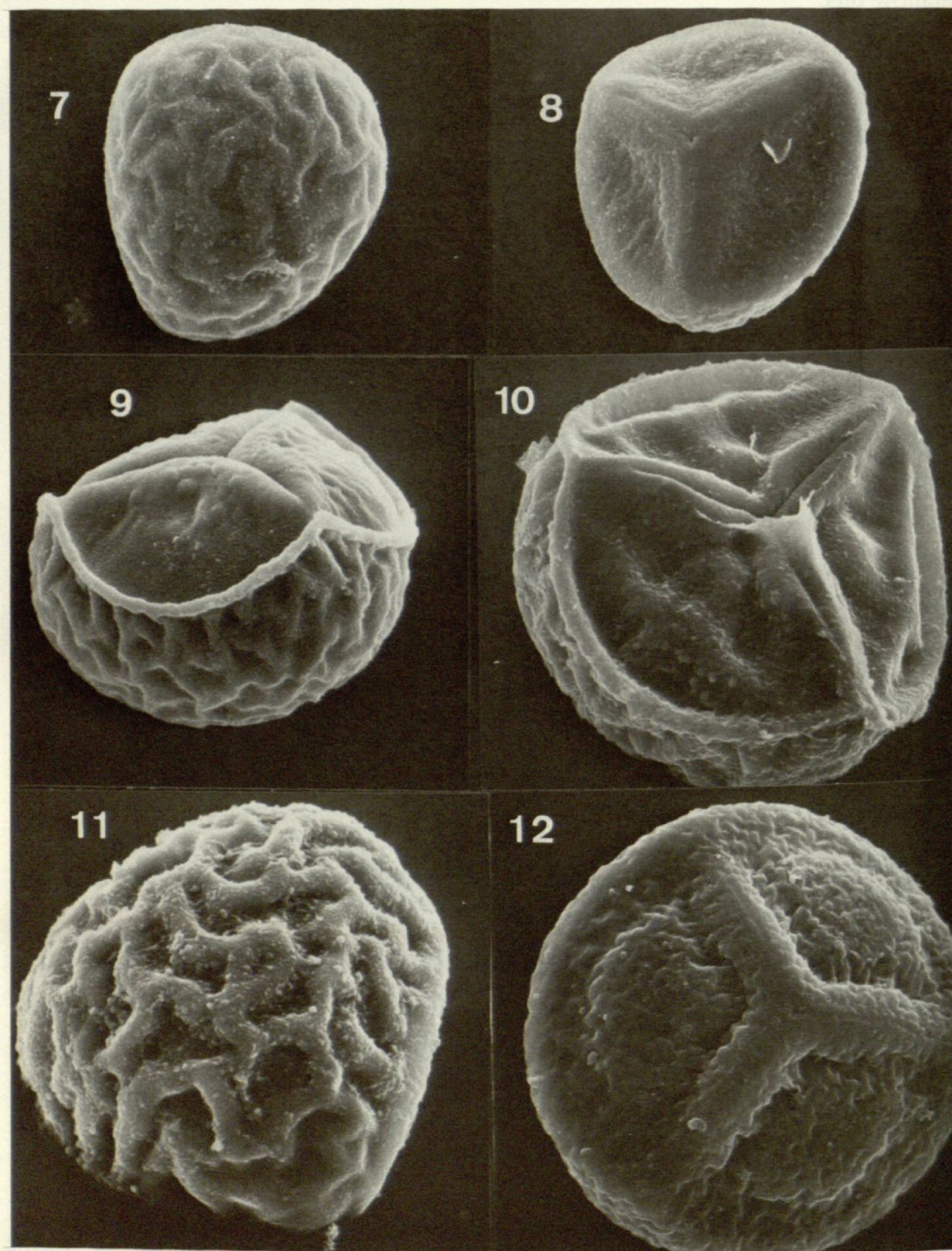
The cluster of species with spores falling into the rugulate group thus far coincides exactly with *Lepidotis* Palisot as redefined by Rothmaler (1944). Spores in this group are circular or nearly so in outline, with grooved laesurae having a usually prominent margo. The distal ornamentation ranges from prominent anastomosing ridges that approximate a reticulum (Fig. 11) to nearly no ornamentation at all with only slight surface undulations (*Lycopodium pendulinum*). Surface textures range from nearly smooth to coarsely pebbled. Within this group are two easily recognizable related spore types.

THE CERNUUM TYPE (Figs. 7–8).—Distal ornamentation rugulate to nearly absent, depending upon the species (acetolysis seems to accentuate the ornamentation slightly). The proximal surface is unornamented or faintly undulating, with a raised margo; the triradiate scar is obscured completely in a groove, the groove normally about $\frac{2}{3}$ the radius of the spore and not conspicuous. Species examined with spores of this type are: *Lycopodium cernuum*, *L. convolutum*, *L. eichleri*, and *L. pendulinum*.

THE CAROLINIANUM TYPE (Figs. 9–12).—Distal ornamentation is rugulate to almost reticulate and is bounded at the equator by a more or less well-defined rim (Fig. 9). The proximal surface is rugulate to merely wrinkled, or becomes verrucate to verrucate-gemmate. The tetrad scar may or may not be visible in the usually conspicuous groove (less conspicuous in *L. laterale*, Fig. 12), and reaches or almost reaches the margin. The margo is raised and generally prominent, straight-sided to sharply notched, and variously ornamented depending upon the species; it may be almost smooth or may closely match the pattern on the rest of the contact face. Spore variation between species is greater within this type than between spores of the Cernuum Type. Species examined with spores of the Carolinianum Type are: *Lycopodium adpressum*, *L. alopecuroides*, *L. carolinianum*, *L. duida*, *L. inundatum*, and *L. laterale*.

THE RETICULATE GROUP

All but two of the remaining species studied may be placed in this broad group, which includes *Diphasium* and *Lycopodium* as defined by Rothmaler (1944). Although basically tetrahedral, spores of some species that have decidedly convex contact faces become subglobose. Spore outline ranges from subtriangular to nearly circular. Distal surfaces are ornamented with high, narrow ridges (muri) that join to form a reticulum. Proximal surfaces are entirely unornamented or partially covered by a reticulum. When present, the proximal reticulum may or may not



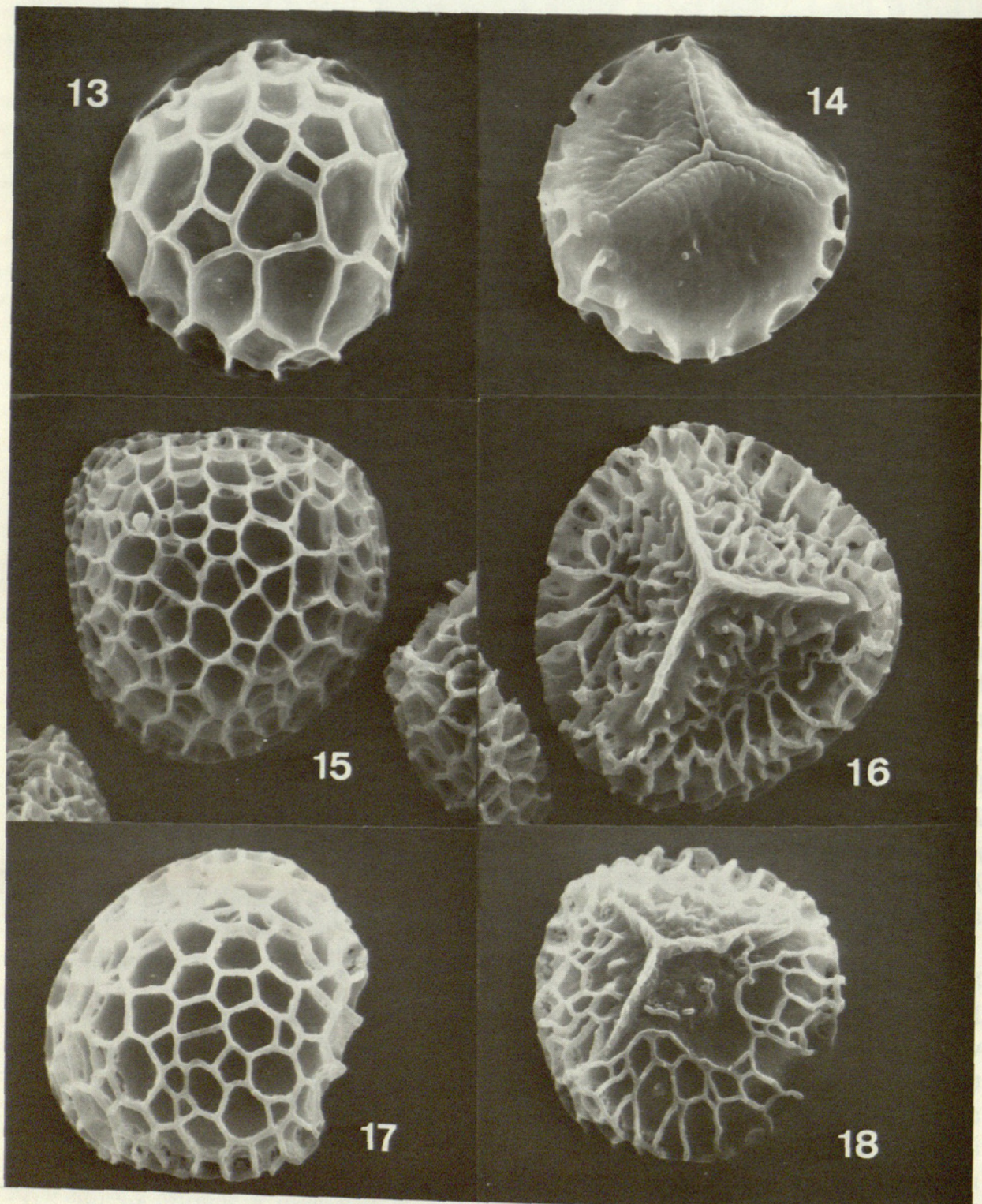
Lycopodium spores. Fig. 7. Distal view of *L. cernuum*, $\times 1400$ (San José, Costa Rica, Skutch 2217, GH). Fig. 8. Same, proximal view, $\times 1400$. Fig. 9. Equatorial view of *L. alopecuroides*, $\times 1280$ (Cuba, 9 Sept 1940, Hodge, Howard & Godfrey, MASS). Fig. 10. Proximal view of *L. carolinianum*, $\times 1280$ (British Honduras, O'Neill 8391, GH). Fig. 11. Same, distal view, $\times 1280$. Fig. 12. Proximal view of *L. laterale*, $\times 1280$ (New Zealand, Hollaway 324, MASS).

closely resemble that of the distal surface. In a few species the proximal reticulum has been reduced to scattered free ridges and knobs. Four related spore types may be recognized within the Reticulate Group.

THE SCARIOSUM TYPE (Figs. 13–14).—Contact faces are much flattened, giving the spore a somewhat semicircular profile, the distal surface being broadly convex. The distal reticulum is regular with a large, open mesh (larger lacunae measure up to $12\ \mu$ in greatest dimension; small lacunae under $4\ \mu$ are rare). Muri are $1\text{--}1.5$ (rarely 2) μ high and only occasionally become bridges through erosion of their sides. Proximal surface is without ornamentation except for slight undulations not visible with light microscopy. The tetrad scar extends $\frac{2}{3}$ the radius to nearly reaching the margin, and is situated in and sometimes is partially obscured by a shallow groove. Taxa examined having spores of the Scariosum Type are: *Lycopodium canceris*, *L. gayanum*, *L. holtonii*, *L. jussiaei*, and *L. scariosum*. It is likely that not all these are good species; their status is under investigation.

THE CLAVATUM TYPE (Figs. 15–18).—The distal reticulum is more or less regular, the polygons normally complete although on a single spore they may vary greatly in size. Muri on individual spores are relatively uniform in size and thickness, ranging from 2 to $4\ \mu$ high, depending upon the species, and normally slightly higher at the equator than near the distal pole. Mural erosion is common on the sides, resulting in windows and bridges. Proximal surfaces in most taxa are at least partially reticulate, the ornamentation approaching the laesurae to a greater extent in some than in others (Figs. 16, 18). The proximal reticulum may be more delicate than the distal reticulum (*L. obscurum*) or it may be more irregular and broken (Fig. 18), sometimes being so reduced and broken as to no longer form a reticulum (*L. annotinum*). Laesurae are prominent, narrow ridges ranging from 1.5 to $2\ \mu$ high and extend from $\frac{2}{3}$ the radius to nearly reaching the margin. There is noticeable variation between species as to pattern detail. The following taxa examined have spores of the Clavatum Type: *Lycopodium alpinum*, *L. annotinum*, *L. clavatum*, *L. complanatum*, *L. contiguum*, *L. flabelliforme*, *L. japonicum*, *L. multispicatum*, *L. obscurum*, *L. platyrhizoma*, *L. sabinifolium*, *L. sitchense*, *L. thyoides*, *L. tristachyum*, *L. veitchii*, *L. venustulum*, *L. vestitum*, and *L. wightianum*.

THE FASTIGIATUM TYPE (Figs. 19–21).—The distal reticulum is irregular, both in size and shape of lacunae and in height (up to $2\ \mu$) and thickness of muri. Erosion of muri takes place from all directions, producing numerous incompletely walled polygons, bridges, and lower muri. The reticulum is a finer mesh than in the previous types; a large lacuna in this group measures not more than $5\text{--}6\ \mu$ across. Reticula extend slightly over the equator and onto the proximal surface, and end rather abruptly at the edge of the contact faces, but without forming a rim or fringe. Contact faces are often slightly concave near the reticulate margin (possibly an artifact produced by drying, but in any case a feature of this type of spore not seen in other types), but they become more convex near the tetrad scar. Laesurae form prominent narrow ridges extending to the edge of the reticulum. The Fastigiatum Type spore was found in the following species examined: *Lycopodium fastigiatum*, *L. magellanicum*, *L. paniculatum*, and *L. spurium*.



Lycopodium spores. Fig. 13. Distal view of *L. scariosum*, $\times 1400$ (New Zealand, 14 Mar 1927, Setchell & Setchell, UC). Fig. 14. Same, proximal view, $\times 1400$. Fig. 15. Distal view of *L. clavatum*, $\times 1400$ (White Mt. Nat. Forest, New Hampshire, Wilce 53-70, MASS). Fig. 16. Same, proximal view, $\times 1400$. Fig. 17. Distal view of *L. complanatum*, $\times 1400$ (Yukon, Wilce study coll. 78, DAO). Fig. 18. Same, proximal view, $\times 1400$.

THE VOLUBILE TYPE (Figs. 22–24).—The distal reticulum is irregular, with many incomplete polygons. Muri range up to $2.5\text{--}3\ \mu$ high; erosion produces isolated ridges, pillars, and numerous bridges and windows. The reticulum ends abruptly at the equator. The proximal surface is unornamented except for a delicate rim completely encircling the outer margin of the contact faces. This rim, “frill,” or “fringe,” as it has been called by Knox (1950) and Harris (1955), measured up to $5\ \mu$ high in air-dried material. Behind the rim, and completely hidden by it in apical view, is a slightly concave, unornamented region extending to the equator (Fig. 22). The laesurae are prominent, narrow ridges up to $3\ \mu$ or $4\ \mu$ high that extend to the edge of the proximal rim. *Lycopodium volubile* is the only species known to have this type of spore. It seems more closely related to the Fastigiatum Type than to others of the Reticulate Group.

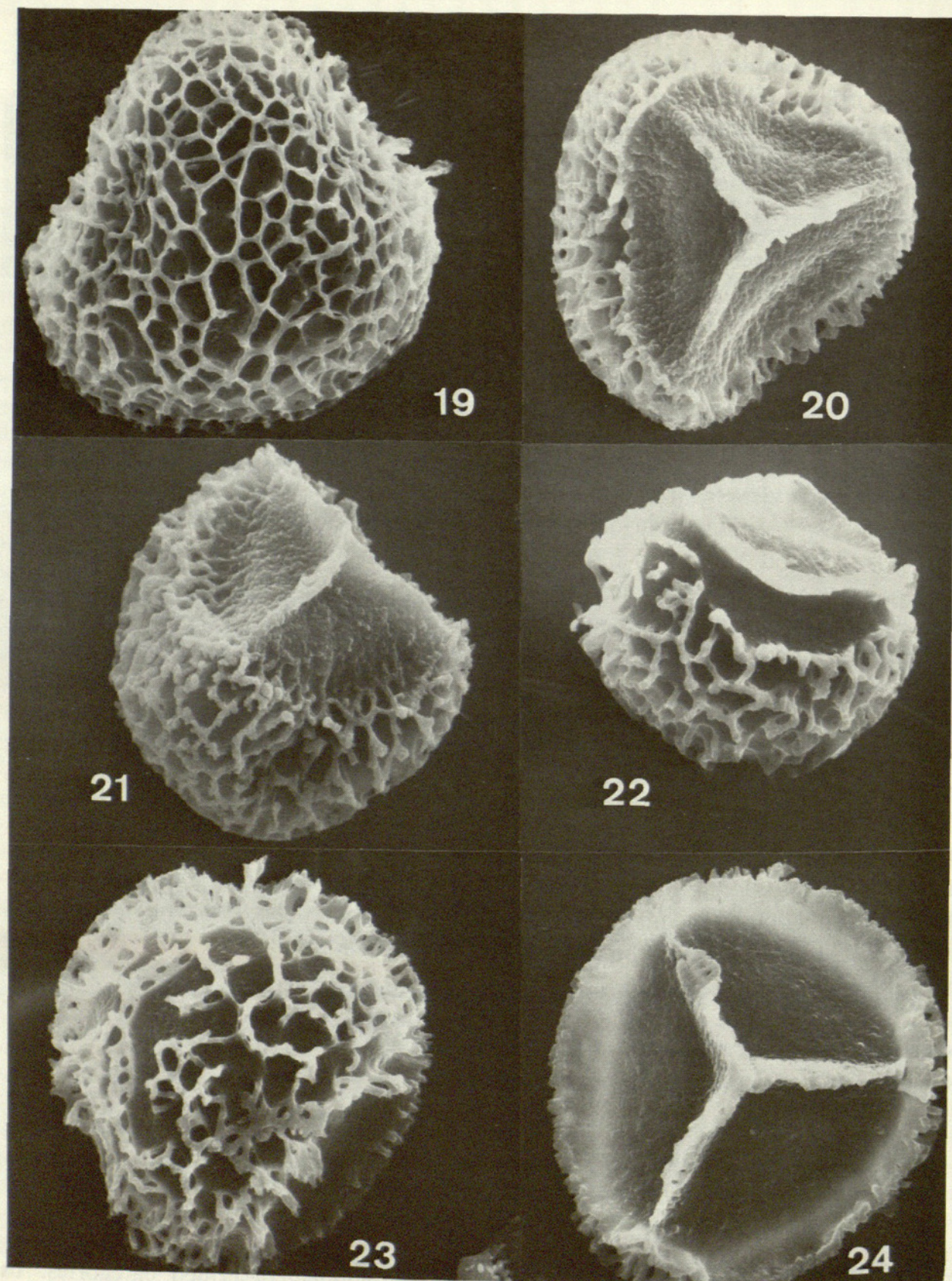
THE BACULATE SPORE

Lycopodium deuterodensum Herter is more widely known as *L. densum* Labill., unfortunately an illegitimate later homonym of *L. densum* Lam. This species is the only lycopod known to have baculate spores (Figs. 25–27). Herter (1950) lists *L. riofrioi* Sod. as a closely related species, but material was not available for this study, and its spores are still unexamined.

The spores are, subtriangular in polar view, with the distal portion broadly hemispherical and the contact faces somewhat flattened. The distal surface is covered with baculate projections rather uniformly $2.5\text{--}3\ \mu$ high and nearly $1\ \mu$ thick which are normally only slightly (if at all) thicker at the base, almost always truncate, and only rarely appear spinose. [Knox (1950) describes the spores as “spinose” and Harris (1955) refers to them as “echinulate,” although noting the truncate tips. In most cases the tapering is so slight that I feel the term “baculate” most adequately describes the condition.] The projections are generally $3\text{--}5\ \mu$ distant, and at higher magnifications can be seen to be covered by the same small, rounded bodies that cover the rest of the distal spore surface (Fig. 27). The proximal surface is unornamented. Laesurae are prominent as a rounded ridge $1\ \mu$ wide and at least $1.5\text{--}2\ \mu$ high which extends nearly to the margin. Knox (1950) has called attention to the resemblance of spores of *L. deuterodensum* to the microspores of certain species of *Selaginella*.

THE SCABRATE SPORE

This spore type has been observed only in *Lycopodium casuarinoides* Spring (Figs. 28–30). Knox (1950) describes and figures the spore of some other taxon under this name, placing it in the group with Phlegmaria Type spores. The spores of this species, however, fit into none of the previously described categories. In apical view they appear subtriangular with very rounded angles and straight to concave sides and contact faces—a bit similar in shape to spores of *L. selago*, although more rounded. Both proximal and distal surfaces are irregularly scabrate; the rounded projections range from $0.25\ \mu$ to just under $1\ \mu$, and average $0.5\ \mu$ in diameter. The distribution of projections is not uniform. At high magnifications



Lycopodium spores. Fig. 19. Distal view of *L. fastigiatum*, $\times 1400$ (Australia, Burcham 92, US). Fig. 20. Same, proximal view, $\times 1400$. Fig. 21. Equatorial view of *L. magellanicum*, $\times 1400$ (Juan Fernandez Isl., C. & I. Skottsberg 482, US). Fig. 22. Equatorial view of *L. volubile*, $\times 1400$ (Benguet, Philippines, Santos, Bureau Sci. 31776, US). Fig. 23. Distal view of *L. volubile*, $\times 1400$ (Luzon, Philippines, Sulit, Phil. Nat. Herb. 5119, GH). Fig. 24. Same, proximal view, $\times 1400$.

these projections are seen to carry numerous, smaller, globose bodies which cover the remainder of the spore as well (Fig. 28). These features are present in air-dried material, but are better viewed in acetylated spores. Laesurae are low and narrow, relatively inconspicuous ridges extending nearly to the margin.

DISCUSSION

There can be no doubt that *Lycopodium* is a more heterogeneous genus than are many others; certain natural groupings of species have been recognized by nearly every systematist working with the group. But botanists have failed to agree on how the group should be further subdivided—or even if it should be.

Both Knox (1950) and Harris (1955) felt that none of the various systems advanced for *Lycopodium* by other authors adequately fit the data provided by spore morphology, although certain groupings found more support than others. Knox, for instance, says that “. . . it should be admitted that Pritzel's division into two sub-genera, based on spore characters, is more easily maintained than the division into six sub-genera [a reference to Herter's (1909) system adopted by Walton and Alston in “Manual of Pteridology” (1939)], since the spores fall into two major well-defined groups, the pitted and the reticulate.”

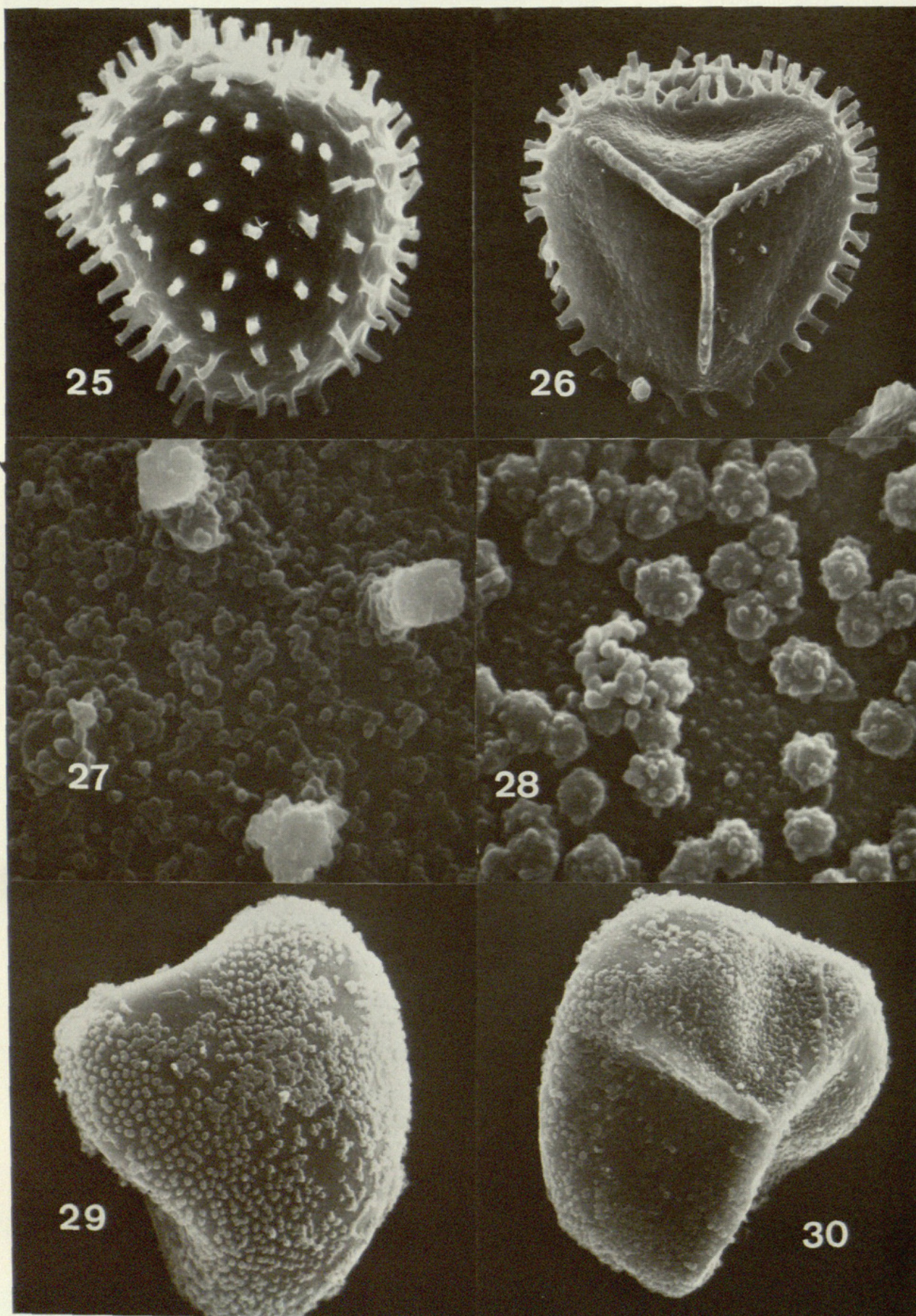
Leaving aside for the moment the baculate spores of *Lycopodium deuterodensum* and the scabrate spores of *L. casuarinoides*, in my view there are not two, but three major well-defined groups, recognizing the rugulate as distinct from the reticulate, a separation Knox does not make. If these groups are taxonomically meaningful, then some correlation with other consistent group characteristics should be noted.

Holloway (1919) made this correlation, except for the spore information. In his detailed study of the New Zealand species of *Lycopodium*, he divided them into sections *Selago*, *Phlegmaria*, *Inundata*, *Cernua*, and *Clavata*. He compared five features recognized as important: (1) growth habit and external form, (2) stem anatomy, (3) character of the fertile region, (4) form and structure of the prothallus, and (5) form of the young plantlet. It is not necessary to repeat the details of his findings; those interested will find Holloway's own account worth careful reading.

For ease of comparison, Holloway combined his discussion of those sections he found most similar in total character. He recognized that sections *Selago* and *Phlegmaria* are closely related, that sections *Inundata* and *Cernua* are a second natural grouping, and that section *Clavata* stands by itself. This grouping of sections conforms exactly with the three large spore groups, showing the expected correlation between spore pattern and overall morphology.

The spore groups also fit with Rothmaler's (1944) treatment of the genera *Huperzia*, *Lepidotis* and *Lycopodium*, but not with his fourth genus, *Diphasium*. Nor does *Diphasium* distinguish itself from *Lycopodium* on other grounds when Holloway's (1919) study of *Lycopodium scariosum* and Wilce's (1965) treatment of section *Complanata* are considered.

Rothmaler based his separation of *Diphasium* from *Lycopodium* purely on prothallial shape and the bilateral nature of the branchlets in *Diphasium*. Löve and



Löve (1958) reinforce Rothmaler by calling attention to the lower chromosome number in *Diphasium*, but weaken his case by suggesting that prothallial shape may have been taxonomically overvalued.

Lang (1899), Holloway (1919), Bower (1935), Löve and Löve (1958), and Wilce (1965), all believe that prothallial shape is not significant. This can hardly be doubted now that experimental studies have shown the differences to be mainly environmentally controlled (Freeberg & Wetmore, 1957; Freeberg, 1962).

Bilateral branches are not restricted to *Diphasium*, nor are all *Diphasium* taxa flat-branched, and so this character does not separate *Diphasium* from *Lycopodium*. Further, numerous species throughout *Lycopodium* show a bilateral leaf orientation, which requires only a broadening of the lateral leaf bases to produce the flat-branched condition. So minor a vegetative adjustment seems an unlikely generic character.

Chromosome number is of possible generic significance, but recent investigations (Wilce, unpubl.) place the haploid number of *L. jussiaei* (type species of *Diphasium*) at ca 34–36, putting it close to that of *L. clavatum* ($n = 34$), rather than to *L. complanatum* ($n = 23$). If a generic separation is to be made based on chromosome number, the Complanatum Group must stand alone, not as *Diphasium*. I cannot consider a difference in chromosome number sufficient basis for any genus, however, and there is little additional support.

There are, then, three major non-arbitrary groups (using “arbitrary” and “non-arbitrary” in the sense of Simpson, 1951) within *Lycopodium*. The basic continuity within these groups and the discontinuity which separates them can be expected to receive additional confirmation as more systematic data come in from the fields of ecology, biosystematics, cytogenetics and biochemistry. I do not believe we should call these three groups genera.

Many authors have discussed the problem of higher taxonomic categories. Mayr (1942) summarizes his view this way:

The genus is based on the fact that the species are not evenly distinct from one another, but are arranged in smaller or larger groups, separated by smaller or larger gaps. The genus is therefore based on a natural phenomenon. How many of such groups are to be included in one genus and how the genus should be delimited from other genera are matters of convenience to be left to the judgment of the individual systematist. The genus of the systematist is his own artificial creation and not a natural unit. The same is true for the higher categories above the genus (family, order, and so forth); the groups on which they are based may be natural but their terminologies and comparative values are not [*italics mine*].

Taking this view, a systematist is not obligated to divide a genus into several genera, even though he can make a morphological case for doing so. In fact, if dividing a genus does not result in a more manageable system, he should resist

Lycopodium spores. Fig. 25. Distal view of *L. deuterodensum*, $\times 1400$ (Mt. Koghi, New Caledonia, Oct 1906, Franc, GH). Fig. 26. Same, proximal view, $\times 1400$. Fig. 27. Same, acetylated, $\times 8550$. Fig. 28. Distal surface, acetylated spore of *L. casuarinoides*, $\times 12,800$ (Kwangtung, China, Tsang 20677, GH). Fig. 29. Same, air dried spore, distal toward equatorial view, $\times 1400$. Fig. 30. Same, proximal view, $\times 1400$.

such a division. In such a situation, recognition of the natural species groupings is sufficient to satisfy the goals of modern systematics.

The case for dividing *Lycopodium* into splinter genera is not strong enough. The discontinuities between the species groups are not as great as some authors have suggested. To leave the genus intact is not a move that obscures the phylogenetic relationships between its members—these are approachable as it is. To divide the genus certainly adds nothing to our understanding of it. Finally, to leave *Lycopodium* whole is to maintain a genus that anyone can recognize at a glance, an attribute not to be discarded lightly.

What status, if not generic, should be given these natural species groups? Mayr (1942), with zoological bias, regards the subgeneric category as unnecessary, preferring an informal recognition of species groups without nomenclatural status. I feel that in botanical classification the subgeneric category is of definite value. Formal recognition of these groups as subgenera of *Lycopodium* also may help to satisfy “splitters,” whereas informal status might not.

None of the earlier formal subdivisions of *Lycopodium* quite fits our present knowledge. Holloway's (1919) informal groupings, as noted earlier, are consistent with the biological facts. The scheme presented below merely assigns available subgeneric names to those groups, and modifies his subgroups (sections) only slightly. Some sections have no names available at any rank; these require Latin diagnoses, which, with their formal naming, is deferred for a later paper in which the subgenera and sections will be treated in greater detail. At this time, however, informal recognition is desirable. The subdivision of *Lycopodium* I adopt is:

- Subgenus *Urostachys* Pritzel (1900)
 - Section 1. *Selago* Dill. ex Pritzel (1900)
 - Section 2. *Phlegmaria* (Baker) Pritzel (1900)
- Subgenus *Lepidotis* (Palisot) Baker (1887)
 - Section 1. *Cernua* (Baker) Pritzel (1900)
 - Section 2. *Inundata* (Baker) Pritzel (1900)
 - Section 3. *Lateralia* Baker (1887)
- Subgenus *Lycopodium*
 - Section 1. *Lycopodium*
 - Section 2. *Complanata* Victorin (1925)
 - Sections 3–7 not yet formally named

Sections 3–7 represent the following elements: the Scariosum Group, the Fastigiatum Group, the Volubile Group (possibly monotypic), *Lycopodium deuterodensum*, and *L. casuarinoides*.

The sections containing the latter two species are placed in the subgenus *Lycopodium* only tentatively. Closer study of *L. deuterodensum* will probably confirm its position here. Its striking, baculate spores could be derived from the reticulate type; in other important characters it conforms to the subgenus. The case is less clear for *L. casuarinoides*. Its spores do not closely resemble any others within the subgenus, and although its stele is of the banded type, it differs from the other banded steles of the genus. It may prove to be secondarily derived from the “mixed” stele type. Chromosome number and gametophyte type, so far as I know, are

unknown for this species. As the species becomes better known, the section may require elevation to subgeneric status.

This revised classification for *Lycopodium* is offered in earnest hope that it will satisfy botanists' need to recognize nomenclaturally the biological discontinuities within this ancient group of plants. At the same time, it reaffirms the view that *Lycopodium* represents a relatively non-arbitrary clustering of related elements that do not require, and should not receive, generic recognition.

LITERATURE CITED

- BAKER, J. G. 1887. Handbook of the fern-allies. London.
- BOIVIN, B. 1950. The problem of generic segregates in the form-genus *Lycopodium*. Amer. Fern J. **40**: 32-41.
- BOWER, F. O. 1935. Primitive land plants also known as the archegoniatae. London.
- FAEGRI, K. and J. IVERSEN. 1950. Textbook of modern pollen analysis. Munksgaard, Copenhagen.
- FREEBERG, J. A. 1962. *Lycopodium* prothalli and their endophytic fungi as studied in vitro. Amer. J. Bot. **49**: 530-535.
- , and R. H. WETMORE. 1957. Gametophytes of *Lycopodium* as grown in vitro. Phytomorph. **7**: 204-216.
- HARRIS, W. F. 1955. A manual of the spores of New Zealand Pteridophyta. N. Z. Dept. Sci. Indust. Research Bull. 116. Wellington.
- HERTER, W. 1909. Beiträge zur Kenntnis der Gattung *Lycopodium*. Bot. Jahrb. Engler **43**: Beibl. **98**: 1-31.
- . 1950. Systema Lycopodiorum. Estudios Botánicos en la Region Uroguaya XXI. Montevideo.
- HOLLOWAY, J. E. 1919. Studies in the New Zealand species of the genus *Lycopodium* III. The plasticity of the species. Trans. N. Z. Inst. **51**: 161-261.
- KNOX, E. M. 1950. The spores of *Lycopodium*, *Phylloglossum*, *Selaginella* and *Isoëtes* and their value in the study of microfossils of Paleozoic age. Trans. Bot. Soc. Edin. **35**: 209-357.
- LANG, W. H. 1899. The prothallus of *Lycopodium clavatum* L. Ann. Bot. **13**: 279-317.
- LÖVE, A. and D. LÖVE. 1958. Cytotaxonomy and classification of lycopods. The Nucleus **1**: 1-10.
- MAYR, E. 1942. Systematics and the origin of species, Chap. 10. The higher categories and evolution. pp. 275-298. Columbia University Press, New York.
- PRITZEL, E. 1900. Lycopodiaceae in A. Engler & K. Prantl, Nat. Pflanz. **1**(4): 563-606. W. Engelmann, Leipzig.
- ROTHMALER, W. 1944. Pteridophyten-studien. I. Rep. Sp. Nov. Fedde **54**: 55-82.
- SIMPSON, G. G. 1951. The species concept. Evolution **5**: 285-298.
- WALTON, J. and A. H. G. ALSTON. Chapter 17, Lycopodiinae in F. Verdoorn, ed. Manual of Pteridology. M. Nijhoff, The Hague.
- VICTORIN, Fr. M. 1925. Les Lycopodiniées du Quebec et leurs formes mineures. Contrib. Lab. Bot. Univ. Montréal **3**. Montréal.
- WILCE, J. H. 1965. Section *Complanata* of the genus *Lycopodium*. Nova Hedw. Beih. **19**. J. Cramer, Weinheim.
- WILSON, L. R. 1934. The spores of the genus *Lycopodium* in the United States and Canada. Rhodora **36**: 13-19.



Wilce, Joan H . 1972. "Lycopod Spores, I. General Spore Patterns and the Generic Segregates of Lycopodium." *American fern journal* 62, 65–79.
<https://doi.org/10.2307/1546437>.

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