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FOSSIL REMAINS OF THE GENUS HUMIRIA.

BY

OLOF H. SELLING.

Introduction.

The subfamily Humirioidae of the Linaceae is a small group of trees and shrubs occurring mainly in tropical South America (and Trinidad), only one species being confined to tropical West Africa, from Sierra Leone to Gabon. It comprises about 35 species, divided among three genera, Humiria J. St. Hil., Sacoglottis Mart. and Vantanea Aubl. Only the two latter are recorded in the fossil state, seven fossil species having been described on endocarps in the Tertiary of South America and Germany. Four of the species have been referred to Sacoglottis (Berry 1922 a, b, 1924 a, 1927, 1929 a, b, d, Reid 1933, Weyland 1938) and three to Vantanea (Berry 1924 b, 1929 b, c). No fossil species of the remaining genus, Humiria, has so far come to light.

While working on some collections of plants from the South American Tertiary, however, I met with a Brazilian endocarp, which undoubtedly belongs to this genus. A revision of the previously published fossil species of this assemblage showed that one of those referred to Sacoglottis, too, should be brought to Humiria. The aim of the present paper is to discuss these determinations and their bearings. The Brazilian material will be dealt with first. It may be added that no fossil leaves to be correlated with the genus have been discovered.
On the Occurrence of Humiria in the Tertiary of Brazil.

*Humiria bahiensis* n. sp.  
(Figs. 1—12).

**Description:** Carbonized endocarp, $14 \times 7$ mm, longest diameter 7.3 mm, shortest 6.4 mm, equatorial circumference 22 mm, outline of base almost ovoid, apex tapering, acuminate (the very apex slightly damaged). Endocarp five-carpelled, syncarpous. A very short, angular remnant of a stalk (about $1 \times 1$ mm; not seen in the pictures) originally present in the central pentagonal area left at the base by the carpels. The continuation of the vascular supply angular in cross section also half-way towards the apex of the endocarp (Fig. 5 b). Carpels mostly sterile, only one fertile, all of them of wedge-shaped cross section and radially grouped, the septa completely fused round the axis. Distal surface of each carpel about 4 mm across and provided with a longitudinal, tongue-shaped facet surrounded by a shallow furrow marking a zone of weakness in the wall (easily observed in cross sections of the endocarp), and outside this furrow by a slightly

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1 When germination took place, the part of the wall surrounded by this furrow was probably shed, as is the case in recent species of the subfamily (Staff in Monus 1895, p. 66; Reid 1933, p. 211, Pl. XIV, fig. 6). This view appears the more likely as Berry (1929 b, p. 157) reports that »isolated seeds [= valves] are almost as common as the stones [drupes] [= complete endocarps] of the Tertiary »Saccoglottis« (= Humiria; cf. p. 264) at Belen, Peru. Already Mrs. Reid (l. c.) has pointed out that Berry in 1922 b mistakenly figures and describes the valves as seeds, and this is true also of the other papers in which the latter author touched the question; the base of the endocarp is, besides, spoken of as the chalaza.

The peculiar type of dehiscence of the humirioid endocarps appears to have escaped the attention of the taxonomists dealing with the relationships of the group, and the carpologists familiar with these endocarps do not seem to have dealt with the possible bearing of their construction. Being hampered by lack of material I cannot go particularly far into the question but have to confine myself to the following short remarks:

The type of dehiscence referred to, which incidentally appears to be of rare occurrence in drupes, is strongly suggestive of the type found in certain capsules with pyxidate carpels. According to Winkler's recent interpretation (1941, p. 34—37), such capsules are found also in two families of the *Gruinales*, viz., *Geraniaceae* and *Linnanathaceae*. Since there is no truly fundamental difference between capsules and drupes, it may be asked whether the occurrence of valvate dehiscence in the fruits of the *Humirioidae* as well as of the said families is due to mere analogy. The answer to this question would be of interest to the problems of the relationships and taxonomic status of the *Humirioidae* (cf. Mauritzson 1934). At any rate, no close counterparts of these drupes appear to be known in the *Linaceae*.  

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Figs. 1—11. *Humiria bahiensis* n. sp. — 1: lateral view (1/1); 2: from the opposite direction (1/1); 3: apical view (1/1); 4: basal view (1/1); 5 a: inside view of basal part of fertile carpel showing pinching of the locule, cf. Fig. 7 (2/1); 5 b: same view as in Fig. 2, with the part shown in Fig. 5 a removed, the light, angular dot in the centre = oblique section of the vascular bundle (2/1); 6: same part as in Fig. 5 a, enlarged to show impressions of two seeds (bracketed), the top seed represented by only basal impression (c. 16/1); 7: same part as in Figs. 5 a and 6, seen from aside, immersed in xylol to show the brown coating of the locule (10/1); 8: upper part of the opened endocarp of Fig. 5 a, photographed from the base to show the continuation of the locule towards the apex (= site of the top seed) (10/1); 9, 10, and 11: same views as in Figs. 3, 1, and 4, respectively, enlarged (2/1). × in Fig. 9: fertile locule (cf. Fig. 12). — Photos by K. E. SAMUELSSON.
bulging, marginal ridge, formed by the distal portions of the thick septa. This ridge broadest at the base of the carpels and only separated from those of the neighbouring carpels by a very narrow and shallow furrow (or just a line) at the site of the suture. The tongue-shaped facet extending to about 3 mm from the apex of the endocarp and measuring about $11 \times 2$ mm (in the fertile carpel somewhat broader than the average); in the fertile carpel, where it reaches to the base of the endocarp itself, being about 1 mm at the base; in the sterile carpels gradually narrowing and disappearing a short distance before the base of the endocarp is reached. Sterile carpels devoid of distinct locules; instead, a three-branched structure can be seen in cross sections of each of the almost solid carpels, with two branches along the valve (Fig. 12). Valve of the fertile carpel, corresponding to the afore-mentioned facet, about 1 mm thick, its texture in cross section very minutely granular and devoid of prominent vesicles. Fertile locule about 1.5 mm across towards the apex and the base, at the middle of its longitudinal axis provided with a pinching (Fig. 5 a). Distinct impressions of two seeds, one above the other, present in the locule and corresponding to the two widened spaces of the latter (Fig. 6). Walls of the locule with a continuous light brown coating of the otherwise black material (Fig. 7), its texture very minutely granular (not visible without magnification, and little distinct also when seen $\times 25$). Impressions of seeds about 3 mm long.

**Locality:** Brazil: state of Bahia, steep immediately E of Maranhú, lat. S $14^\circ 8'$, long. W $38^\circ 55'$.

**Horizon:** Miocene or Pliocene, according to the geological map in Branner 1919. No data on this point are to be had from a comparison with other species of *Humiria* (see p. 262—265), and according to the label no other determinable fossils were seen.
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in the locality. Only a few minute pieces of carbonized wood could be found in addition to this single endocarp.

Type specimen in Riksmuseets Paleobotaniska Avdelning, Stockholm. Collected by Dr Fredrik Enquist (now professor of geography, University of Göteborg, Sweden), January, 1921.

Discussion of the species. The generic reference appears to leave no room for mistake. Outside the Humirioidae there is no assemblage to match the fossil fruit in construction. Among the genera belonging here Sacoglottis may be dismissed, because in this genus the carpels are one-seeded (see, e.g., Winkler 1931). Further, the literature on its about 19 species contains nothing of the occurrence of surface markings closely corresponding to those found in the fossil endocarp, though the general construction is the same. In Vantanea we find two seeds per locule (l.c.), but — just as in Sacoglottis — no occurrence of surface markings approaching those of H. bahiensis is reported, and the measurements of the fruits, if sufficient in number to rely upon, provide further negative evidence. There is no report of any smaller drupe than in V. micrantha, which measures 20—25 × 14—22 mm (Ducke 1938); the values are generally much higher, the highest being 50—100 × 35—45 mm (V. macrocarpa; Ducke 1935).

In Humiria, however, there is agreement in number of seeds per locule, surface pattern, and general size. As to surface markings, a reference to the detailed discussion in Urban 1877 may suffice. In the fossil endocarp there are no structures like those seen at the apices of Urban's endocarps, but this difference is only apparent. As emphasized already by Bailon (1860—1861, p. 209), such wall gaps merely denote immature endocarps. Also the slight differences in the shape of the valves and in the outlines of the endocarps appear to be reduced in mature specimens. Urban's material was of H. floribunda Mart.; I have seen essentially the same pattern in H. balsamifera (Aubl.) St. Hil. (specimen in the Riksmuseum, Stockholm), a species whose fruits were unknown to Urban (l.c.) and the endocarps of which are not mentioned in Bakhuizen's short description (1941, p. 415). I have little doubt that it will be found elsewhere in the genus, too, but for lack of material this cannot be definitely stated. As regards size, the available reports give values rather close to those of H. bahiensis: The endocarp of H. crassifolia Mart. measures 12.5 × 7 mm (Martius 1826, Tab. 198), and Urban (1877, col. 440) found the drupe of
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*Humiria floribunda* to be 8—14 × 5—8 mm including a 0.5—1 mm thick, fleshy mesocarp. All the drupes of *H. balsamifera* that I have seen were immature, but appeared to be of the same order of magnitude. Conditions in the other species of *Humiria* seem to be unknown or undescribed.

Turning to the possibilities of distinguishing the Brazilian fossil endocarp as a separate species, the serious lack of recent material for comparison does not affect the standpoint taken here, which accords with palaeobotanical usage. The fossil should have a name for the sake of reference. It would moreover no doubt be more hazardous to claim identity of a plant of this age with a recent species. The only question to settle is whether the Brazilian endocarp can be referred to any pre-Quaternary species hitherto described. This does not appear to be the case, though some endocarps previously brought to *Sacoglottis*, which will be dealt with below, come rather close to it. So far as any comparison can be made when only figures are available of the latter specimens, *H. bahiensis* differs in shape sufficiently to be given a name of its own (cf. p. 265).

The question of the relationships of *H. bahiensis* must be left until more is known of endocarp morphology in the recent species. Three of them (*H. Cassiquiari* Suesseguth et Bergdolt, *H. savannarum* Gleason, and *H. subcrenata* Benth.) seem to be quite unknown in this respect, and our knowledge of two others [*H. balsamifera* and *crassifolia* (see above)] leaves much to be desired. Still, the Brazilian find gives rise to some further remarks, which will be included in the general discussion (p. 267).

**Additional Fossil Species of Humiria.**

Several years ago Berry (1924 a) described four fossil endocarps from the Guaduas formation of Cipacón (or Zipacón) in the Province of Cundinamarca, Colombia, under the name of *Sacoglottis cicaconensis*. They had been collected by Brother Aristé (Dr. Maurice A. Rollot) of the Institute de la Salle in Bogotá, in a Tertiary deposit, the exact age of which was unknown but considered by Berry to be late Eocene or early Oligocene.¹ His age

¹ Weyland (1938, p. 157) states that Berry, in 1929 d, recognized the possibility of the Cipacon material being of Miocene age. I can find nothing of this sort in the paper referred to, and in the same year Berry (1938, p. 44) actually restated his view that the endocarps of *Sacoglottis* are most likely Oligocene in age. This conclusion is, however, open to discussion.
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Figs. 13—17. *Humiria cipaconensis* (Berry) Selling from the early Tertiary of Cipacon, Dept. of Cundinamarca, Colombia. From Berry 1929 d, Pl. I, Figs. 1—5, respectively. — All 1/4.

Figs. 18—22. *Humiria peruviana* (Berry) Selling from the early Tertiary of Belen, Dept. of Piura, Peru. From Berry 1929 b, Pl. I, Figs. 14—18, respectively. — All 1/4.

determination was based on a comparison with abundant remains of similar, silicified endocarps from Belen, Dept. of Piura, Peru, which were later described and figured under the same name (Berry 1927). Still later Berry (1929 b; cf. 1929 d), after having received more material from Cipacon, arrived at the conclusion that the Peruvian endocarps deserved varietal rank, being prevailingly five-carpelled (5—6), whereas the Colombian is prevailingly six-carpelled (5—8) and also differs in shape and certain of its size values. He therefore called them var. *peruviana* (1929 b, p. 155).

Berry does not in any of his papers discuss why these remains were brought to *Sacoglottis* and to no other genus of the *Humirioideae*. A certain but not close similarity to the modern *S. amazonica*, well known from previous and more recent studies on plant dispersal (see, e.g., Morris 1895, Guppy 1917, Ridley 1930), and to a Pliocene ally of the latter species from Bolivia (Berry 1922 a, b), appears to have induced him to make the generic reference without ascertaining the number of seeds per locule, a point of fundamental significance to the question. Nor did he consult Urban's detailed study of the *Humirioideae* and the figures given there (1877). The latter work was evidently also overlooked by Weyland (1938), who dealt with the species in detail and appears to have held it to be an undoubted representative of *Sacoglottis*. Weyland dissected two endocarps of the Peruvian material to ascertain their construction, but did not note any impressions of seeds.

The exterior similarity of *Sacoglottis cipaconensis* to the Brazilian fossil endocarp described above as a species of *Humiria*, is close
enough to suggest generic identity. The evidence obtained from studies of recent material supports this view. The interior agreement of the endocarps also adds weight to it. Weyland (l. c. p. 157) thus found exactly the same light brown coating in the locules of *S. cipaconensis* that I have seen in *Humiria bahiensis*. It may not be entirely wasted labour to look for the number of seeds in this material, for the rough sketches published in Weyland’s paper do show that in his material the locules were not of uniform width throughout, and they appear likely to contain impressions of the seeds, just as the Brazilian species does. His Fig. 15 of Taf. XIX (3) shows exactly the same inward bulging of the wall as Figs. 5 a. 6, and 7 of the present paper, and at the same time it is evident that the said locule cannot have ended as far from the base of the endocarp as the picture might suggest. The most likely is that these locules, too, were two-seeded. Though lacking the ultimate proof of observation on this point, I find the balance of the evidence in favour of transferring *Sacoglottis cipaconensis* to *Humiria*, irrespective of the phytogeographic consequences, which incidentally may then seem less unexpected. Whether the Peruvian form should be regarded as variety or a separate species might be a matter of taste. In order to indicate the uncertainty of the true relationship of the two forms, I prefer not to include it in the said species. If anybody still wants to take the other view, I have little objection. The transfers are listed below.

**Humiria cipaconensis** (Berry) Selling n. comb.  
(Figs. 13—17)

*Saccoglottis cipaconensis* Berry 1924 a, p. 64—66, Figs. 20—22 (p. 62), Berry 1927, p. 121 (in part), Berry 1929 b, p. 155—157 (in part), 1929 d, p. 6, Pl. 1, Figs. 1—5.


**Humiria peruviana** (Berry) Selling n. comb.  
(Figs. 18—22)

*Saccoglottis* Berry 1924, p. 65, 1929 a, p. 345.

*Saccoglottis cipaconensis* Berry 1927, p. 124 (in part), pl. 20, figs. 8—16.

*Saccoglottis cipaconensis* Weyland 1938, S. 156 (in part), 161—162, Taf. XVIII (2), Abb. 6—8, Taf. XIX (3), Fig. 8—16.

*Saccoglottis cipaconensis peruvianus* Berry 1929 b, p. 155—157 (in part), Pl. I, Figs. 14—18. (Cf. Berry 1929 d, p. 6.)

The difference between these two species is brought out in Berry 1929 b and d (cf. Figs. 13—22 of the present paper). They differ from H. bahiensis chiefly in shape, as is apparent from a comparison of Berry's figures (p. 263) with Figs. 1, 2, 5 b or 10 on p. 259.

**General Discussion.**

Modern students of the taxonomy of the genus *Humiria* appear to recognize six species, all confined to tropical South America:

*H. balsamifera* (Aubl.) St. Hil. — A tree, 15—40 m high, in forests and savannas from the Amazonas Territory of Venezuela and further east to French Guyana, south to the Rio Negro region of the Brazilian Amazonas (cf., e.g., Urban 1877, Gleason 1931, Benoist 1933, Bakhuizen 1941).

The Amazonas locality, Furos de Breves region, in Huber 1902 a, p. 498, 1902 b, p. 23, is by Ducke (1922, p. 176) considered a mistake for *H. floribunda*.

*H. Cassiquiare* Suessenguth et Bergdolt — A small tree (4—6 m high) from forests on the banks of the River Cassiquiare in southern Venezuela (Suessenguth 1935).

*H. crassifolia* Mart. — A small tree, 2.5—4 m, in the summit region of Serra de Arafa-Coara on the Peruvian border of western Brazil (Martius 1826; Bentham 1853; Urban 1877).

*H. floribunda* Mart. (Fig. 23). — A polymorphic species, no doubt deserving detailed study. Reported from a wide area in a number of varieties, some apparently rather rare and of disrupted distribution (cf., e.g., Gleason 1931), other of common occurrence. It occurs in Peru (Depts. of San Martin and Loreto), Venezuela, British Guyana, Suriname and French Guyana, and is — judging from the literature and the small material available — found comparatively far south in Brazil (Amazonas, Bahia, Matto Grosso, Minas Geraes, Pará, Rio de Janeiro). Its habit varies: shrubs (1—) 2—4 (—9) m high to trees 30 m high (cf. Ducke 1922, Bakhuizen 1941), and the same applies to its habitats: sand reefs, rocky tops, dry slopes, savannas, mountain forests, etc. At least in Pará, the species chiefly occurs in the campinas, where it is one of the leading trees (Ducke 1922).

*H. savannarum* Gleason — A lowland species of unknown habit from the Tree savannas at Esmeralda in the Cerro Duida region of Venezuela (Gleason 1931).

*H. subcrenata* Benth. — Inadequately known, and of unknown habit, gathered by Martin in Cayenne, French Guyana. (Bentham 1843, 1853, Urban 1877).

As seen from this brief survey, the genus is one of wide and sometimes disrupted distribution. This in itself suggests no small age, even though some of the gaps may be bridged by future ex-
Fig. 23. *Humiria floribunda* MART., large-leaved form from Peru: Dept. of Loreto, Balsapuerto, alt. about 220 m, in forest (tree 4 m high), Jan. 1933; G. Klug 2846 (Riksmuseum, Stockholm). — Slightly more than 1/3 (1/2.5).

Fig. 24. Tertiary occurrences of the genus *Humiria*. Colombia: *H. cipaconensis* (Berry) Selling; Peru: *H. peruviana* (Berry) Selling; Brazil: *H. bahiensis* Selling. The recent distribution of the genus comprises Peru (Depts. of San Martin and Loreto), Venezuela, the Guyanas, and Brazil south towards the tropic of Capricorn, but is not sufficiently known to deserve mapping in this connexion.
ploration. It is therefore of interest to find that the genus is well represented in the Tertiary, dispersed (see map, Fig. 24) over even greater areas than where it is now known, and that some of these fossil species (*H. cipaconensis*, *H. peruviana*) appear to belong to the earlier part of the period. As regards the western area of the genus, *H. peruviana* and the recent *H. floribunda* are the only representatives in Peru, while *H. cipaconensis* (from a locality now at an altitude of about 8000 ft in the Eastern Andes at no great distance from Bogotá) is the only Colombian representative so far discovered. Whether the fossil fruits belong to the neighbourhood of the widespread *H. floribunda*, which occurs also in the same general region as the late Tertiary *H. bahiensis* and in which similar endocarps are found, cannot be decided at present. Ample material from all the recent species must first be secured, and — a point of equal importance — described in detail. It cannot be denied that present-day taxonomic descriptions more often leave the reader in ignorance of rather important details than do those of the 19th century, thus causing obstacles — not least to the palaeobotanist — which might easily have been avoided.

**Summary.**

Of the South American genus *Humiria*, previously unknown in the fossil state, three fossil species are recognized on characteristic endocarps: *H. bahiensis* n. sp. (late Tertiary of Marahui, state of Bahia, Brazil), *H. cipaconensis* (Berry) n. comb. (early Tertiary of Cipacon, Prov. of Cundinamarca, Colombia), *H. peruviana* (Berry) n. comb. (early Tertiary of Belen, Dept. of Piura, Peru), the two latter hitherto recorded as a single species (with a variety) of *Sacoglottis*. No fossil leaves to be correlated with the genus have so far been discovered.

The construction of the endocarps is dealt with in detail. In this connexion the bearing of their valvate dehiscence to the problems of the relationships and taxonomic status of the *Humirioideae* is briefly touched.

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1 It also remains an open question whether the presence of *H. cipaconensis* does imply that the rainfall at Cipacon would have to be greater than now at the time when this species occurred there (Berry 1924 a, p. 61).
The fossil endocarps show that the genus is of considerable age and that its distribution in the Tertiary (see map, p. 266) was even wider than it is now. *H. cipaconensis* is the only either recent or fossil representative of the genus so far discovered in Colombia, and the only members of it in Peru are the early Tertiary *H. peruviana* and the recent *H. floribunda*. For lack of material, and partly for lack of detailed descriptions, it is impossible to say whether or not any of the fossil species may be considered closely allied to the latter species (which also occurs in the state of Bahia).

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TWO X-RAY INDUCED AUXO-HETEROTROPHIES.

BY

NILS FRIES.

Introduction.

In a series of physiological mutations induced by X-ray irradiation of ascospores from *Ophiostoma multiannulatum*, two mutants, i.e. Strain 225 and Strain 617 were characterized by the inability to synthesize biotin and p-aminobenzoic acid respectively. Contrary to certain mutations of different type which were isolated on several occasions, these types of physiological mutations were no more produced in any further irradiation experiment. Strain 225 and Strain 617 had retained their characteristic auxo-heterotrophies though they had been maintained in culture for 18 months and 6 months respectively, and reinoculation had been made approximately once a month. If these characteristics really were the results of mutations one is bound to assume that they were even hereditary transmissible through a series of sexual generations. That this actually is the case, will become apparent from the following statements, which also show that the induced requirement for growth substances — the induced auxo-heterotrophy — is quantitatively in fairly good agreement with that which certain other organisms normally show.

Method.

The method used for X-ray irradiation and isolation of the mutants was described in a previous paper (Fries 1945).

All strains of *Ophiostoma multiannulatum* were grown on malt agar in culture tubes (2.5 % malt extract, 1.5 % agar-agar). Tubes containing malt agar were even used in the mating experiments though the malt extract content used on these occasions was lower
because acceleration of perithecia formation was aimed at. For
the physiological experiments Erlenmeyer flasks of Jena glass of
100 ml capacity were used, each of which contained 25 ml nutrient
solution consisting of glucose, NH₄-tartrate, inorganic salts, aneurin
(vitamin B₁), and adermin (vitamin B₉) (as regards composition
see Fries l. c., p. 3). As has been shown earlier, normal strains
of Ophiostoma multiannulatum require the two last mentioned
vitamins for growth. Mutant Strain 225 required in addition biotin
which was added in the form of α-biotin-methylester supplied
by Kögl’s Laboratory in Utrecht; the p-aminobenzoic acid required
by Mutant Strain 617, was added in the form of a preparation
provided by Schering-Kahlbaum.

The Quantitative Action of Biotin and p-Aminobenzoic Acid on
the Two Mutants.

As only small quantities of biotin were available, I did not
test the effect of many different dosages of biotin on Strain 225.
Table I shows, however, that even a quantity of 5 mg per flask
(concentration 2·10^10) seems to induce optimal growth. On the
whole, growth is rather poor on all substrates — poorer than
that of strains which are physiologically normal. At any rate,
the amount of biotin reported, produced (in 10 days) a yield of

<table>
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<tr>
<th>Added per flask</th>
<th>Average dry weight of mycelium in mg after 10 days</th>
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<tbody>
<tr>
<td>0 (Control)</td>
<td>0.2</td>
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<tr>
<td>5 mg biotin</td>
<td>10.8</td>
</tr>
<tr>
<td>1 mg inositol</td>
<td>0.3</td>
</tr>
<tr>
<td>5 mg biotin + 1 mg inositol</td>
<td>9.7</td>
</tr>
<tr>
<td>100 mg malt extract</td>
<td>10.3</td>
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mycelium which quantitatively agreed almost exactly with that
obtained with 100 mg of malt extract per flask. It may be assumed
that as regards Oph. multiannulatum, the most favourable growth
response is induced with malt extract.

The action of biotin if added in very small quantities was studied
in a separate experiment. The following quantities were added
to three different series: 0.2 mg, 0.5 mg and 5 mg respectively. Since Strain 225 grew considerably slower than the majority of the biotin-heterotrophic strains in the f₁ and f₂ generations (see Fig. 2), a comparatively rapidly growing mycelium was selected out of the f₂ generation, i.e. (225 × 2) (1 × 4) 6. The chief aim of this experiment was to clarify the question whether this strain was characterized by absolute inability to synthesize biotin, and whether, this being true, biotin exercised a quantitative action. Fig. 1 shows, that a fairly large yield of mycelium was obtained in the control flasks. This was most likely caused by the fact that inoculation was made with small bits of mycelium from malt agar.
plates which, as is known, are fairly rich in biotin. At the end of two months, growth was practically completed, both in the control series and in the series in which suboptimal amounts of biotin had been added. At the end of the experiment the control flasks were found to contain 3.3 mg mycelium (dry weight), the series to which 0.2 mg biotin had been added, 4.8 mg, and the series in which 0.5 mg were present, 6.7 mg mycelium. After deduction of the control value the mycelium-biotin quotient could be calculated; it amounted to about 7,000,000. This value is in the same order of magnitude as that obtained by Lindeberg (1944) for Marasmius androsaceus and which amounted to 4,000,000.

Thus, the experiment showed that the X-ray induced mutation in Strain 225 evidently signified a complete loss of the ability to synthesize biotin, at any rate under the conditions of the experiment reported.

Strain 617 required for growth the addition of p-aminobenzoic acid, a fact which in analogy to the case just related was interpreted as a loss of the ability to build up this indispensable substance. In this case, one could not speak of complete loss of the synthesizing power because bits of mycelium after having laid for about a month in nutrient solution not containing any p-aminobenzoic acid, began to grow, though initially only slowly, but subsequently more and more rapidly. If, however, the experiment was carried on over a short period (10 days) the mycelium responded readily even to minute amounts of the vitamin. As small quantities as 0.01 γ per flask (4 × 10⁻⁹) resulted in appreciable, and 1 γ per flask (4 × 10⁸) in optimal growth (Table II).

Table II. — The Effect of p-Aminobenzoic Acid on the Growth of Strain 617.

<table>
<thead>
<tr>
<th>Quantity per flask</th>
<th>Average dry weight of mycelium in mg after 10 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 (Control)</td>
<td>0</td>
</tr>
<tr>
<td>0.001 γ</td>
<td>0</td>
</tr>
<tr>
<td>0.01 γ</td>
<td>0.4 ± 0</td>
</tr>
<tr>
<td>0.1 γ</td>
<td>15.8 ± 1.8</td>
</tr>
<tr>
<td>1 γ</td>
<td>77.0 ± 3.3</td>
</tr>
<tr>
<td>10 γ</td>
<td>87.4 ± 6.7</td>
</tr>
</tbody>
</table>

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Streptobacterium plantarum which is usually used as test organism in quantitative assays for this vitamin, responds by far more sensibly. Even a concentration of $1 : 10^{11}$ (Kuhn and Schwarz 1941) induces optimal growth.

The type of physiological mutation which Strain 617 represents, was even produced earlier, i.e. by Beadle and Tatum (1941) in irradiation experiments with Neurospora. These authors likewise exhaustively studied both its requirement of p-aminobenzoic acid and the possibilities of substituting this vitamin by several substances related to it (Tatum and Beadle 1942, cited out of the Exp. Stat. Record, 88, 1943). In this instance, complete loss of the ability to synthesize p-aminobenzoic acid had, apparently, occurred.

A fungus normally requiring p-aminobenzoic acid, does so far not seem to be known.

The Stability of the Induced Auxo-Heterotrophies.

Ophiostoma multiannulatum is bipolar heterothallic and the two incompatibility groups are in the following designed by + and −. In order to induce the formation of perithecia a one spore mycelium must be put together with another one spore mycelium belonging to the opposite group. After mating Strain 225 with Test Strain 2, representing the −-group, numerous perithecia were obtained. Strain 225 could, therefore, be classified as +-mycelium. On the other hand, Strain 617 proved to be a −-mycelium.

For the purpose of testing the heredity of the induced biotin-heterotrophy, the f₁-generation obtained from the perithecia which were formed in the combination 225 × 2, was investigated. 20 one spore mycelia, grown from spores of the perithecia mentioned, were isolated and investigated, firstly to determine their possible biotin-heterotrophy, and secondly to ascertain to which of the two incompatibility groups they should be assigned. Out of these 20 mycelia, 8 were biotin-autotrophic + -mycelia, 4 biotin-autotrophic −-mycelia, 3 biotin-heterotrophic + -mycelia, and 5 were biotin-heterotrophic −-mycelia. Though the material available was very limited it may nevertheless be deduced that the changed gene and the gene which was responsible for the classification of the mycelia in incompatibility groups, were not strongly linked.

As biotin-heterotrophic one spore mycelia of both the + - and −-type occurred in f₁ it should be possible, by means of matings
The progeny of the mating between the p-aminobenzoic-acid-heterotrophic Strain 617 (–) and Test Strain 1 (+) was studied in the same manner as described above. The hereditability of the X-ray-induced physiological property of Strain 617 was clearly demonstrated. Since this result was essentially in agreement with the results obtained on Strain 225 regarding biotin-heterotrophy, I did not consider it necessary to report these experiments in detail.

Crosses between the Mutants 225 and 617 representing opposite incompatibility groups, gave rise to perithecia. As was expected, the spores of these gave rise to four, physiologically different types of one spore mycelia. 16 strains were examined: 1 strain required biotin, 7 required p-aminobenzoic acid, 2 required both biotin and p-aminobenzoic acid and 6 did not require any of these substances.
On the other hand, if two mycelia belonging to the same incompatibility group were mated, and of which the one required biotin and the other p-aminobenzoic acid — (225 × 2) (1 × 4) 6 × 617 for instance — there occurred, of course, no perithecium formation. The mixed mycelium which originated, most likely, was of a type which would have warranted the designation miktohaplont. On the basis of the principle of “artificial symbiosis” it could be expected that this mixed mycelium would grow in a substrate in the absence of both biotin and p-aminobenzoic acid. This was also actually the case.

Attempts to induce Reversion of Mutation.

As regards mutations in morphological properties — in plants as well as in animals — various authors have demonstrated that they in several cases are reversible, i.e. the original genotype could be reformed. Was this also possible as regards the mutation to biotin-heterotrophy discussed in this paper?

The previously mentioned completely biotin-heterotrophic, perithecia-forming combination culture (225 × 2) 1 × (225 × 2) 4 offered possibilities of studying this question. A dense suspension of ascospores from perithecia grown in the culture mentioned, were X-rayed. Subsequently, the suspension of spores was diluted and transferred into several flasks containing a nutrient solution the composition of which was the usual one. Now, if in any one of the millions of X-rayed spores reversion of mutation to biotin-autotrophy had occurred, this single spore would have grown out in the biotin-free nutrient solution. In none of the culture flasks, however, did mycelia develop, a fact which warrants the assumption that no reversion of mutation had occurred.

In this connection it is in order to mention some other experiments of a similar type. They were made in the attempt to restore the ability to synthesize thiazole to the normal strain (stock culture) of Ophiostoma multiannulatum. Earlier experiments have shown that the Ophiostoma-species though in general incapable of building up the pyrimidine component of aneurin, possessed, however, the ability to synthesize its thiazole component. Out of the species studied, Ophiostoma multiannulatum was the only one which even lacked the ability to form thiazole. As this mutation might have occurred phylogenetically fairly late, it seemed to me that there might be a possibility of restituting the ability to synthesize this
substance by inducing reversion of mutation. Three experiments were made with irradiation of ascospores obtained from the stock culture. After irradiation the spores were transferred to the usual solution in which aneurin was substituted by pyrimidine alone. None of the experiments, however, yielded any thiazole-forming strain.

The demonstration of auxo-heterotrophic mutants necessitates not only the isolation of numerous one spore mycelia but also the exhaustive study of each individual one spore mycelium, whereas experiments of the type just reported readily permit of isolating possibly appearing auxo-autotrophic mutants out of a comprehensive heterotrophic material. The experiments described in this paper seem to suggest that the mutations into auxo-heterotrophy are irreversible. To furnish definite evidence that this is actually true, is, of course, a matter of great difficulty. As regards the possible irreversibility of these mutations it would, however, seem rather bold to draw definite conclusions from the negative results obtained with the limited number of experiments reported in this paper. The solution of this problem will have to await the advent of further data determining — at least approximately — the frequency of mutations of this type.

Summary.

1. Out of two X-ray induced physiological mutations in *Ophionostoma multiannulatum*, one, *Strain 225*, required the addition of *biotin*, and the other, *Strain 617*, the addition of *p-aminobenzoic acid* to the substrate. In both instances the synthesizing power which was previously doubtlessly present, was completely or almost completely lost. Owing to this fact the substances mentioned assumed the character of vitamins in relation to the two mutants.

2. The experiments showed that Strain 225 was entirely dependent on the addition of biotin and that it responded quantitatively to biotin-additions. Strain 617, however, possessed the though very weak ability to synthesize p-aminobenzoic acid.

3. The hereditability of the two auxo-heterotrophies was demonstrated.

4. The experiments to induce reversion of auxo-heterotrophy into auxo-autotrophy by means of X-ray irradiation were unsuccessful.

Institute of Physiological Botany, University of Uppsala, June 21, 1945.
LITERATURE CITED.


POLLEN MORPHOLOGY AND PLANT TAXONOMY. IV.
LABIATAE, VERBENACEAE, AND AVICENNIACEAE.

BY

G. ERDTMAN.

Labiatae.

Taxonomically *Labiatae* is considered a very hard-worked field particularly from the fact that its members, in contradistinction to the members of many other families, exhibit but a comparatively slight range of variation as to morphology and anatomy. Pollenmorphologically *Labiatae* is characterized by two pollen types, *viz.*, tri- (or tetra-) and hexacolpate grains (Fritzsche 1832, and others). A tentative rearrangement of the subfamilies and tribes of *Labiatae*, based on pollen morphology alone, has recently been proposed by Risch (1940; in this paper, however, the importance of certain minor pollenmorphological features seems to be over-emphasized, and in some cases — *e.g.* Pogostemon — the morphology of the pollen grains is not adequately described). Pollen grains, however, have been taxonomically evaluated also from reasons other than morphological. Thus in some plants the pollen grains, at the time of shedding, are binucleate whilst in other plants they are trinucleate. This is to some extent — although in some cases rather uncritically — recorded in Engler und Diels 1936. When it was published, no thorough information as to the pollen caryology in *Labiatae* was available. Such information has later been supplied by Lörner (1942). A comparison between the pollenmorphological data and the cytological facts presented by Lörner tends, as far as our present experience goes, to show that
in *Labiatae* tricolpate grains are binucleate and hexacolpate grains trinucleate (which, by the way, possibly may be due to coupled genes). Striking as is this coincidence of cytological and taxonomical features it may, eventually, support a tentative division of *Labiatae sensu Briquet* (1894—95) into the following groups, which possibly deserve the rank of subfamilies:

One group would include plants with tricolpate (or, exceptionally, tetracolpate), binucleate pollen grains, *viz.* (according to the subdivision of *Labiatae* presented in *Engler und Diels* 1936):

- **Ajugoideae (Rosmarineae excepted)**
- **Prostantheroideae**
- **Prasioideae**
- **Scutellarioideae**
- **"Stachyoideae"-Marrubieae**

The other group would include plants with hexacolpate, trinucleate pollen grains, *viz.*:

- **Ajugoideae-Rosmarineae**
- **Lavanduloideae**
- **"Stachyoideae"-Nepetae**
- **"Stachyoideae"-Brunnerlinae** (Brazoria excepted)
- **"Stachyoideae"-Salvieae**
- **"Stachyoideae"-Monardeae**

According to this tentative classification "*Stachyoideae*, "*Stachyeae*, "*Brunellinae*, and "*Pogostemoneae* include heterogeneous elements and, therefore, should not be retained as group names.

The rearrangements suggested are also supported by facts other than cytological and pollenmorphological. Thus an amalgamation of *Perilomia* and *Scutellaria* has been proposed by *Epling* (1936). *Pogostemon* differs anatomically from other *Pogostemoneae*, as *Tetradenia, Colebrookea*, and *Elsholtzia* (*Mayer* 1909). The position of *Rosmarinus* and *Lavandula* has for long been a matter of controversy (*cf. Gams in Hegi* 1927, p. 2275 and 2518). *Brazoria*, finally, was placed by *Briquet* in the same group as *Brunella* and *Cleonia*. As to the morphology of sepals and anthers etc., it has, however, several traces in common with representatives of the *Melittinae* group, *e.g.*, *Chelonopsis, Physostegia*, and *Synandra*.
**Verbenaceae.**

As to *Verbenaceae*, Junell (1934) has suggested a considerable reduction in order to make it a more natural unit. Only the nucleus *Verbenaceae-Verbenoideae* has been left within the confines of *Verbenaceae*, whilst most of the remainder of the family has been transferred to *Labiatae*. This transfer, if justifiable, would apparently have no influence on *Labiatae-Nepetoideae*, as hexacolpate grains have not been encountered in *Verbenaceae sensu Briquet*. It would, on the other hand, greatly affect the demarcation line between *Verbenaceae* and *Labiatae-Lamioideae*. A proper statement of the way in which these families abut upon each other constitutes a difficult problem which will not be discussed here, insufficient as many data, cytological, pollenmorphological, and others, still are. In future investigations, however, pollenmorphology should be able to furnish useful hints both in this connexion and in connexion with monographical studies of genera, or sections, within *Verbenaceae*, particularly *Verbenaceae-Verbenoideae*, a group which pollenmorphologically is much more diversified than *Labiatae*. A few illustrations (figs. 2—6, 8) will provide an idea of some of the possibilities in this line.

Fig. 8 exhibits a pollen grain of *Bouchea prismatica* (L.) Kuntze, Fig. 3 a grain of *Chascanum marrubiifolium* Walp. (as to the name of this species, see Sprague 1939). The genus *Bouchea* was established by Chamisso (1832), *Chascanum* by Meyer (1837). They were amalgamated by Schauer (1847), who divided *Bouchea s. lat.* into two sections, *Rhogocarpium* and *Chascanum*. Subsequent authors followed as a rule Schauer's inclusive generic interpretation of the group until Grenzebach (1926) and Moldenke (1938, 1940) treated *Bouchea* and *Chascanum* as separate genera.

Pollenmorphologically there are considerable differences between *Bouchea* and *Chascanum*. In the latter genus the pollen grains, as far as investigated, are tricolporate (fig. 3), whilst the grains in *Bouchea*, likewise as far as investigated, are usually triporate and of a rather strange appearance (fig. 8). This is the case in *B. fluminensis* (Vell.) Mold., *B. prismatica* (L.) Kuntze, and *B. Rusbyi* Mold. In contradistinction to the species mentioned, *B. linifolia* A. Gr. is provided with tetra- or pentacolpate pollen grains (average size about 75 by 65 µ) and, furthermore, with unpetiolate leaves. Closely allied to *B. linifolia* is *B. spathulata* Torr. (pollenmorphology
unknown). Future investigations will show if it is appropriate to divide Bouchea Cham. into two sections, one with colpate grains of the *linifolia*-type, the other with porate grains of the *fluminensis*-type. Pollenmorphologically this would form some sort of a parallel to the two sections in *Morina* mentioned in Erdtman 1945.

**Labiatae or Verbenaceae.**

Figs. 5 and 6 show some of the pollen types in *Caryopteris*. According to P‘ei (1932) this genus includes 15 species in Central and Eastern Asia. In China there are a dozen species which may be referred to two natural groups, viz. the *mongolica*-type with the species *Forrestii, glutinosa, incana* (*Mastacanthus*), *mongolica, tangutica, and trichosphaera*, and a second group with the species *divaricata, nepetaefolia, odorata, paniculata, siccanea, and terniflora*.

Ten of these have been investigated pollenmorphologically. *Caryopteris nepetaefolia* (Benth.) Max. and *C. terniflora* Max. have tricolpate, spheroidal grains with scattered spines (fig. 5). *Caryopteris divaricata* (S. et Z.) Max. has triporate, oblate spheroidal to subprolate grains (fig. 6) of about the same size and sculpturing as in the grains of *C. nepetaefolia*, although the ektexine is comparatively much thicker. The triporate condition is a striking feature which, no doubt, may serve to support following lines by Junell (l.c. p. 119): "Bei einer eingehenden Bearbeitung dieser Gattung wird *C. divaricata* sicher nicht in dieselbe Gattung aufgenommen werden wie die Arten von *C. incana*-Typus (*Mastacanthus*)".

*Caryopteris Forrestii* Diels (Forrest n. 10432), *C. incana* (Thunb.)

Figs. 1—8. Pollen grains in Labiatae and Verbenaceae. All × 670; 1 mm in the figures represents about 1.5 μ (for the sake of uniformity (cf. Erdtman 1944, p. 414) the figures have been drawn to the scale 1500:1 and subsequently reduced 2½ times for reproduction; the numbered sketches attached to some of the figures show the changing appearance of the sculpturing according to the adjustment of the microscope from high to low. 1: *Catopheria chiapensis* A. Gr. — Polar view; 112 μ (von Türcheim 1360); possibly the largest hexacolpate Labiatae pollen so far encountered; usually the diameter of hexacolpate Labiatae pollen is much less, about 30—40 μ. 2: *Avicennia officinalis* L. — Equatorial view; 28 × 28 μ (Schleiden 5787). 3: *Chaseanum marrubifolium* Walp. — Equatorial view; 61.5 × 55 μ (Kotschy 32). 4: *Amethystea coerulea* L. — Equatorial view; 55 μ (Karlo 257). 5: *Caryopteris nepetaefolia* (Benth.) Max. — Polar view; 55 μ (H. Smith 2270). 6: *Caryopteris divaricata* (S. et Z.) Max. — Equatorial view; 61 × 67 μ (cult., Uppsala, 1987). 7: *Pogostemon auriculata* Hook. — Equatorial (21 × 17 μ) and polar (19 μ) view (Java 1897; E. Nyman s. n.). 8: *Bouchea prismatica* (L.) Kuntze. — Equatorial view; 140 by 76 μ (Colombia, 1826; Bot. Mus. Ups.); the average size of the grains is bigger — about 155 × 95 μ — than in the grain figured.
Miq. (Tsushima, Sept. 1912; Riksmuseum, Stockholm), *C. mongolica* Bge (leg. Tatarinow; ibid.), *C. odorata* (Buch.-Ham.) B. L. Robins. (Stewart 1560), *C. paniculata* (Kurz.) Clarke (Henry 10408 A), *C. tangutica* Max. (H. Smith 12238), and *C. trichosphaera* W. W. Sm. (Forrest 18990) have tricolpate grains, either apparently smooth (*C. mongolica*), provided with a faint reticulation (*C. incana, C. tangutica*), or thickly beset with minute, faintly sloping conical elements (*C. odorata*). The grains are subprolate, except in *C. odorata*, where they are prolate.

On pollenmorphological as well as on other evidence, *Amethystea coerulea* L. (cf. fig. 4) ought to be closely related with and, consequently, placed in the same family as *Caryopteris nepetaefolia* and *C. terniflora*. Briquet refers *Amethystea* to Labiatae (1895), *Caryopteris* to Verbenaceae (1894). Arguments will not be presented here as to which family these plants should rightly belong. It is evident, however, that an eventual transfer of *Caryopteris* — including *C. divaricata* — to Labiatae would lessen the remarkable pollenmorphological uniformity of that family. The triporate condition of the pollen grains in *C. divaricata* may possibly be regarded as an extreme development of the tricolpate pollen type in *C. nepetaefolia* just as the apparently triporate grains in *Bouchea prismatica* etc. (cf. fig. 8) may be regarded as an extreme development of the tricolporate grains in *Chascanum* (fig. 3).

**Avicenniaceae.**

A few words ought finally to be said about *Avicennia*. Arguments have recently been put forward for its being referred to Labiatae (Junell l. c.). So much, however, does *Avicennia* deviate from the true Labiatae stock, pollenmorphologically (cf. fig. 2) as well as in other respects, that it probably should be regarded as forming a family of its own. This idea was foreshadowed by Endlicher more than a century ago and was later adopted by van Tieghem (1898) and others.

The author is indebted to Dr E. Asplund and Professor E. Hultén, Stockholm, to Professor J. A. Nannfeldt and Dr H. Smith, Uppsala, and to Professor W. Wright Smith, Edinburgh, for information, herbarium facilities, and material for study.
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POLLEN MORPHOLOGY AND PLANT TAXONOMY. V.
ON THE OCCURRENCE OF TETRADS AND DYADS.

BY
G. ERDTMAN.

Nearly a century ago H. G. REICHENBACH (1852) published a thesis on the pollen grains in Orchidaceae. In this thesis single pollen grains are termed monads, whereas composite grains made up of two, three, four, six, eight etc. grains are aptly styled dyads, triads, tetrads, hexads, octads, etc. REICHENBACH's thesis, however, seems to have landed in the dead-letter office, for pollen morphologists as FISCHER and WODEHOUSE do not mention it in their treatises on pollen. In the present paper an attempt will be made to save some of REICHENBACH's terms from oblivion; monads, for example, ought in special cases to be a very convenient term. The main purpose of the paper is, however, to provide a list of plants with pollen grains united in pairs into dyads or in fours into tetrads. The list, as given here, is admittedly incomplete and of a preliminary character only. Its publication may, nevertheless, be justified since misleading statements as to the occurrence of tetrads and dyads are still to be found even in modern text-books. It is hoped, moreover, that the list may stimulate others to extend and render more precise our knowledge of this meeting-ground, often debated but poorly explored, of pollenmorphological, cytological, and taxonomical ratiocinations.

1 In cytology the terms monad, dyad, triad, pentad, ... polyad denote the number of cells originating by meiosis from one pollen mother cell. Consequently a tetrad, cytologically speaking, may not be the same as a tetrad in a pollen-morphological sense, etc. For the moment this state of affairs can be maintained without much inconvenience. A growing collaboration between cytologists and pollen morphologists may, however, be anticipated. In consequence the terminology should be revised in order to eliminate any possibility of misunderstanding in the future.
The families, where plants with pollen tetrads or pollen dyads occur, are cited in alphabetical order. The names of the families are in accordance with Engler und Diels (1936). If the occurrence of tetrads or dyads has been announced several times only the oldest record encountered is usually cited. The nomenclature is in conformity with Index Kewensis or later publications (thus Anona tripetala mentioned by Fritzsche in 1837, is quoted as Annona Cherimolia Mill., etc.). An asterisk indicates that the species thus marked is represented in the author’s collection of pollen slides. Roman figures denote the type of tetrad in accordance with fig. 1.

![Fig. 1. Different types of tetrads. I: tetrahedral tetrad; II: cross tetrad; III: square tetrad; IV: rhomboidal tetrad; V: linear tetrad.](image)

**ACTINIDIACEAE.**
*Saurauia elegans* (Choisy) F.-Vill. (Luzon: Van Overbergh 379). — Erdtman 1938; types I, II.

[Tetrads do not occur in *S. brachybotrys* Turcz., *S. cauliflora* DC., *S. oligolepis* Miq.]

**AMARYLLIDACEAE.**
*Fourcroya Bedinghausii* K. Koch (Mexico: Pringle 6669). — Type III.
*F. gigantea* Vent. (cult. Copenhagen 1932). — Type III.
*F. longaeva* Karw. et Zucc. — Mohl 1834.

**ANNONACEAE.**
*Annona Cherimolia* Mill. — Fritzsche 1837, tab. IV: 7 (type III); Samuelsson 1914 (types III, IV).
*A. reticulata* L. — Fischer 1890 (type III).

*Monodora Myristica* Dum. (Kamerun: Mildbraed 4530). — Type III.
*Uvariodendron* R. E. Fr. — »Pollinis cellulis in tetradibus uniserialiter dispositae» (Fries 1930, p. 51).

Acc. to Martius (1856, Tab. VII: 12) Hornschuchia Bryotrophe Nees has pollen composed >e globulis sub-16, quorum 8 in centro, 8 in peripheria collocaeti sunt<. Acc. to S. J. Golub »the pollen of the Annonaceae not infrequently tends to be more or less coherent in tetragonal tetrads at the time of shedding» (Bailey and Nast 1942) [quoted from a letter from Mrs S. Watson Smith; the original publication not available].

**APOCYNACEAE.**
*Willoughbya globosa* Elm. (Luzon: Elmer 15199). — Types I, II.

Tetrads, furthermore, characterize the genera of the Apocynoideae subfamily (cf. Woodson 1930), viz., Apocynum L., Poacynum Bail., and Trachomilum Woodson. Examples:
*Apocynum androsaemifolium* L. — Koelreuter 1811; type III.
*Trachomitum venetum* (L.) Woodson (Batum: Holmberg 2259). — Type III.

ARACEAE.
*Caladinter striatipes* Schott (Paraguay; Jorgensen 4023). — Type III

ASCLEPIADACEAE.
Tetrads characterize the Periplocoideae subfamily: »Massae pollinis 5—20, granulosae (granulis e sphaerulis 4 compositis) [Brown 1809; cf. also Koelreuter 1811 (»conventui exhib. die 11 Januarii 1804»; tetrads in Periploca africana L.). Examples:

Atherandra pubescens Bl. — Blume 1849—51 (types IV, V).
*Curroria decidua* Planch. (S v Afr.: Dietzel 4211). — Type I.

BERBERIDACEAE.
*Podophyllum Emodi* Wall. — Fischer 1890 (type I); tetrads of type II are also found.

BIGNONIACEAE.
*Catalpa bignonioides* Walt. — Purkinje 1830, tab. IX: 15 (type I).
*P. graeca* L. (Bithynia: Bornmüller May 1929). — Mohl 1834; types I, IV (Drahowzal 1936, p. 259: »In 210 von 300 Fällen lagen die Pollenkörner einer Tetrade in einer Ebene, in den übrigen Fällen waren sie anähnend tetraedrisch vereinigt»); cf. also Bourge 1892.

CHLAENACEAE.
*Eremolaena Humblotiana* Bail. — Smith 1934.
E. rotundifolia P. Dansdy — Smith 1. c.
*Rhodolaena parviflora* F. Gerard. — Smith 1. c.; tetrad »easily separated«.
Fig. 2. *SclerooIaena Richardi* BailL., pollen tetrads. A: tetrad in the same position as the tetrad Fig. 1: 1. The central triangular area represents the distal polar cap of the upper grain. Broken lines mark the boundaries between the three lower grains. B: the same tetrad as in A, seen from underneath. Three distal polar caps appear in NW, NE, and S, respectively. The fourth cap is represented by the central triangle (sides marked by broken lines). There are six equatorial germinal apertures in all. The central, upper and greater part of Fig. 2 A is occupied by one grain, whilst the corresponding part in Fig. 2 B is made up from parts of three different pollen grains [the pollen boundaries within that area are marked by hatched radii (N, SW, and SE)].

*Schizolaena cauliflora* Dup. Ehs. — Smith l. c.; tetrad »rather easily separated». *Scleroooloaena Richardi* BailL. (*Xylochlaena Richardii* BailL.). — Type I.

Material of *Scleroooloaena Richardi* was supplied by Prof. Humbert through the good offices of Prof. Skottsb erg. Its pollen grains are firmly united in tetrahedral tetrads (Fig. 2). Schumann (1895) regarded the tetrads as single grains (»ihre Gestalt is bei allen untersuchten Gattungen gleich, kugelförmig und von 6 tiefen Furchen durchlaufen, die nach den Kanten eines Tetraeders geordnet sind«), whilst Smith (l. c.) regarded them as »tetraquartets» constituted from 16 grains (»the outer wall which covers the four quartets probably represents the modified spore-mother cell wall«; l. c. p 85). According to Smith »tetraquartets» also occur in *Lep-tolaena multiflora* Thou., *Rhodolaena Bakeriana BailL., Sarcolaena codo-nochlamys Baker, S. multiflora Thou., and *Xerochlamys Bojeriana BailL.*

The *Chlaoenaceae* family was established by Du Petit-Thouars (1806), who, although tentatively, referred it to *Malvales*. It seems, however, to have more in common with *Theales* (cf., e. g., *BailLON 1873*).

**CUCURBITACEAE.**


Mohl (1834) describes tetrads in *Citrullus Colocynthis* (L.) Schrad., whilst Griebel (1931) mentions tetrads in (cf.) *C. vulgaris* Schrad. As a rule, however, there are no permanent tetrads in these species.

[DATISCACEAE and DIDIEREACEAE].

[According to old statements (Koelreuter 1811 and Schnizlein, 1843—70, Taf. 184: 8) the grains of *Datisca cannabina* L. are united in loose tetrads.

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Acc. to Mohl (1834) and the testimony of my pollen slides the grains of this species are not coherent.

Loose tetrahedral tetrads have been observed in *Didierea madagascariensis* Bail. (Madagascar: Decary 3352; material supplied by Prof. Humbert); it is uncertain whether the mature grains are united into tetrads or not.[

**DROSERACEAE.**

The pollen grains are, as far as is known, firmly united into tetrads, except in *Drosophyllum lusitanicum* Link (Lang 1901), the taxonomically most isolated member of the family.

**EMPETRACEAE.**

As far as is known the pollen grains are always united into tetrads, usually with the grains in tetrahedral arrangement; cf., e. g., Mohl 1834 and Gray 1848 (Tab. I: 5: *Corema Conradi* Torr.; types I, II).

**EPACRIDACEAE.**

In several genera, e. g., *Dracophyllum, Epacris,* and *Prionotes,* the pollen grains are united into tetrads of the same type as in *Empetraceae* and *Ericaceae.* Archeria is provided with loose tetrads (Granwell 1942). In *Styphelia* both tetrads and monads occur, tetrads e. g., in *S. Tameianae* (Cham. & Schl.) F. Müell. (Kruai, T. H., 1938: Selling) and *S. Douglasii* (A. Gr.) F. Müell. (Selling mscr.), monads in *S. triflora* Andr. and *S. tubiflora* Sm. (Mohl 1834). — The occurrence of both monads and tetrads in this family was first mentioned by Brown (1810). Further references to the pollen morphology is found in other taxonomical papers and in Purkinje (1830), Fritzche (1832), Schnizein (1843—1870), etc.

**ERICACEAE.**

The pollen grains are as a rule united into tetrads (type I; less often types II and IV). The occurrence of tetrads was already mentioned by Koelreuter (1761; cf. also Koelreuter 1811 and Mirbel 1815). Fischer (1890) frequently encountered dyads and triads in *Erica spp.* Monads occur in *Blaceria ericoides* L. (Mohl 1834), *Brackenthalia sp* califolia Rchb. (Mohl l. c.), *Erica stricta* Donn. (Samuelsson 1913) and *Salaxis flexuosa* Klotzsch (Pl. Schlecht. 10474; *S. octandra* Klotzsch and *S. Sieberi* Benth. have tetrads).

**GENTIANACEAE.**

Pollen tetrads were already observed by Martius (1826). According to Gilg (1895) tetrads characterize the Helieae group (cf. also Köhler 1905), e. g., *Helia brevifolia* Cham. (Rio Grande do Sul 1902: Malme; type I) and *Prepsa connata* Gardn. (Köhler i. c., fig. 26; type II).

**GOODENIACEAE.**

In this family only the species belonging to the genus *Leschenaultia* R. Br. are characterized by tetrads (Pollinis granula in omnibus speciebus e 4-sphaerulis coalitis composita, quà notā, minutaquamvis, optimo dis-
tinguntur a reliquis ordinis, et praesertim a genere finitimo Anthotio« (Brown 1810, p. 581), e. g., *L. biloba* Lindl., *L. formosa* R. Br. (Fritzsche 1837, Tab. VI: 10), *L. laricina* Lindl., and *L. linarioides* DC.

**HYDROCHARITACEAE.**


*Halophila Thourars.* — Goebel 1923, p. 1709, 1711.

[In *Elodea callitrichoides* (Rich.) Casp., *E. densa* Casp. (cf. Holm 1885, p. 21), and *E. Matthewsii* (Planch.) St. John the pollen grains are not united in tetrads.]

**HYDROSTACHYACEAE.**

*Hydrostachys verruculosa* A. Juss. (Madagascar 2. IX. 1912: Afzelius; types I, IV). — Warming 1891.

**JUNCACEAE.**

Tetrahedral tetrads (cf., e. g., Mohl 1834) occur throughout, e. g., in *Prionium Palmira* E. Mey.

**LACTORIDACEAE.**


**LEGUMINOSAE.**

Compound grains of plants belonging to this family have been described by Engler (1876), Wodehouse (1935), and others. Examples of species with pollen tetrads:

*Acacia dealbata* Link (Melbourne 1936: Mauritson s.n.). — Type I.

Ina spp. — Cf. Wodehouse l. c., p. 430.

*Mimosa casta* L. — Rosanoff 1865—66; diameter of tetrads 9.8 μ (»tetrades perminutae»).

*M. hirsuta* Spreng. — Rosanoff l. c.

*M. laxiflora* Bth. (Mexico 1936: Scott 2343).

*M. pudica* L. — Rosanoff 1865—66; tetrads were, however, sketched more than half a century earlier by F. Bauer (cf. Wodehouse l. c., p. 34).

*M. verrucosa* Bth. — Engler 1876 (type III).

*Schrankia angustata* Torr. & Gray — Engler l. c. (type III).

*S. uncinata* Willd. — Rosanoff l. c.

Vachellia. — Cf. Wodehouse l. c., p. 430.

**MAGNOLIACEAE.**

*Drimys Winteri* Forst. — Mohl 1834 (type I).

In »Winteraceae« tetrads occur throughout (cf. Bayley and Nast 1943, 1945).

**MONIMIACEAE.**


**MYROTHAMNACEAE.**

NEPENTHACEAE.
As far as is known the pollen grains are united into more or less 
»droseroid« tetrads (cf. SCHNIZLEIN 1843—70, vol. II, Taf. 115:7, and STERN 1916, p. 235); in the species mentioned below the tetrads are of type I, less frequently of type II.
*Nepenthes alata* Blanco (Luzon: van Overbergh 53).
*N. Phyllanthora* Willd. (Ambonäa).
*N. Vieillardii* Hook. f. (New Caled.: Bonatti 17).

NYMPHAEACEAE.
*Victoria regia* Lindl. — Fischer 1890 (type I); cf. also ERDTMAN 1943 (fig. 268, p. 113, sub nom. *V. Cruziana*).

OENOTHERACEAE.
*Boisduvalia densiflora* S. Wats. — RAIMANN 1893.
*Epilobium hirsulum* L. — Loose tetrads, acc. to MOHL (1834) and Dra-howzal (1936).
*[E. montanum* L. — Loose tetrads, acc. to MOHL (l. c.) and Biourge (1892); author’s collection: monads].
*E. parviflorum* Schreb. — RAIMANN l. c.
*E. roseum* Schreb. — Triads acc. to Hassall (1842), monads acc. to Fischer (1890), tetrads acc. to Drahowzal (l. c).
*Jussieuia erecta* L. — MOHL l. c.
*[J. suffruticosa* L. — Tetrads acc. to Fischer (l. c.); monads or tetrads acc. to RAIMANN (l. c.); author’s collection: monads (monads also occur in *J. grandiflora* R. & P.)].
*Zauschneria californica* Presl. — GOEBEL 1927.

ORCHIDACEAE.
References to the occurrence of pollen tetrads are often found in the literature as taxonomists recognized at an early date the importance of pollen investigations in this family [cf., e.g., BROWN 1810, KOELBEUTER 1811 (tetrads in Neottia Nidus-avis), RICHARD 1818 (types I, III, IV), BISCHOFF 1833, MOHL 1834, REICHENBACH 1832, GUIGNARD 1882, etc.]. The first observations on the occurrence of tetrads in Orchidaceae were probably those of FRANCIS BAUER. In 1791, he commenced the sketches to BAUER 1830—1838 and a large number of them, particularly those of European species, was executed between 1791 and 1798. The tetrads illustrated belong mostly to types II and IV, less often to type I. A tetrad of Satyrium erectum Sw., shown in Tab. VIII, shows a pollen tube protruding from one of the grains. Tab. X: 9 shows tetrads of *Vanilla planifolia* ANDR. [types I, III, IV; this seems, in fact, to be a more natural state of affairs than the pollenmorphological features (triporate monads) briefly mentioned by myself (ERDTMAN 1944) as a result of a series of observations on pollen slides of *Vanillae*; the matter certainly merits further investigation].

PEDALIACEAE.
*Sesamothamnus Lugardii* N. E. Br. — BREMEKAMP 1942 (type I).
PHILYDRACEAE.

*Philydrum lanuginosum* Banks — Fritzsch 1837, Tab. IV: 8 (type III).

PODOSTEMONACEAE.

A part of the genera is characterized by monads, another part by dyads. Acc. to Schinzlein (1843—70, vol. II, Tab. 85: 14), Warming (1882—1901), and Engler (1930) the latter is the case in, e. g., Anastrophaea, Cladopus Nymani Engl., Dicræa elongata (Gardn.) Tulk., Dicræanthus africanus Engl., Hydrobryum, Inversodicræa minima Engl., Mniopsis Glazioviana Warmg., Pohliella laciniata Engl., Podostemon [e. g., *P. selaginoides* (Wedd.) Michx.], Polypleurum Schmidliana Warming, Saxicolella nana Engl., and Zeylanidium olivaceum (Gardn.) Engl.

In some species, e. g., Leiothylax Quangensis (Engl.) Warming, and Lophogyne aureifera Tulk. et Wedd. the pollen grains are either single or united into pairs (Warming 1888, 1899).

PYROLACEAE.

Tetrads have been described by Koelreuter (1811; *Pyrola rotundifolia* L.), Schinzlein [1843—70, vol. II, Tab. 161: 18, 19; Chimaphila umbellata (L.) Barton], and others. In addition, tetrads are found in *Moneses uniflora* (L.) A. Gr., *Pyrola aphylla* Sm., *P. chlorantha* Sw., *P. media* Sw., *P. minor* L., etc.


RUBIACEAE.

Cacasia. — Fagerlind 1942.


G. Brighamii Mann — Selling mscr. (type I).

*G. jasminoides* Ellis (Kiusiu 30.6. 1908). — Type I.


*Oxyanthus speciosus* DC. — Fritzsch 1837 (Tab. VII: 5; type I); the tetrads of this species were already sketched by F. Bauer (cf. Wodehouse 1935, p. 33).


*»R. obcordata* Wats.» (Mexico; Gentry 2269). — Types I—Ill.

SAPINDACEAE.

Tetrads have apparently only been found in Magonia (Radlkofer 1933), e g., *M. glabrata* A. St. Hil. and *M. pubescens* A. St. Hil.

SAXIFRAGACEAE.

*Carpodetus serratus* Forst. (N. Zeal. 1874: S. Berggren s. n.; type I; tetrads of about the same size and shape as the tetrads in Ericales). — Cranwell 1942.
The taxonomic position of *Carpodetus* has been much debated and still remains unsettled.

**Scheuchzeriaceae.**
*Scheuchzeria palustris* L. — Dyads (cf. Pohl 1929).

**Solanaceae.**
*Petunia nyctaginiflora* Juss. — Levant 1942 (in 11 among 34 cultivated plants the ripe pollen, after the dehiscence of the anthers, still remained hanging together in tetrads).
*Salpiglossis sinuata* R. et P. — Hassall 1842.

**Thurniaceae.**
*Thurnia Jenmani* Hook. f. — Erdtman 1944.
*Thurnia* ought no doubt to be included in *Juncaceae*.

**Typhaceae.**
*Typha latifolia* L. — Koelreuter 1811.
*T. minima* Hoppe — Mohl 1834.
*T. Shuttleworthii* Koch et Sonder. — Goebel 1880.

**Velloziaceae.**
*Vellozia aloefolia* Mart. — Mohl 1834 (types II, III). [*V. elegans* Talbot has monads.]

**Appendix. Tetrads and dyads of gymnosperms and archegoniates.**

*Glyptostrobus.* — »The grains of *Glyptostrobus* which are sometimes united in tetrads, are joined together by their dorsal surfaces, each with its pore facing outward« (Wodehouse 1935).

*Selaginella deflexa* Brack.—Selling 1945 (ill.). Also single spores. In Hawaiian Late Quaternary deposits both tetrads and monads occur (l. c.).
*S. rupestris* Spring — This is, according to Graustein (1930), an apogamous species with microspores in dyads »like many apogamous angiosperms«.
*S. selaginoides* (L.) Link — Cf., e. g., Erdtman 1914, fig. 488, p. 149. The spores also occur singly. In Late Quaternary deposits both tetrads and monads of this species have been found.

*Notothyllas.* — »Sporae quaternatim aggregatae« (Sullivan 1847, p. 64).
*Sphaerocarpus terrestris* (Mich.) Sm. — Cf., e. g., Goebel 1918.
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SMÄRRE UPPSATSER OCH MEDDELANDEN.

Föreningens medlemmar uppmanas att till denna avdelning insända meddelanden om märkliga växtfynd o. d.

Elodea canadensis funnen i Jämtland.


Genom fiske känner jag väl dessa delar av sjön fram t. o. m. 1922. Växten var då fullständigt okänd härstadies. Det är tänkbart, att den inkommit till sjön med det älyngel, som utplanterats i Alsensjön. Älynglet brukar komma från Trollhätta täckt av «nate» (mest Potamogeton perfoliatus), och i packningsmaterialet kunna Elodea-skott lätt ha medföljt. Arten finns som bekant på flera ställen i Värner och Göta älv [jfr utbredningskartan hos G. Samuelsson i Acta Phytogeogr. Suec. VI (1934)].

Summary. — Elodea canadensis found in the Prov. of Jämtland, Sweden. In summer, 1944, the species was found by the author in Lake Alsensjön, par. of Alsen, about 30 km NW of Östersund. It must have been introduced during the last 23 years, possibly with eel fry. As to the hitherto known range of the species in Sweden, see map in Samuelsson, Acta Phytogeogr. Suec. VI (1934), p. 120.

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