THE OVERPOWERING ROLE OF MORPHOLOGY IN TAXONOMY

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ABSTRACT

The aim of the taxonomist is to prepare a natural system of classification bringing out the phylogenetic relationships between plants. To achieve this aim evidence must be collected from all possible angles. External morphology is the first of these and it is quite remarkable that many taxa created on the basis of such studies alone have also been found to be perfectly natural assemblages when other criteria are taken into account.

However, a large number of examples may be cited where external morphology has proved inadequate and it is important to study the internal structures. Characters of the cuticle, stomata, secondary xylem, glands, hairs, pollen grains, embryo sac, endosperm and seed coat have all proved to be of value.

To illustrate the significance of internal morphology and embryology a reference will be made to the following taxa in particular : *Ephedra, Exocarpus, Kingdonia, Paeonia, Phyllocladus, Scyphostegia,* and *Sequoia.*

(1) *Ephedra* is more closely related to the cordaites and conifers than to the Gnetales and should be placed in a separate order Ephedrales ; (2) *Exocarpus* does not belong to the Taxaceae as proposed by one botanist or even close to it, but is a member of the Santalaceae ; (3) The genus *Kingdonia* should perhaps be removed from the Ranunculaceae and assigned to a new family Kingdoniaceae ; (4) *Paeonia* cannot be assigned to the Ranunculaceae and is not even related to *Helleborus* as suggested by Hutchinson ; (5) *Phyllocladus* is confirmed as a member of the Podocarpaceae all of whose genera are characterized by certain peculiarities in the development of the male gametophyte and the embryo ; (6) The genus *Scyphostegia* is in no way related to the Urticales, Celastrales or Monimiaceae ; its real affinities are still undecided ; (7) *Sequoia gigantea* is too different from *S. sempervirens* to be included in the same genus ; the former must be put in a separate genus *Sequoiadendron* as recommended by Buchholz.

Internal morphology generally corroborates the conclusions based on external morphology. However, it has a special value in cases of controversial nature. Sometimes it fails to provide an immediate solution but reorients our ideas in more fruitful directions.

The student of taxonomy has to face his own share of troubles just like any other scientist. The more fragmentary the material, the greater these difficulties sometimes resulting in serious errors. Thus *Casuarina, Ephedra, Equisetum, Leptadenia* and *Restio* may be mistaken for each other if only the vegetative parts are present. The habit and netted venation of the leaves of *Gnetum* make it look like a dicotyledon. A few years ago a botanist collected a big jar of *Oxalis* thinking it to be *Marsilea.* Another brought a bottle of stems of *Leptadenia* under the impression that the plant was a species of *Ephedra.* The marratiaceous genus *Kaulfussia* has leaves which would hardly be identified as those of a fern if the sori are absent. On the other hand, *Stangeria* was actually taken to be a fern and it is only the discovery of the cones that enabled its identification as a cycad. Many fossil gymnosperms were for long classed under the ferns and quite a sensation was created in 1903 by the discovery of seeds associated with the leaves after which the plants were transferred to a new class called the Cycadofilicales or Pteridospermales. A fossil, originally labelled as *Zamia gigas,* later turned out to be a member of the Cycadeoidales (Bennettitales) and was transferred to the genus *Williamsonia.* Even in the earlier part of this century it was hard to tell whether a pinnate fossil leaf belong-ed to the Cycadales or the Bennettitales, although their fructifications are quite different. Cuticular studies by Thomas & Bancroft (1913) and Harris (1932) showed that while the Bennettitales have stomata of the syndetocheilic type, those of the Cycadales are of the haplocheilic type. Several fossil genera, originally given names like *Cycadites, Zamites* and *Dioonites,* were later found not to belong to the cycads at all but to the Cycadeoidales. It is possible to multiply examples but I shall mention only one more. An algologist collected the pollinia of *Acacia* which were floating on the surface of a pool and erected a new genus for its reception !

From this cursory account of errors and illusions we may now pass on to specific examples where morphology (as understood in a broad sense) has either substantiated some previous views on taxonomic relationships or given new orientations to our ideas even if a final solution is not yet in sight.

ALISMATACEAE

The monocotyledons are usually considered to be a monophyletic group. According to Hutchinson (1959) and many others they show a close relationship with the dicotyledons at one point only—the Butomaceae and Alismaceae. He writes: "These share with the Ranales an apocarpous gynoecium, and they often possess numerous stamens ;

Moreover . . . the Butomaceae correspond very closely with the follicular-carpelled Helleboroideae, whilst the Alismataceae resemble the achenial Ranunculoideae of the family Ranunculaceae.". Concerning one rare Malayan plant usually placed under the Alismataceae, Hutchinson (1959) states: "But for its solitary cotyledon and lack of endosperm, the genus *Ranalisma* Stapf might equally well be placed in Ranunculaceae. As may be inferred from the name, it combines the characteristics and appearances of *Ranunculus* and *Alisma*. The carpels of *Ranalisma* are densely aggregated in a head, after the manner of *Ranunculus*, and its leaves have pinnate nervation."

While no one has yet studied the anatomy or embryology of *Ranalisma*, there are many other members of the Ranunculaceae as well as the Alismataceae which have received attention. Metcalfe (1961) has recently emphasized the anatomical differences between the two families: (a) the stomata of the Ranunculaceae are anomocytic, while those of the Alismataceae are paracytic or tetracytic (see Fig. 1) ; (b) the spongy parenchyma of the marshy and aquatic members of the Ranunculaceae is made up of loosely arranged cells, while in the Alismataceae there is a complex network and the intercellular cavities are traversed by transverse plates of specialized cells ; (c) the metaxylem of the Ranunculaceae consists of vessel elements with simple perforations, while in the stems of the Alismataceae there are long tracheids tapering to a rounded point at either end (vessels occur only in the roots) ; and (d) raphides are absent in the Ranunculaceae, but occur sporadically in many members of the Alismataceae. To these may be added one

more point: the Ranunculaceae are devoid of laticiferous cells ; in the Alismataceae their occurrence is a common feature.
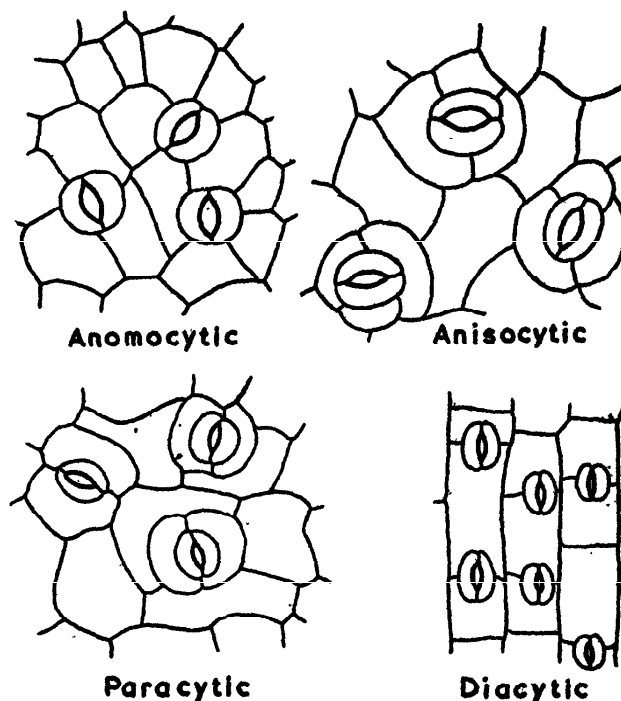

Fig. 1. Types of stomata.

The work of several scholars in my laboratory on the families Ranunculaceae and Alismataceae shows that even in the characters of the pollen, grains, embryo sac and embryo there are wide differences between two (Table I):

TABLE I

Ranunculaceae	Alismataceae
Tapetum glandular with binucleate cells	Tapetum forms a true periplasmodium
Divisions of microspore mother cells simultaneous	Divisions of microspore mother cells successive
Pollen grains 2-nucleate or 3-nucleate	Pollen grains uniformly 3-nucleate with clearly demarcated male cells
Ovules may have one or two integuments ; wall cells may or may not be cut off	Ovules have uniformly two integuments ; wall cells not cut off
Embryo sac usually of Polygonum type	Embryo sac always of Allium type
Antipodal cells usually polyploid, large and persistent	Antipodal cells (or nuclei) ephemeral, often fewer than three
Endosperm Nuclear, persistent in seed	Endosperm Nuclear or Helobial ; not persistent in seed
Development of embryo shows a rather irregular sequence of divisions. In some species embryo small and immature at time of shedding of seed	Development of embryo follows a very regular pattern with a large haustorial basal cell having a prominent nucleus. Embryo well-developed at time of shedding

The conclusion is unavoidable that there is no close relationship between the Ranunculaceae and Alismataceae and that the derivation of the latter from the former is most unlikely. Naturally it would be interesting to make a fuller investigation of *Ranalisma* to see if this belongs to the Ranunculaceae or the Alismataceae or some other family.

PAEONIACEAE

The genus *Paeonia* has been variously assigned to the Berberidaceae, Magnoliaceae and Ranunculaceae. Corner (1946) pointed out that in *Paeonia* the order of development of the stamens is centrifugal and that its proper place is near the Dilleniaceae. On the other hand, Hutchinson (1959) writes: "I

consider *Paeonia* to be something of a link between the Magnoliaceae and Helléboraceae, but much more closely related to the latter."

Murgai (1962) in my department has made a careful study of the embryology of some species of this genus. Although her account is at variance with that of some other workers and a few points are still not clear, *Paeonia* differs from all the families to which it has been assigned from time to time in one important respect. After fertilization the nucleus of the zygote divides as usual by a transverse wall but surprisingly one of these cells degenerates while the other undergoes a series of free nuclear divisions resulting in a large coenocytic structure. Cell formation occurs after a while following which certain meristematic areas are laid out and it is from one of these that the embryo differentiates. This type of embryogeny is unique in the whole class of angiosperms and supports the view that Paeonia should be assigned to a separate family Paeoniaceae. Neither *Helleborus* nor any member of the Dilleniaceae shows this peculiar feature.
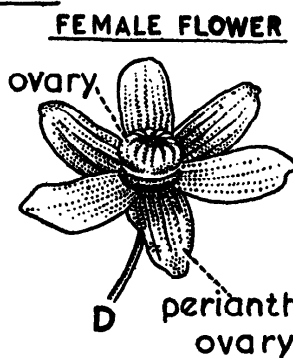
SCYPHOSTEGIA

The genus *Scyphostegia*, with a single species *S. borneensis* occurring in Borneo, was originally referred to the family Monimiaceae although not with any degree of certainty. Hutchinson (1926) created a new family Scyphostegiaceae and placed it tentatively in the Urticales, adding that "when male flowers are known this genus may be found to belong to Moraceae." However, in the new edition of his book (1959) he has transferred it to the Celastrales close to the Capusiaceae in which the disk completely encloses the carpels.
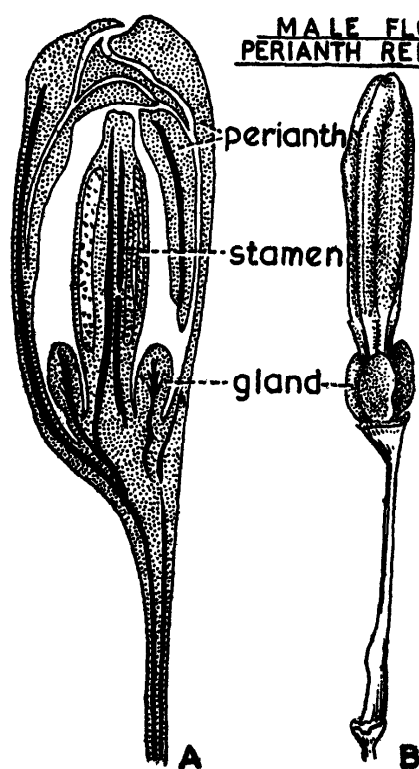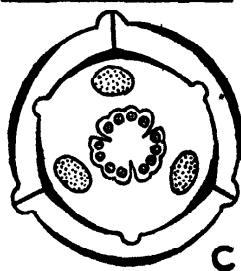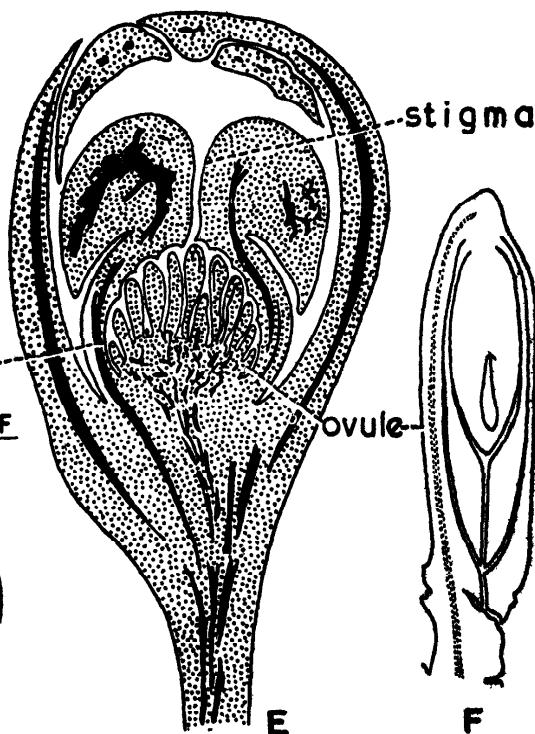

Fig. 2. Male and female flowers of *Scyphostegia* (*After* Swamy, 1953).

Swamy (1953) has made a detailed study of the structure of the flower and shown that all these assignments are based on certain misconceptions. To begin with, the male and female flowers are borne in separate inflorescences which look like compound racemes. In the male flower the perianth is united into a tube whose individual lobes become free about the mid-height of the flower. The outer whorl comprises three somewhat fleshy lobes and may be regarded as sepaline. The members of the inner whorl are thinner and this may be regarded as petaline. The third whorl comprises three fleshy knob-like glands situated opposite to the lobes of the second whorl. Finally there are the three stamens, confluent by their adaxial surfaces.

Like the male flower the female flower also has six perianth lobes in two alternating whorls, but these are somewhat fleshy and free right from the base. There is nothing to match the glands of the male flower. Instead, there is a fleshy urceolate

structure whose free upper part is conspicuously deflexed and which encloses a single cavity communicating with the outside through a narrow passage. The floor of the cavity is slightly raised and bears numerous structures which have been interpreted in the past as carpels or as female flowers while the urceole has been regarded as an overdeveloped disk. The merit of Swamy's work lies in showing that the urceole is really the ovary and the structures within it are ovules which bear peculiar funicular outgrowths at the base.

The details given by Swamy (see Fig. 2) make it impossible to consider any alliance between Scyphostegia and either the Urticales or the Celastrales. Nor is any relationship with the Ranales worthy of serious thought. Scyphostegia remains a challenge to taxonomists who must think afresh on its systematic position. Morphologists must meanwhile supply further details about the embryology, cytology and anatomy of the plant so that a positive assignment can be made.

KINGDONIA

This is a monotypic genus with a single species *K. uniflora*, discovered by F. Kingdon Ward in 1913 (see Foster, 1959) at an elevation of 4,000 metres in the Chinese-Tibetan borders. On the basis of the original description of Balfour & Smith (1914) the flower consists of 5 sepals, o petals, 10-15 stamens and 5-7 uniovulate carpels, and appeared to be of the ranalian type. However, Foster (1959) has called attention to the peculiar venation of its leaves which is open and dichotomous and thus strikingly like that of *Ginkgo biloba* and certain ferns. In the angiosperms the reticulate type of venation is almost universal, and *Kingdonia* is an uncomfortable exception (Foster & Arnott, 1960).

Four bundles constitute the vascular supply of the leaf and since they depart from a single point, the node is unilacunar. On the other hand, in the Ranunculaceae the leaves of nearly all the genera have three or more traces and the nodes are trilacunar or multilacunar. Thus the venation, node and leaf trace provide no support for the supposed relationship of *Kingdonia* with the Ranunculaceae.

More recently, Foster (1961) has also examined the flower of *Kingdonia*. It is borne on a naked scape 7-10 cm long. A well-defined calyx is absent, but there are 5 tepals each supplied by two vascular traces. The androecium comprises 8-12 spirally arranged staminodes and 3-6 fertile stamens. The gynoecium is composed of 5-8 spirally arranged carpels. After pollination the tepals, staminodes and stamens fall away while the styles become recurved over the dorsal edges of the ovaries so as to form beak-shaped structures. The stamens are clearly demarcated into anther and filament—a rather advanced feature.

In Foster's opinion the totality of the morphological and anatomical evidence indicates that *King-*

donia is a relict genus without obvious affinity to any, ranalian family including the Ranunculaceae. Among its most unique features are: (a) unilacunar nodes ; (b) dichotomous venation of the leaf ; and (c) a two trace vasculature of the tepals. Further, the pollen grains are tricolporate and thus different from those of the Ranunculaceae. A study of the tracheary elements, seedling anatomy and embryology of *Kingdonia* still remains to be carried out. Foster believes that when this is done, the plant will probably be assigned to an independent family within the order Ranales.

PHYLLOCLADUS

Turning now to the gymnosperms, the systematic position of *Phyllocladus* was long in doubt. Some authors assigned it to the Podocarpaceae, others to the Taxaceae, and still others erected a separate family Phyllocladaceae. The studies of J. T. Buchholz and J. Doyle have shown that the Podocarpaceae is a fairly homogeneous family whose members are characterized by the following common features: (a) the pollen grains are winged and the prothallial cells multiply so that the pollen tube contains several other nuclei besides the two male gametes, the tube nucleus and the stalk nucleus ; (b) the body cell remains in the pollen grain for a long time, perhaps in a period of rest, and later gives rise to two equal male cells ; (c) there is a single megaspore mother cell which is surrounded by a well developed spongy tissue ; (d) the megaspore membrane is thick and comprises two layers ; (e) the arche-
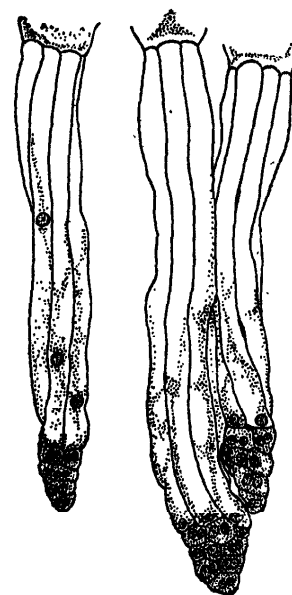

Fig. 3. *Phyllocladus alpinus*. Proembryos showing binucleate phase. (*After* Buchholz, 1941).

gonia are long, narrow and pointed and each has a single-tiered neck ; (f) a ventral canal nucleus is present ; (g) the zygote undergoes free nuclear divi-

sions to form a 16-nucleate stage before walls are formed ; (h) the proembryo shows a characteristic binucleate phase, as shown in Fig. 3, which is unknown in other gymnosperms ; and (i) a single proembryo is formed from each archegonium.

In the development of its winged pollen grains and the pollen tube *Phyllocladus* shows marked podocarp affinities. It also has a definite megaspore membrane and a tapetal or spongy tissue around the embryo sac. Although Holloway (1937) missed the binucleate stage—so characteristic of podocarps—this was demonstrated later by Buchholz (1941). Doyle & Looby (1939) write that the inherent unity of *Phyllocladus, Saxegothaea, Dacrydium* and *Podocarpus,* as shown by their gametophytes and embryos, is further confirmed even in their physiology, especially the pH of the leaf sap (*see* also Doyle, 1954 ; Florin, 1958).

In spite of a few superficial similarities with the Taxaceae, today there can be no reasonable doubt that *Phyllocladus* is correctly placed in the Podocarpaceae and there is no reason for retaining an intermediate family for this genus as was once done by some systematists.

LIBOCEDRUS

The genus *Libocedrus,* belonging to the Cupressaceae, was formerly considered to comprise several species widely scattered in areas bordering the Pacific Ocean : 3 in New Guinea ; 2 in New Zealand ; 2 in New Caledonia ; 1 in Southern China ; 1 in Formosa ; and 1 in Pacific North America. However, there are morphological differences in the organization of the female cones between the northern and southern species, due to which Pilger (1926) made two subgenera—*Heyderia* for the northern species and *Eulibocedrus* for the southern. On the basis of epidermal structures Florin (1930) segregated the Chilean *L. uvifera* into a new monotypic genus called *Pilgerodendron.*

From a detailed study of the cone scales Li (1953) suggested still other changes. The genus *Libocedrus* is to comprise only such members which have four valvate cone scales. All of these belong to the Southern hemisphere. The three species from New Guinea, which have bracteate ovuliferous scales and spirally arranged microsporophylls, are assigned to a new genus *Papuacedrus.* The generic name *Heyderia* is used for the three northern species with six imbricate cone scales.

TABLE II

Sequoiadendron	Sequoia
Buds naked	Buds scaly
Pollen tube long and slender, enlarged only near archegonia	Pollen tube shorter and stouter ; broader in middle region
Cone scales bearing 3-12 or more erect ovules in double crescentic row	Cone scales with 3-7 erect ovules in single arched row
Ovules mature in two seasons	Ovules mature in one season
Female cone remains green and attached to tree for many years	Female cone turns brown and is shed at maturity
Only one megaspore mother cell ; produces single linear row of three cells consisting of two megaspores and one dyad cell	Many megaspore mother cells, forming groups of megaspore tetrads which vary in form from tetrahedral to linear
Single functioning megaspore showing normal growth	Many megaspores forming downward tubular processes
Spongy tissue massive and permanent	One-layered spongy tissue of short duration
Micropyle symmetrical	Unsymmetrical development of the closing cells of the micropyle
Only one female gametophyte per ovule	Several female gametophytes in early stages
Female gametophyte alveolar like that of many other conifers	Female gametophyte alveolar only in middle ; free nuclei at the ends
Megaspore membrane relatively thick (2-3μ)	Megaspore membrane relatively thin, less than 1μ.
Archegonia few (±20) with prominent jacket cells	Many archegonia (50-200) with large and irregularly arranged jacket cells
Proembryo with free-nuclear stage	Zygote divides by wall formation—a unique feature in gymnosperms
Embryo has 3, 4 or 5 cotyledons	Embryo has 2 cotyledons

Florin's extensive studies of the epidermis and stomata of gymnosperms have fully confirmed the above rearrangements. Further, Florin & Bouteije (1954) have shown that one more species—*Liboce-drus chilensis*—differs rather widely from the others and should be assigned to a new genus *Austrocedrus*. Thus we have now five genera instead of one: (1) *Heyderia* with 3 species, 1 in Pacific North America and 2 in subtropical south-east Asia ; (2) *Libocedrus* with 6 species, 3 in New Caledonia, 2 in New Zealand and 1 in Southern Chile and Argentina ; (3) *Papuacedrus* with 3 species in New Guinea and the Moluccas ; (4) *Pilgerodendron* with 1 species along the Western slopes of the Andes ; (5) *Austro-cedrus*, with 1 species from the lower slopes of the Andes.

SEQUOIA

For more than a hundred years the genus *Sequoia* was said to comprise two species: *S. sempervirens* (the redwood) and *S. gigantea* (the big tree). Buchholz (1939 a, b, c), who made a thorough study of the external and internal morphology of the two, became convinced that they were too different to be members of the same genus. Accordingly he renamed the big tree as *Sequoiadendron giganteum* (Lind.) Buchholz. Many people objected to this and some still do so. However, a study of Table II will leave no doubt

that Buchholz is right and the two plants definitely belong to two different genera (cf. John & Krauss, 1954). Looby & Doyle (1937, 1942) also wrote: "It is clear that the two redwoods differ essentially in practically every phase of their life history. . . We, therefore, without hesitation agree with him (J. T. Buchholz) that the Sierra Redwood and the Big Tree, commonly now known as *Sequoia gigantea*, can no longer be retained as a species of *Sequoia*, a generic title to which *Sequoia sempervirens* has priority claim."[1]

CEPHALOTAXUS

The genus *Cephalotaxus* was at first included in the Taxaceae but Neger (1907) created a new monogeneric family Cephalotaxaceae. Pilger (1926) assigned *Amentotaxus* also to this family. Pulle (1937) has included both Taxaceae and Cephalotaxaceae under the order Taxales. Takhtajan (1953) too considers these two families to be closely allied to each other.

Singh (1961) has made a detailed study of *C. drupacea* and supports Neger's (1907) view that *Cephalotaxus* should be assigned to a separate family Cephalotaxaceae, while *Amentotaxus* should be included in the Taxaceae.

The following table brings out the contrast between the Taxaceae and Cephalotaxaceae:

TABLE III

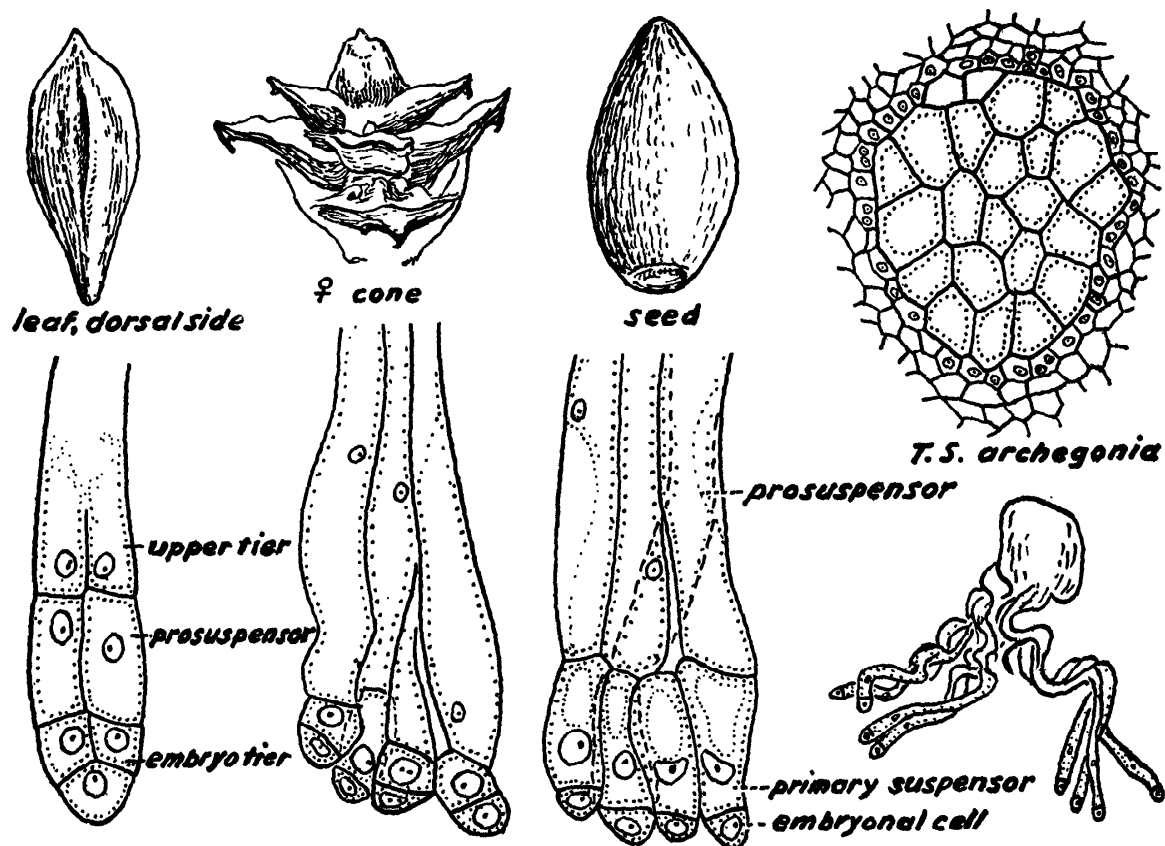| Taxaceae	Cephalotaxaceae
Leaves spiral	Leaves opposite and decussate
Microsporophylls with perisporangiate microsporangia	Microsporophylls with hyposporangiate microsporangia
Ovules borne singly and terminally on short fertile shoots	Two ovules borne laterally on a short axis lying in the axil of the bract scale
Aril present	Aril absent
Ovule supplied by a variable number of normally oriented bundles	Ovule supplied by two inverted bundles
Female gametophyte shows wall formation by alveoli	Wall formation by centripetally advancing cells
Cleavage polyembryony present ; proembryo without cap cells	Cleavage polyembryony absent ; proembryo with prominent cap cells
Integument not fleshy (the fleshy part is the aril)	Integument has a thick outer fleshy layer

In *Amentotaxus* the ovules are borne singly and appear terminal on the floral axis, while in *Cephalotaxus* they are borne in cones and are lateral on the floral axis. Florin (1931) has pointed out that in *Amentotaxus* the stomatic bands are thickened while in *Cephalotaxus* they are unthickened. Further, the stomatal apparatuses of the two genera also differ in arrangement and structure. It may be concluded that the Taxaceae comprise five genera—*Taxus, Torreya, Austrotaxus, Amentotaxus* and *Pseudotaxus*—while *Cephalotaxus* occupies an isolated position under a separate family Cephalotaxaceae.

BIOTA

There is a long standing controversy regarding the genus *Biota* which was set up in 1847 by Endlicher. Lindley (1853) merged this in *Thuja* and gave it the same old name *Thuja orientalis*. However, Peirce (1937), Buchholz (1948), and Martin (1950) have added new data supporting Endlicher's view. Singh & Oberoi (1962) do the same on the basis of a detailed embryological study of *Biota orientalis*, a commonly grown shrub in our gardens. The differences between the two genera are shown in Fig. 4 and tabulated below:

[1] Later, Doyle (1945) modified this opinion but the original arguments given by Looby & Doyle (1942) are more convincing.

BIOTA

leaf, dorsal side

♀ cone

seed

T.S. archegonia

upper tier

prosuspensor

prosuspensor

embryo tier

primary suspensor

embryonal cell

THUJA

leaf, dorsal side

♀ cone

upper tier

pro-suspensor

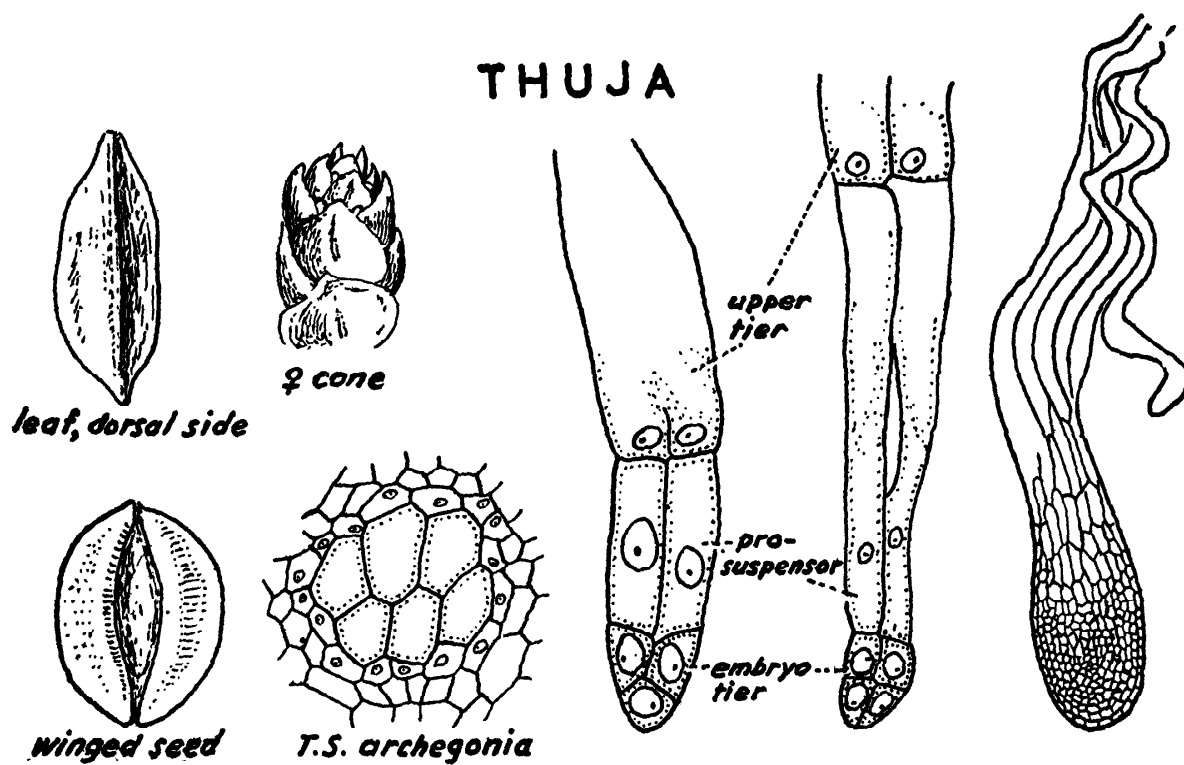embryo tier

winged seed

T.S. archegonia

Fig. 4. Diagrams showing comparison of *Biota* and *Thuja*.

TABLE-IV

Thuja	Biota
Young branches horizontal	Young branches vertical
Raised gland on abaxial surface of leaf	Groove on abaxial surface of leaf
Scales of female cone erect at time of pollination, thin and papery in seed	Scales thick and fleshy, and strongly recurved at time of pollination, woody at maturity and bearing a prominent recurved spine
No spongy tissue around functioning megaspore	Well developed spongy tissue around functioning megaspore
Number of free nuclei in female gametophyte about 512 ; 5-8 archegonia in a complex ; ventral canal nucleus reportedly absent	Number of free nuclei is nearly 4,000 ; 15-28 archegonia in a complex ; ventral canal nucleus present
Simple polyembryony present, but no cleavage poly-embryony	Both simple and cleavage polyembryony are present
Seed thin with two papery wings	Seed thick and unwinged

It is thus clear that *Thuja orientalis* should be raised to the status of a separate genus *Biota*.

EPHEDRA

This genus is usually included, along with *Welwitschia* and *Gnetum*, in the order Gnetales. A few years ago, Eames (1952) discussed this point in considerable detail and arrived at the conclusion that *Ephedra* is nearer to the conifers and cordaites than to *Welwitschia* and *Gnetum*. With this opinion I am in full agreement. While Eames has devoted much space in his paper to the organization of the male and female strobili, additional support of a convincing nature is derived from vegetative anatomy and embryology. Eicke (1957), who made an electron microscope study of a number of gymnosperm woods, confirms that the bordered pits of *Ephedra* show a close similarity with those of conifers. On the other hand, the bordered pits of *Gnetum* lack a torus and thus stand apart from those of *Ephedra*. The male and female gametophytes of *Ephedra* are also typically gymnospermous. The pollen grains have two prothallial cells, a tube nucleus, a stalk nucleus and a body cell. On the other hand, *Welwitschia* and *Gnetum* have a single prothallial cell, a tube nucleus, and a generative cell which divides directly to produce the two male gametes ; a stalk cell is absent. The female gametophyte shows a tent pole—also found in *Ginkgo* and some conifers —and typical archegonia with a large number of neck cells. The resemblance extends even to the occurrence of lateral archegonia which we have observed in *E. foliata* and a few other species. Fertilization and embryogeny too offer no deviation from the condition in conifers. We may conclude with Eames that *Ephedra* is not related phylogenetically to the other genera of the Gnetales and belongs instead to the general cordaite-conifer line.

PALYNOLOGY

Among the branches of morphology, that have proved useful in taxonomy. special mention must

he made of the structure of pollen grains. They are small, only about 10-150μ in diameter, but provide a wealth of information. To give a couple of examples, a few years ago, some botanists—all specialists in the flora of Africa—tried to identify a shrub from Tanganyika but failed to do so. They sent to Dr. G. Erdtman of Sweden a few dried stamens who reported that the pollen grains resembled those of *Montinia*, a little known genus of the Saxifragaceae. This gave the desired clue ; the plant was identified as a new species of the genus *Montinia* which is now placed in the Montiniaceae (see Erdtman, 1954, 1958).

While the evidence from pollen morphology is not always quite so decisive, it is nevertheless very helpful. For example, if in a disputed case 50 per cent of the evidence points one way and 50 per cent the other way, the taxonomical compass-needle must be considered to move in favour of the family with which the pollen grains show a good resemblance. Thus, *Nepenthes* is believed by some botanists to be related to *Drosera* but others keep the two quite apart and Wettstein (1935) in particular declared: "die vielfach vermutete Verwandtschaft der Nepenthaceen mit den Droseraceen ist höchst unwahrscheinlich." However, the pollen grains of *Nepenthes* are not only joined in tetrads but also have other features similar to those of *Drosera* so that an alliance between the Nepenthaceae and Droseraceae is by no means unlikely.

Pollen grains have been used to identify the sources of samples of honey and to determine fossil plants. During recent years it has also proved feasible to cut ultra thin sections of pollen grains for studying the sporoderm under the electron microscope and obtaining further details.

Like any other single character, the evidence from pollen morphology must, however, always be used with caution. For example, in *Sanicula*—a member of the Umbelliferae—even anthers of the same plant show pollen grains of two different types. Some are spherical and others are ellipsoidal.

HOST AND PARASITE

A knowledge of parasites is sometimes quite useful in giving clues to relationships of their hosts. Gibbs (1954) writes: "Those parasites which have thus become highly specialized are, we may be sure, adapted to the chemistry and physiology of their hosts. It is therefore likely that groups of closely related parasites will attack groups of closely related hosts."

To give an example, the rust *Chrysomyxa* (Melampsoraceae) has 14 species of which 11 occur on members of the Ericaceae, 2 on the Pyrolaceae, and 1 on *Empetrum nigrum*. This fungus is thus an excellent indicator of a biochemical affinity between all the families and provides further proof of Samuelsson's view (1913) that the Empetraceae belong to the Ericales rather than to the Sapindales (Lawrence, 1951) or Celastrales (Hutchinson, 1959). The saying that "you can't fool the fungus" has certainly proved true in this case. Similar data are available about certain gall insects which are excellent taxonomists even to the extent of identifying species or varieties.

CONCLUSION

In concluding this talk I should like to recall that it is morphological evidence which led to the recognition of new families like the Degeneriaceae, Winteraceae (*Drimys, Bubbia, Belliolum, Pseudowintera, Exospermum* and *Zygogynum*), Trochodendraceae (*Trochodendron*), Tetracentraceae (*Tetracentron*), Amborellaceae (*Amborella*), Scyphostegiaceae (*Scyphostegia*), and many others. *Indenburgia* turns out to be cogeneric with *Nouhuysia* whose affinities remain undetermined, and *Ascarina alticola* is merged with *Paracryphia*. These are only a few of many examples (see Swamy, 1958). Morphology has also given timely warning of many pitfalls such as the attempt to transfer *Casuarina* to a new class intermediate between gymnosperms and angiosperms, and another suggesting a removal of *Exocarpus* from the Santalaceae to the Gymnosperms.

One of the difficulties in the use of the morphological approach to taxonomic problems is the lack of properly preserved material. Embryological studies, in particular, cannot be carried out on poorly fixed specimens. Many times the sepals and petals must be removed and the ovules excised before fixation. This involves much inconvenience and a lot more patience than most people are capable of under the tropical sun and rain. There are two suggestions that come to mind: (1) the staff of the Botanical Survey should have some training in the fixing and sending of material so that it reaches in good condition, and they can greatly increase the scope and quality of their service to botanists in other fields; and (2) adequate grants should be provided to University teachers to

go on plant collecting trips to regions like Eastern Assam, the Western Ghats, and the Andaman and Nicobar Islands. Many treasures still lie there unexplored. It is a pity that today field botany is in danger of disappearing from University curricula. We must all raise our voice against it and induce the authorities concerned to generously finance collecting trips in the summer and autumn vacations when many teachers and students have no other exacting duties.

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