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CONTENTS

BOTANY VOLUME 3

No. 1. A revision of the genera Buchenavia and Ramatuella. By A. W. Exell and C. A. Stace

No. 2. The diatom genus Capartogramma and the identity of Schizostauron. By R. Ross

No. 3. Angiosperms of the Cambridge Annobon Island Expedition. By A. W. Exell

No. 4. A revision of the genus Petrorhagia. By P. W. Ball and V. H. Heywood

No. 5. Marine algae of Gough Island. By Yvonne M. Chamberlain

No. 6. The Ceylon species of Asplenium. By W. A. Sledge

Index to Volume 3

PAGE

1
47
93
119
173
233
279
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A. W. EXELL
AND
C. A. STACE

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A REVISION OF THE GENERA
BUCHENAVIA AND RAMATUELLA

By A. W. EXELL and C. A. STACE

The two genera Buchenavia Eichl. and Ramatuella Kunth are confined to tropical America, in common with two other genera of the family Combretaceae (Bucida and Thiloa). While one of us (C. A. S.) was undertaking a detailed study of the cuticular anatomy of Buchenavia and Ramatuella, as part of a comprehensive survey of the whole family, it became apparent that the taxonomy of the former genus was badly in need of revision. Although twenty-eight specific names had appeared under Buchenavia it had never been revised. Since certain changes in the taxonomy of Ramatuella also seemed advisable, a joint revision of both genera was undertaken.

As many of the earlier, and some of the later, species of Buchenavia and Ramatuella have been very inadequately described, and the discovery of new species has revealed further characters of diagnostic significance, descriptions of all the species of these two genera are included in this paper.

Our work is based mainly on the collections in the herbaria of the British Museum (Natural History) (BM) and the Royal Botanic Gardens, Kew (K). Loans were also received from the Chicago Natural History Museum (F), Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad (LE), Botanische Staats-sammlung, Munich (M), New York Botanical Garden (NY), Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris (P), U.S. National Museum, Washington (US), and Naturhistorisches Museum, Vienna (W). We are grateful to the Directors of these Institutions, and especially to the Botanical Institute of the Academy of Sciences of the U.S.S.R., and to Dr. J. Cuatrecasas of Washington, for the donation to the British Museum of duplicate specimens. Concurrently with the commencement of this revision a fairly large and very useful collection of the two genera concerned was received at the British Museum from the Instituto Agronómico do Norte, Belém, Brazil (IAN).

The abbreviations indicated parenthetically above are used in the citation of specimens throughout the paper. Other institutions cited are: Natuurwetenschappelijk Museum, Antwerp (AWH); Botanisches Museum, Berlin (B); Jardin Botanique de l'État, Brussels (BR); Museu Paraense Emílio Goeldi, Belém (MG); Jardim Botânico, Rio de Janeiro (RB); Botanical Department, Naturhistoriska Riksmusem, Stockholm (S).

1 During this investigation C. A. S. was receiving a grant from the Department of Scientific and Industrial Research, for which he is most grateful.
BUCHENAVIA Eichl.

Buchenavia Eichl. in Flora 49:164 (1866); in Mart., Fl. Brasil. 14 (2): 95 (1867).

Type: B. capitata (Vahl) Eichl.

Buchenavia belongs to the tribe Terminalieae of the family Combretaceae and is most closely related to Terminalia, from which it differs in that the filaments of the stamens are adnate to the back of the anthers and the calyx lobes are only very slightly or scarcely all developed. In Terminalia the anthers are versatile and the calyx lobes well developed, usually triangular in shape and acute at the apex.

As in all genera of the Combretaceae except Strephonema, the "receptacle" of Buchenavia is composed of two morphological components: an upper portion ("upper receptacle" or "calyx tube"), cup-shaped in this genus (sometimes considerably elongated in Combretum and Quisqualis), and a lower portion ("lower receptacle") surrounding and fused with the ovary and (in this genus) extended above it. As it is usually not easy or possible to ascertain from gross morphological studies which part of the "upper receptacle" is in fact receptacular rather than appendicular (although in Laguncularia and Lumnitzera the presence of adnate bracteoles indicates the probable receptacular origin of at least part of that organ), we have used the term "hypanthium" rather than "receptacle". In Buchenavia the cupuliform upper hypanthium is almost always broader than long and bears five scarcely developed calyx lobes, ten stamens, no petals, and a well-developed hairy disk. It is usually more elongate (i.e. campanulate) in Terminalia. The lower hypanthium is also characteristic in Buchenavia, consisting of a proximal portion surrounding the sessile ovary and a distal portion tapering from the apex of the ovary and simulating a pedicel, bearing the upper hypanthium at its apex. In most species the portion surrounding the ovary is pubescent, while the distal portion and the whole of the outside of the upper hypanthium are glabrous or almost so. In one or two species, however, the lower portion is also glabrous. In Terminalia the whole hypanthium is usually uniformly hairy or (less often) glabrous, but a few species have the Buchenavia pattern of indumentum. Some species of Terminalia possess a lower hypanthium shaped as in Buchenavia, but the majority lack the long pedicel-like distal portion.

Eichler (1866, 1867) included eight species in the genus: one (B. capitata (Vahl) Eichl.) previously known in Bucida and also in Terminalia; one (B. oxyarpa (Mart.) Eichl.) previously known in Terminalia; and the other six newly described. Since then twenty additional names have appeared in the literature (three of these being nomina nuda, the rest validly published) but the genus has not been revised. Out of the 25 valid names we recognize 21 species, and we also describe three additional ones. From various herbarium specimens we have seen it seems that there may be several more awaiting description but they are at present insufficiently known.

The genus is confined to but fairly widespread in tropical America where it is centred on the Amazon basin (see Figs. 1, 2). It occurs throughout the West Indies (one species) from Cuba (within 150 kilometres south of the Tropic of Cancer) to
Trinidad; in Panama (one species); Venezuela (five species); Colombia (five species); the Guianas (four species); Brazil (twenty species); Peru (two species); and Bolivia (one species). One outlying species (*B. kleinii*) occurs 500 kilometres

![Map of the distribution of Buchenavia and Ramatuella species](image-url)

**Fig. 1.** Distribution of Buchenavia (part) and Ramatuella: 1, *B. capitata* (insular); 2, *B. parvifolia*; 3, *B. kleinii*; 4, *B. ochroprunna*; 5, *Ramuella* (all species); C, *B. capitata* (continental); S, *B. sericocarpa*. 
south of the Tropic of Capricorn in southern Brazil. This distribution pattern follows that of the family as a whole (in the New World) and is a typical pattern for a predominantly tropical group. The largest two genera, *Combretum* and *Terminalia*, are almost pantropical; the two small genera *Laguncularia* and *Conocarpus* are found on both sides of the Atlantic; *Buchenavia* is the largest genus of *Combretaceae* confined to one hemisphere, this being due no doubt to the well-known phenomenon of prolific speciation in the Amazonian forest region; *Bucida*, *Ramatuella* and *Thiloa*, the other three American genera, are also confined to the New World.
Eichler (1866) recognized two groups of species in *Buchenavia*: "Flores fructusque capitati" and "Flores fructusque vel saltum fructus spicati". It is still possible to recognize these two groups with ease, and we have used this character in the key. We have refrained, however, from giving the two groups taxonomic status, since there appear to be no other constant differences between them, and from a study of other genera in the *Combretaceae* (especially *Combretum*) it seems that the capitate inflorescence has arisen on several separate occasions in rather distantly related groups. Furthermore, the capitate *B. sericocarpa* is otherwise almost identical (as far as we can tell) with the spicate *B. acuminata*.

In the flowering state it is usually very easy to distinguish between species of the two groups, as the inflorescences of one are long and slender, the flowers in many cases being well separated from each other, while in the other group the flowers are crowded together on a rhachis rarely as long as the peduncle. In the fruiting state the distinction is no more difficult, although usually very few fruits reach maturity in each infructescence. The presence of a spicate inflorescence is, however, always evident, even when the peduncle bears but a single fruit, since the scars of the fallen flowers may be seen at intervals along the rhachis. In this spicate group the rhachis often elongates considerably during ripening of the fruits.

Much of the difficulty encountered in the genus is due to the incompleteness of our knowledge of several species which are known from fruits and leaves or from flowers and leaves only. The leaves are frequently of a very different appearance at flowering and fruiting stages. Fortunately, although the fruits of *Buchenavia* do not differ from those of *Terminalia* as a whole, all the American species of the latter genus apparently have conspicuously winged fruits, while all species of *Buchenavia* have fruits without wings or with very narrow ones. The greatest development of wings is shown by *B. pterocarpa* and *B. punctata*. In using this character to separate the two genera, the only possible source of error would be in the case of *Terminalia catappa*, now widespread in tropical America, but this is an introduced Asiatic and Australasian species easily recognizable by its large thin obovate leaves usually with a cordate or subcordate base.

*Buchenavia* species are shrubs or trees from about three to fifty metres tall. Ecologically they may apparently be roughly divided into two main groups: small trees or shrubs of lowland forest often inundated by water, frequently growing on river banks, by lakes and in swamps; and tall trees of more upland rain forest. The latter are said to flower "very seldom" (Ducke in Bol. Téc. Inst. Agron. Norte 4: 25 (1945)).

**Key to the Species**

In the following key we have used the characters which are most likely to be present on herbarium specimens: thus, unless absolutely necessary, fruit characters alone are not used. This has sometimes resulted in long couplets citing exceptions but is thought to be justified by the added usefulness in identifying incomplete specimens. The flowers unfortunately appear to be of very little taxonomic help in this genus. As in the descriptions, the terms "tomentellous" (a diminutive of "tomentose") and "puberulous" (a diminutive of "pubescent") are taken to

BOT. 3, 1.
indicate not a lesser amount of indumentum but a shorter length of the hairs. "Pseudostipe" indicates a stalk-like basal portion of the fruit, a true pedicel being absent. Leaf length always includes the petiole (except, of course, when leaf-lamina is specified). In cases where the lamina is decurrent into the petiole it is not feasible to determine an exact point at which to distinguish between them. We have occasionally referred to the indumentum (or lack of indumentum) of the "ovary", this being merely a short way of saying "that part of the lower hypan-thium enclosing the ovary". This part usually differs in indumentum from the apical narrowed part.

Flowers in short ovoid or capitate spikes usually less than 1·5 cm. long; peduncle usually longer than the rhachis; spikes not elongating in fruit:

Fruit glabrous or rarely very sparsely pubescent:

Leaf-lamina coriaceous when mature, c. 2–8 × 1–4 cm., narrowly to broadly obovate; major lateral nerves rather conspicuous, c. 2–6 pairs; petiole c. 4–20 mm. long, usually rather stout; peduncle slender or stout; flowers with densely pubescent ovary; fruit 18–30 × 10–20 mm.; endocarp markedly longitudinally ridged; smallest twigs rather stout (widespread throughout tropical America from Cuba to S. Brazil).

1. B. capitata

Leaf-lamina chartaceous when mature, c. 1·5–4 × 0·5–2 cm., narrowly to broadly obovate; major lateral nerves rather inconspicuous, c. 5–12 pairs; petiole c. 2–5 mm. long, slender; peduncle slender; flowers with glabrous ovary; fruit 14–20 × 8–12 mm.; endocarp indistinctly longitudinally ridged; smallest twigs very slender (Amazon and Orinoco basins only)

2. B. parvifolia

Fruit pubescent or puberulous:

Fruit densely but minutely puberulous, obtuse or acute at the apex; leaves obovate, usually broadly so, rounded, obtuse or rarely very shortly apiculate at the apex (S. Brazil only)

3. B. kleinii

Fruit densely tomentose; leaves narrowly to broadly obovate, rounded to long-acuminate at the apex (N. Brazil only):

Fruit silvery- or grey-tomentose, obtuse at the apex, smooth-surfaced; leaf-lamina oblong-obovate, 5–12 cm. long, apex abruptly caudate-acuminate with an acute acumen; lateral nerves 7–9 pairs

4. B. sericocarpa

Fruit ferrugineous-tomentose, long-beaked, markedly and irregularly ridged; leaf-lamina obovate to oblanceolate, 4–8 (10) cm. long, apex rounded; lateral nerves 3–5 pairs

5. B. ochroprumna

Flowers in long narrow spikes usually 4 cm. long or more, if in shorter spikes then the latter elongating in fruit:

Leaf-lamina chartaceous, up to 15 cm. long, very narrowly obovate to oblanceolate, subacute to acute at the apex, conspicuously but minutely pellucid-punctate; fruit very strongly and symmetrically 5 (6)-ridged, apiculate to shortly (to 3 mm.) acuminate at the apex, 27–31 mm. long

6. B. punctata

Leaf-lamina various, but never pellucid-punctate; fruit usually more or less
terete or obscurely ridged, or if strongly ridged then 2 ridges much more developed than the others or apiculus 3–9 mm. long:
Leaves at anthesis and usually for some time afterwards densely rubiginous-to ferrugineous-pubescent to -tomentose below, pubescent and nearly always drying reddish-brown above; reticulation usually very conspicuously raised below at maturity, connecting the 5–15 pairs of lateral nerves:
Leaf-lamina (2) 5–26 (36) × 1–7 (12) cm., narrowly elliptic to oblanceolate, obtuse to acute or shortly apiculate at the apex; inflorescence 7–18 cm. long; fruit ferrugineous- or rubiginous-tomentose or densely pubescent, apiculate to acuminate at the apex . . . . 7. B. reticulata
Leaf-lamina 3·5–13·5 × 1·5–7 cm., elliptic or obovate (narrowly elliptic or oblanceolate when very young), rounded at the apex (obtuse or more pointed when very young); inflorescence 2·5–13 cm. long; fruit sparsely ferrugineous-pubescent, rounded at the apex:
Leaf-lamina rather conspicuously reticulate below when mature; inflorescence 3·5–13 cm. long; flowers c. 4·5 × 2·5–4 mm.; fruit 22–31 × 15–25 mm., rather to very sparsely puberulous 8. B. tomentosa
Leaf-lamina very conspicuously reticulate below when mature; inflorescence 2·5–5·5 cm. long; flowers c. 2·5–3 × 1·75–3 mm.; fruit 21–23 × 12–15 mm., puberulous . . . . 9. B. callistachya
Leaves becoming sparsely pubescent to almost glabrous some time before anthesis, rarely drying reddish-brown above; reticulation never conspicuously raised (though lateral nerves often so):
Leaves almost or quite glabrous, up to 11·5 cm. long but often much shorter; lateral nerves inconspicuous below, scarcely or not at all raised, domatia entirely absent from their axils; fruit flattened or terete, glabrous, with a distinct apiculus up to 4 mm. long:
Leaf-lamina narrowly elliptic or oblanceolate to elliptic or obovate (usually obovate); fruit 24–30 mm. long, more or less terete, apiculus usually straight; endocarp smooth, almost round in transverse section
10. B. suaveolens
Leaf-lamina narrowly elliptic or obovate to narrowly obovate; fruit 14–28 mm. long, flattened with two narrow lateral wings and three additional facial ridges, apiculus usually curved; endocarp irregularly furrowed, with two lateral wings . . . . 11. B. pterocarpa
Leaves various; lateral nerves conspicuous below, the major nerves considerably or somewhat raised and very often with domatia in some or all of their axils; fruit various, often long-beaked or rounded at the apex:
Inflorescence with conspicuous bracts c. 7–13 mm. long subtending and exceeding the flowers; bracts persistent at least until anthesis or after; leaf-lamina 8–23 cm. long, oblanceolate, acuminate at the apex; petiole up to 1·5 cm. long . . . . 20. B. longibracteata
Inflorescence with small narrow bracts subtending the flowers, bracts rarely equalling the length of the open flowers, up to c. 5 mm. long,
usually caducous before anthesis; (flowering material unknown in *B. pulcherrima*, but this with petiole over 3 cm. long):
Fruit with an apical beak (3) 5–20 mm. long and abruptly constricted from the rest of the fruit:
Fruit scarcely or not pseudostipitate at the base, beak up to 13 mm. long; leaf-lamina up to 13 × 5 cm., lateral nerves 3–9 (12) pairs:
Leaves with (4) 6–9 (12) pairs of lateral nerves; fruit quite glabrous
12. *B. oxycarpa*

Leaves with 3–4 pairs of lateral nerves; fruit tomentellous
13. *B. discolor*

Fruit with a pseudostipe 2–7 mm. long, beak 10–20 mm. long; leaf-lamina c. (15) 20–32 × 5–10 cm., lateral nerves (9) 10–14 pairs
14. *B. megalophylla*

Fruit rounded to acute or apiculate at the apex, apiculus when present very short (abnormally in young *B. fanshawei* apiculus up to 2 mm. long):
Leaf-lamina up to 11 × 4 cm., oblanceolate, abruptly and acutely apiculate or mucronate or shortly acuminate at the apex; lateral nerves 5–7 pairs, arising at about 40° or less and then curving towards the leaf-apex at about 25° or less for most of their length; reticulation conspicuous, very slightly raised below with very small inter-reticular spaces; fruit glabrous, ellipsoid-ovoid
15. *B. pallidovirens*

Leaf-lamina various, often much larger than 11 × 4 cm., if smaller rarely acutely apiculate or acuminate at the apex; lateral nerves 3–numerous pairs, very rarely or never less than about 40° to the midrib for their proximal half; fruit various, often pubescent:
Leaf-lamina up to 10 × 5.5 cm. but rarely over 8 × 4 cm.; apex acute to rounded or retuse, never apiculate or acuminate; lateral nerves 4–7 pairs; inflorescence 2–7 cm. long; fruit densely greyish-brown-tomentellous; domatia never as in *B. fanshawei* (q.v.) . . . . . . 16. *B. viridiflora*

Leaf-lamina usually in all or most leaves over 8 cm. long, if less then apex apiculate or acuminate, except in *B. fanshawei* (with distinctive domatia, q.v.) and *B. grandis* (with glabrous fruit and ovary often glabrous):
Leaf-lamina up to 9.5 × 5 cm., elliptic or narrowly elliptic, apex obtusely or acutely acuminate; domatia never as in *B. fanshawei* (q.v.); fruit densely silvery-brown-tomentellous
17. *B. acuminata*

Leaf-lamina in all or most leaves usually 10 cm. or more long, if less then apex not acuminate (but apiculate to rounded or retuse) except in some forms of *B. macrophylla* (with less hairy brownish fruit) and of *B. fanshawei* (with fruit similar to the latter and distinctive domatia):
Leaf-lamina up to 14 × 6 cm., rounded to apiculate (acuminate) at the apex; lateral nerves 3–5 pairs; petiole sometimes but usually not biglandular near the apex; distinctive domatia present in nerve axils on lower surface of lamina on some or most leaves of older or sometimes young branchlets, opening of domatium narrower than its diameter; fruit rather densely but minutely tomentellous

18. B. fanshawei

Leaf-lamina various, often over 15 cm. long; lateral nerves (4) 6–c. 14 pairs, if 5 or less then leaf apex apiculate or acuminate and petiole biglandular; domatia absent or present and then simple and triangular, pocket-like, with the opening as wide as the diameter of the domatium; fruit various:

Petiole conspicuously biglandular in most leaves; fruit minutely but rather densely brownish-tomentellous

19. B. macrophylla

Petiole without glands or petiolar glands inconspicuous; fruit either glabrous or densely greyish-brown- or rufous-pubescent:

Leaf-lamina 27–29 × 8–10 cm., apiculate at the apex; petiole 3 cm. or more long; inflorescence c. 10–15 cm. long; fruit rounded to obtuse at both ends, densely rufous-velutinous (British Guiana only)

21. B. pulcherrima

Leaf-lamina not over 16 cm. long; petiole up to about 3·2 cm. long; fruit glabrous or pubescent and then apiculate at the apex, usually shortly pseudostipitate at the base when mature (N. Brazil only):

Fruit densely pubescent or tomentose at maturity, indumentum wearing off when fruit very old but still visible in parts.

22. B. huberi

Fruit glabrous from an early stage; ovary sometimes also glabrous:

Leaves not very densely clustered at branchlet tips, up to 14 cm. long; lateral nerves 6–9 pairs; petiole up to 2 cm. long; fruit with a pseudostipe c. 2–3 mm. long, acutely apiculate at the apex

23. B. grandis

Leaves very densely clustered at the branchlet tips, 10–18 cm. long; lateral nerves 9–13 pairs; petiole 2–3 cm. long; fruit with a pseudostipe under 2 mm. long or not pseudostipitate, rounded to more or less obtuse at the apex

24. B. congesta

Bucida capitata Vahl, Eclog. Amer. 1:50, t. 8 (1796).
Bucida angustifolia Spruce ex Eichl., loc. cit. (1867), nom. syn.; non B. angustifolia DC. (1828).
Buchenavia ptariensis Steyerl. in Fieldiana, Bot. 28:423 (1952).

Leaf-lamina membranous when young, coriaceous when mature, very variable in size, narrowly to broadly obovate, retuse or rounded at the apex, sometimes obtuse or subacute when very young, cuneate and sometimes narrowed at the base, decurrent into the petiole, densely pubescent when very young but becoming glabrous except on the midrib and lateral nerves when mature, often ciliate at flowering time; midrib and major lateral nerves usually conspicuous below, the latter variable in number, 2–6 pairs; reticulation usually distinct when mature, slightly raised below; petiole 4–20 mm. long, usually rather stout. Peduncle slender or stout, c. 6–23 mm. long, almost glabrous to rufous-pubescent when young, almost glabrous at maturity; rhachis under 10 mm. long, often only 3 mm. long; flowers in sparse or dense capitula, 10–many in each inflorescence; bracts very small and caducous before anthesis. Upper hynanthium 1–1.5 mm. long, 2–3 mm. across, glabrous or sparsely pubescent outside, pubescent within and ciliate on the margin; lower hynanthium pedicel-like with the ovary at the base, 1.5–3 mm. long, densely rufous-sericeous. Stamens exserted for c. 0.5–1.5 mm. Fruit ellipsoid, 5-ridged to subterete, 18–30 × 10–20 mm., apiculate or acute to broadly obtuse at the apex, narrowed below into a very short pseudostipe, glabrous or rarely very sparsely pubescent, apparently rarely more than one ripening in each infructescence; endocarp markedly longitudinally ridged, usually about five ridges more prominent than the rest.

B. capitata is by far the most variable, abundant and widely distributed species in the genus. It is found in the West Indies from Cuba (within 150 kilometres south of the Tropic of Cancer) to Trinidad; Panama; Colombia (Vaupés); Venezuela (Amazonas and Bolívar); Dutch and French Guiana; Brazil (Amazonas, Maranhão, Ceará, Pernambuco and Rio de Janeiro within 150 kilometres north of the Tropic of Capricorn); and Bolivia (Santa Cruz and La Paz). It is the only Buchenavia found in the West Indies, where it occurs as a common tree of river banks and lowland forest. It also appears to be frequent in similar conditions in north-east South America, becoming rare westwards in Colombia and Venezuela and southwards in southern Brazil and Bolivia (Fig. 1). Glaziou says (in Mém. Soc. Bot. France 1 (3):203 (1908)) that it is cultivated in Rio de Janeiro.

As it is a well-known species, described in many Floras, we have not cited the numerous specimens preserved in herbaria.

We consider that B. ptariensis Steyerl. and B. vaupesana Cuatrec. fall within the wide range of variation shown by B. capitata. In the West Indies plants of B. capitata are characterized by the large number of flowers in each inflorescence, the rather small flower size and the relatively stout peduncles. Plants from the Amazon basin
tend to have fewer rather large flowers in each inflorescence and often more slender and more glabrous peduncles. Specimens from coastal areas of the mainland are often more or less intermediate in these characters. We are of the opinion that, in the present state of our knowledge, this variation does not lend itself to subdivision of the species into lower categories, but that it represents an ecocline from the West Indies through the coastal areas of the South American continent to the Amazon basin.

_B. vaupesana_ appears to be an extreme example of the Amazon type, with rather few large flowers and slender peduncles. We have seen the other characters by which this "species" is said to differ from _B. capitata_ (narrow somewhat pointed leaves and long petioles) in other specimens of _B. capitata_, mostly due to immaturity. The single known gathering (_Cuatrecasas 6828_), of which we have seen an isotype (US), is the only record we have of _B. capitata_ from Colombia. It is in flower.

_B. ptariensis_ of which we have seen the only known gathering, _Steyermark 60038_ (F, holotype), is a very small-leaved plant lacking flowers and fruit. We have no evidence that it actually has a capitate inflorescence but it appears to fall at one extreme of the _B. capitata_ range of variation and we can see no reason for keeping it separate. The leaves are of quite a different texture, shape and venation from those of _B. parvifolia_, as the author points out. It is one of only two specimens of _B. capitata_ that we know of from Venezuela.

It seems quite possible that at some future date, when the material of _B. capitata_ is really representative throughout its wide range, it will become advisable to divide the species into infraspecific units.

Vahl, when originally describing _Bucida capitata_, cited specimens collected by Ryan in Montserrat which, after being described by Vahl, were sent to Banks. They are now in the British Museum Herbarium (W. R. Dawson, Banks Letters: 727 (1958); letter of 1 May 1794). There are two specimens, one with flowers, young leaves and old fruits corresponding well with Vahl's t. 8 [fig. 1], and the other with adult leaves and extremely young inflorescences fitting his fig. 2. Since Vahl (tom. cit.: 51) refers to the latter as "Aliam quoque in Montserrat legit Ryan" and later (op. cit. 3: 55 (1807)) indexes it as "varietas?" it is reasonable to regard the former specimen, with flowers and old fruits, as the holotype of _B. capitata_.

The vernacular name is given as "Tanibuca" by Glaziou (in Mém. Soc. Bot. France 1 (3): 203), and Exell (Fl. Suriname. 3 (1): 175 (1935)) quotes "Katoelima", "Toekoeli", "Toekadi", "Matakki" and "Gemberhout".


Leaf-lamina chartaceous when mature, rather small, c. 1.5–4 × 0.5–2 cm., narrowly obovate to obovate, usually rounded but sometimes slightly retuse or very broadly obtuse at the apex, cuneate at the base, narrowed and decurrent into the petiole, almost glabrous except for sparse pubescence on the midrib and lateral nerves when mature; major lateral nerves often not very distinct, rather numerous for small size of leaf and often with many minor lateral nerves almost as conspicuous, c. 5–12 pairs;
petiole slender and short, c. 2–5 mm. long. Inflorescences (fide Ducke) more or less as in B. capitata; peduncle c. 10–18 mm. long, slender. Ovary completely glabrous. Fruit ellipsoid or less often obovoid, more or less terete, sulcate when dry, c. 14–20 mm. long, usually shortly apiculate, sometimes rounded or obtuse at the apex, rounded to acute at the base, glabrous; endocarp very slightly longitudinally ridged, very slightly flattened but without prominent lateral ridges.

**Venezuela**: Amazonas: Cerro Sipapo, “buttressed tree 30 m. high, 40 cm. diam., dense low elevation forests”, 24 Nov. 1948, Maguire & Politi 27370 (BM).


Ducke also recorded the species “inter flumina Cuminá-Mirim et Ariramba affl. Rio Trombetas”, Ducke 13584 (RB), and as sterile trees near Belém, Breves and Faro, all in the state of Pará.

But for Maguire & Politi 27370, which was originally named B. capitata, this species has been found only near the Amazon and its tributaries in northern Brazil. The Venezuela specimen is from a locality close to the Rio Orinoco some 1,250 kilometres from Manáos, the nearest Brazilian locality. The distinctive leaves, however, make its identification quite definite.

No specimen we have seen has flowers, those of Ducke 17686 (which we have chosen as lectotype) having just fallen. The ovary in this gathering is glabrous, and as Ducke also states this it seems that this character provides a further good means of distinguishing B. parvifolia from B. capitata. By far the greater number of Buchenavia species have densely pubescent ovaries, the indumentum often disappearing to give quite glabrous fruits (e.g. B. oxyacarpa). B. grandis appears to be the only other species with a glabrous ovary.


Leaf-lamina chartaceous when young, subcoriaceous when mature, 2–9 × 1.5–5 cm., obovate to broadly obovate, rounded or obtuse or subacute or apiculate at the apex, acute-cuneate but not decurrent at the base, densely pubescent when very young, becoming glabrous except on the midrib and lateral nerves when mature; major lateral nerves 4–8 pairs; petiole distinct, fairly long in most cases, 8–20 mm. long. Inflorescences as in *B. capitata*; peduncle rather stout, 10–20 mm. long. Fruit ellipsoid or less often obovoid, 17–28 × 11–14 mm., apiculate or less often rounded at the apex, densely but minutely rufous-puberulous, becoming less hairy when very old; endocarp very similar in shape to that of *B. parvifolia*.

**Brazil**: Santa Catarina: Mata do Hoffmann, Brusque, 13 Jan. 1951, Klein 22 (BM; S, holotype). Cunhas, Itajai, 10 m., 29 Nov. 1954, Klein 870 (BM); same

This species is known only from the south-eastern corner of Santa Catarina, southern Brazil, although it may well occur elsewhere. The area is south of the Tropic of Capricorn, *B. kleinii* being the only species of the genus (and one of the comparatively few members of the Combrezaceae) known outside the tropics. Its vernacular name is given as "Guarajuba".

*B. kleinii* appears to be most closely related to *B. capitata*, but its puberulous fruits and characteristic leaf-shape make it quite easily identifiable. In the shape of its endocarp it approaches *B. parvifolia* more closely than *B. capitata*.


Leaf-lamina subcoriaceous, 3-12 × 1-6 cm., narrowly elliptic to elliptic, short-to rather long-acuminate at the apex, cuneate and narrowed into the petiole at the base, very sparsely pubescent to almost glabrous when mature (except for appressed pubescence on the midrib and lateral nerves on both surfaces); midrib and lateral nerves conspicuous and raised below; major lateral nerves 5-10 pairs; petiole distinct, c. 7-30 mm. long, appressed-fuscous-pubescent. Peduncle fairly stout in fruit, c. 20-25 mm. long, rather sparsely appressed-pubescent; rhachis extremely short, up to c. 8 mm. long. Fruit narrowly ellipsoid-oblong, more or less terete, c. 20-25 × 7-10 mm. at maturity, rounded to very broadly obtuse at both ends, densely but shortly appressed-pale-tawny-pubescent.

*Brazil: Amazonas*: Manãos, Estrada do Bombeamento, "Capoeirão, terra firme, árvore pequena", 26 Nov. and 30 Dec. 1943, *Ducke 1481* (K; RB, holotype, not seen).

Known only from the type gatherings (presumably made from the same tree).

This species is very different from all others of the genus with a capitate inflorescence in its highly distinctive leaves. There is a remarkable similarity between this species and *B. acuminata*, so much so that there is scarcely any other difference that we can detect apart from the elongate inflorescences of the latter. This could be a striking example of parallel evolution but would seem to be more probably
the comparatively recent evolution of a species by the appearance of a single but very distinctive character expressing one of the fundamental tendencies in the family towards massing of the flowers in a condensed inflorescence. A close parallel is shown in the relationship between Combretum punctatum subsp. squamosum (Roxb. ex G. Don) Exell and C. punctatum Blume subsp. punctatum, but in that case the difference in the form of the inflorescence is not so clear-cut and is considered to be of no more than subspecific value.


Leaf-lamina subcoriaceous when mature, c. 2–9.5 × 1–4.5 cm., oblanceolate to obovate, usually rounded but sometimes very broadly obtuse or (when damaged?) retuse at the apex, cuneate and somewhat decurrent into the petiole at the base, almost glabrous when mature except on the midrib and lateral nerves; major lateral nerves 3–7 pairs; petiole rather short, 4–15 mm. long, usually rather stout. Peduncle 6–30 mm. long, slender at flowering time, stout in fruit. Fruit ellipsoid or ovoid, indistinctly 5-angled, markedly and irregularly ridged when dry, 18–25 × 7–15 mm. including beak, long-beaked at the apex, rounded at the base, densely but minutely ferrugineous-tomentose; beak 4–8 mm. long, narrow, straight or somewhat curved; endocarp markedly longitudinally ridged (more so than in B. capitata), often about 5 ridges more prominent than the rest.


This species is thus known only from the lower regions of the Amazon. Eichler cited only Spruce 309, which he saw in Herb. Leningrad and Herb. Munich. We have seen the latter specimen, which we select as the lectotype. Ducke 17287, labelled B. oxyacarpa, is almost certainly B. ochroprumna as shown by the rather distinctive leaves. Besides their shape, the leaves of B. ochroprumna are usually characterized by a ferrugineous colour on their under surfaces when dry. This specimen is the only one we have seen in flower. The flowers do not appear to differ from those of B. capitata.

B. ochroprumna differs from all other species of the genus in its highly characteristic fruits, and may also be distinguished by its leaves.

*Terminalia punctata* Spruce ex Eichl., loc. cit. (1867), nom. syn.; non *T. punctata* Roth (1821) nec Eichl., tom. cit.: 85 (1867).

Leaf-lamina chartaceous when mature, c. 6–15 × 2.5–4.5 cm., conspicuously but minutely pellucid-punctate, very narrowly obovate to oblanceolate, acute to subacute at the apex, very narrowly cuneate but not decurrent into the petiole at the base, very sparsely pubescent above, pubescent on the midrib and nerves and sparsely pubescent elsewhere below; midrib and major lateral nerves raised and very conspicuous below; reticulation rather inconspicuous; major lateral nerves c. 7–11 pairs; petiole short and stout, 5–15 mm. long, eglandular, pubescent. Peduncle stout, c. 35 mm. long; rhachis long (over 25 mm., but material fragmentary). Fruit ellipsoid, radially symmetrical, markedly 5(6)-ridged along its length, 27–31 × 12–19 mm., conspicuously apiculate at the apex, narrowed into a very short but distinct pseudostipe at the base, very sparsely pubescent between the ridges, glabrous elsewhere; apiculus 1–3 mm. long.


This species is very distinct from all other of the genus in both its fruits and leaves. Only *B. pterocarpa* has fruits as conspicuously ridged. Since the flowers are unknown we cannot, of course, be absolutely certain that this species belongs to *Buchenavia*, but as the fruit is distinctly less winged than that of any American species of *Terminalia* we have seen it seems safe to include it in *Buchenavia*. Its locality is completed isolated from that of any other *Buchenavia* yet discovered and is one of only two records of the genus for Peru.


Leaf-lamina more or less chartaceous when mature, (2) 5–26 (36) × 1–7 (12) cm., narrowly elliptic to oblanceolate, obtuse to acute or shortly apiculate at the apex, narrowly cuneate but not decurrent at the base, ferrugineous-tomentose over the whole of the lower surface at flowering time and during fruit maturation but tomentum wearing off after fruit-fall, ferrugineous- to rubiginous-tomentose or -pubescent on midrib and lateral nerves of upper surface at flowering time but indumentum wearing off during fruit maturation, sparsely pubescent and becoming glabrous elsewhere on upper surface; midrib very conspicuous and markedly raised below; major lateral nerves conspicuous and markedly raised below, 5–15 pairs, arising at c. 45° or less; reticulation at and after flowering time prominent and raised below, mostly consisting of secondary venules connecting the major lateral nerves; petiole distinct but usually short, c. 6–23 mm. long, stout, ferrugineous- or rubiginous-tomentose, most often conspicuously biglandular towards the apex. Peduncle
fairly stout, c. 20–30 (40) mm. long, ferrugineous- or rubiginous-tomentose; rhachis c. 50–140 mm. long, ferrugineous- or rubiginous-tomentose; flowers rather large, c. 4–5 mm. long. Lower hypanthium ferrugineous- to rubiginous-tomentose round the ovary, almost glabrous and c. 1–2 mm. long above it; upper hypanthium c. 1.5–2 × 2.5–3.5 mm., almost or quite glabrous outside. Fruit narrowly ellipsoid to ellipsoid, irregularly and rather slightly longitudinally furrowed or scarcely so, sometimes slightly flattened, c. 19–28 × 8–12 mm., apiculate to acuminate at the apex, shortly (1–2 mm.) pseudostipitate at the base, shortly ferrugineous- to rubiginous-tomentose and rather velvety all over; apiculus 1–6 mm. long, straight or slightly curved; endocarp variable, very slightly to conspicuously longitudinally furrowed, more or less circular in section to rather flattened, sometimes with 2 very narrow lateral wings.


From Spruce’s records for Rio Guainia and Rio Atabapo it seems probable that this species also occurs in Colombia (see footnote under *Ramatuelle argentea* concerning *Spruce* 3498, p. 41 below).

This very distinct species has very large or large leaves although it is a rather small tree. It is apparently abundant in the upper Rio Negro-Orinoco region (*fide* *Spruce* 3453), and thus entirely separated from the other two species with reticulate tomentose leaves (*B. tomentosa* and *B. callistachya*) which occur only in the lower regions of the Amazon basin and further south (Fig. 2).

The fruits of this species show a remarkable range in the form of the endocarp. In some specimens it is round in section and only slightly longitudinally furrowed, while in others it is conspicuously flattened, markedly longitudinally ridged, and has two lateral wings, although these are not as well developed as in *B. pterocarpa*. 

**Terminalia tomentosa** Mart. ex Eichl., loc. cit. (1867), *nom. syn.*; non *T. tomentosa* Wight & Arn. (1834).


Leaf-lamina chartaceous at flowering time, coriaceous when mature, c. 3.5–13.5 × 1.5–7 cm., narrowly elliptic or oblanceolate to (probably always at maturity) elliptic or obovate, rounded at the apex but obtuse or more pointed when very young, cuneate at the base, often involuted at the margin, ferrugineous- or rubiginous-tomentose or densely pubescent all over both surfaces at flowering time, indumentum beginning to wear off soon afterwards; midrib very conspicuous and markedly raised below; major lateral nerves conspicuous and somewhat raised below, c. 9–14 pairs, arising at about 45°; reticulation not prominent before flowering time but rather conspicuously so afterwards, though less so than in *B. reticulata* and *B. callistachyia*, less regular than in *B. reticulata*; petiole distinct, c. 3–18 mm. long, stout, densely rubiginous- or ferrugineous-velutinous when young, sometimes biglandular. Peduncle c. 6–20 mm. long, usually stout, densely rubiginous-velutinous when young; rhachis c. 3–11 cm. long, densely rubiginous-velutinous when young; flowers very like those of *B. reticulata*, c. 4–5 mm. long, indumentum identical. Upper hypanthium c. 2.5–4 mm. across. Fruit ellipsoid to more or less spherical, probably more or less terete when fresh, 22–31 × 15–25 mm., more or less rounded at both ends, rather sparsely ferrugineous-pubescent when mature.

**Brazil:** "Brasilia", *Pohl* 83 (W, lectopartotypes). **Pará:** Serra Pontada, in the Jutahy region between Almeirim and Prainha, "silva, arbor magna", 11 Sept. 1923, **Ducke** 17677 (K, isotype of *B. corrugata*). Santa Cruz dos Martírios, região do Araguáia, "árvore de 10 m., frutos comestíveis", 15 June 1953, **Fróes** 30018 (BM). **Piauí:** Banks Gurgia (= Rio Gurgeia ?), "a large tree called Biriba—fruit acid and bitter—liked by deer", Aug. 1839, **Gardner** 2657 (K). **Goiás:** Between Alegre and Ponte do Sevorino, "arbre de petite taille", 2 Oct. 1895, **Glaziou** 21125 (K; P). In woods and plains, Serra da Chapada, "arbor 15–20 ped.", Sept. 1827, **Martius** 1180 (LE, lectotype). **Minas Gerais:** Biribiry (*fide* Glaziou), 1892, **Glaziou** 19144 (K). On sandy plains between Alegres and Rio São Francisco, "arbor 8–20 ped.", Sept. 1834, **Riedel** 2641 (BM; K; LE, lectotype and lectoparatype; W).

**Glaziou** 21125 is unlocalized in Herb. Kew, but the Paris specimen bears a label concurring with the locality cited by Glaziou (1908). This sheet also bears a label identical to that of *B. macahensis* (*nomen nudum*; see p. 37 below), **Glaziou** 18218, but the actual specimen bears a tag numbered 21125 and other pieces of evidence conclusively show that the presence of the second label is due to an error in mounting.

Eichler (1866) cited specimens of *B. tomentosa* in Herb. Munich, Herb. Martius, Herb. Vienna and Herb. Leningrad, but those in the first two herbaria do not appear to have survived. Of the three specimens in Herb. Vienna (W) one is a duplicate of one of the Leningrad specimens whilst the other two (both *Pohl* 83) are mounted on the same sheet. There are also three specimens in Leningrad: one collected by Martius and two (duplicates) by Riedel. We have selected the better Riedel
specimen as the lectotype as duplicates of this are also present in the British Museum, Kew and Vienna Herbaria.

*B. corrugata* shows considerable similarity to *B. callistachya*, but the differences noted by Ducke and ourselves appear to be sufficient to keep the two separate, at least for the present. Comparison of them with the type specimens of *B. tomentosa* leads us to the opinion that *B. corrugata* is conspecific with the latter.

*B. tomentosa* seems to be a species which does not extend up the Amazon, in contrast with *B. reticulata* which is confined to the upper Amazon and Orinoco tributaries (Fig. 2). The vernacular name is noted as “Tanebuco” by Pohl.


Leaf-lamina coriaceous when mature, c. 5·5–10·5 × 2·5–5·5 cm., elliptic to slightly obovate, rounded at the apex, cuneate at the base, inrolled at the margin when young, lower surface at flowering time densely ferrugineous-pubescent except tomentose on the midrib and nerves, indumentum beginning to wear off soon afterwards but midrib and nerves densely pubescent below even after fruit-fall; midrib very conspicuous and markedly raised below; lateral nerves also markedly raised below, c. 8–11 pairs, arising at 45° or slightly more; reticulation very prominent below after flowering time, less regular than in *B. reticulata*; petiole distinct, stout, ferrugineous- to rubiginous-tomentose at flowering time, c. 6–16 mm. long, sometimes biglandular. Peduncle c. 10 mm. long or less at flowering time, up to 15 mm. long in fruit, stout, densely rubiginous-velutinous at flowering time, densely pubescent in fruit; rhachis 15–25 mm. long at flowering time, up to 45 mm. in fruit; flowers smaller than in *B. reticulata* and *B. tomentosa*, c. 2·5–3 mm. long, indumentum as in the two preceding species. Upper hypanthium c. 1.75–3 mm. across. Anthers also smaller. Fruit ellipsoid wrinkled when dry, probably more or less terete when fresh, 21–23 × 12–15 mm., rounded at the apex, rounded or very shortly pseudo-stipitate at the base, finely ferrugineous- to rubiginous-puberulous when mature.


*B. callistachya* is clearly closely allied to *B. tomentosa*, from which it differs in a few characters which remain constant with regard to the rather few specimens of each species known. The recently collected fruiting specimen (*Pires & Black 2095*) almost certainly belongs to this species, its leaves being very similar to those of the type. It is just possible, however, that we have confused the fruiting specimens of *B. callistachya* and *B. tomentosa*, or that *B. callistachya* itself may prove to be conspecific with the latter. These points must await more and better material for elucidation.
10. **Buchenavia suaveolens** Eichl. in Flora 49:166 (1866); in Mart., Fl. Brasil. 14 (2): 97 (1867). (Fig. 3 e, f.)

**Buchenavia oxycarpa** Eichl. in Flora 49:165 (1866) pro parte, quaod Schomburgk 854; in Mart., loc. cit. (1867) pro parte, quaod Schomburgk 854.

**Terminalia suaveolens** Spruce ex Eichl., loc. cit. (1867), nom. syn.

**Terminalia vasivae** Spruce ex Eichl., loc. cit. (1867), nom. syn. (Spruce also used a third manuscript name which was not cited by Eichler.)

Leaf-lamina coriaceous when mature, 1-8-8 × 0-3-4-3 cm., narrowly elliptic or oblanceolate to elliptic or obovate, retuse to rounded at the apex, narrowly to very narrowly cuneate and somewhat decurrent into the petiole at the base, almost glabrous when mature except on the midrib; midrib fairly conspicuous, slightly raised below; major lateral nerves inconspicuous to very inconspicuous, but usually over 6 pairs visible below, scarcely or not raised; reticulation not visible; petiole fairly long and distinct, c. 3-20 mm. long, very sparsely and minutely pubescent, eglandular. Peduncle usually rather slender, sparsely pubescent, up to c. 25 mm. long; rhachis up to 65 mm. long at flowering time, sparsely pubescent; flowers scarcely different from those of *B. capsilata*, but ovary usually rather more sparsely pubescent. Fruit ellipsoid to slightly obovoid, more or less terete when fresh, 24-30 × 10-14 mm., conspicuously apiculate at the apex, narrowed into a short but distinct pseudostipe at the base, glabrous, the apiculus 1-3 mm. long, more or less straight; endocarp ellipsoid, almost round in section, c. 20 × 9 mm., obtuse at each end, more or less smooth.

**Venezuela**: Amazonas: On the rivers Casiquiare, Vasiva and Pacimoni, 1853-54, Spruce 3198 (BM; K; LE, lectoparatype). On the banks of Lake Vasiva, also observed on Rio Pacimoni, Dec. 1853, Spruce 3190 (K). Rio Sanariapo, 120 m., 2 July 1842, Williams 15955 (F).

**Venezuela or Colombia**: On the banks of Rio Guainia, “Drupa viridis carnosa, recens vix obsolete prismatica”, June 1854, Spruce 1887 in part (K). On Rio Guainia above its confluence with Rio Casiquiare, 1854, Spruce 1887 in part (K). (See footnote under **Ramatuella argentea** concerning Spruce 3498, p. 41 below.)


*B. suaveolens* is thus confined, like *B. pterocarpa* and *B. reticulata*, to the upper Amazon-Orinoco region (Fig. 2).

The distinction between *B. suaveolens* and *B. pterocarpa* is made under the latter species.

Eichler (1866) cited specimens in Herb. Leningrad and Herb. Martius, of which we have seen the former. The two gatherings are Spruce 1887 and Spruce 3198 (which Eichler gives in error as 3189), and there are duplicates of both at the British Museum and Kew. We have selected Spruce 1887 as the lectotype as there
Fig. 3. Buchenavia pterocarpa Exell & Stace (holotype): a, habit (× ½); b, c, two views of fruit (× 1); d, fruit in transverse section (× 1). B. suaveolens Eichl. (Fröes 28309): e, fruit (× 1); f, fruit in transverse section (× 1).
is no confusion about the number and other specimens (from another locality) also with this number bear fruits.

_Schomburgk_ 854 is labelled "Guiana" but according to the collector's notebooks he was actually at the Falls of the Rio Branco, Brazil. _Schomburgk_ 814 is similarly labelled and since his note-book states that this number was a herbaceous plant it seems most probable that 814 is an error for 854, which it resembles in every detail. _B. suaveolens_ is otherwise not known from British Guiana. Eichler (1866, 1867) cites _Schomburgk_ 854 under _B. oxycarpa_ (in 1867 as an unnamed variety), but this is clearly a misidentification.

**II. Buchenavia pterocarpa** Exell & Stace, sp. nov. (Fig. 3 a–d.)

_Arbor_ parva ad c. 10 m. alta; ramuli griseo-fusci, fere glabri, apice non clavati. _Folia_ spiraliter ordinata ad ramulorum apices congesta; lamina subcoriacea, 1·5–9·5 × 0·5–2·8 cm., anguste elliptica vel ob lanceolata ad anguste obovata, integra, apice obtusa rotundata vel retusa, basi acuta decurrens, fere glabra, costa media infra prominenti, nervis lateralisbus inconspicuis; petiolus c. 3–18 mm. longus, sparse minuteque puberulus eglandulosus. _Inflorescentiae_ axillares, elongato-spicatae; pedunculus gracilis, c. 10–17 mm. longus, sparse minuteque puberulus; rhachis c. 15–53 mm. longa, puberula; flores ferruginoe-virides; bracteae parvae, ante anthesin caducae. _Hypanthium inferum_ gracile, 1–2 mm. longum, ovario in parte basali puberula inclusu, parte apicali sparse minuteque puberula; _superum_ c. 1–1·5 × 2–3 mm., extus sparse puberulum, intus pubescens, margine saeppe fere integrum. _Stamina_ 10, ad 0·5–1 mm. exserta. _Stylus_ ad c. 1·5 mm. exsertus, filiformis, glaber. _Fructus_ (plerumque singulus tantum pro infructescentia matur-escens) latissime applanato-ellipsoideus vel obovoideus, c. 14–28 × 10–16 mm. et 5–8 mm. crassus, apice abrupte apiculatus, basi rotundatus vel breviter (ad 3 mm.) pseudostipitatus, glaber, apiculo ad 4 mm. longo curvato, alis 2 lateralibus angustis et angulis 3 prominentibus instructus; endocarpium lignosum, lateraliter bialatum, irregulariter longitudinaliter sulcatum.

**Venezuela:** _Amazonas:_ Occasional along Rio Yatua, near Laja Catipan, Casiquiare, 100–140 m., "flat-topped riverine tree, 6–8 m. high, fruit green", 6 Feb. 1954, _Maguire, Wurdack & Bunting_ 37543 (BM, holotype). Common and subdominant along Cana Catua, Cerro Yapacana, Rio Orinoco, 125 m., 19 Nov. 1953, _Maguire, Wurdack & Bunting_ 36555 (BM). Caño Yapacana, below port to Cerro Yapacana, Rio Orinoco, 6 Jan. 1951, _Maguire, Cowan & Wurdack_ 30763 (BM).

**Brazil:** _Amazonas:_ Santa Izabel, Rio Negro, in flooded riparian forest, 8 Oct. 1932, _Ducke_ 25018 in part (K); same locality, 9 Mar. 1936, _Ducke_ 25018 in part (K). Igarapé Imutá, tributary of Rio Negro, "terra firme", 12 Mar. 1952, _Fröes_ 27937 (BM).

All the specimens we cite, other than _Fröes_ 27937, were previously labelled _B. suaveolens_. In the absence of fruits it does not always seem to be possible to
distinguish between *B. suaveolens* and *B. pterocarpa*, but in most cases the leaves of the former are broader and more markedly obovate. The fruits of the two species are, however, quite different (see Fig. 3). The fruit of *B. suaveolens* is more or less terete, narrower in proportion to its length and with a usually straight apiculus abruptly delimited from the obtuse or rounded apex. In our new species on the other hand the fruit is considerably flattened with two narrow lateral wings and three extra ridges (one on one face and two on the other), is broader in comparison with its length and has a usually curved apiculus very abruptly delimited from the usually rounded or truncate or even retuse apex. The endocarp is also markedly different in the two fruits, that of *B. pterocarpa* having two lateral wings and an irregularly furrowed surface, while that of *B. suaveolens* is smooth and almost round in cross-section. The bilateral symmetry of the fruit of *B. pterocarpa* is not found so greatly developed elsewhere in the genus, although some species (notably *B. reticulata* and less conspicuously *B. parvifolia* and others) show tendencies towards it.

Comparison of recent collections of *B. suaveolens* and *B. pterocarpa* with Spruce's collections of the former shows that it is the flattened-fruited species which needs to be described as new. Although Eichler did not see fruits of *B. suaveolens* (none of his cited specimens is in fruit, and he states "Fructus ignotus" in Fl. Brasil.) it seems clear that it was the terete-fruited species that he described. The evidence for this is that both Leningrad specimens are broad-leaved, and that other specimens of Spruce 1887 (not duplicates of those which Eichler cited from Barra and Barcellos) from the Rio Guainia which are in Herb. Kew possess the distinctive terete fruits.


*Terminalia oxycarpa* Mart. in Flora 24, Beibl. 2 : 22 (1841).

Leaf-lamina chartaceous, 1–13 × 0·5–5 cm., very narrowly elliptic or oblanceolate to obovate, rounded to acute at the apex, narrowly cuneate but scarcely decurrent at the base, almost glabrous when mature except on the midrib; midrib fairly conspicuous, slightly raised below; major lateral nerves fairly conspicuous, very slightly raised below, (4) 6–9 (12) pairs; reticulation fine but fairly conspicuous; petiole very distinct, 4–25 mm. long, sparsely and minutely pubescent to almost glabrous, eglandular. Peduncle slender, rather sparsely pubescent, up to 55 mm. long; flowers very similar to those of *B. capitata* but ovary pubescent or more usually very sparsely pubescent to almost glabrous, and always glabrous soon after flowering. Fruit ellipsoid, wrinkled and slightly flattened to conspicuously 5–6 (7)-angled when dry, 19–30 × 9–15 mm., abruptly acuminate at the apex, rounded to obtuse at the base, glabrous; acumen 3–9 mm. long, pointed, more or less straight or slightly curved; endocarp strongly longitudinally ridged, 5 ridges stronger than the rest, more or less radially symmetrical but 2 lateral ridges sometimes the most prominent.


Out of Martius's eight syntypes we have selected a specimen possessing leaves, flowers and fruits as the lectotype.

B. oxycarpa is a very distinct species, although Eichler (1866, 1867) cited a gathering of B. suaveolens (Schomburgh 854) under it. The endocarp of the present species is markedly ridged and more or less radially symmetrical, a feature only as greatly developed elsewhere in B. punctata. The fruits are markedly ridged in some specimens (e.g. in Martius's syntypes) and in Eichler's figures. Spruce's specimens show no sign of these ridges, having slightly flattened and minutely wrinkled fruits. Fruits of Duche 402 are, however, more or less intermediate in this feature. Again, in Krukoff 1241 and Krukoff 6174 the ovaries are completely glabrous at anthesis or just after, while those of Asplund 14302 are ferrugineous-tomentose. The ovaries of the flowers of Riedel 744 are completely intermediate in pubescence. The inflorescences of Asplund 14302 are additionally unusual in that the whole peduncle and rhachis are tomentose; the long pedicel-like distal portion of the lower hypanthium and the outside of the upper hypanthium are, however, glabrous.

Eichler also recorded the species from the state of Mato Grosso (on banks of Rio Paraguay), Brazil. Since he cites Riedel as the collector from this locality, the specimen in question may well be the Riedel specimen referred to above under unlocalized records for Brazil.

Leaf-lamina chartaceous or coriaceous, c. 6–7:5 × 4 cm., obovate, obtuse to emarginate at the apex, narrowly cuneate at the base, sparsely pubescent below; major lateral nerves prominulous below, 3–4 pairs, venules inconspicuous; petiole 10–15 mm. long. Peduncle plus rhachis 20–30 mm. long. Fruit ellipsoid, 5-angled, c. 15 mm. long excluding acumen, abruptly acuminate at the apex, tomentellous; acumen up to 10 mm. long. (Ex descr. orig.)


The only known specimen, which was in the Berlin Herbarium, has been destroyed. The species appears to be very distinct. Diels states that *B. discolor* is close to *B. oxycarpa* but differs in the structure of the leaves (mainly in having only three or our pairs of lateral nerves) and in the tomentellous fruit. It is quite possible, if the inflorescences have been misinterpreted by Diels, that this species is the same as *B. ochrophyrumna*, which has capitate inflorescences.


Leaf-lamina subcoriaceous when mature, 14–31 × 5–10 cm., narrowly obovate to oblanceolate, obtusely apiculate to shortly acuminate at the apex, very narrowly cuneate at the base but not decurrent into the petiole, almost glabrous above except on the midrib and lateral nerves, shortly pubescent on the midrib and lateral nerves below, almost glabrous to very sparsely puberulous elsewhere below; midrib very prominent and raised below, slightly sunken above; lateral nerves conspicuous below, (9) 10–14 pairs; reticulation quite conspicuous, mostly connecting the lateral nerves; petiole distinct and stout, 12–23 mm. long, usually conspicuously biglandular towards the apex, shortly pubescent. Peduncle rather stout, densely puberulous, c. 20–30 mm. long; rhachis fairly stout, densely puberulous or tomentellous, c. 70–125 mm. long; flowers rather large, c. 4 × 3 mm. Ovary tomentellous. Upper hypanthyum almost glabrous outside. Fruit very large, 30–48 mm. long, rather abruptly narrowed into a long acumen at the apex and into a pseudostipe at the base, ferrugineous-tomentellous; body of fruit ellipsoid, 18–26 × 11–13 mm., slightly compressed, conspicuously 5-ridged; pseudostipe often relatively long and slender, 2–7 mm. long; acumen rather various, straight or markedly curved, slender or rather stout (5, damaged?) 10–20 mm. long.

**BRITISH GUIANA**: *Demerara*: “Demerara”, without date, *Parker* (K, as *Pamea guianensis*). *Essequibo*: Mazaruni Station, “shrub or small tree 8 ft. high from sand bank by river”, 11 Sept. 1942, *Field No. F845* in part = *Forest Dept. 3581* in part (K); same locality, 11 Apr. 1943, *Field No. F845* in part = *Forest Dept. 3581* in part (K).

The type of this species is said to be in “herb. van Heurck” (AWH) but we have been informed that it is not to be found there now. It was said (Van Heurck &
Muell. Arg., op. cit.: 212) to have been sent to Mlle. Hermine Reichenbach, probably from Demerara, under the name *Pamea guianensis* Aubl., but collector and date are not given. A specimen at Kew (cited above) bears the annotation "Mr. Parker Demerara. Alloshabbo yielding excellent timber. *Pamea guianensis*. Aubl. *Terminalia Pamea*. Aubl." This was in Herb. Hooker, presented to Kew in 1867, three years before Van Heurck and Mueller's publication. It seems very likely that the Kew specimen, with which *Forest Dept.* 3581 is obviously conspecific, is a duplicate of the specimen described by Van Heurck and Mueller. However, in the absence of confirmation of this and of the fact that Van Heurck's specimen is actually missing we cannot give the Kew specimen the status of a type.

A further difficulty is that in their lengthy description Van Heurck and Mueller state that the inflorescences of this species are capitate, whilst the specimens we have seen all have very long spicate inflorescences. The rest of the description, notably of the leaves and fruits, fits the Kew Demerara specimen exactly. Without seeing Van Heurck's specimen it is not possible to account for this discrepancy with certainty, but it seems probably that the specimen described had incomplete inflorescences which had been broken off. We believe, like Sandwith (in sched.), that the inflorescences of this species were misinterpreted by Van Heurck and Mueller, and that they are in fact elongate spikes as stated in our description. There remains the unlikely possibility, however, that *B. megalophylla* has a truly capitate inflorescence and that the three Kew specimens represent a new species.


Leaf-lamina subcoriaceous, 3–11 × 1–3.7 cm., oblanceolate to narrowly elliptic or oblong-lanceolate, abruptly and sharply apiculate or mucronate or shortly acuminate at the apex, narrowly cuneate but scarcely decurrent into the petiole at the base, almost glabrous above except sparsely puberulous on the midrib and lateral nerves, very sparsely puberulous or almost glabrous below except sparsely pubescent or pubescent on the midrib and lateral nerves; midrib conspicuous and raised below; lateral nerves conspicuous and raised below, 5–7 pairs, very distinctive, arising at about 40° or less to the midrib and then curving rather abruptly inwards towards the apex and running at about 25° or less to the midrib for most of their length and nearly parallel with the leaf margin at their apex; reticulation conspicuous, very slightly raised below, forming very small inter-reticular spaces; petiole often long, 5–13 mm. long in flowering material, pubescent, obscurely bil glandular at the extreme apex in most leaves, 10–26 mm. long in fruiting material, sparsely or very sparsely pubescent, not glandular or rather conspicuously bil glandular at about the middle. Peduncle 25–33 mm. long in flowering material, 8–18 mm. long in fruiting material, slender, sparsely pubescent, rhachis c. 40–70 mm. long, slender, pubescent; flowers c. 3 × 2.5 mm. Ovary densely pubescent. Upper hypanthium pubescent on the outside. Fruit (immature) ellipsoid-ovoid, probably terete when fresh, up to 12 × 6 mm., subacute to obtuse at both ends, glabrous.


In the above description “flowering material” refers to Cuatrecasas 19939 and “fruiting material” to Pires 1043. These are the only two specimens known to us, and it is of interest to note that they are from rather widely separated areas. It is unfortunate that we have to compare a flowering specimen with a fruiting specimen from a distant locality, but Pires 1043 seems most probably to belong to the same species as the type. The peculiar nervation and reticulation of the leaves are common to both specimens and we have not met with them elsewhere in the genus. The main point of difference is that the glands of Pires 1043 are, when present, near the middle of the long petiole, while in Cuatrecasas 19939 they are either absent or very inconspicuous and at the extreme apex of the petiole.


Leaf-lamina subcoriaceous, 1-10 x 0·5-5·5 cm. (but rarely over 8 x 4 cm.). oblonglanceolate or narrowly elliptic to obovate or elliptic, acute or subacute to rounded or retuse at the apex, narrowly cuneate and often somewhat decurrent into the petiole at the base, almost glabrous except sparsely to very sparsely pubescent on the midrib and sometimes on the lateral nerves above, almost glabrous to sparsely puberulous on the midrib and lateral nerves below; midrib conspicuous and raised below; lateral nerves conspicuous and raised below, 4-7 pairs; reticulation rather inconspicuous; petiole (4) 8-16 mm. long, pubescent, usually not glandular but some very small (not young) leaves markedly biglandular at the apex of the petiole. Peduncle 5-27 mm. long, slender, pubescent; rachis 12-50 mm. long, slender, pubescent; flowers 3-4·5 x 2-3 mm. Lower hypanthium densely pubescent round the ovary, sparsely so above; upper hypanthium almost glabrous outside. Fruit more or less terete, up to 24 x 13 mm., subacute to very shortly apiculate at the apex, rounded to subacute at the base, densely greyish-brown-tomentellous; endocarp terete, slightly longitudinally ridged, acute at the apex, rounded at the base.

The leaf-shape of this species is apparently variable. In Ducke 1378, 25022 and 25023 the lamina is usually oblanceolate with a rounded apex, but some leaves on the first of these have acute or subacute apices, showing a connexion with Ule 7682 which has larger, more or less elliptic acute leaves. Leaves on the fruiting branch of Ducke 25022 (fruits are actually lacking in the specimen at Kew) are obovate and rounded or retuse at the apex, which is the shape found in Fröes 22698. It seems, however, that all the specimens cited belong to this species. Some of the inflorescences of the last specimen are very short, barely exceeding 3 cm. long with a floriferous part little over 1 cm. long.

17. Buchenavia acuminata Exell & Stace, sp. nov.

Arbor ad 20 m. alta; ramuli grisco-fusci, sparse pubescentes, apice non clavati. Folia spiraliter ordinata ad ramulorum apices congesta; lamina chartacea, 2–9·5 × 0·8–5 cm., anguste elliptica vel elliptica, integra, apice obtuse vel acute acuminata (acumine ad 15 mm. longo), basi acute cuneata, fere glabra costa media nervisque lateralis pubescentibus exceptis, costa media infra prominenti, nervis lateralis infra prominentibus 5–8-paribus, venulis inconspicuis; petiolus c. (4) 8–24 mm. longus, pubescens, plerumque apice conspicue biglandulosus. Inflorescentiae axillares, elongato-spicatae; pedunculus gracilis, c. 15–30 mm. longus, sparse pubescens; rhachis gracilis, c. 15–30 mm. longa, sparse pubescens; flores parvi; bracteae parvae, ante anthesin caduae. Hypanthium inferum gracile, c. 2 mm. longum, ovario in parte basali dense pubescenti inclusu, parte apicali pubescenti; superum c. 1-1·5 × 2–2·5 mm., extus sparse puberulum, intus pubescens, margine saepe fere integrum. Stamina 10, ad 0·75 mm. exserta. Stylus inclusus (semper?). Fructus (pauci pro infructescencia maturescentes) ellipsoides vel obovoides, terei-tiusculus, immaturus ad 11 × 5 mm., apice rotundatus, basi breviter pseudostipitatus, dense argenteo-brunneo-tomentellus.


The rather small-long-acuminate leaves, long slender petioles and densely tomentellous fruits make this species quite distinct from all others except B. serico-carpa, which has a capitate inflorescence. Apart from this single but very conspicuous and easily recognizable difference we have been unable to separate these two species, and they occur in the same area of Brazil. It is possible that here is a case of a dimorphic species but until this is actually demonstrated it seems more advisable to treat the plant with the elongate inflorescence as a different (new) species.


Leaf-lamina coriaceous at maturity, 1–14 × 0·5–6 cm., narrowly elliptic or ob-lanceolate to elliptic or obovate, rounded to apiculate or less often acuminate or
acute at the apex, narrowly cuneate and often rather decurrent into the petiole at the base, when mature almost glabrous above except sparsely pubescent on the midrib, almost glabrous to very sparsely pubescent below except pubescent to sparsely pubescent on the midrib and lateral nerves; midrib conspicuous and raised below; lateral nerves conspicuous and raised below, 3–5 pairs; reticulation rather inconspicuous or fairly conspicuous, not close; petiole slender to rather stout, 6–24 mm. long, pubescent to sparsely pubescent, usually not glandular but very small leaves often conspicuously biglandular near top of petiole and some specimens with normal leaves also biglandular; some or most leaves on mature-leaved specimens with conspicuous domatia (in the axils of the lateral nerves on the lower surface) with a conspicuous opening smaller than the diameter of the domatium itself. Peduncle slender at first, stouter in fruit, 6–30 mm. long, pubescent or puberulous; rhachis 7–38 mm. long, puberulous, often densely so; flowers yellowish-green, c. 2.5–4 × 2–4 mm., seen on a rhachis up to only 20 mm. long. Fruit rather variable, ovoid to ellipsoid- or oblong-ovoid but when ripe often becoming pressed almost circular in outline, more or less terete when fresh or slightly flattened, up to 24 × 14 mm., subacute to rounded at the apex or rarely apiculate or shortly acuminate at the apex with a beak up to 2 mm. long, rounded or shortly pseudostipitate at the base, very shortly but rather densely tomentellous, indumentum wearing off when very old; endocarp slightly flattened, slightly longitudinally ridged, acute to subacute at both ends.

**British Guiana:** Essequibo: Mazaruni Station, "100 ft. tree 16 in. diam. from mixed forest ... fr. oval to oblong, yellow when ripe—pulp whitish, slightly sweet—seed oval, whitish, veined, stone very hard", 7 Sept. 1942, Field No. F844 = Forest Dept. 3580 (K). Mazaruni Station, "60 ft. tree 10 in. diam. from secondary mixed forest on brown sand ... fls. in axill. revolute spikes, yellow-green—perianth shaped like a flat bowl, barely lobed", 5 May 1943, Field No. F1270 = Forest Dept. 4006 (K). Mazaruni Station, seedlings of Forest Dept. 3580 ten weeks old from forest nursery, no date, Field No. F1616 = Forest Dept. 4352 (K). Mazaruni Station, seedlings (no source) three weeks and seven months old from forest nursery, no date, Field No. F2233 = Forest Dept. 4999 (K). Mazaruni Station, towards Labbakabra Creek, 27 Aug. 1937, Sandwith 1219 (BM; K). Bank of Potaro River, Tumatumari, 4–6 July 1921, Gleason 401 (K). Riverside below Tukeit, Potaro River Gorge, rare, 16 May 1944, Maguire & Fanshawe 23499 (BM; K; NY, holotype). Mahdia River, Potaro River, 172 km. along Bartica-Potaro road, 16 Jan. 1943, Field No. F1039 = Forest Dept. 3775 (K); same locality, 21 Jan. 1943, Field No. F1064 = Forest Dept. 3800 (K). Basin of Kuyuwini River, tributary of Essequibo River, about 240 km. from mouth, 12 Feb. 1938, Smith 3033 (K). Berbice: New River, Courantyne River, 5 Oct. 1911, Anderson 749 (K).

**Brazil:** Amazonas: Cachoeira Baixa, Rio Tarumá, Manáos, "árvore mediana; flór pardo avermelhado clara; fruto amarelado páldido", May 1950, Ducke 2278 (BM).

Although not recorded from the third British Guianan county, Demerara, or from Surinam, *B. fanshaweii* probably occurs in both.
B. fanshawei is a variable species, but is usually quite easily recognized in all of its states. It appears to be most closely related to B. macrophylla, although in their typical forms the two are extremely different in aspect. Some specimens of B. macrophylla, however, have very small leaves with few nerves and stout inflorescences, while some specimens of B. fanshawei have acuminate leaves, biglandular petioles and undeveloped or no domatia. The two species apparently overlap only in the Manáos region of the middle Amazon (Fig. 2).

Leaves on more juvenile branches of B. fanshawei (but not juvenile leaves on older branches) show characters more approaching those of B. macrophylla, since the leaf-apex is commonly acuminate and the petioles may be glandular. These branches flower freely, however, and do not appear to be suckers. The more mature branches are swollen at the tips with the leaves more densely tufted at the apex. The seedlings (Forest Dept. 4352 and 4969) are interesting since the leaves have a long acute acumen, although they do not appear to be glandular. The cotyledons are about 2-2.5 by 3-4 cm., truncate or very shallowly retuse at the apex and very weakly cordate to rounded at the base.

The domatia are of unique structure in the genus, although they are of a type commonly found in Terminalia. On mature branches they are found usually on some or most of the leaves, in the axils of the major lateral nerves on the lower surface. They are often very small, but may be up to about 1.5 mm. across, and are frequently dome-shaped in general outline, with a pore either centrally placed or at the end of the domatium distal to the nerve axil. The pore is never as broad as the total diameter of the domatium. In all other known species of Buchenavia domatia, if present, are simple more or less triangular pocket-like structures formed by the epidermal and cortical layers of the midrib and nerve overarchings the nerve axil. In these cases the pore is thus positioned at and therefore always as wide as the maximum diameter of the domatium and faces parallel to the leaf surface. As in all species, the domatia of B. fanshawei are frequently marked by a persistent axillary tuft of hairs in the young stage. Very often, at an early stage, the domatium is a simple wart-like object, the pore appearing later by the rupture of the wart. This is not the case in the other types of domatium (e.g. in B. capitata). In a survey of domatia in the family Combretaceae, of thirty American species of Terminalia examined twenty-three were found to lack domatia, three to possess domatia like those of B. capitata and four to have domatia like those of B. fanshawei. In Buchenavia, of the twenty-three species available for study (B. discolor being, as stated, unavailable) nine (ns. 7-11, 14 and 19-21 of this revision) lack domatia, thirteen (ns. 1-6, 12, 15-17 and 22-24) possess domatia like those of B. capitata and none except B. fanshawei has the other type.

B. fanshawei is not separable from B. macrophylla on any single character, although a number of characters are very nearly constant. A combination of characters, however, will give a good separation in all specimens we have encountered. The single Brazilian specimen of B. fanshawei is in fact fairly typical of the species, not approaching B. macrophylla. It has very conspicuous domatia typical of B. fanshawei.
19. **Buchenavia macrophylla** Eichl. in Flora 49: 166 (1866); in Mart., Fl. Brasil. 14 (2) : 98 (1867).

*Terminalia macrophylla* Spruce ex Eichl., loc. cit. (1867), nom. syn.
*Buchenavia stellae* Cuatrec. in Fieldiana, Bot. 27 (1) : 109 (1950).

Leaf-lamina subcoriaceous to coriaceous at maturity, 3–34 × 1.5–11 cm., (narrowly elliptic) oblanceolate to narrowly obovate, minutely apiculate to long-acuminate (or rarely rounded) at the apex with an acumen up to 2 cm. long, acutely to very narrowly cuneate and often markedly narrowed and sometimes decurrent into the petiole at the base, almost glabrous except pubescent on the midrib and lateral nerves on both surfaces; midrib very conspicuous and raised below; lateral nerves very conspicuous and raised below, (4) 6–14 pairs; reticulation rather inconspicuous or fairly conspicuous, not close; petiole rather slender to stout, very variable in length, 6–32 mm. long, densely to sparsely pubescent, nearly always conspicuously biglandular from below the middle to at the top. Peduncle not stout, 6–32 mm. long, shortly pubescent; rachis 20–100 mm. long, densely puberulous; flowers as in *B. fanshawei*. Fruit oblong-ellipsoid to ovoid-ellipsoid, terete or very slightly flattened when fresh, up to 23 × 12 mm., rounded to subacute (apiculate) at the apex, rounded to very shortly pseudostipitate at the base, very shortly but densely ferrugineous-tomentellous, indumentum wearing off when very old; endocarp as in *B. fanshawei*.

**Colombia**: Caqueta: Florencia, in the cerros La Estrella, 400 m., 30 Mar. 1940, Cuatrecasas 8863 (US, isotype of *B. stellae*).


*B. macrophylla* is apparently the most abundant species of the genus in its area of distribution. It has not been recorded from Venezuela, although it seems likely to occur there. It probably also occurs further up the Vaupés in Colombia.
The fruits of *B. macrophylla* are distinct from those of all other species than *B. fanshawei*, the difference between *B. macrophylla* and that species being discussed under the latter. In their typical form the leaves are also quite characteristic and distinctive.

We have little hesitation in including *B. stellae*, of which we have seen an isotype, under the present species. It is the only record of *B. macrophylla* which we know of from Colombia. All the characters by which *B. stellae* is supposed to differ (notably its longer petioles) are found quite frequently in various forms of *B. macrophylla*. Although *B. stellae* was compared by the author with *B. reticulata*, it and *B. macrophylla* in general are very distinct from that species.


Leaf-lamina chartaceous at anthesis, 8–23 × 4–8 cm., usually oblanceolate, shortly acuminate at the apex, narrowly cuneate but not decurrent into the petiole at the base, almost glabrous above except tomentose on the midrib and densely pubescent on the lateral nerves, conspicuously ciliate on the margin, sparsely pubescent below except densely pubescent on the midrib and lateral nerves (at flowering time); midrib conspicuously raised below; lateral nerves conspicuously raised below, c. 12–16 pairs; petiole short and stout, c. 6–13 mm. long, shortly pubescent, conspicuously biglandular. Rhachis c. 55–110 mm. long, densely pubescent; flowers c. 3.5 × 3 mm., with a pubescent ovary but a glabrous upper hypanthium; bracts relatively large and conspicuous, foliaceous, c. 7–13 × 1–2 mm., with a conspicuous midrib, pubescent, exceeding the flowers. Fruit so far unknown.

**BRAZIL**: Amazonas: Cachoeira das Araras, Rio Vaupés (near the Colombian frontier), “Árvore, 5 m.”, 1 Nov. 1945, Fréses 21308 (IAN, holotype, not seen; K).

This species is very distinct in its large leafy bracts which, as far as is known, are unique in the genus. Apart from this character, however, it scarcely seems possible to distinguish it from *B. macrophylla*, and indeed it may be an abnormal form of that species. As the fruits are unknown (the only gathering being in flower) we prefer to maintain the species for the present. The locality is within the range of *B. macrophylla* but we have not seen the slightest trace of large leafy bracts or of a ciliate leaf-margin in the latter species.

21. *Buchenavia pulcherrima* Exell & Stace, sp. nov.

*Arbor* c. 20 m. alta; ramuli griseo-fusci, fere glabri, apice clavati. *Folia* spiraliter ordinata ad ramulorum apices congesta; lamina subcoriacea, 27.5–29 × 8–10 cm., anguste obovata vel oblanceolata, integra, in toto fere glabra, apice abrupte acute mucronata vel apiculata (apiculo ad 8 mm. longo), basi anguste cuneata, costa media infra valde prominenti; nervis lateralibus infra prominentibus 9–11-paribus, venulis conspicuis vix prominentibus; petiolus 30–38 mm. longus, triquetrus, inconspicuissime glandulosus vel eglandulosus. *Inflorescentiae* axillares, pendulae,
elongato-spicatae; pedunculus gracilis, c. 30-42 mm. longus, sparse rufo-pubescent; rhachis gracilis, c. 70-110 mm. longa, rufo-pubescent. Fructus ellipsoideus, teretiusculus, immaturus ad 12 x 8 mm., apice basique rotundatus vel latissime obtusus, pulchre dense rufo-velutinus.

British Guiana: Essequibo: 172 km. along Bartica-Potaro road, "60 ft. tree 10 in. diam. basally swollen from Clump Wallaba forest—lvs. tufted to branch ends, thinly leathery, primary nerves prominent beneath—young fr. on drooping stalks from below lvs., oval, rusty-velvety pubescent", 15 Nov. 1943, Field No. F1485 = Forest Dept. 4221 (K, holotype); same locality, "Seedlings of 4221 with cotyledons only—perhaps 10 days old, from below parent tree", 15 Nov. 1943, Field No. F1486 = Forest Dept. 4222 (K).

This species is very different from the other two species of the genus known from British Guiana: B. fanshawei with small leaves and very shortly brownish-pubescent fruits; and B. megalophylla with large leaves and long-beaked fruits. It is also distinct from all other members of the genus in its fruits.

The specimen Forest Dept. 4222 in the Kew Herbarium consists of two seedlings each of which has only a pair of cotyledons on a short hypocotyl. The cotyledons are very like those of B. fanshawei from the same area: 3.5-3.8 by 4.5-5.5 cm., truncate at the apex, obtusely cuneate to almost truncate at the base. We have not seen cotyledons of any other species of Buchenavia.

The vernacular name for both B. fanshawei and B. pulcherrima is given as "Fukadi".


Leaf-lamina coriaceous, 2.5-14 x 1.3-6.7 cm., narrowly obovate or obovate to elliptic-obovate, rounded or very shallowly retuse or broadly obtuse or very shortly apiculate (apiculus up to 4 mm. long) at the apex, acutely cuneate at the base and not or scarcely decurrent into the petiole, almost glabrous except rather sparsely pubescent on the midrib and lateral nerves on both surfaces; midrib conspicuous and raised below; major lateral nerves conspicuous and raised below, 5-10 pairs; reticulation fine but quite conspicuous, close, forming very small inter-reticular spaces; petiole distinct and stout, 14-25 mm. long, sparsely pubescent or pubescent, eglandular or very inconspicuously glandular near the apex. Peduncle slender, 12-24 mm. long, puberulous, indumentum greyish or rufous; rhachis slender, c. 35-95 mm. long, rufous- or cano-puberulous; flowers with a densely canescent-sericeous ovary and a glabrous upper hypanthium. Fruit ellipsoid to ellipsoid-obovoid, more or less terete, 28-31 x 13-14 mm. (c. 20 mm. broad fide Ducke—fresh material?), abruptly and shortly apiculate (up to 2 mm.) at the apex, shortly pseudostipitale (2-3 mm.) at the base, cano- or rufous-tomentose at first, indumentum wearing off but still visible in very old fruits in wrinkles of drupe and at the ends; endocarp almost terete, slightly longitudinally ridged, c. 25-30 x 12-15 mm., subacute at the apex, more or less rounded at the base.

Ducke also mentions specimens (Ducke 1308 (RB)) collected from the same locality (same tree?) as the lectotype on 12 Aug. 1943 (subadult flowers) and on 5 Oct. 1943 (young fruits). Apparently the first specimen known was a tree in the gardens of Belém (Pará) Museum (Pará State) introduced in 1904 by Dr. J. Huber from the mid region of the Rio Perús (Amazonas State). There is a specimen from this tree (Ducke 1281 (RB)) with mature fruit.

This species appears to be very distinct from all others in its characteristic fruits, perhaps being closest to the glabrous-fruited B. grandis. Very old fruits seem quite glabrous but on examination remains of the tomentum can be seen in the wrinkles and at the ends. In the original description Ducke says that the fruits have a grey tomentum, and this is true of Krukoff’s two gatherings. Ducke’s two gatherings, however, have a conspicuously rufous tomentum. Such a change of indumentum from a greyish to a reddish colour during drying is also known in leaves of Chrysophyllum species. We do not know of it elsewhere in Buchenavia: B. sericocarpa has retained its greyish-pubescent fruits in the herbarium and B. pulcherrima is described in a field note as having “rusty-velvety pubescent” fruits in the fresh state.


Leaf-lamina chartaceous or subcoriaceous, 4·5–12 × 2–5 cm., obovate to narrowly obovate, rounded to subacute or rarely apiculate at the apex, narrowly cuneate but scarcely decurrent into the petiole at the base, almost glabrous (or sometimes very sparsely pubescent below) except sparsely puberulous to puberulous on the midrib and lateral nerves on both surfaces; midrib conspicuous and raised below; major lateral nerves fairly conspicuous and somewhat raised below, c. 6–9 pairs; reticulation rather conspicuous and close, forming fairly small inter-recticular spaces; petiole distinct, not stout, (5) 10–20 mm. long, puberulous to sparsely puberulous, eglandular. Peduncle slender, c. 13–24 mm. long, rufous-puberulous; rachis slender, c. 22–100 mm. long, rufous-puberulous; flowers c. 3–4 × 2–3 mm. Ovary glabrous to densely rufous-puberulous. Distal portion of lower hypanthium glabrous to sparsely rufous-puberulous; upper hypanthium glabrous or very sparsely puberulous. Fruit ellipsoid, slightly 4–5-angled when dry, c. 24–27 × 11–13 mm. (17 mm. wide fide Ducke), rather gradually acutely apiculate (up to 2 mm.) at the apex, shortly pseudo-stipitate (c. 2–3 mm.) at the base, glabrous; endocarp (fide Ducke) compressed, longitudinally ridged, 20–22 × 12–13 mm., 8–10 mm. thick, acute at each end.
BRAZIL: Pará: Obidos, 9 Mar. 1909, Ducke 10235 (BM; MG, lectotype, not seen); same locality, wood in elevated places, "arbor magna fl. viridibus", 15 Sept. 1927, Ducke 21349 (K). Oriximiná, by Rio Trombetas, 5 Feb. 1918, Ducke 16976 (BM, lectoparatype). In forest in the Quataquara hills near the middle of Rio Tapajoz, "arbor magna", 13 Aug. 1923, Ducke 17687 (K, lectoparatype).

Ducke has recorded the species elsewhere in the State of Pará: between Mt. and Lake Curumú (Ducke 17682 (RB)); by the Rio Tapajoz waterfalls near Bella Vista (Ducke 17688 (RB)); and in the Serra de Santarém. He has also recorded it from Maranhão: near Codo on the Rio Itaperurú (Ducke 658 (MG)); and near Mirador on the same river (Lisboa 2351 (MG)). Besides Ducke’s four gatherings cited above we have seen no other specimens of this species, although specimens of other species have been placed here (e.g. of B. pallidovirens and B. huberi).

It is possible that the specimens mentioned represent more than one taxon, although there is no direct evidence for this besides the great variation in pubescence noted by Ducke. He states that specimens from Tapajoz have glabrous ovaries and less densely pubescent inflorescences (i.e. rachides), specimens from Obidos and Trombetas have moderately pubescent ovaries and inflorescences; and that specimens from Maranhão have very densely pubescent ovaries and inflorescences. We have, however, noted this range of pubescence in B. oxycarpa, where an increased pubescence is probably correlated with a drier habitat. This is also very likely the case in B. grandis, as noted by Ducke since he says that trees from the drier regions (in Maranhão) are smaller (20 m. as opposed to 30–45 m. high). The Maranhão specimens are also more pubescent.

This is a plant from the lower regions of the Amazon and coastal areas, which may well account for the fact that we have seen no recent collections of it. It appears to be most closely related to B. huberi and B. congesta.

Ducke’s specimens 10235 and 16976 (and probably others) were originally determined (by J. Huber fide Ducke) as Terminalia lucida Hoffmanns. ex Mart., as there is some resemblance between the leaves of the two species. The fruits, however, are quite different, those of T. lucida having very broad wings and a dense indumentum. Two gatherings of B. oxycarpa (Krukoff 1241 and 6174) and one of B. fanshaweii were also originally determined as T. lucida, although the Terminalia is quite unrelated and bears only the most superficial resemblance to any species of Buchenavia. We do not know of any other Terminalia species which has been confused in this way.


Leaf-lamina chartaceous or subcoriaceous, 8–15 × 3–7 cm., obovate or narrowly obovate, rounded and very sharply and abruptly shortly apiculate (apiculus up to c. 3 mm.) at the apex, narrowly cuneate and slightly decurrent into the petiole at the base, very sparsely puberulous to almost glabrous except puberulous on the midrib and lateral nerves above, sparsely puberulous at flowering time to very sparsely puberulous or almost glabrous except puberulous on the midrib and lateral
nerves below at fruiting; midrib conspicuous and raised below; lateral nerves conspicuous and raised below, slightly raised above, c. 9–13 pairs; reticulation rather conspicuous, slightly raised below and above, forming small inter-reticular spaces; petiole not stout, c. 20–30 mm. long, puberulous or densely puberulous, eglandular. Peduncle rather slender, 20–35 mm. long, densely rubiginous-puberulous at flowering time to rather sparsely so in fruit; rhachis rather slender, c. 35–85 mm. long, rather densely rubiginous-puberulous; flowers c. 3–4 × 2–3 mm. Lower hypantherum densely rubiginous-puberulous; upper hypantherum rather to very sparsely rubiginous-puberulous. Fruit oblong-ellipsoid, very slightly flattened to more or less terete, 22–25 × 9–12 mm., rounded to broadly obtuse at the apex, more or less pseudostipitate (pseudostipe under 2 mm. long) at the base, glabrous from a very young stage.

Brazil: Amazonas: Manáos, near Cachoeira do Mindú in a non-flooded wood in a humid spot, "arbor sat. magna" (over 30 m. fide Ducke in descr.), 3 Dec. 1943, Ducke 1465 (F; RB, lectotype, not seen); same locality, 4 Oct. 1946, Ducke 2003 (RB, lectoparatype, not seen); same locality, "Árvore grande; flôr verde branacenta da árvore tipica", 25 Sept. 1947, Ducke 2104 (BM).

Apparently only one tree of this species is known and from it all three of the above gatherings were made. From these we select Ducke 1465 as lectotype since this bears mature fruits: Ducke 2003 has young fruits and Ducke 2104 (which was not cited by Ducke) has flowers.

In its densely congested long-petioled leaves and oblong-ellipsoid glabrous fruits this species appears to be quite distinct from all others, perhaps approaching most closely B. grandidis and to a lesser extent B. macrophylla.

Insufficiently known species


Based on Glaziou 5855 from the State of Rio de Janeiro, Brazil. We have examined the specimen in Herb. Paris and a fragment in the British Museum Herbarium from the specimen in Herb. Copenhagen. They both consist of young sterile material alone, which makes their determination quite impossible even to the extent of specifying Buchenavia or Terminalia as the genus.


Based on Glaziou 18218 from the State of Rio de Janeiro, Brazil. We have examined the specimen in Herb. Paris and confirmed the genus as Buchenavia. The specimen consists only of leaves and very young inflorescences and this makes a comparison with known species extremely difficult. We consider the specimen too immature to warrant description as a new species or to allow its identification, although there are a number of similarities with B. viridiflora. A further possibility is that the inflorescences would have been capitate. A second sheet in Herb. Paris bears an identical label to the previous specimen, in addition to the correct collector's ticket and tag with n. 21125. This specimen is clearly B. tomentosa and was recorded...
as such by Glaziou (loc. cit.). It was doubtless erroneously mounted with a label of *B. macahensis*.

*Excluded species*


Based on Glaziou 6142 from the State of Rio de Janeiro, Brazil. We have examined the two specimens in Herb. Paris and found them to be an unknown species of *Terminalia*.

**RAMATUELLA** Kunth

*Ramatuelle* Kunth, Nov. Gen. & Sp. Pl. 7 : 253 (1825) (“*Ramatuela*”).

*Type:* *R. argentea* Kunth.

Kunth originally used the spelling *Ramatuela*, naming the genus after a French horticulturist whom he called “*Ramatuel*”. De Candolle (Prodr. 3 : 16 (1828) stated that the correct spelling of this Frenchman’s name was Ramatuelle (actually given as M. de Ramatuelle in a paper published by the latter in Journ. Hist. Nat. 2 : 233 (1792)) and thus rightly corrected the spelling of the generic name to *Ramatuela*.¹

*Ramatuela* also belongs to the *Terminalieae*, differing from the other six genera in the tribe by having 4–5-winged actinomorphic fruits crowded in spherical masses. It is confined to the headwaters of the Rio Orinoco and Rio Negro and some of their tributaries in the Amazonas district of Venezuela, the Vaupés district of Colombia and the Amazonas district of Brazil (see Fig. 1), the whole region consisting of inter-connecting waterways since the upper Orinoco divides in such a way that some of its waters, curiously enough, flow into the Amazon via the Rio Negro. The area of distribution of the genus lies within latitudes 1° S. and 4° N., and occupies only about 8° of longitude. There appear to be no ecological or geographical differences between the species.

The genus is closely related to *Terminalia* and it is highly probable that it was derived from an original *Terminalia* stock. As in *Terminalia* and *Buchenavia* (and indeed all the *Terminalieae*) *Ramatuela* is apetalous. The lower hypanthium is constricted at the apex but not extended into a long neck as in *Buchenavia*. It and the cupuliform upper hypanthium, which bears 4 or 5 triangular calyx-lobes, are pubescent on the exterior. The 8 or 10 stamens are in two whorls, one opposite to and one alternate with the calyx teeth, and are conspicuously exserted, as is the style. In bud the stamens are bent double, the anthers being well protected in the base of the upper hypanthium which possesses a very well-developed hairy disk. As in *Terminalia* the anthers are versatile. All species usually have tetramerous and pentamerous flowers in the same inflorescence. In *Ramatuela*, as is frequently the case in *Buchenavia*, male and bisexual flowers are mixed in the same inflorescence, in the present genus the former sometimes being the more abundant. The lower

¹ Poiret (Dict. Sci. Nat. 44 : 427 (1826)) had used the spelling *Ramatuela* two years previously, but he gave no reasons for this.
flowers of the inflorescence are more usually male, so that the floriferous rhachis may be three or more cm. long but give rise to a more or less capitate infructescence.

Ramatuella was surveyed fairly recently by Maguire (in Mem. New York Bot. Gard. 8: 130-132 (1953)), who recognized four species, one consisting of two varieties. The acquisition of further material has now led us to recognize six species and, apart from the fact that Maguire gave no descriptions, is the only reason for revising the genus after such a comparatively short interval. These species all consist of small to medium-sized evergreen trees of riverine forest.

Key to the Species

Lower surface of leaves and fruit densely silvery-sericeous; wings of fruit short and broad, very abruptly narrowed at the base into a pseudostipe and at the apex into a beak 2-4 mm. long

1. R. argentea

Lower surface of leaves for the greater part glabrous or only rather sparsely hairy, not silvery or sericeous; fruit various, the wings relatively long; beak more or less absent to long:

Fruit 10-20 mm. long, lanceolate to circular in outline, rounded or curved at the margin; beak up to 1 mm. long, or 2 or more mm. long and then the wings gradually narrowing into it:

Leaves glabrous or very sparsely pubescent over the whole of both surfaces; fruit acuminate at the apex, beaked, the beak 2-5 mm. long at maturity:

Leaf-lamina 2.5-11 × 1-5 cm.; petiole 4-15 mm. long; fruit silvery, ovate in outline; beak c. 2-5 mm. long, rather slender; pseudostipe c. 2 mm. long

2. R. maguirei

Leaf-lamina 8-14 × 4-7 cm.; petiole 20-30 mm. long; fruit fulvous, narrowly ovate to lanceolate in outline; beak c. 2-4 mm. long, rather stout; pseudostipe absent

3. R. virens

Leaves rather densely pubescent at the base of the midrib on the lower surface; fruit truncate to obtuse at the apex, beakless or with a beak not exceeding 1 mm. long:

Leaf-lamina ob lanceolate to narrowly oblong; fruit broadly elliptic to circular in outline, 12-18 mm. wide, truncate to rounded-retuse at the apex; wings markedly crisped, rather thin

4. R. latifolia

Leaf-lamina obovate to oblong; fruit oblong to ovate in outline, 8-15 mm. wide, obtuse to almost truncate at the apex; wings undulate, rather thick

5. R. crispialata

6. R. obtusa

Fig. 4. *Ramatuella maguirei* Exell & Stace (holotype): a, habit (×3); b, fruit (×2). 
*R. argentea* Kunth (Spruce 3498): c, fruit (×2). 
*R. virens* Spruce ex Eichl. (*Maguire, Cowan & Wurdack* 30764): d, fruit (×2). 
*R. latifolia* Maguire (holotype): e, fruit (×2). 
*R. obtusa* (Maguire) Exell & Stace (holotype): f, fruit (×2). 
*R. crispialata* Ducke (*Fröes* 28040): g, fruit (×2).
Leaf-lamina coriaceous, 2-10 \times 1-4 \text{ cm.}, oblanceolate to narrowly obovate, retuse to rounded at the apex, narrowly cuneate and slightly decurrent into the petiole at the base, almost glabrous above except sparsely or very sparsely puberulous on the midrib, densely silvery-sericeous below; midrib conspicuous and raised below; major lateral nerves inconspicuous, c. 5-11 pairs; reticulation not visible; petiole usually distinct, 5-16 mm. long, appressed-puberulous. Peduncle (in fruit) rather slender to stout, 5-35 mm. long, appressed-puberulous; rhachis up to 6 mm. long. Fruits crowded into spherical capitula, 8-12 \times 8-13 \text{ mm.}, densely silvery-sericeous; pseudostipe stout, abruptly delimited from upper regions, 2-3 mm. long; beak rather slender, abruptly delimited from lower regions, 2-4 mm. long; body of fruit with 4-5 short and broad (1-5 \times 3-6 \text{ mm.}) wings; margin of wings sharply or bluntly pointed, not undulate.

**VENEZUELA or COLOMBIA:** Rio Atabapo, Humboldt \& Bonpland (P, holotype, not seen). Rio Guainia, above its confluence with Rio Casiquiare, May 1854, Spruce 3498 (BM; K).\(^1\)

**COLOMBIA:** Vaupés: Rio Atabapo, drowned river margin, frequent on the Colombian bank between San Fernando and Cacaqual, to 30 m., "bushy tree 7 m. high, fruit tan", 18 Nov. 1953, Maguire, Wurdack \& Bunting 36264 (BM). Rio Vaupés (not seen; \textit{fide} Maguire).

**BRAZIL:** Amazonas: Íçana, bank of Rio Cubato, "Árvore 4 m. com ramagens densas", 19 Nov. 1945, Froés 21421 (K).

In its densely silvery-sericeous lower leaf surfaces and characteristic fruits (see Fig. 4) this species is very distinct from all the other five.

2. **Ramatuellla maguirei** Exell \& Stace, sp. nov. (Figs. 4 a, b; 5 a, b.)

*Arbor* parva vel media, c. 20 m. alta; ramuli griseo-fusci, fere glabri, apice clavati. *Folia* spiraliter ordinata ad ramulorum apices congesta, 2-11 \times 1-4 \text{ cm.}; lamina subcoriacea, oblanceolata vel elliptico-obovata, apice retusa, basi acuta in petiolum decurrens, integra, costa infra minute puberula excepta glabra, costa media supra inconspicua subtus prominenti, nervi lateralibus inconspicuis; petiolus c. 3-11 mm. longus, sparse puberulus. *Inflorescentiae* axillares, spicatae vel capitatae; pedunculis vix validis, 15-50 mm. longus, sparse puberulus; rhachis ad 33 mm. longa; flores masculini et bisexuales in eandem inflorescentiam dispositi. *Hypanthium inferior* c. 3-7 \times 1-2 mm., dense adpresso-pubescent, apice in floribus masculinis angustatum, in floribus bisexualibus brevissimum et angustissimum; *superum* c. 3-4 \times 3.5-5 mm., adpresso-pubescent vel sparse adpresso-pubescent. *Calycis lobi* 4 (vel 5?), c. 1-5 mm. longi, obtusi. *Stamina* 8 (vel 10?), exserta ad 6 mm. *Stylus* ad c. 5 mm. exsertus, filiformis, glaber. *Fructus* dense congesti, 8-9 \times 9-11 mm., (4) 5-alati, rhomboidei vel late ellipsoidei, olivaceo-fusci, minute argenteo-pubescentes, rostro 0.5-1 mm. longo, alis tenuibus in rostrum stipamque abrupte

\(^1\) Both the Rio Atabapo and the Rio Guainia form the Venezuelan-Colombian frontier, and we cannot be certain to which country these collections belong. No other collection of this species appears to have been made in Venezuela, although it undoubtedly occurs there.
contractis amplis lateriliter obtuis vel obtuso-rotundatis margine planis vel leviter undulatis.

**Venezuela**: Amazonas: Alto Rio Orinoco, Caño Yapacana from laguna to mouth, 125 m., "tree 20 m. high, occasional waterside", 17 Mar. 1953, Maguire & Wurdack 34606 (BM, holotype).

**Brazil**: Amazonas: Rio Curicuriary, tributary of Rio Negro, "super cataractas, ad ripas inundatas. Arbor parva fl. albidis", 23 Nov. 1936, Ducke 34638 (K); same locality, 20 Nov. 1936, Ducke 34639 (K); same locality, 22 Feb. 1936, Ducke 34640 (K).

We have pleasure in naming this distinct species, which has been distributed as *R. virens*, after one of its collectors, Bassett Maguire, author of a previous paper on the genus.

*R. maguirei* is easily distinguished from the other species of the genus by its rather small almost glabrous leaves and by its fruits, the wings of which are deltate in outline and abruptly narrowed above into the very short but distinct beak and below into a stalk-like base. The fruits are also less pubescent than in any other species and smaller than in all but *R. argentea*, to which it is perhaps most closely related (except in its lack of sericeous indumentum).

The Venezuelan specimen has mature fruits, while of the three Brazilian specimens one (*Ducke 34640*) has mature fruits and all three have open flowers.

There are two distinct types of mature fruit among the material which has hitherto been identified as *R. virens*. These are represented by (a) Maguire, Cowan & Wurdack 30764, and (b) Ducke 34640 and Maguire & Wurdack 34606. They obviously belong to two distinct species. We have, however, had great difficulty in deciding which of them should be linked with Spruce 3758 (the type collection of *R. virens*) since the latter has flowers and only very immature fruits. The very young fruits and ovaries at anthesis give very little clue to their shape at fruiting time. *Ducke 34640* has both flowers and fruits and the former differ slightly from the flowers of *R. virens* (*Spruce 3758*), the upper hypanthium being somewhat less pubescent and the calyx lobes more obtuse (see Fig. 5). Moreover, the very young fruits have less sinuate wings. We have therefore decided that Maguire, Cowan & Wurdack 30764 belongs to *R. virens* and that *Ducke 34640* and *Maguire & Wurdack 34606* represent a new species, described above.

*Ducke 34638* and 34639 are interesting in that the rather elongate inflorescences consist almost entirely of male flowers, the bisexual flowers being confined to one or two at the extreme apex of the rhachis.

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Leaf-lamina coriaceous, 2-5-11 × 1-5 cm., oblanceolate to obovate, refuse to rounded at the apex, narrowly cuneate and slightly decurrent into the petiole at the base, almost glabrous on both surfaces except sparsely puberulous on the midrib below; midrib conspicuous and raised below; major lateral nerves inconspicuous,
c. 8-15 pairs; reticulation not visible; petiole usually fairly distinct, 4-15 mm. long, sparsely puberulous. Peduncle (in fruit) rather slender, 30-70 mm. long, appressed-puberulous; rhachis up to 25 mm. long. Flowers as in B. maguirei (but see discussion thereunder). Fruits usually crowded into spherical capitula, but sometimes a few below the head, c. 13-17 × 6-10 mm., ovate in outline, densely silvery-sericeous when mature; pseudostipe abruptly delimited from upper regions, c. 2 mm. long; beak rather slender, gradually contracted from lower regions, 2-5 mm. long; body of fruit with 4-5 long and rather narrow (8-12 × 2-4 mm.) wings; margin of wings gradually curved, conspicuously but minutely sinuate; wings rather thin.


**Venezuela or Colombia**: Rio Guainia, above its confluence with Rio Casiquiare, Nov. 1854, Spruce 3758 (type collection; BM; K); from type locality, Schultes & Lopez 9359 (not seen; fide Maguire).

**Brazil**: Amazonas: Rio Negro, Enuixy, Matozinho, 18 May 1947, Froes 22340 (BM).

The problem of the identification of fruiting specimens with Spruce’s type collection of *R. virens* (in flower) is discussed above under *R. maguirei*.


(Fig. 4 e.)

Leaf-lamina coriaceous, 8-14 × 4-7 cm., oblancoolate to obovate, refuse to rounded at the apex, cuneate and scarcely decurrent into the petiole at the base,

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1 See footnote on p. 41 concerning Spruce 3498 under *R. argentea*.
almost glabrous on both surfaces except sparsely puberulous on the midrib below; midrib conspicuous and raised below; major lateral nerves quite conspicuous below, c. 8–16 pairs; reticulation visible, irregular; petiole distinct, (10) 20–30 mm. long, very sparsely puberulous. Peduncle (in fruit) rather slender, 50–70 mm. long, densely puberulous; rhachis up to c. 6 mm. long. Fruits crowded into spherical capitula, 14–18 × 6–10 mm., narrowly ovate to lanceolate in outline, densely tawny-puberulous when mature; pseudostipe absent; beak rather stout, gradually contracted from lower regions, 2–4 mm. long; body of fruit with 4–5 long and rather narrow (10–13 × 2–4 mm.) wings; margin of wings gradually curved, conspicuously but minutely sinuate; wings rather thick.


This species is obviously very closely related to *R. virens* and may ultimately even prove to be conspecific. The fruits (see Fig. 4) and leaves, however, show rather small but distinct differences. The “cuticular exfoliation” to which Maguire refers is of very dubious taxonomic value. Whatever is exfoliated (perhaps it is a surface layer of wax) it is certainly not the leaf-cuticle since in this genus the latter is extremely thick and extends well down between the epidermal cells.


—Maguire in Mem. New York Bot. Gard. 8: 131 (1953) excl. var. obtusa. (Fig. 4 g.)

Leaf-lamina coriaceous, 6–13 × 2.5–7.5 cm., oblanceolate to narrowly obovate, retuse at the apex, cuneate but scarcely decurrent into the petiole at the base, almost glabrous except sparsely puberulous on the midrib above, very sparsely puberulous to almost glabrous except densely puberulous on the midrib below; midrib conspicuous and raised below; major lateral nerves quite conspicuous below, c. 8–18 pairs; reticulation visible, irregular; petiole distinct, c. 12–17 mm. long, puberulous. Peduncle (in fruit) rather slender, 50–95 mm. long, densely puberulous; rhachis up to c. 12 mm. long. Fruits crowded into spherical capitula, 16–20 × 12–18 mm., broadly elliptic to circular in outline, densely tawny-puberulous when mature; pseudostipe absent; beak absent or up to 1 mm. long, very abruptly contracted from the truncate or retuse apex of the fruit; body of fruit with 4–5 broad and long (15–20 × 5–7 mm.) wings; margin of wings rounded, conspicuously crisped; wings rather thin.


The large broad-winged fruits of this species render it very easily identifiable. Even sterile specimens can readily be determined owing to the distinctive shape, size and pubescence of the leaves.
6. *Ramatuella obtusa* (Maguire) Exell & Stace, stat. nov.  (Figs. 4 f; 5 d.)


Leaf-lamina coriaceous, 3·2–13 × 1·7–7 cm., narrowly obovate to obovate or narrowly elliptic to elliptic, retuse to rounded at the apex, cuneate to broadly cuneate and scarcely decurrent into the petiole at the base, very sparsely puberulous to glabrous except puberulous to sparsely puberulous on the midrib above, very sparsely puberulous except densely puberulous on the midrib below; midrib conspicuous and raised below; major lateral nerves quite conspicuous below, c. 8–18 pairs; reticulation visible, irregular; petiole distinct, 7–25 mm. long, densely puberulous. Peduncle (in fruit) rather slender to rather stout, 50–110 mm. long, densely puberulous; rhachis up to 15 mm. long; flowers male and bisexual in the same inflorescence. Lower hypanthium 4–6 × 2–4 mm., very densely appressed-pubescent, slightly constricted at the apex; upper hypanthium 3–4·5 × 4–6 mm., densely appressed-pubescent to more or less tomentose. Calyx lobes 4 (or 5?), c. 1·5 mm. long, obtuse, rather thick. Stamens 8 (or 10?), exserted to 4 mm. Style exserted to 3 mm., stout, densely pubescent for at least the proximal three-quarters. Fruits usually crowded into spherical capitula but sometimes a few below the head, 10–20 × 8–15 mm., ovate to oblong in outline, densely tawny-puberulous when mature; pseudostipe absent; beak absent or up to 1 mm. long, abruptly contracted from the obtrue to almost truncate apex of the fruit; body of fruit with 4–5 broad and long (9–18 × 3–6 mm.) wings; margin of wings rounded, conspicuously undulate; wings rather thick.

**Venezuela.** Amazonas: Cerro Yapacana, Rio Orinoco, "tree to 7 m. high, fruit brown, occasional in Caatinga about Yapacana Savanna I.", 7 Jan. 1951, **Maguire, Cowan & Wurdack 30796** (NY, holotype).

**Brazil.** Amazonas: Rio Aracá, subtributary of Rio Negro, Campinarana, "árvore de 2 m., flor esbranquiçada, sólido arenoso", 24 Oct. 1952, **Fröes & Addison 29040** (BM).

Maguire recognized five taxa (four species, one having two varieties) in the genus *Ramatuella*. These fall readily into three easily defined groups:

1—*R. argentea*, with silvery-sericeous fruits and under surfaces of the leaves, the fruits with short wings abruptly narrowed at the base and at the apex into a fairly long beak (Fig. 4 e).

2—*R. virens* and *R. latifolia*, with nearly glabrous leaves, and fruits with long wings gradually tapering at the apex into a rather long beak (Fig. 4 d, e).

3—*R. crispialata* vars. *crispialata* and *obtusa*, with leaves nearly glabrous except for a rather dense brownish indumentum at the base of the midrib on the lower surface, and fruits with long broad wings abruptly narrowed to a very short beak at the apex (Fig. 4 f, g).

*R. maguirei*, our new species, forms a fourth group (see above).

In group 2, Maguire separated *R. latifolia*, known only from the type specimen, from *R. virens* by several small though well-defined characters (see key) which we regard as sufficient to maintain them as specifically distinct. In group 3, we consider that the differences between *R. crispialata* var. *crispialata* and var. *obtusa* are
comparable to those between *R. latifolia* and *R. virens* and for this reason we have raised *R. crispialata* var. *obtusa* to the rank of species. Maguire himself suggested that this might ultimately prove to be the best course. We have recently received a specimen from a second station for *R. obtusa*, which extends the eastern limit of *Ramatuella* to 63° W. This specimen (*Fróes & Addison 29040*) is of further interest since it bears flowers and unripe fruits, the type having mature fruits. It has almost all the characters described by Maguire, except that the leaf base is not always more obtuse than in *R. crispialata*, although the leaf is broader in comparison with its length. In addition to the characters given by Maguire, the fruit of *R. obtusa* is clearly narrower and less truncate at the apex than is that of *R. crispialata* (see Fig. 4).

Of the six species now recognized, only *R. obtusa*, *R. maguirei* and *R. virens* are known in flower. The last was figured by Eichler (in Mart., Fl. Brasil. 14 (2): t. 26 fig. 2 (1867)) but we have re-examined the flowers of this species and compared them with those of the other two species. The flowers of *R. obtusa* differ from those of *R. virens* and *R. maguirei* chiefly in their greater amount of indumentum, a feature also shown by the leaves. This difference is most evident on the outside of the upper hypantherium and calyx lobes, which are appressed-pubescent in *R. virens* but densely appressed-pubescent to more or less tomentose in *R. obtusa*; and in the style, which is entirely glabrous in *R. virens* but densely pubescent in *R. obtusa*, at least for the proximal three-quarters and sometimes along its whole length. Other parts of the flower are also more pubescent in *R. obtusa*, but the stamens are completely glabrous. A further feature is that the style and stamens, which are of the same length, are somewhat longer in *R. virens*, the filaments being over twice as long as the calyx lobes in the latter species but rarely that length in *R. obtusa*. This character should be used, however, with caution, since the filaments and style elongate considerably at anthesis. The flowers of *R. obtusa* are also slightly larger, the ovary especially so, although the latter, of course, soon enlarges after pollination. Furthermore the ovary is less constricted at the apex in *R. obtusa* (see Fig. 5).
THE DIATOM GENUS
CAPARTOGRAMMA
AND THE IDENTIFY OF
SCHIZOSTAURON

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Pp. 47–92 ; 38 Text-figures ; Plates 1–2

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THE DIATOM GENUS CAPARTOGRAMMA
AND THE IDENTITY OF SCHIZOSTAURON

By R. ROSS

Hustedt (in Rabenh., Krypt.-Fl. Deutsch. 7 (2) : 757 (1959)) has suggested that Stauroneis crucicula (Grun. ex Cleve) Comber and another species for which he used the name S. karstenii\(^1\) constitute a distinct subgenus of Stauroneis Ehrenb. characterized by a forking of the central nodule. However, the structure of these two species is so different from that of the type species of Stauroneis and its near relatives as to justify treating them, and two hitherto undescribed and closely related diatoms, as a separate genus. Stauroneis has the central nodule transversely expanded so that it forms a single band of thickening across the valve, reaching almost or quite to the margin and interrupting the striae. In the species under discussion, on the other hand, the valve is convex and the central nodule is connected to the margin of the valve by two diverging strands of silica on either side. These are not mere thickenings of the valve surface but are deep and narrow flanges running between two striae that are scarcely, if at all, more widely separated than the rest.

Those authors who have treated these species as belonging to a genus distinct from Stauroneis have referred them to Schizostauron Grun. (Hedwigia 6 : 28 (1867)), but this name is typified by a totally unrelated species whose correct position is in Achnanthes Bory. However, the monotypic genus Capartogramma Kuff. (Expl. Hydrobiol. Lac Tanganyika (1946–1947), Res. Sci. 4 (3) : 27 (1956)) is based on the species called by Hustedt Stauroneis karstenii. Kufferath’s description shows that he did not fully understand the structure of the diatom, especially of its valve view, and he did not realize that it was one already described and figured by O. Müller (in Engler, Bot. Jahrb. 45 : 88, t. 2 figs. 17, 18 (1910)) and given the name Schizostauron karstenii by Zanon (Atti R. Accad. Ital., Mem. Sci. Fis. Mat. Nat. 12 : 494 (1941)) ; O. Müller, although he used that name, did not give it valid publication. Nevertheless, Kufferath’s description and figures make it impossible to doubt that his name is based on this species.

When it had been established that Schizostauron was a synonym of Achnanthes, the correct position and name of all the species that had at any time been referred to the genus were investigated. In some cases this revealed confusions with species which have never been placed in Schizostauron. The detailed account of Capartogramma is accordingly followed by a discussion of Schizostauron, including both its typification and the identity of all the species which have been placed in it, and this concludes with annotated synonymies of all the species taken into consideration. Where accurate descriptions are not available in the literature, these have been given, and in such cases all the specimens I have seen are listed.

\(^1\)This is not a validly published name. See under Capartogramma karstenii below (p. 58).
All the specimens cited in this paper are in the diatom collection of the British Museum (Natural History), unless there is an indication to the contrary. I am much indebted to the Director of the Botany Department of the Naturhistorisches Museum, Vienna, and the Directors of the Botanical and Palaeobotanical Departments of the Naturhistoriska Riksmuseum, Stockholm, for the loan of specimens from the collections in their charge, and to Mr. H. S. Job and Mr. Manfred Voigt for the loan of specimens from their private collections.

**CAPARTOGRAMMA** Kuff.


E *Naviculaceis*. Valvae symmetricae vel lunatae, convexae, pseudosepto in utroque polo instructae. Nodulus centralis tigillis binis cum ambobus marginibus valvae conjunctus; tigilla quattuor figuram litteram “X” ad instar facientia.

**Type**: *C. jeanii* Kuff. (= *C. karstenii* (Zanon) Ross).

The characteristic feature of this genus is the form of its central nodule and associated structures. The nodule is rectangular, its longer axis being transapical and with a length of one-fifth to one-third of the width of the valve. From each corner a strut of silica runs to the margin of the valve, the four struts forming a figure in the shape of the letter “X”. These struts are flattened, ribbon-like strands of silica and one edge is attached to the inner surface of the valve. The cross-section of these struts is curved, at least near the margin of the valve, and the inner, or free, edge is turned towards the apex of the valve; this edge is continuous with an inwardly projecting flange that runs along the valve margin and connects with the pseudoseptum. The term used in the Latin diagnoses for these struts is *tigillum* (= a little beam). One or more of the struts is at times duplicated or forked, a single row of puncta, rarely more, lying between the two forks. This frequently occurs in the smallest specimens of *C. crucicula* (Grun. ex Cleve) Ross (Plate 1 b) and on the ventral side in *C. amphoroides* Ross (Fig. 14), and also, but much more rarely, in *C. karstenii* and on the dorsal side in *C. amphoroides*.

The struts and pseudosepta of *Capartogramma* are laid down subsequently to the formation of the rest of the valve. In dividing frustules containing young valves at the appropriate stage, these can be seen to have the raphe and striae completely formed but no trace of the tigilla or pseudosepta. It is possible in such specimens to see that there is no appreciably larger gap between the striae where the tigilla will form.

Using the light microscope it was not possible to be sure of the detailed form of the struts, or whether they were attached to the valve surface throughout their length. The description given above is based on stereoscopic electron micrographs, for which I am much indebted to Dr. K. Little of the Nuffield Orthopaedic Centre, Oxford. *C. karstenii*, *C. crucicula* and *C. amphoroides* were investigated by this technique (Plate 1); *C. rhombicum* Ross, which is much rarer in the material available
to me, shows such great similarity to *C. karstenii* and *C. crucicula* under the light microscope that there can be little doubt that its structure is identical. *C. amphoroides* differs somewhat from the other three species, all of which are symmetrical about the apical axis. It, on the other hand, has the form characteristic of the genus *Amphora* Ehrenb. ex Kütz.; the valves are lunate, with a convex dorsal margin and an almost straight ventral one, and the girdle is wider on the dorsal side. The struts on the dorsal side are not very divergent and the electron micrographs show that they are very similar to those of the other species; those on the ventral side are more divergent and are much more expanded parallel to the valve surface, leaving only a small gap between the two at the centre. It is clear, however, that the differences between this species and the other three are no more than minor modifications of the same plan. The fact that these four species all clearly belong to the same genus raises the question of the taxonomic status of *Amphora* and supports the view, tentatively put forward by Cleve in his *Synopsis of the Naviculoid Diatoms* (K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 27 (3) : 99 (1896)), that the various subdivisions of that genus are more closely related to symmetrical forms of similar structure than they are to one another.

The electron micrographs also provide information about the structure of the striae part of the valve. Between each pair of striae there is a low rounded ridge of thickening on the inner surface of the valve. Each stria consists of a single row of holes (alveoli) through the main substance of the valve; these are broadly elliptic to circular, the long axis of the elliptic ones being across the striae, i.e. parallel to the raphe (Plate 2 ; Fig. 1 a). On the outer side of the valve each alveolus opens through a bar-shaped slit, which is normally parallel to the raphe and is about one and a half times as long as the alveolus and one-third as broad as it. These slits are not formed in a separate membrane but in the outer layer of the main membrane of the valve (Plate 2 c). On the inner side of the valve a fine membrane with pores in triangular tesselation stretches across each alveolus. As the walls slope inwards for a short distance from this surface, the area covered by the membrane is somewhat larger than the minimum section of the alveoli. In all three species examined the centre-to-centre spacing of the pores in this fine membrane is c. 150 Å. Alveoli of similar structure occur in some species of *Navicula* sect. *Lineolatae*, e.g. *N. cryptocephala* Kütz. (Helmcke & Krieger, Diatomeenschalen in Elektronen-mikroskopischen Bild 1 : t. 69 (1953)), and in *Scoliopleura tumida* (Bréb. ex Kütz.) Rabenh. (Helmcke & Krieger, op. cit. 2 : t. 177 (1954), whilst those of *Pleurosigma angulatum* (Quekett) W. Smith (Helmcke & Krieger, op. cit. 1 : tt. 61–64 (1953)) and other species of that genus are of the same general plan; the spacing of the fine pores in the inner membranes of all these species is also of the same order, from about 135 Å. to about 180 Å. In the specimens of *Capartogramma* examined

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1 Although the title-page of this work is dated 1895, it does not appear to have been published before 1896. A copy was received by the Royal Microscopical Society between 15 April and 20 May 1896 (Journ. R. Microsc. Soc. 1896 : 368 (30 June 1896)), and it was not noticed elsewhere until later, viz.: Nat. Nov. 18 : 326 (second half of June 1896) ; Nuova Notaristia 7 : 94 (July 1896) ; Hedwigia 35 : (104) (30 October 1896). It is also clear that Schütt had not seen a copy when preparing his account of the *Bacillariaceae* for Engler and Prantl's *Natürlichen Pflanzenfamilien* (t (1, b) "Gedruckt im Juli 1896"; cf. p. 33), and Van Heurck had only seen a manuscript when writing his *Treatise on the Diatomaceae* (cf. pp.105, 125), the preface of which is dated 19th September 1896.
there seems, however, to be another thin amorphous membrane within that in which the alveoli lie; this seems the only explanation for the fact that a small number of alveoli in which both the bar-shaped slit and the pattern of fine pores can be seen are appreciably more electron-transparent than the remainder (Plate 2 A). No such membrane has been reported previously in any diatom and it may be that it is not part of the silica valve but the consequence of imperfect cleaning or washing. This seems unlikely, however, for the specimens were cleaned by boiling in a mixture of concentrated hydrochloric and nitric acids, followed by boiling in concentrated sulphuric acid into which crystals of potassium chlorate were sprinkled, and were washed in dilute ammonia and at least seven changes of distilled water.

![Diagrammatic cross-sections through alveoli at right-angles to (i) and along the line of (ii) the striae](image)

**Fig. 1.** Diagrammatic cross-sections through alveoli at right-angles to (i) and along the line of (ii) the striae: a, *Capartogramma crucicula* (Grun. ex Cleve) Ross; b, *Stauroneis smithii* Grun.; c, *S. anceps* Ehrenb. (All × 50,000; the horizontal scale exact but the vertical scale only approximate.)

Cleve (K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 26 (2) : 141–143 (1894)), in his discussion of the classification and affinities of *Navicula* sect. *Microstigmaticae*, in which he placed *Capartogramma crucicula* and all the species of *Stauroneis* then known, attached considerable importance to the presence or absence of intercalary bands in the girdle and used their presence as the character distinguishing one of the groups into which he suggested the section should be divided. It is of interest, therefore, to note that intercalary bands are present in *C. karstenii*, *C. rhombicum* and *C. amphoroides* but not in *C. crucicula*. The close resemblance between these species in all other respects makes it clear that here at least this character is not of importance above the specific level.

Since the two species of *Capartogramma* already known have been treated in
The past as belonging to or being closely related to *Stauroneis*, stereoscopic electron micrographs were taken of four species of that genus: *S. phoenicenteron* (Nitzsch) Ehrenb., which is the type species, *S. anceps* Ehrenb., *S. smithii* Grun., and *S. acuta* W. Smith. The specimens of the first three all came from a gathering from Western Wood, Cheldon, Devon, collected and cleaned by the late R. F. Bastow, and those of the last from Petersdorf, near Gleiwitz, Silesia (now Gliwice, Poland), the gathering distributed as Rabenh., Alg. Mitteleur. n. 847. The last two of these species resemble *Capartogramma* in having pseudosepta at the apices, whilst the other two do not possess these.

The stauros of *Stauroneis phoenicenteron*, *S. anceps* and *S. acuta* is as broad as the central nodule is long and widens outwards. It is an area of moderate thickening, not projecting further into the interior of the frustule than the central nodule itself, and in *S. anceps* it becomes thinner as it approaches the margin, often so much so that there are short striae opposite it at the margin. In *S. smithii*, on the other hand, the stauros is much narrower than the length of the central nodule; the width of the gap between the striae on either side of it is only twice that between the other striae. It is also very deep, projecting much further into the interior of the frustule than the central nodule does, and near the margin its inner edge expands and continues as a flange along the valve margin. At the poles this flange widens to form the pseudoseptum. *S. smithii* thus resembles a species of *Capartogramma* with the two tigilla on either side fused into one.

*Stauroneis smithii* resembles *Capartogramma* more closely than it does *S. phoenicenteron*, *S. anceps* and *S. acuta* in the fine structure of the valve also. Its striae, like those of *Capartogramma*, are separated by a rounded ridge and the individual alveoli are more or less circular (Fig. 1 b). They open on the outer side through broadly elliptic pores, whose long axis is across the striae, i.e. parallel to the raphe, and is somewhat longer than the diameter of the alveoli, whilst their short axis is about three-quarters of that diameter. On the inner side of the alveoli there is a fine membrane with pores in triangular tesselation, but no indication of an amorphous third membrane was seen in this species.

In *Stauroneis phoenicenteron*, *S. anceps* and *S. acuta* the striae are sunk into the inner surface of the valve in steep-sided troughs and consist of elliptic alveoli whose long axis is in the direction of the striae (Fig. 1 c). The distance between the alveoli is only about half the length of the alveoli themselves, and about half-way between each pair a narrow flange runs across the trough in which the striae lie. The alveoli open to the outside through broad slits parallel to the direction of the striae; these slits have rounded ends and parallel sides, and are almost as long as the alveoli and one-half to one-third as wide as them. There is a fine membrane with pores in triangular tesselation on the inner side of the alveoli stretching from the tops of the flanges across the trough and thus covering all of this. No trace of an amorphous membrane was seen.

*Stauroneis smithii*, as will be appreciated, resembles *Capartogramma* much more closely than it does the other species of *Stauroneis* examined. In *S. smithii* var. *sagittta* (Cleve) Hust., of which no unmounted specimens for examination with the
electron microscope were available, the stauros on one or both sides is often divided so that it forms two parallel bars of thickening with a single stria between them. As far as can be seen with the light microscope the stauros is deeper than wide, as in the specimens of S. smithii var. smithii examined under the electron microscope, and these divided arms of the stauros thus resemble closely the divided tigilla sometimes found in Capartogramma and especially frequent in specimens of C. crucicula from Lake Tanganyika.

There are various other species of Stauroneis whose appearance under the light microscope suggests that in them the stauros is a deep and narrow bar of thickening rather than a broad area of not very deep thickening such as is found in S. phoenicenteron, S. anceps and S. acuta. It is probable, therefore, that when it has been possible to study the majority of the many species of the genus with the electron microscope it will be found necessary to divide it. This division, however, will not be that originally suggested by Cleve (K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 26 (2): 141 (1894)) into those with and those without pseudosepta, for S. acuta has pseudosepta whilst S. phoenicenteron and S. anceps do not, but both the stauros and the fine structure of all three are the same. If and when sufficient information to justify a division of the genus Stauroneis has been accumulated, it will be possible to decide whether S. smithii and its allies should be treated as a separate genus closely related to Capartogramma or included within that genus. Meanwhile it seems best to restrict Capartogramma to those species with two tigilla on either side of the central nodule and not to transfer Stauroneis smithii from its present position.

**Key to the Species**

Frustules symmetric about the apical axis; valves rhombic lanceolate or elliptic:

Valves strongly convex, about 4μ deep, apices narrow, long-rostrate; striae not more than 17 in 10μ, parallel or convergent at the apices; pseudosepta markedly inclined to the apical plane, as long as the rostrate apices

1. *C. karstenii*

Valves not strongly convex, about 2μ deep, with apices not produced, subrostrate, or rostrate and broad; striae radiate throughout or 20 or more in 10μ; pseudosepta almost parallel to the valvar plane, much shorter than the apices when these are rostrate:

Valves rhombic or lanceolate, apices acute, sometimes subrostrate; striae radiate throughout; pseudosepta 2-5μ long or more. 2. *C. rhombicum*

Valves elliptic or oblong, apices broad, rostrate, subrostrate or not produced; striae parallel at the apices; pseudosepta 2μ long or less. 3. *C. crucicula*

Frustules asymmetric about the apical axis; valves lunate. 4. *C. amphotroides*

1. *Capartogramma karstenii* (Zanon) Ross, comb. nov. (Plates 1 A, 2 B, C; Figs. 2, 3.)

*Schizostauron crucicula* sensu G. S. West in Journ. Linn. Soc. Lond., Bot. 38: 156, t. 8 fig. 12 (1907) pro parte; non Cleve.
Frustulum rectangulare, angulis rotundatis, cingulo et copulis composito. Valva 35-60μ longa, 9-13μ lata, valde convexa, c. 4μ alta, anguste elliptica, marginibus plerumque leniter triundulatis, rostrata, apicibus angustis longis ad finem truncatis. Pseudosepta c. 6μ longa, in planitiem valvarem inclinata, marginibus interioribus crassis. Raphe filiformis, leniter undulata, poris centralibus distantiioribus, fissis terminalibus in idem latus inclinatis. Area axialis angusta; area centralis circularis. Noduli terminales parvi; nodulus centralis rectangularis. Tigilla duo in altero latere inter se angulam 30°-60° facientia. Striae leniter radiatae, in apicibus paralleis convergentesve, tenues, 11-17 in 10μ; puncta c. 25 in 10μ.

In tropical African fresh waters; recent from Lakes Victoria, Tanganyika, Zwai (fide Zanon), Nyassa (fide O. Müller and Monteiro) and Malomba (fide O. Müller), and in a stream near Utengule, Tanganyika (fide O. Müller); fossil in a pleistocene deposit near Bularaba, Nigeria.


TANGANYIKA: Western Province: Lake Tanganyika, near Kirando, plankton, 1 Dec. 1904, Cunningham 175 (B.M. 34180). Lake Tanganyika, Kala Langabo Bay, near Kigoma, on stone in water c. 50 cm. deep, 30 Jan. 1953, Ross 1457 (B.M. 72100); same locality, on stems and adventitious roots of Phragmites mauritianus, 30 Jan. 1953, Ross 1458 (B.M. 72102). Lake Tanganyika, Kigoma, on submerged leaves of Paspalidium geminatum, 31 Jan. 1953, Ross 1468 (B.M. 72108); same locality, on Potamogeton pectinatus, 31 Jan. 1953, Ross 1470 (B.M. 72110, 72111, 72116, 72117); same locality, on Lagarosiphon sp. floating in harbour, 31 Jan. 1953, Ross 1473 (B.M. 72129); same locality, on roots of Phragmites mauritianus c. 1 m. deep, 31 Jan. 1953, Ross 1474 (B.M. 72131); same locality, on Ceratophyllum demersum in harbour, 31 Jan. 1953, Ross 1477 (B.M. 72137); same locality, scrapings from jetty wall, 31 Jan. 1953, Ross 1478 (B.M. 72139); same locality, bottom mud in harbour, 2 Feb. 1953, Ross 1512 (B.M. 72141, 72142). Lake Tanganyika, c. 1 km. off mouth of Luichi River, on shells brought up in trawl, 3 Feb. 1953, Ross 1531 (B.M. 72143); same locality, on roots brought up in trawl, 3 Feb. 1953, Ross 1532 (B.M. 72145); same locality, mud from large mussel shell brought up in trawl, 3 Feb. 1953, Ross 1533 (B.M. 72147). Lake Tanganyika, c. 1.5 km. S.W. of Ujiji, bottom mud, 80 m., 3 Feb. 1953, Ross 1535 (B.M. 72149, 72150). Lake Tanganyika, c. 1 km. off mouth of Luichi River, bottom mud, 15 m., 3 Feb. 1953, Ross 1536

This name is not validly published. (see p. 57).
CAPARTOGRAMMA AND SCHIZOSTAURON

Lake Tanganyika, Kigoma, scrapings from hull of M.V. "Sangala", 31 Jan. 1953, Ross 1537 (B.M. 72153). Lake Tanganyika, c. 500 m. offshore between Ujiji and Bangwe Point, on various weeds tangled in trawl from c. 8 m. deep, 4 Feb. 1953, Ross 1539 (B.M. 72157, 72158); same locality, tangled in meshes of trawl from c. 8 m. deep, 4 Feb. 1953, Ross 1540 (B.M. 72150). Lake Tanganyika, Bangwe Point, on rocks just below water level, but exposed during moderate swell, 4 Feb. 1953, Ross 1541 (B.M. 72161); same locality, pool c. 30 cm. above water level, often entered by swell, 4 Feb. 1953, Ross 1543 (B.M. 72166). Lake Tanganyika, Kigoma, bottom sand, c. 1-5 m., 4 Feb. 1953, Ross 1549 (B.M. 72171, 72172, 72173, 72174).

Figs. 2–3. Capartogramma karstenii (Zanon) Ross. Fig. 2, valve view (B.M. 72116, specim. n. 1); Fig. 3, girdle view (B.M. 72116, specim. n. 5). (Both × 1,000.)

Fossil: Pleistocene:


O. Müller's and Monteiro's records of this species from Lake Nyassa, O. Müller's from the shallow Lake Malomba, and G. S. West's from Lake Tanganyika are based on specimens from plankton hauls made close inshore. Zanon reported the species as being frequent in gatherings of bottom mud from Lake Zway, and Kufferath found it in bottom mud from Lake Tanganyika. It was rare in the two of my gatherings from Lake Victoria in which it occurred; both these were bottom muds. In my gatherings from Lake Tanganyika it was commoner in bottom samples than in epiphytic ones. It thus seems probable that it is primarily a free-living benthic form, occurring not only on the bottom but also in the films of diatoms and other algae growing as epiphytes on higher plants, but that it is, in addition, a facultative plankter, surviving and multiplying in the plankton when lifted into the water mass by wave action or similar causes. The species composition of the Nigerian diatomite in which it occurs indicates deposition close inshore in a freshwater lake.
The specimens I have seen and the published accounts of the species indicate that it varies very little, but occasionally one of the tigilla is forked. O. Müller, at the conclusion of his account of it, distinguished a variety in which the longitudinal margins of the frustule when seen in girdle view are convex, not straight. The size range of the specimens he referred to this variety is near the lower limit for the species, and this convexity is possibly a characteristic of small cells and, as such, not a justifiable basis for a taxonomic distinction. There is also the possibility that this variety was based on frustules of *C. amphiroides*. Careful examination is often necessary to distinguish large frustules of that species in which the longitudinal margins are scarcely convex (see Fig. 13) from those of *C. karstenii*, and if it were rare in the samples O. Müller examined and he only saw whole frustules in girdle view, he might have failed to realize that he was dealing with a distinct species.

Neither in G. S. West's collection nor among the slides he sent to the British Museum (Natural History) on completion of his report on the algae collected by Cunnington on the Third Tanganyika Expedition is there any material of *Cunnington 81* or *Cunnington 135*. There is, however, a preparation of cleaned diatoms from *Cunnington 175*, the third of the gatherings from which West reported *Schizostauron crucicula*. This contains *Capartogramma karstenii* and not *C. crucicula*. West's figure, also, is clearly of *C. karstenii*; the dimensions he gives and his description of the outline both fit *C. karstenii*, but his value for the closeness of the striae is that characteristic of *C. crucicula*. He shows no striae in his figure and one is left to wonder whether *C. crucicula* was present in one of the gatherings cited or whether his value for striation density is an error. (Was it copied from Cleve's account of *C. crucicula* in the *Synopsis of the Naviculoid Diatoms*)?

O. Müller's description of the species is a full and accurate account of it and appears under the name *Schizostauron karstenii*. Above it is the heading ""Sectio *Schizostauron* Cl. N. D. I. p. 141 ", and the typography of this indicates that it is a subsidiary heading under the main heading ""Naviculaceae Microstigmaticae Cl."" O. Müller, in his treatment of *Naviculaceae*, followed that in Cleve's *Synopsis of the Naviculoid Diatoms* (for which see pp. 63–64 below). It is clear that he cannot be considered as having validly published the specific name *Schizostauron karstenii*, for he did not regard *Schizostauron* as the name of a genus, and ""the name of a species is a binary combination consisting of the name of the genus followed by a single specific epithet "" (Art. 23 of the *International Code of Botanical Nomenclature*, 1961 edition). Neither can he be held to have published the name *Navicula* (sect. *Schizostauron*) *karstenii* for he did not definitely indicate that the specific epithet was to be used in that particular combination (cf. Art. 33 of the *International Code*); there is no reason for supposing that he was not aware of the previous publication of *Navicula karstenii* Pant. for a different species.

Mills (Index Gen. & Sp. Diat.: 1438 (1934)) lists the name ""Schizostauron Karsteni", but with a query and in the type that indicates that the name is a synonym. Therefore he cannot be regarded as accepting the species and accordingly he did not give the name valid publication, in spite of his recognition of *Schizostauron* as a genus and his citation of O. Müller's description. Zanon, in 1941, accepted
Schizostauron as a genus and S. karstenii as a distinct species and gave the latter name valid publication by reference to O. Müller's description. Hustedt in 1959 used the name Stauroneis karstenii in discussion and gave a figure of the species but no description nor any reference to O. Müller's description or Zanon's valid publication of the name; he therefore did not give the name Stauroneis karstenii valid publication either as a new combination or as an independently published new name.

Kufferath's account of his Capartogramma jeani is very inadequate. He apparently worked with fluid mounts and only saw whole frustules. In consequence he had great difficulty in getting a valve view. His drawing of this aspect of the diatom shows apices that are much too broad for C. karstenii and his representation of the central nodule and struts is no more than a caricature. Nevertheless the slope of the pseudopecta and the depth of the valve shown in his figure of the girdle view of a frustule show clearly that his name was applied to this species.

2. **Capartogramma rhombicum** Ross, sp. nov. (Figs. 4–7.)

Frustulum rectangulare, angulis rotundatis, cingulo e copulis composito. Valva 20–55 µ longa, 4.5–12.5 µ lata, plana (parte prope marginem excepta), c. 2 µ alta, lanceolata, anguste lanceolata vel rhombica, aliquando subrostrata, apicibus angustis rotundatis. Pseudopecta 2.5–5 µ longa, planitie valvari fere parallela, marginibus interioribus paullo incrassatis. Raphe filiformis, fere recta, poris centralibus approximatis, fissis terminalibus in idem latus inclinatis. Area axialis angustissima; area centralis rectangularis, parva. Noduli terminales parvi; nodulus centralis rectangularis, parvus. Tigilla duo in altero latere inter se angulum 30°–60° facientia. Striae leniter radiatae, 15–22 in 10 µ, dense punctatae.

**Figs. 4–7.** *Capartogramma rhombicum* Ross. Fig. 4, valve view (holotype); Fig. 5, valve view (B.M. 72115, specim. n. 4); Fig. 6, girdle view (B.M. 72115, specim. n. 5); Fig. 7, valve view (in B.M. 72143). (All x 1,000.)


¹ The second specimen from the left-hand end of the row as seen under the microscope, the top of the labels on the slide being to the left.
Tanganyika: Western Province: Lake Tanganyika, Kigoma, on Potamogoton pectinatus, 31 Jan. 1953, Ross 1470 (B.M. 72110, 72111, 72114, 72115); same locality, on Lagarosiphon sp. floating in harbour, 31 Jan. 1953, Ross 1473 (B.M. 72129); same locality, on Ceratophyllum demersum in harbour, 31 Jan. 1953, Ross 1477 (B.M. 72137); same locality, bottom mud in harbour, 2 Feb. 1953, Ross 1512 (B.M. 72175). Lake Tanganyika, c. 1 km. off mouth of Luichi River, on shells brought up in trawl, 3 Feb. 1953, Ross 1531 (B.M. 72143).

This species has so far been found only in five of my gatherings from Lake Tanganyika. Three of these were of epiphytes from flowering plants in the harbour at Kigoma, the fourth of bottom mud at the same place, and the fifth of a growth of algae and diatoms on empty shells of a freshwater snail brought up in the trawl from a haul made about 1 km. off the mouth of the Luichi River. This suggests that the characteristic habitat of the species is the algal felt that grows on solid substrata in shallow water. It is probably free-living in this habitat and not attached.

The specimens from Kigoma harbour (Figs. 4-6) and those from off the mouth of the Luichi River (Fig. 7) clearly belong to two different populations. The latter are smaller (20-32μ long as against 27-55μ) and more slender (4.5-6μ broad as against 9-12μ), especially when compared with the shorter specimens from Kigoma harbour; they have more radiate striae and more divergent tigilla. More material is necessary, however, before one can decide whether these differences are indicative of infraspecific taxonomic separation.

Within the population from Kigoma harbour there are differences correlated with total size. The largest specimens (Fig. 4) have a rhombic outline with acute apices that are not produced, and the pseudosepta are 4-5μ long, whilst the smaller specimens (Fig. 5) have a lanceolate outline, subrostrate apices, and shorter pseudosepta only about 2.5μ long; also the tigilla of the larger forms are much broader parallel to the valvar plane. The variation in these characters is, however, clearly continuous. That in outline is of interest in that it is unusual for produced apices to be characteristic of the smaller diatoms in a population when the apices of the larger ones are not produced.

3. Capartogramma crucicula (Grun. ex Cleve) Ross, comb. nov. (Plates I B, 2 A; Figs. 1 a, 8-11.)


Stauroneis crucicula (Grun. ex Cleve) Cleve, op. cit. 26 (2): 151 (1894).1


1 This name, although used here by Cleve, was not validly published by him (see pp. 63-64).


Schizostauron brasiliense Zimmerm. in Broteria, Bot. 16: 86, t. 2 fig. 3 (1918).


Stauroneis grunowii sensu Choln. in Hydrobiologia 19: 104 (1962); non Rabenh.

Frustulum rectangularare, angulis rotundatis, cingulo sine copulis. Valva 10–35μ longa, 4½–9μ lata, plana (parte prope marginem excepta), c. 2μ alta, elliptica vel oblonga, apicibus obtusis vel truncatis, non productis vel subrostratis vel late rostratis. Pseudopecta curta, c. 1½μ longa, planitiei valvari fere parallela. Raphes filiformis, recta, poris centralibus distantioribus, fissis terminalibus in idem latus inclinatis. Area axialis angusta; area centralis parva, circularis vel transverse elliptica. Noduli terminales minores; nodulus centralis parva, rectangularis. Tigillia duo in altero latere inter se angulum c. 30° facientia. Striae leniter radiatae, in apicibus plerumque parallelae subconvergentesve, 20–25 in 10μ, dense punctatae.

Figs. 8–11. Capartogramma crucicula (Grun. ex Cleve) Ross. Fig. 8, valve view (in B.M. 32046); Fig. 9, girdle view (in B.M. 68168); Fig. 10, valve view (B.M. 72119, specim. n. 3); Fig. 11, valve view (B.M. 72119, specim. n. 1). (All x 1,000.)

In fresh and slightly brackish waters of temperate and tropical America and of Africa south of the Sahara, and fossil in pleistocene deposits from the same regions.


Tanganyika: Western Province: Lake Tanganyika, Kala Langabo Bay, near Kigoma, on stems and adventitious roots of Phragmites mauritianus, 30 Jan. 1953, Ross 1458 (B.M. 72102). Lake Tanganyika, Kigoma, on submerged leaves of

1 This combination is not validly published (see p. 57).
Paspalidium geminatum, 31 Jan. 1953, Ross 1468 (B.M. 72108, 72109); same locality, on Potamogeton pectinatus, 31 Jan. 1953, Ross 1470 (B.M. 72110, 72111, 72118, 72119, 72120); same locality, on Potamogeton schweinfurthii, 31 Jan. 1953, Ross 1472 (B.M. 72127); same locality, on Lagarosiphon sp. floating in harbour, 31 Jan. 1953, Ross 1473 (B.M. 72129); same locality, on roots of Phragmites mauritianus c. 1 m. deep, 31 Jan. 1953, Ross 1474 (B.M. 72131); same locality, on leaves c. 120 cm. below surface of water, 31 Jan. 1953, Ross 1475 (B.M. 72133); same locality, on Ceratophyllum demersum in harbour, 31 Jan. 1953, Ross 1477 (B.M. 72137); same locality, scrapings from jetty wall, 31 Jan. 1953, Ross 1478 (B.M. 72139); same locality, bottom mud in harbour, 2 Feb. 1953, Ross 1512 (B.M. 72141, 72142, 72146); same locality, scrapings from hull of M.V. "Sangala", 31 Jan. 1953, Ross 1537 (B.M. 72153).


Fossil: Pleistocene:

Most of the previous records of this species have been based on gatherings from rivers, streams or ponds. I, however, found it frequently in epiphytic and, to a lesser extent, benthic habitats in Lake Tanganyika at Kigoma. It would seem therefore to be a species of the layer of diatoms and other algae that grows on higher plants and other solid substrata in shallow water, and its occasional occurrence in plankton is fortuitous. In this it resembles *C. rhombicum* and *C. amphiroides*, but these two are confined to Lake Tanganyika, as far as is at present known, whilst *C. crucicula* has a much wider geographical range and occurs as frequently in rivers and streams as in lakes. The records by Zimmermann from Santos, Brazil, by Frenguelli from the estuary of the River Plate, and by Hustedt from Venezuela are based on gatherings from estuarine localities, but salinity data are only available for the last of these; the water from which this sample was taken had a sodium chloride content of 1.0 parts per mille. In most of the gatherings in which I have seen this diatom it has been uncommon.

Cholnoky (Österr. Bot. Zeitschr. 103: 87 (1956)) questions the accuracy of Zanon's record of this species from Upper Volta, saying: "Zanon... teilt die Art aus Französisch-Mittelafrika (Niger-Fluss) mit, seine Zeichnungen (l. c., T. 2, F. 12, zwei Abbildungen) beziehen sich aber auf eine Form aus der Verwandtschaft der *S[tauroneis] obtusa* Lgst." He had, however, failed to notice that there is a misprint in the text of Zanon's paper, but not in the explanation of the plate, where t. 2 fig. 12 is stated to represent *Stauroneis obtusa* var. *minor* and t. 2 fig. 13 *Schizostauron crucicula*. The three illustrations which constitute fig. 13 are only about 2 cm. away from fig. 12, and they are unmistakable representations of *C. crucicula*.

There is considerable variation in outline in this species, but little in other respects, except for the occurrence of divided tigilla. The larger specimens (Fig. 8) have long, broad, rostrate apices, whilst the smaller ones (Figs. 10, 11) are not at all produced at the apex. There appears to be a continuous variation between the two extremes. However, the specimens in Cholnoky's gatherings from the Tugela District in Natal and mine from Kigoma in Lake Tanganyika appear to represent very distinct populations. The majority of the Natal specimens are 25 µ long or more and have long rostrate apices, and the smallest specimens from there are 10 µ long and are distinctly substratum. The largest of the Lake Tanganyika specimens is little longer than this and is no more markedly substratum, whilst the smallest ones from there are as little as 10 µ long and have no trace of production of the apices. Forking or duplication of the tigilla is also frequent in the Lake Tanganyika specimens (Plate 1 B), but elsewhere it is rare, although it does occur (Fig. 9). O. Müller found forms similar to the Lake Tanganyika population in a sample from a pool at Manda (formerly Wiedhafen) on the shores of Lake Nyasa; he described them as [*Navicula sect.*] *Schizostauron crucicula* forma *obtusa*. Somewhat similar though rather larger specimens from Sierra Leone were named *Stauroneis merrimacensis* var. *intermedia* by Woodhead and Tweed. In view of the identity in appearance of the largest of the Lake Tanganyika specimens and the smallest of the Natal ones, the present state of our knowledge does not justify the maintaining of these taxa as distinct.
As well as the variation with length of valve in the extent to which the apices are produced, there are also differences in the length-breadth ratio and the convexity of the valve margin between individuals of the same length. Whilst specimens in a single gathering usually show considerable uniformity, amongst the different gatherings a continuous series between the extremes can be found, and therefore it does not appear justifiable to maintain as distinct [Navicula sect.] Schizostauron crucicula forma gracilior O. Muel., which is based on slender specimens with almost straight sides from the plankton of Lake Nyasa and the Songwe River.

Cleve originally intended to use a different epithet for this species and his type specimen is labelled with this and not Schizostauron crucicula. He gives his reason for using a different name in a footnote to his protologue which reads: "In printing this paper I have been informed by Mr. Grunow that he has found the same form abundantly in pools of the Rio Purus, Brazil, and that he has named it in Linnaean Society Journ. of May 1880 [.] I consequently adopt his name."

Until very recently most authors have called this species Stauroneis crucicula, a later homonym of S. crucicula W. Smith (Synops. Brit. Diat. 1: 60 (1853)), but Woodhead and Tweed have recently published a legitimate substitute, S. merri-macensis. Zimmermann's independently described Schizostauron brasiliense, however, provides an earlier epithet which would have to be adopted if the species were placed in the genus Stauroneis. Cholnoky (Hydrobiologia 19: 104 (1962)), without referring to the new name proposed by Woodhead and Tweed, recently suggested that, since the name Stauroneis crucicula could not be used for this species, it should be called S. grunowii Raben. (Fl. Eur. Alg. 1: 251 (1864)), founded on S. crucicula var. minuta Grun. (Verh. Zool.-bot. Ges. Wien 10: 567, t. 6 fig. 15 (1860)); contrary to what Cholnoky says, however, this is based on small forms of Stauroneis crucicula W. Smith (= Navicula crucicula (W. Smith) Donkin) and not of S. crucicula (Grun. ex Cleve) Comber (= Capartogramma crucicula). More recently still Cholnoky (Revista Biol. 3: 69 (1962)) uses the name Stauroneis merrimacensis for this species without referring to his suggestion that S. grunowii is its correct name.

The combination Stauroneis crucicula is usually attributed to Cleve, but this is incorrect, for he did not recognize Stauroneis as a separate genus. In his Synopsis of the Navicoloid Diatoms his treatment above the specific level is chaotic. His major groups are all treated taxonomically as if they are of equal status, but nomenclaturally some are treated as genera and some as sections of Navicula. There is no description of the genus Navicula as such in the whole work, and the various sections of that genus described under such headings as Naviculae Fusiformes and Naviculae Lineolatae are not grouped together but are interspersed among the accounts of genera he recognized both taxonomically and nomenclaturally. In the section headed Naviculae Microstigmaticae, with which we are here concerned, the situation is even more confused. The account begins with a description of the section, and this is followed by:

"This large section comprises a number of species, hitherto placed in Navicula, Stauroneis, Pleurostauron, Schizostauron and Schizonema. They may be classed in the following divisions:
1. Stauroneis. . . .  
2. Pleurostauron. . . .  
3. Schizostauron. . . .  
4. Libellus. . . .  
5. Microstigma. . . .  

"This division of the whole group cannot be completely carried out at present, as the connecting zones of many species have not been observed. I consequently class all the forms now in two groups, viz. those with transversely dilated central nodules in Stauroneis, and those without such dilated central nodules in Microstigma; at the same time indicating as far as can yet be made out to which of the five groups named above each species belongs."

There is no intervening heading between the key to the species and the individual accounts of them. In these accounts the names are given thus: "S. . . ." or "S. (Libellus) . . ." or "S. (Pleurostauron) . . .". After species n. 27 there is a heading "Subdivision Schizostauron Grun.", under which the species names are given thus: "S. . . ."; the six species under this heading include "S. crucicula". There is then a further heading: "Subdivisions Microstigma and Libellus", under which the species names are given as "N. . . ." or "N. (Libellus) . . ." or "N. (Schizonema Libellus) . . ." or, in one case, "N. (Scoliopleura) . . .". (Elsewhere in the Synopsis Cleve treats Scoliopleura as a separate genus!) That the "S." of "S. crucicula" represents Stauroneis and not Schizostauron is indicated by the feminine terminations of the adjectival specific epithets under the same heading, but in the index Schizostauron Cruciculum (sic) is indicated as a correct name and Stauroneis crucicula as a synonym. Cleve accordingly cannot be held to have regarded Stauroneis as a genus, and hence the combination Stauroneis crucicula is not validly published in this work.

Boyer (Proc. Acad. Nat. Sci. Philad. 79, Suppl.: 426 (1928)) realized this, but thought that the combination had first been validly made by himself (Diat. Philad.: 89 (1916)). It was in fact made earlier by Comber, but the Welwitsch specimens to which he applied it are, as examination of his original preparations shows, Navicula exiguiformis Hust.

Frenguelli (Rev. Mus. La Plata, Nueva Ser., Bot. 3: 245 (1941)) suggested that Pinnularia signata Ehrenb. (Mikrogeologie: t. 34 VI A fig. 7 (1854)) from Florida might be this species, but this seems unlikely; Ehrenberg's figure shows coarse striae, whilst his optical equipment was such that he would not have been able to detect those of Capartogramma crucicula, and also the outline of his figure is quite different from that of this species.

4. Capartogramma amphoroides Ross, sp. nov. (Plate 1 c; Figs. 12–14.)

Frustulum marginibus longitudinalibus convexis vel arcuatis, cingulo latiore in parte dorsali quam ventrali, e copulis composito. Valva 20–50 μ longa, 6·5–9·5 μ lata, maxime convexa, lunata, margine ventrali recto vel leniter convexo, aliquando medio gibboso, apicibus subrostratis. Pseudosepta 2·5–6·5 μ longa, planitiei valvari fere parallela, marginibus interioribus crassis. Raphe filiformis, fere recta, poris
centralibus distantioribus, fissis terminalibus in idem latus inclinatis. Area axialis angusta; area centralis parva, circularis. Noduli terminales minimi; nodulus centralis minor, rectangularis. Tigilla duo dorsalia inter se angulum 20°–30° facientia, duo ventralia multo latius digredientia. Striae leniter radiatae, dorsales 13–22 in 10μ, ventrales 18–22 in 10μ.


From the shores of Lake Tanganyika near Kigoma.

**Figs. 12–14. Capartogramma amorphoides** Ross. Fig. 12, valve view (holotype); Fig. 13, girdle view (B.M. 72113, specim. n. 5); Fig. 14, girdle view (in B.M. 72137).

(All × 1,000.)

**TANGANYIKA: Western Province:** Lake Tanganyika, Kala Langabo Bay, near Kigoma, on stems and adventitious roots of *Phragmites mauritianus*, 30 Jan. 1953, Ross 1458 (B.M. 72102); same locality, on tree root in c. 15 cm. of water, 30 Jan. 1953, Ross 1461 (B.M. 72104). Lake Tanganyika, Kigoma, on submerged leaves of *Paspalidium geminatum*, 31 Jan. 1953, Ross 1468 (B.M. 72108, 72109); same locality, on *Potamogeton pectinatus*, 31 Jan. 1953, Ross 1470 (B.M. 72110, 72111, 72112, 72113); same locality, on *Potamogeton schweinfurthii*, 31 Jan. 1953, Ross 1472 (B.M. 72127); same locality, on *Lagarosiphon* sp. floating in harbour, 31 Jan. 1953, Ross 1473 (B.M. 72129); same locality, on roots of *Phragmites mauritianus* c. 1 m. deep, 31 Jan. 1953, Ross 1474 (B.M. 72131); same locality, on leaves c. 120 cm. below surface of water, 31 Jan. 1953, Ross 1475 (B.M. 72133); same locality, mud from roots c. 120 cm. below surface of water, 31 Jan. 1953, Ross 1476 (B.M. 72135); same locality, on *Ceratophyllum demersum* in harbour, 31 Jan. 1953, Ross 1477 (B.M. 72137); same locality, scrapings from jetty wall, 31 Jan. 1953, Ross 1478 (B.M. 72139); same locality, bottom mud in harbour, 2 Feb. 1953, Ross 1512 (B.M. 72141). Lake Tanganyika, c. 1 km. off mouth of Luichi River, on roots brought up in trawl, 3 Feb. 1953, Ross 1532 (B.M. 72145); same locality, mud from large mussel shell brought up in trawl, 3 Feb. 1953, Ross 1533 (B.M. 72147). Lake Tanganyika, Kigoma, scrapings from hull of M.V. "Sangala", 31 Jan. 1953,

1 The specimen at the left-hand end of the row as seen under the microscope, the top of the labels on the slide being to the left.
Ross 1537 (B.M. 72153). Lake Tanganyika, Katabi Bay, near Kigoma, bottom sand, 20 m., 4 Feb. 1953, Ross 1538 (B.M. 72155, 72156). Lake Tanganyika, c. 500 m. offshore between Ujiji and Bangwe Point, on various weeds tangled in trawl from c. 8 m. deep, 4 Feb. 1953, Ross 1539 (B.M. 72157, 72158); same locality, tangled in meshes of trawl from c. 8 m. deep, 4 Feb. 1953, Ross 1540 (B.M. 72159, 72160). Lake Tanganyika, Bangwe Point, on rocks just below water level, but exposed during moderate swell, 4 Feb. 1953, Ross 1541 (B.M. 72161). Lake Tanganyika, Kigoma, bottom sand, c. 1-5 m., 4 Feb. 1953, Ross 1549 (B.M. 72171).

This species, like *C. rhombicum* and *C. crucicula*, is primarily an inhabitant of the felt of algae and diatoms that grows in shallow water on solid substrata such as higher plants, rocks, etc. In my gatherings from Lake Tanganyika it is more common than any of the other three species of the genus, and it is therefore somewhat surprising that it has not been found previously either by G. S. West in Cunningham's collections or by Kufferath in the material from the Belgian hydrobiological survey of the lake.

Whilst *C. ampheroides* differs markedly in symmetry from the other members of the genus, its resemblance in all other respects is extremely close and there can be no question but that it is correctly placed here. It is somewhat variable in the density of striae on the dorsal side of the valve and also in the outline of the frustule, some specimens being much more inflated than others, but the variation in these characters is continuous and not of taxonomic significance at any level. The ventral tigilla of this species are frequently forked (Fig. 14) and occasionally a dorsal tigillum is forked.

Boyer (Diat. Philad.: 60, t. 16 fig. 13 (1916)) described and figured a specimen which he identified as the raphe valve of *Achnanthes danica* (Flögel) Grun. The description and the outline as shown in the figure are consistent with its being a raphe valve of *A. fimbriata* (Grun.) Ross, a species long confused with *A. danica* (cf. p. 75 below), but if the central area is correctly drawn it cannot belong to that species and may well represent an unknown species of *Capartogramma* with three struts on either side of the central nodule.

THE IDENTITY OF SCHIZOSTAURON

*Schizostauron* was established by Grunow (Hedwigia 6: 28 (1867)) for four marine species with ovate or broad-lanceolate valves and a central nodule which was transverse, linear, and bifid at either end. There is a formal Latin description of the genus and of one of the species, *S. lindigianum*, the only one found in the material from Honduras on which he was reporting. The diagnostic characters of the remaining three, *S. reichardtianum*, *S. ovatum* and *S. fimbriatum*, are mentioned in the discussion in German which follows. Grunow, however, said that he was doubtful whether it was correct to place *S. fimbriatum* in the same genus as the other three species.

Ten years later Grunow published another version of his account of the diatoms of Honduras. In this he repeated, slightly modified, his Latin diagnoses of *Schizo-
stauron and S. lindiganum and gave a latin diagnosis of S. reichardtianum, spelling
the epithets “Lindigii” and “Reichardtii” respectively. He also figured the two
species (Month. Microsc. Journ. 18: 181, t. 195, figs. 17, 18 (1877)). Both figures
show the stauros as a narrow transverse band reaching about half-way to the margin
on either side and there forking into curved and tapering bands, whose general
direction is longitudinal.

The types of Grunow’s species are preserved in the Botany Department of the
Naturhistorisches Museum, Vienna, and I have been able to examine both these
and Grunow’s notes and sketches relating to them. On the slide (Coll. Grunow n.
839€) indicated by Grunow as that on which the type of S. lindiganum is to be
found there is only one specimen that agrees with his description and figure. On
close examination, using phase contrast as well as transmitted light, this was found
to be a specimen of Cocconeis dirupta Greg. It consists of a raphe-less valve and
two raphe valves back to back, one of these with its central portion broken away.
There is a transverse fascia on both intact valves, but what Grunow interpreted
as the bifid prolongation of the stauros is no more than a line of contact between
the two valves. This line is obvious because the slide is a dry mount and a certain
amount of dirt has accumulated along it. The expansions of the central area are
also artefacts of a similar nature.

The types of S. reichardtianum and S. ovatum come from a gathering made by
Reichardt in the Adriatic near the town of Mali Lošinj, formerly known as Lussin
Piccolo, on the island of Lošinj in the Gulf of Kvarner. In his second account
of S. reichardtianum Grunow also cited a specimen on Codium bursa from Dalmatia
collected by Dr. Bartsch. Both the type (Coll. Grunow n. 864a) and this latter
specimen (Coll. Grunow n. 1133) are whole frustules of the species of Achnanthes
recently described as new by Proschkina-Lavrenko under the name A. lyrata (Not.
(1961)). This species is related to A. baldjickii (Brightw.) Grun., A. danica (Flögel)
Grun. and A. fimбриata (Grun.) Ross. It has ovate valves with rounded rostrate
apices, striae on the raphe-less valve consisting of single hyaline alveoli and much
finer striae on the raphe valve, whose central area divides on either side into two
curved tapering branches; between these there is a triangular striae area on which
the striae are not alternately longer and shorter. Grunow clearly did not realize
that he was looking at two valves and he described and figured his specimen as if
it were a single valve with a raphe and the central area of the raphe valve but the
coarser unbroken striae of the raphe-less one. Proschkina-Lavrenko’s interpretation
of the raphe valve seems to be based on a similar error.

Cleve (Ann. & Mag. Nat. Hist., Ser. 7, 10: 29 (1902)), in the course of a series of
annotations on Karsten’s Die Diatomeen der Kieler Bucht, wrote as follows: “I
have once found in plankton from Skagen a diatom the lower valve of which agreed
with fig. 117, but the upper valve was identical with Grunow’s Schizostauron
Reichardtianum, which thus belongs to Achnanthes, s. l.” Karsten’s fig. 117 is
labelled Cocconeis apiculata A. Schmidt and depicts a raphe-less and a raphe valve,
both with slightly radiate continuous striae about 10 in 10μ. It is thus clear that
the specimen to which Cleve refers was something quite different from Grunow’s species or was thoroughly misinterpreted by him. Cleve’s remarks do not, of course, constitute publication of the combination *Achnanthes reichardtiana*, but this was validly published by Hustedt (in Rabenh., Krypt.-Fl. Deutsch. 7 (2) : 429 (1933)), who wrongly attributed it to Cleve.

*S. ovatum*, like *S. lindigianum*, proves on examination of the type material to be based on a specimen of *Cocconeis dirupta* Greg. On this specimen, however, the marks which Grunow misinterpreted as bifid prolongations of the stauros are inclined to one another at a much smaller angle and there is no artefact giving the appearance of expanded axial areas.

Grunow did not designate a type species of *Schizostauron*, and, since he was doubtful whether *S. fimбриatum* was correctly placed in the genus, one of the other three species originally included in it must be chosen as lectotype. As has been pointed out, the character which Grunow considered diagnostic of the genus, viz. the bifid stauros, is possessed by only one of these, *S. reichardtianum*, and this must accordingly be chosen. In the other two species the bifid stauros is only simulated by an artefact and neither of them can be accepted as the type of the genus, even although they have never been removed from *Schizostauron* whilst *S. reichardtianum* has been transferred to *Achnanthes*. Since the correct taxonomic position of the type species is in that genus, *Schizostauron* must be regarded as a synonym of *Achnanthes*.

A number of species other than the three considered above have been referred to *Schizostauron* by various authors. Whilst two are, like the type of the genus, species of *Achnanthes*, most belong to other genera.

*S. fimбриatum* Grun. (Hedwigia 6 : 28 (1867)), doubtfully referred to the genus *Schizostauron* when it was first established, proves on examination of the type material (Coll. Grunow n. 869, Porto Zubzamki, Sušak Island, Gulf of Kvarner, Jugoslavía, leg. Reichardt) to be the raphe valve of the species currently known as *Achnanthes manifera* Brun. Grunow’s name provides the earliest specific epithet for this, and the necessary new combination is accordingly made below (p. 72). This species has been confused with *A. danica* (Flögel) Grun., which has in its turn been confused with the diatom hitherto known as *A. lorentziana* (Grun.) Cleve but named here (p. 82) *A. baldjickii* subsp. *lorentziana* (Grun.) Ross. An account of the confusion between these species accompanies their synonymies and descriptions (pp. 72–84 below).

Cleve, in his original account of *S. andicola* (Öfvers. K. Vetensk.-Akad. Förhandl. Stockh. 38 (10) : 12, t. 16 fig. 8 (1882)), expressed doubt as to whether it was correctly placed in *Schizostauron*. It was subsequently transferred to *Achnanthes* by Østrup (Danske Diat.: 128 (1910)), who referred it to *A. hungarica* (Grun.) Grun. as a distinct variety. In the following year Hustedt (Abhandl. Naturwiss. Ver. Bremen 20 : 279 (1911)) treated it as a distinct species of *Achnanthes*. Examination of the type material shows that the species was based on large specimens of *A. hungarica*.

De Toni (Nuova Notarisia [1] : 196 (1890)) transferred *Stauroneis tatrica* Gutw. to
Schizostauron. Cleve, in his Synopsis of the Naviculoid Diatoms, treated this as a synonym of Navicula pupula Kütz., and it would appear from Gutwinsky's account and figure (Sprawozd. Kom. Fizyjogr. 25 : (24), t. i fig. 20 (1890)) that he was correct in so doing.

De Toni (Syll. Alg. 2 : 225 (1891)) also transferred Stauroneis verbania De Not. to Schizostauron. Examination of the type material (Erb. Critt. Ital., Ser. 2 : n. 434 (1871)) shows that this too is Navicula pupula.

Stauroneis sagitta Cleve (K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 18 (5) : 15, t. 3 fig. 45 (1881)) is listed by Cleve in his Synopsis (op. cit. 26 (2) : 151 (1894)) under the subdivision Schizostauron of the Naviculae Microstigmaticae. Hustedt (in Rabenh., Krypt.-Fl. Deutsch. 7 (2) : 811 (1959)) reduces this taxon to a variety of Stauroneis smithii Grun. As explained above (p. 53), that species resembles Capartogramma more closely than it does the type species of Stauroneis, but there is not yet sufficient information to justify its transfer either to Capartogramma or to a new genus.

When the original material of Schizostauron rhombicum M. Perag. (in Temp. & Perag., Diatomées, ed. 2 : 398, n. 825 (1913)) was examined, it was found to be a Navicula with a transverse fascia widening outwards but not reaching the margin. This species has apparently not been reported by any other author and, as the name Navicula rhombica is pre-occupied (Gregory in Quart. Journ. Microsc. Sci. 3 : 40 (1855)), a new name is proposed for it on p. 91 below.

The only other species that has been referred to Schizostauron is S. portaregiense Å. Berg (Ark. Bot., Andra Ser., 2 : 30, 36, t. 4 fig. 57 a-c (1952)). I cannot find anything to match Berg's illustration in his type material. He reports, however, that he examined some uncleaned material mounted in Viscol of the gatherings in which he found this species, and I believe that his name is based on specimens of Navicula rhyncocephala var. amphiceros (Kütz.) Grun. with remains of cell contents simulating a stauros and apical septa. The identity of his species must, however, remain doubtful, although it is clearly neither a Capartogramma nor a Stauroneis.

**Species Investigated—Synonymies, Descriptions and Notes**

*Cocconeis dirupta* Greg. in Trans. R. Soc. Edin. 21 : 491, t. 9 fig. 25 (1857).—Hust. in Rabenh., Krypt.-Fl. Deutsch. 7 (2) : 354, fig. 809 (1933).

*Cocconeis diaphana* var. β W. Smith, Synops. Brit. Diat. 1 : 22, t. 33 fig. 254β (1853).


Schizostauron lindigianum Grun. in Hedwigia 6 : 28 (1867) ; in Month. Microsc. Journ. 18 : 181, t. 195 fig. 17 (1877).

Schizostauron ovatum Grun. in Hedwigia 6 : 28 (1867).

*Cocconeis bellmeyeri* Janisch ex A. Schmidt, Atl. Diat.: t. 196 fig. 23 (1894).

*Cocconeis delicata* A. Schmidt, tab. cit. fig. 24 (1894).

Stauroneis lindigiana (Grun.) Cleve in K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 26 (2) : 151 (1894).¹

Stauroneis ovata (Grun.) Cleve, loc. cit. (1894).¹


Stauroneis ovata (Grun.) Mills, op. cit.: 1464 (1934).

¹ These combinations, although used here by Cleve, were not validly published by him (see pp. 63–64).
For description and figure, see Hustedt (loc. cit.).

A cosmopolitan marine littoral epiphyte.


**Scotland**: Corriegills, Isle of Arran, on *Corallina*, Miles (B.M. 1420, isotype).

**Jugoslavia**: Mali Lošinj, Lošinj Island, Gulf of Kvarner, Reichardt (Coll. Grunow n. 864b in Herb. Vienna, holotype of *Schizostauron ovatum*).

**Honduras**: On *Sargassum*, Lindig (Coll. Grunow n. 839 in Herb. Vienna, holotype of *Schizostauron lindigianum*).

W. Smith, in his protologue of *Cocconeis diaphana*, cites two gatherings, one from Jersey and one from Sidmouth, without indicating which represents his var. β. However, the material from Jersey matches his fig. 254, and that from Sidmouth his fig. 254β and his description of var. β, which is said to have a stauros. The Jersey specimens are identical with the type material of *C. molesta* Kütz., showing that *C. diaphana* is correctly regarded as a synonym of that species, whilst those from Sidmouth belong to the species later described by Gregory as *C. dirupta*.

**Achnanthes reichardtiana** (Grun.) Hust. in Rabenh., Krypt.-Fl. Deutsch. 7 (2) : 429 (1933).—Mills, Index Gen. & Sp. Diat.: 1439 (1934), 1699 (1935). (Figs. 15, 16.)

*Schizostauron reichardtianum* Grun. in Hedwigia 6 : 28 (1867) ; in Month. Microsc. Journ. 18 : 181, t. 195 fig. 18 (1877).

*Stauroneis reichardtiana* (Grun.) Cleve in K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 26 (2) : 151 (1894).¹

*Stauroneis reichardtiana* (Grun.) Mills, op. cit.: 1468 (1934).


Figs. 15-16. *Achnanthes reichardtiana* (Grun.) Hust. (holotype). Fig. 15, raphe valve ; Fig. 16, raphe-less valve. (Both x 1,000.)

Valve broadly elliptic with short subrostrate to rostrate apices, 30-40μ long, 18-23μ broad. Raphe-less valve with a linear or very narrowly lanceolate pseudoraphe and a narrow central area tapering outwards; striae slightly radiate, slightly curved, 8-11 in 10μ, each consisting of a single hyaline alveolus, rather distant throughout most of their length but widening and becoming almost contiguous at the margin. Raphe valve with a straight filiform raphe lying in a thickened rib ;

¹ This combination, although used here by Cleve, was not validly published by him (see pp. 63-64).
central pores approximate; terminal nodules small; axial area linear, narrow; central area a narrow transverse fascia bifurcating half-way to the margin on either side into two curved tapering branches; striae punctate, strongly radiate throughout except within the bifurcation of the central area, sinuous adjacent to the central area, curved near the apices, 22–24 in 10μ, puncta about as distant as the striae.

Marine, from the coast of Jugoslavia and from the Black Sea.

**JUGOSLAVIA:** Mali Lošinj, Lošinj Island, Gulf of Kvarner, Reichardt (Coll. Grunow n. 864a in Herb. Vienna, holotype). Dalmatia, on Codium bursa, Bartsch (Coll. Grunow n. 1133 in Herb. Vienna).

This is an uncommon species, only a single example being present in each of the two preparations on which it occurs, and in both cases the specimen is somewhat broken. In the material from Mali Lošinj the related species *Achnanthes fimbriata* and *A. baldjickii* also occur and are more common. The only other record is Proschkina-Lavrenko’s from the island of Tendra in the Black Sea, U.S.S.R.

*A. reichardtiana* has a raphe-less valve closely resembling that of *A. baldjickii*, the striae each consisting of a single alveolus without secondary markings visible under the light microscope; Proschkina-Lavrenko comments on this similarity. The raphe valve, however, is much more like that of *A. fimbriata*, the striae being close and not double near the margin nor alternating there with costae. It was not easy to be certain of some details of the structure of the raphe valve; the only specimens available are whole frustules mounted in air, and the coarser structure of the raphe-less valve obscures the finer markings of the raphe valve. In consequence it was impossible to see whether the marginal alveoli of the raphe valve were elongated, as they are in *A. fimbriata* and *A. danica*.

According to Proschkina-Lavrenko, the striae on the raphe valve are considerably more widely spaced than I found in the Adriatic specimens. Moreover, her drawing (t. 1 fig. 13) of this valve shows the striae as only slightly radiate and interrupted by the branches of the central area. However, her photograph that purports to be of the raphe valve (t. 2 fig. 19), like Grunow’s original illustration of the species, shows the raphe and central area superimposed on the markings of the raphe-less valve, which appear interrupted as a result of interference from the much finer striae of the raphe valve. Proschkina-Lavrenko, like Grunow, seems not to have detected these.

The combination *A. reichardtiana* is usually attributed to Cleve (Ann. & Mag. Nat. Hist., Ser. 7, 10: 29 (1902)), but, as is pointed out above (p. 68), he did not publish it; this was first done by Hustedt. Cleve did publish the combination *Stauroneis reichardtiana*, but not validly (cf. pp. 63–64 above). Mills was apparently the first to give the combination valid publication, but he appears to have done so by oversight. In the entry for Schizostauron reichardtianum on pp. 1438–1439 of his Index he indicates that *Achnanthes reichardtiana* is the correct name for the species and does not cite *Stauroneis reichardtiana* as a synonym. On p. 1468 he lists *Stauroneis reichardtiana* as a correct name with *Schizostauron reichardtianum* as a synonym but no mention of *Achnanthes reichardtiana*. In the addenda, on p. 1699, he lists *A. reichardtiana* as a correct name, with *Schizostauron reichardtianum*
as the only synonym. Hustedt’s treatment of *Achnanthes* in the *Kryptogamen-Flora* was published during the period when Mills’s *Index* was coming out, and it would seem that Mills accepted Cleve’s and Hustedt’s view that the species belonged to that genus but failed to correct the entry under *Stauroneis* that referred to it.

*Achnanthes fimbriata* (Grun.) Ross, comb. nov. (Figs. 17–22.)

**Schizostauron fimbriatum** Grün. in Hedwigia 6: 28 (1867).

*Achnanthes heteropsis* Grun. ex Cleve & Möller, Diatoms 3: 6, ns. 154, 155 (1878), nom. nud.

*Navicula fimbriata* Grun. ex Cleve & Möller, loc. cit. (1878), nom. syn.

*Stauroneis cornuta* Led.-Forthm., Cat. Diat. Ceyl.¹ : 37, t. 3 fig. 36 (1879).


*Achnanthes stroemii* Hust. in Rabenh., *Krypt.-Fl. Deutsch. 7* (2) : 393, fig. 841B (1933) (“ Strómi ”).

Valves ovate to rhombic-lanceolate, subrostrate, 20–120μ long, 7–40μ broad, often with one margin slightly gibbous opposite the central nodule. Raphe-less valve with the pseudoraphe linear or slightly widened in the central part of the valve and with a small hyaline space at each apex ; striae distant, slightly to moderately radiate, sometimes a few opposite the central nodule short, 5–15 in 10μ, alveolate ; alveoli several per stria, those adjacent to the pseudoraphe always considerably longer than broad and usually the longest in the stria ; divisions between the alveoli transverse or occasionally oblique but never bifurcating or Anastomosing ; faint continuations of the striae present on the central portion of the pseudoraphe on those specimens where this is widened. Raphe valve with a straight filiform raphe with approximate central pores ; terminal nodules small, terminal fissures hooked ; axial area moderately broad at the centre, tapering uniformly to the apices ; central area transverse, expanded outwards or slightly narrowed outwards and then expanded, a half of the width of the valve or more, its outer margin ragged ; striae arcuate, strongly radiate throughout, especially near the apices, longer and

¹ This publication is a reprint from *Mémoires de la Société d’Emulation des Côtes-du-Nord*. I have been unable to trace a copy of the original.
shorter opposite the central nodule, 12–30 in 10µ in the central part of the valve, closer towards the apices, alveolate; alveoli punctiform and scarcely longer than broad except for the marginal one of each stria, which is 1–4µ long.

From the coasts of the North Atlantic, the Mediterranean and the Indian Ocean and the western border of the Pacific Ocean, and fossil from marine and brackish deposits in eastern Europe.

**Figs. 17–22. Achnanthes fimbriata** (Grun.) Ross. Fig. 17, raphe valve (in B.M. 13079) (× 1,000); Fig. 18, detail of same valve as Fig. 17 (× 2,000); Fig. 19, raphe-less valve (in B.M. 13079) (× 1,000); Fig. 20, raphe valve (B.M. 37339, specim. n. 4) (× 1,000); Fig. 21, detail of same valve as Fig. 20 (× 2,000); Fig. 22, raphe-less valve (Coll. F. W. Adams n. Bess. 896, specim. n. 1) (× 1,000).


**Spain**: Balearic Islands (B.M. 36256 = Cleve & Möller, Diatoms, n. 154).

**Italy**: Capri (B.M. 33068).

**Norway**: Grip (Cleve & Möller, Diatoms, n. 311 in Coll. F. W. Adams in Herb. Brit. Mus.).

**U.S.A.**: Connecticut: Morris Cove (B.M. 14577 = Temp. & Perag., Diatomées,


Ceylon: Colombo, Craven (B.M. 8986, syntype of Stauroneis cornuta); same locality, harbour mud, Voigt (Coll. Voigt nos. 14099, 30056).

Indonesia: Celebes, from holothurians (Coll. Voigt n. 29018).

China: Kwangtung, from holothurians (Coll. Voigt nos. 36053, 36060).

Chekiang: Chusan Archipelago, Voigt (Coll. Voigt n. 3040).


Australia: Queensland: Flinder's Passage (B.M. 31942).

Fossil: Miocene:


Pliocene:


As will be seen, the range of density of striation on both the raphe-less and the raphe valves of this species is very wide. It is found to vary continuously, however, when a considerable number of specimens from a variety of localities is examined, and the variation on the two valves is not closely correlated. There are nevertheless some differences between the ranges found in recent and fossil specimens, although there is much overlap. Recent specimens (Figs. 17–19) range in size from 20 μ by 7 μ to 75 μ by 26 μ, whilst the fossil ones (Figs. 20–22) range from 24 μ by 11 μ to 120 μ by 40 μ; the striae on the raphe-less valve of recent specimens range from 5·5 to 14 in 10 μ, whilst those on fossil ones range only from 7·5 to 13 in 10 μ; on raphe valves the striae of recent specimens range from 18 to 30 in 10 μ in the centre part of the valve whilst those of fossil specimens range from 12 to 21 in 10 μ. Another variable feature is the direction of the striae on the raphe-less valve; in some specimens these are definitely although not strongly radiate and a few short striae are present in the centre of the valve, whilst others have almost parallel striae and no short ones. Short striae are present on all fossil specimens but only on some recent ones. These differences between fossil and recent specimens are too indefinite to serve as a basis for an infraspecific division, and accordingly Achnanthes danica var. maxima, proposed by Cleve for fossil specimens of this species from Balchik, is not maintained here as a separate variety.

The striae on the raphe-less valve of this species are always separated by a distinct gap, usually equal to at least half their own width, but in the coarsest specimens occasionally somewhat less. On most of Hustedt's figures of this valve of the species (viz.: A. Schmidt, Atl. Diat.: t. 415 figs. 9, 11, 13–15, 18 (1937); Bull. Duke Univ.
Mar. Sta. 6 : t. 6 figs. 5, 7, 8 (1955)) they are represented as contiguous. Whilst this may to some extent be due to the drawing convention adopted, it is misleading.

_Achnanthes fimбриata_ is less common in the miocene and plioene deposits from Hungary than it is in the plioene deposit from Balchik, Bulgaria, and even there it is infrequent. It is not common, either, in any of the recent gatherings in which I have seen it, but nevertheless it has a wide distribution, from the Atlantic Coast of North America, through Europe and the Mediterranean to Ceylon, the East Indies and the western borders of the Pacific.

Grunow expressed doubt about the correctness of referring this species to _Schizostauron_ when first describing it, and by 1877 he had decided that it did not belong there; the phrase in the original diagnosis of the genus which especially refers to it, "(vel laciniato fimбриato?)" was deleted from the version published in that year (Month. Microsc. Journ. 18: 181 (1877)). Grunow's notes show that when he first decided that the species was not a _Schizostauron_ he considered that it should be placed in _Navicula_ but that he then found whole frustules in the material from the Balearic Islands issued as Cleve & Möller, _Diatoms_, ns. 154, 155 (1878), and realized that it was an _Achnanthes_. He apparently considered "fimбриata" an inappropriate epithet for the species when it was placed in this genus. The list of species in the preparations forming the third series of Cleve and Möller's _Diatoms_, which includes ns. 154, 155, is headed "All the slides have been examined by M. Grunow", and the list for those numbers includes "_Achnanthes heteropsis_ Grun. (= _Navicula fimбриata_ Grun.)". Neither of these names had been published previously and both must accordingly be regarded as _nomina nuda_; the identity of epithet is insufficient to connect them with the previously published description of _Schizostauron fimбриatum_ Grun., although Grunow's manuscript notes show that they were new names for that species.

Between 1878 and 1880 Grunow formed the opinion that this species was identical with _Cocconeis danica_ Flögel and he accordingly made the new combination _Achnanthes danica_, quoting _A. heteropsis_ as a synonym. This mistake was probably the result of his receiving, apparently from Weissflog, material of a further gathering from the Balearic Islands in which there was true _A. danica_ but no _A. fimбриata_. From his notes it appears that he did not at any stage associate the raphe valves he called _Schizostauron fimбриatum_ in the material from the Gulf of Kvarner with the raphe-less valves also present in his preparations of these gatherings. When he found specimens in the Cleve and Möller material from the Balearic Islands that caused him to decide that his _S. fimбриatum_ was the raphe valve of an _Achnanthes_, he made no drawing of the raphe-less valve. He did, however, make drawings of both valves of _A. danica_ from specimens in the Weissflog material and, misled by the similarity of the raphe valves, failed to realize that he was dealing with a different species from that in Cleve and Möller's material from the same locality and also in their material from Pensacola, Florida, which he saw at about the same time. As a result of Grunow's error, _A. fimбриata_ and _A. danica_ have been confused ever since 1880. Thus Cleve took specimens of _A. fimбриata_ in the material from the Balearic Islands issued as Cleve & Möller, _Diatoms_, ns. 154, 155, as representative
of *A. danica*, and consequently in the *Synopsis of the Naviculoid Diatoms* he applied that name to *A. fimbriata* and misidentified true *A. danica* with *A. lorenziana* (Grun.) Cleve (= *A. baldjickii* subsp. *lorenziana* (Grun.) Ross). The way in which the name *A. danica* has been applied is analysed in the account of that species below (pp. 79-81).

When Brun found specimens of this species in Tempère's material from Morris Cove, Connecticut, he realized that they were not conspecific with *Cocconeis danica* and so described them as a separate species, *Achnanthes manifera*. Such other authors as have recognized that this species is distinct from *A. danica* have, in general, used Brun's name for it, but European specimens have for the most part continued to be identified as *A. danica*. The exceptions are those from Norway described by Hustedt as the separate species *A. stroemii*, and the two from the Balearic Islands figured by him (in A. Schmidt, Atl. Diat.: t. 415 figs. 15, 16 (1937)) as *A. manifera*.

Clevé (in Nordensk., Vega-Exped. Vet. Iaktt. 3 : 512 (1883)) was the first to treat *Stauroneis cornuta* Leud.-Fortm. as a synonym of *A. danica*. Leuduger-Fortmorel's species is based on a raphe valve and both *A. danica* and *A. fimbriata* occur in the material from Ceylon on which he was reporting. It is therefore impossible to be completely certain to which of the two species his type belongs. Nevertheless, the central area shown in his figure strongly suggests *A. fimbriata* rather than *A. danica* and his inability to resolve the striae points in the same direction.

*Navicula vaszaryi* Pant. from the Hungarian miocene is clearly based on a raphe valve of *Achnanthes fimbriata*, which occurs in the diatomite from Nyermegy from which Pantocsek's type came. Cleve transferred the species to *Achnanthes* on the basis of the resemblance of the raphe valve to that of an *Achnanthes* from Oregon which has a very different raphe-less valve and is clearly unrelated.

Frenguelli (in Chiov., Fl. Somala : 394, t. 49 fig. 14 (1929)) describes and figures a raphe valve from near Mogadiscio in Somalia under the name *Achnanthes manifera*. As Hustedt (Bull. Duke Univ. Mar. Sta. 6 : 18 (1955)) has pointed out, this cannot be identified with absolute certainty in the absence of a raphe-less valve, but its central gibbosity, the shape of its central area, and the closeness of its striae together make it highly likely that it is *A. fimbriata* and not *A. danica*. Hustedt's (loc. cit.) statement that according to Frenguelli the striae on his specimen are 10-11 in 10μ is an error; Frenguelli says that this is the density of the striae on the raphe valve of *A. baldjickii* (Brightw.) Grun., with which he compares *A. manifera*, and that those on his own specimen are 22 in 10μ.

*Achnanthes stroemii* Hust. is founded on specimens of this species with rather close striae on the raphe-less valve and not very close ones on the raphe valve. His type came from Nordasot, Norway. Specimens closely resembling Hustedt's description and figure occur in Cleve & Möller, *Diatoms*, n. 311, from Grip, Norway, which is listed as containing *A. danica*.


Achnanthes lorensiana Grun. ex A. Schmidt, Atl. Diat.: t. 198 fig. 59 (1895).


Figs. 23–26. Achnanthes danica (Flögel) Grun. Fig. 23, raphe valve (in B.M. 71125) (× 1,000); Fig. 24, detail of same valve as Fig. 23 (× 2,000); Fig. 25, raphe-less valve (in B.M. 71125) (× 1,000); Fig. 26, detail of same valve as Fig. 25 (× 2,000).

Valves rhombic-lanceolate, subrostrate, 50–65μ long, 20–25μ broad. Raphe-less valve with the pseudopereae very narrowly lanceolate and a small hyaline space at each apex; striae distant, parallel or very slightly radiate, 4.5–6 in 10μ, each consisting of a single alveolus with oblique or transverse, sometimes bifurcating or anastomosing, secondary costae about 18–20 in 10μ. Raphe valve with a straight filiform raphe with approximate central pores; terminal nodules small, terminal fissures hooked; axial area narrow, tapering uniformly to the apices; central area transverse, rhombic, indefinitely bounded at its outer angles; striae strongly radiate, longer and shorter in the centre of the valve, 16–20 in 10μ, somewhat closer towards the apices; alveoli mostly punctiform and 13–17 in 10μ, but those adjacent to the margin 1.5–2μ long; striae near the apices consisting of a single alveolus.

From the coasts of western Europe, the Mediterranean and Ceylon, and fossil from southern Sweden (fide Cleve-Euler; a doubtful record, cf. p. 81).
ITALY: Capri (B.M. 33068, 33069, 33426, 71121, 71122, 71123, 71124, 71125).


CEYLON: Colombo, Craven (B.M. 8986).

This species, although widespread, is far from common, a fact which probably accounts for the inaccuracies in the accounts of it in the literature and for the long confusion of it with *Achnanthes fimbriata* (Grun.) Ross. When the raphe-less valve is observed under the microscope with a lens of less aperture than N.A. 1·3, or when such a lens is used with an inadequate illuminating cone, the striae appear to have a double row of puncta, in places alternating, in others opposite. When a lens of N.A. 1·3 or more is used with an adequate illuminating cone, however, it becomes apparent that this appearance is an optical artefact and that the true structure is as shown in Fig. 26. Similarly, careful observation with a lens of adequate aperture shows that the striae of the raphe valve are not regularly punctate throughout, as depicted by Hustedt, but that there is a row of long alveoli at the margin (Fig. 24).

Although the raphe valve is very similar to that of *A. fimbriata*, the central area is smaller and does not definitely expand outward, as that of *A. fimbriata* always does.

The way in which Grunow confused this species and *A. fimbriata* has been discussed under that species (p. 75 above). It has also been confused with *A. baldjickii* subsp. *lorenziana* (Grun.) Ross (*A. lorenziana* (Grun.) Cleve), firstly by Pantocsek, who misidentified specimens of that subspecies as *A. danica*, then by Cleve, who did the reverse. His account of *A. lorenziana* in the *Synopsis of the Naviculoid Diatoms* is based almost entirely on *A. danica*. Thus he says of the raphe-less valve "Intercostal spaces finely punctate (puncta about 23 in 0·01 mm.), frequently apparently smooth", and his description of the raphe valve would apply to that of *A. danica* or *A. fimbriata*. The localities he cites for the species are "Barcelona, Balearic Islands! Adriatic (Grun.), Bab el Mandeb! Macassar Straits (Grove Coll.)!" and he adds the remark: "I have seen an entire frustule in Grove’s collection, but the coarse structure of the upper valve made the examination of the lower very difficult."

No specimen to which this remark could refer is to be found now in Grove’s collection. About 1890 Thum issued slides of material from the Balearic Islands containing both *A. danica* and *A. baldjickii* subsp. *lorenziana*, but no *A. fimbriata*, and Cleve is certain to have seen some of these. As has already been pointed out (p. 76 above), he applied the name *A. danica* to *A. fimbriata* and, at least as far as the Balearic Island material was concerned, he seems to have identified as *A. lorenziana* the raphe-less valves of both *A. baldjickii* subsp. *lorenziana*, in which the outer membrane to the single alveolus forming each stria is smooth, and *A. danica*, in which that membrane has anastomosing secondary thickening. With these raphe-less valves he
associated the raphe valves of *A. danica*, and he apparently never saw a raphe valve of *A. baldjickii* subsp. *lorenziana* in this material.

Before part II of the Synopsis of the Naviculoid Diatoms appeared, but during its preparation, plate 198 of A. Schmidt’s *Atlas* was published. Figure 59 on this plate is undoubtedly of a raphe-less valve of *A. danica*; its legend is “Nordsee, nach Cleve *Achnanthes* Lorentziana Grunow.” As the name *Achnanthes lorenziana* had not by then been published, and as the figure is sufficient to validate its publication there, *Achnanthes lorenziana* Grun. ex A. Schmidt (Atl. Diat.: t. 198 fig. 59 (1895)) is a legitimate name, typified by the North Sea specimen figured by Schmidt, a synonym of *A. danica* (Flögel) Grun., and an earlier homonym of *A. lorenziana* (Grun.) Cleve (K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 27 (3) : 186 (1896)), whose basionym is *Raphoneis lorenziana* Grun.

In view of the way in which the name *Achnanthes danica* has been so frequently misapplied, it will probably be useful to present here an analysis of all the accounts and records which have been published under it:

Grunow in K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 17 (2) : 21 (1880). The synonym *A. heteropsis* Grun., the lower limit of size of the valves, and the records from the Adriatic and Florida, and in part that from the Mediterranean, all refer to *A. fimбриата*. The remainder of the account is based on *A. danica*.

Cleve & Möller, *Diatoms* 6 : 3, n. 311 ; 4, n. 320 (1882). Both are *A. fimбриата*.

Cleve in Nordensk., Vega-Exped. Vetensk. Iaktt. 3 : 512 (1883). The synonym *Stauroneis cornuta* Leud.-Fortm. refers to *A. fimбриата*. There is no information about the identity of the specimen on which this record is based, but it is most probably *A. fimбриата*, since, as explained above, Cleve later misidentified *A. fimбриата* as *A. danica* and included *A. danica* in *A. lorenziana*.

Grunow in Van Heurck, Typ. Synops. Diat. Belg.: 121, n. 545 (1887). This is *A. fimбриата*.

Pantocsek, Beitr. Kenntn. Foss. Bacill. Ung. 1 : 31 (1886). I have seen no specimen from Dolje to which this record might refer. Both *A. fimбриата* and *A. baldjickii* subsp. *lorenziana*, but not *A. danica*, occur in other Hungarian fossil deposits, and the record is probably based on one or other of these.

Pantocsek, op. cit. 2 : 57, t. 4 fig. 66 (1889). The figure is of *A. baldjickii* subsp. *lorenziana*, but *A. fimбриата* also occurs from material from Bremia, Hungary, and it is probable that Pantocsek did not distinguish the two species and that the record applies to both.

De Toni, Syll. Alg. 2 : 480 (1891). The lower limits of size of the valve, and the synonyms *A. heteropsis* Grun. and *Stauroneis cornuta* Leud.-Fortm., refer to *A. fimбриата*. Of the locality records, Knarrhoi, Jutland, refers to *A. danica*, and so in part do Mediterranean and Ceylon, whilst the others refer to *A. fimбриата*, except that both that species and *A. baldjickii* subsp. *lorenziana* are covered by the record from Bremia, Hungary.

A. Schmidt, Atl. Diat.: t. 198 figs. 60, 61 (1895), as *A. danica* var. *maxima*. These figures depict *A. fimбриата*.

A. Schmidt, tab. cit. fig. 50 (1895). This figure of a raphe valve is probably
correctly identified as *A. danica*. Fig. 59 on the same plate, named by Cleve *A. lorenziana*, is certainly *A. danica*.

Cleve in K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 27 (3) : 186 (1896). The only element in the description which refers to *A. danica* is the statement: "costae [on the raphe-less valve] ... alternating with fine lineolae, twice as close as the costae". The remainder of the description, including that of *A. danica* var. *major* Cleve, and all the synonyms except *Cocconeis danica* Flögel, refer to *A. fimbriata*. The locality records do so also, except "Mediterranean Sea", which is taken from Grunow (1880) and is based on gatherings from the Balearic Islands in which both *A. danica* and *A. fimbriata* are represented.

H. & M. Peragallo, Diat. Mar. France : 7, t. 2 figs. 1–3 (1897). The statement that the costae on the raphe-less valve are 8–13 in 10μ (which is inconsistent with fig. 2, correctly identified as *A. danica*, as also is fig. 1) and the description of the raphe valve refer to *A. fimbriata*, as do the synonym *A. heteropsis* Grun. and the record from "Mer du Nord", also in part that from "Baléares". The fig. 3 also depicts *A. fimbriata*.

Tempère & Peragallo, Diatomées, ed. 2 : 82, ns. 152, 153 (1908). There is no specimen of this or any related species on either of these two slides in the set in the British Museum Herbarium.

Tempère & Peragallo, op. cit.: 185, ns. 346–349 (1909). According to the index (op. cit., Tables : 9 (1915)), the species is only found on ns. 348, 349. In the set in the British Museum Herbarium there is a specimen of *A. fimbriata* on n. 348 but none of this or any related species on any other of the slides. I have found specimens of *A. baldjickii* subsp. *lorenziana* on other preparations of material from the same fossil deposit at Bremia, near Kavna, Hungary.


Tempère & Peragallo, op. cit.: 232, ns. 442, 443 (1910). According to the index (op. cit., Tables : 9 (1915)), the species is to be found on n. 443. There is no specimen of this or any related species on this slide in the set in the British Museum Herbarium.

Hustedt in Rabenh., Krypt.-Fl. Deutsch. 7 (2) : 396, fig. 845 (1933). The description is of *A. danica*, except that the statement that the striae in the centre of the raphe valve are 26 in 10μ would fit *A. fimbriata* but not *A. danica*; "26" is, however, probably an error for "20" since Hustedt's figure of this valve shows only 20 striae in 10μ in the centre of the valve. This figure and that of the raphe-less valve represent *A. danica*. The synonyms *Schizostauron fimbriatum* Grun., *A. heteropsis* Grun., and *Stauroneis cornuta* Leud.-Fortm. refer to *A. fimbriata*. Of the gatherings cited by Hustedt, Cleve & Möller, Diatoms, ns. 154, 155 contain *A. fimbriata*, Tempère & Peragallo, Diatomées, ed. 2, ns. 348, 349 contain *A. fimbriata* and probably also *A. baldjickii* subsp. *lorenziana*, n. 371 contains *A. baldjickii* subsp. *lorenziana*, and n. 443 probably contains one or other of both of these species.

The description of the raphe-less valve refers to *A. danica* but that of the raphe valve repeats Hustedt's error that the striae are 26 in 10μ at the centre. The only original figure, fig. 510 c, is indeterminable, but the density of its striaation and also, to some extent, its shape suggest *A. fimbriata* rather than *A. danica*. If this is so, the fossil record from Skågganäs in Småland also refers to *A. fimbriata*.


**Odontidium baldjickii** Brightw. in Quart. Journ. Microsc. Sci. 7 : 180, t. 9 fig. 10 (1859). 

**Dimeregramma baldjickii** (Brightw.) Ralfs in Pritch., Hist. Infus., ed. 4 : 791 (1861).—Walker & Chase, Not. New & Rare Diat. [1] : 1, t. 1 fig. 3 (1886). 


**Achnanthidium baldjickii** (Brightw.) Grun. ex A. Schmidt, Atl. Diat.: t. 198 figs. 44-48 (1895).

Valves rhombic to lanceolate, sometimes slightly gibbous at the centre, subrostrate to rostrate at the apices, 25–90μ long, 13–40μ broad. Raphe-less valve with a lanceolate or moderately broad linear area, often transversely expanded on one or both sides at the centre; striae each consisting of a single hyaline alveolus, distant, slightly to moderately radiate, some in the centre part of the valve usually short. Raphe valve with an elevated marginal zone; raphe filiform, straight except near the central nodule, where the two halves are slightly bent in opposite directions; axial area narrow; central area transversely expanded; striae sigmoid, very strongly radiate, longer and shorter in the central part of the valve, consisting of a

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Figs. 27–29. *Achnanthes baldjickii* (Brightw.) Grun. subsp. baldjickii. Fig. 27, raphe valve (in B.M. 43404) (× 1,000) ; Fig. 28, detail of same valve as Fig. 27 (× 2,000) ; Fig. 29, raphe-less valve of same specimen as Fig. 27 (× 1,000).

Figs. 30–31. *Achnanthes baldjickii* subsp. lorenziana (Grun.) Ross. Fig. 30, raphe valve (in Coll. Grunow n. 864a) ; Fig. 31, raphe-less valve (in Coll. F. W. Adams n. E 230). (Both × 1,000.)
single row of fine puncta except on the elevated marginal zone, where they are double (?) and treble) rows of puncta separated by costae.

Subsp. **baldjickii**.  (Figs. 27–29.)


Valves rhombic, usually subrostrate and gibbous at the centre, 25–90 μ long, 17.5–40 μ broad. Raphe-less valve with long and short striae in the centre part, striae radiate, gently curved, 3–6 in 10 μ, closer towards the apices. Raphe valve with shortened striae to about half-way to the apices; striae 9–12 in 10 μ at the margin, 6–7.5 in 10 μ against the raphe.

Known only from marine pliocene deposits in Bulgaria and Hungary.

**Fossil:** *Pliocene:*


**Hungary:** Borostelek (B.M. 33350, 70882).

Subsp. **lorenziana** (Grun.) Ross, stat. nov.  (Figs. 30, 31.)


*Raphoneis fluminensis* sensu Van Heurck, Synops. Diat. Belg.: t. 36 fig. 34 (1881); non Grun.

*? Raphoneis scutellum* sensu Petit in Mém. Soc. Sci. Nat. Math. Cherbourg 23: 205, t. 3 fig. 6 (1881); non Ehrenb.

*Achnanthes danica* sensu Pant., tom. cit.: 57, t. 4 fig. 66 (1889); non Grun.


Valves rhombic-lanceolate to lanceolate, subrostrate to rostrate, 25–50 μ long, 13–20 μ broad. Raphe-less valve with one or two short striae opposite the central nodule on one side, usually without other short striae, sometimes with one or two more; striae scarcely to slightly radiate, 6–10 in 10 μ. Raphe valve with shortened striae only opposite the central area; striae 13–16 in 10 μ.

Mediterranean (and possibly other seas—see below), and fossil from marine miocene deposits in Hungary and marine pliocene deposits in Austria, Hungary and Bulgaria.

**Spain:** Balearic Islands (Coll. F. W. Adams ns. E 230, E 231 in Herb. Brit. Mus.).

**Italy:** Capri (B.M. 33068, 71125).

Fossil: Miocene:


Pliocene:


It is not possible to be completely certain that the striae on the raphe valve of Achnanthes baldjickii subsp. lorenziana consist of a double row of puncta near the margin. All the raphe valves seen have been parts of whole frustules and the structure of the striae in the marginal zone is too fine to be resolved with the optical microscope, at any rate in whole frustules where the presence of the other valve interferes with image formation. Nevertheless it is possible to see that the striae broaden as they approach the marginal zone in a way which suggests that they, like those of the type subspecies, are double there. The costae between the striae are certainly present in the marginal zone of both subspecies.

The very characteristic structure of the raphe valve (Figs. 27, 28, 30) of this species has not previously been correctly described or adequately figured. The descriptions by Grunow (K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 17 (2) : 21 (1880)) and by Cleve later in the same periodical (27 (3) : 187 (1896)) do not mention the doubling of the puncta near the margin, nor the costae, and these two features are not shown in Cleve's figure (tom. cit.: t. 3 fig. 5 (1896)) nor in those of A. Schmidt (Atl. Diat.: t. 198 figs. 45, 48 (1895)). It has already been pointed out (p. 78) that the description of the raphe valve of A. lorenziana given by Cleve in the Synopsis of the Naviculoid Diatoms and copied by Hustedt and Cleve-Euler is actually of the raphe valve of A. danica.

In the pliocene deposit from Balchik, Bulgaria, in which both subspecies occur, there are a few individuals which are to some extent intermediate between them in that, whilst having the outline of A. baldjickii subsp. lorenziana and a raphe-less valve with closer and less radiate striae, they have one or two shortened striae on this valve other than the two on one side opposite the central nodule. I have assigned such specimens to A. baldjickii subsp. lorenziana.

The two subordinate taxa within the species have very different ranges in time, and possibly also in space, and when they do occur together in the same fossil deposit intermediates are very few. There is thus adequate basis for distinguishing the two as subspecies, but their close resemblance in morphology and the few intermediates found in the Balchik material preclude separation at a higher taxonomic level.

The type subspecies is only known from the pliocene of Balchik, Bulgaria, and of
Borostelek, Hungary. *A. baldjickii* subsp. *lorenziana*, however, occurs in the mio-
cene of Nyermegy, Hungary, and the pliocene of Bory and Bremia, both in Hungary,
of Balchik and of Styria, and it is also found in recent gatherings. I have seen
only one specimen from Bory and one broken one from Bremia, each consisting
solely of a raphe-less valve. They both have 7–7.5 striae in 10μ, and there is
sufficient of the specimen from Bremia, which is broken across near the centre, to
show that at the centre it has two short striae on one side. Whilst the identifications
of these two specimens are made with confidence, there can be no absolute certainty
in the absence of associated raphe valves. *A. hauckiana* Grun. is present in the
Bremia material, but the specimens referred to *A. baldjickii* subsp. *lorenziana*
have their striae so widely spaced and so narrow that it is unlikely that they are
raphe-less valves of *A. hauckiana*.

The species is rare in recent gatherings. I have only seen it from the Gulf of
Kvarner, from Capri, and from the Balearic Islands. H. Peragallo’s (in H. & M.
Perag., Diat. Mar. France : t. 2 fig. 4 (1897)) figure of a specimen from Barcelona
is obviously correctly identified. Leuduger-Fortmorel (Bull. Soc. Bot. France 25 : 23 (1878)) records it as *Rhaphoneis lorenziana* from Verdelet, Côtes-du-Nord,
France, but gives no figure or description. Cleve records *A. lorenziana* from Bab
el Mandeb and the Macassar Straits, but there can be no certainty as to whether
these records are correct or are based on *A. danica*. He also considers that Petit’s
record of *Rhaphoneis scutellum* from Ning-po, China, is based on this species, but
Petit’s figure is such that this identification, although possible, is doubtful. The
specimens from the Sea of Azov described and figured by Mereschkovsky as *Actinoneis
lorenziana* var. *parva* can also be referred here only with considerable doubt.
Østrup (Danske Diat.: 126 (1910)) records *A. lorenziana* from Vesterhavssøerne,
Denmark, and Cleve-Euler, whose figure is a copy of Grunow’s, records it from
a marine deposit of unspecified age at Robertsfors, Sweden. There is therefore
some possibility that the species may occur recent outside the Mediterranean, but,
in view of the possibility of its being confused with others, this must remain uncertain
in the absence of specimens.

*Achnanthes hungarica* (Grun.) Grun. in K. Svensk. Vetensk.-Akad. Handl., Ny
Följd, 17 (2) : 20 (1880).—Østrup, Danske Diat.: 128, t. 3 fig. 78 (1910).—Hust.
in Pascher, Süssw.-Fl. Mitteleurop. 10, ed. 2 : 201, fig. 283 (1930) ; in Rabenh.,
Krypt.-Fl. Deutsch. 7 (2) : 383, fig. 829 (1933).—Cleve-Euler in K. Svensk.
Vetensk.-Akad. Handl., Ser. 4, 4 (5) : 23, fig. 521 (1953). (Figs. 32–37.)


A *Achnanthidium neglectum* Schum. in Schr. Phys.-ökön Ges. Königsb. 8 : 54, t. 1 fig. 17
(1867).

*Schizostauron andicola* Cleve in Öfvers K. Vetensk.-Akad. Förhandl. Stockh. 38 (10) : 12,
t. 16 fig. 8 (1882) ("andicolum ").

*Stauroneis andicola* (Cleve) Cleve in K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 26 (2) :
151 (1894).1

*Stauroneis andicola* (Cleve) M. Perag., Cat. Gén. Diat.: 829 (1897).

1 This combination, although used here by Cleve, was not validly published by him (see pp. 63–64).
Cocconeis hungarica (Grun.) Schoenf., Diat. Germ.: 126, t. 13 fig. 239 (1907).
figs. 23, 24 (1911) ; in Pascher, Süssw.-Fl. Mitteleur. 10, ed. 2 : 201, fig. 284 (1930) ;
in Rabenh., Krypt.-Fl. Deutsch. 7 (2) : 384, fig. 830 (1933).—Cleve-Euler, loc. cit.,
fig. 522 (1953) excl. β producta.
Microneis hungarica (Grun.) Meister in Beitr. Krypt.-Fl. Schweiz 4 (1) : 98, t. 13 figs. 5, 6
(1912).

Oblong-lanceolate with cuneate ends, the largest specimens sometimes gibbous
in the centre and with subrostrate apices. Raphe-less valve with very narrow, very
slightly oblique pseudoraphe and small circular central area, or, in some of the
largest specimens, with a narrow transverse fascia ; striae parallel in the centre, radiate towards the apices, 18–20 in 10μ, punctate. Raphe valve with a straight
filiform raphe with the terminal fissures turned in opposite directions ; axial area
very narrow ; central area transverse and widened outwards on one or both sides
of the valve ; large hyaline terminal areas on the largest specimens but not on
others ; striae parallel in the centre, radiate towards the apices, 20–22 in 10μ,
punctate.

32–35, raphe valves ; Figs. 36, 37, raphe-less valves. (All × 1,000.)

Cosmopolitan in fresh waters, normally as an epiphyte on aquatic phanerogams,
especially Lemnaceae, and fossil from a freshwater miocene deposit in France.
Because of the wide distribution and frequent occurrence of this species the only
specimens cited are the type of Schizostauron andicola and the slides in published
sets in which the species occurs.

Argentina : Sierra de Velasco, Prov. Rioja (Coll. P. T. Cleve n. 1208 in Herb.
Mus. Stockh., type of Schizostauron andicola).
France : St. Cloud (B.M. 14625 = Temp. & Perag., Diatomées, n. 371 ; B.M.
69016 = Temp. & Perag., Diatomées, ed. 2, n. 666).
Diat. Belg., n. 196).
Cleve records both Achnanthes hungarica and Schizostauron andicola from the type gathering of the latter. In this gathering there are abundant specimens of A. hungarica ranging in length from 15μ to over 40μ. The tranverse fascia in the centre of the raphe valves over 40μ long and a small proportion of those slightly shorter than this widens outwards on both sides (Figs. 32-34), but on the other raphe valves it widens outwards on one side only (Fig. 35). The raphe valves over 40μ long have hyaline areas about 1.5μ long at each apex, and most of these valves have a rather irregular outline, with a tendency to triundulate margins (Fig. 33). I interpret these as being post-auxosporic valves of A. hungarica and find confirmation of this view from a valve 40μ long with a hyaline area at one apex but not the other (Fig. 34). Cleve gives the length of Schizostauron andicola as 36μ and makes no mention of hyaline areas at the apices, nor does his figure show them. His type was accordingly one of the very few specimens with a transverse fascia widening outwards on both sides but no hyaline areas, such as that illustrated in Fig. 32.

In a small proportion of the raphe-less valves over 40μ long there is a moderately broad transverse fascia that widens outwards (Fig. 37); in the type preparation there are appreciably fewer of these valves than of raphe valves with hyaline apices. All the remaining raphe-less valves, even the largest, have no transverse fascia (Fig. 36).

The material from St. Cloud distributed by Tempère and Peragallo also contains, among abundant A. hungarica, a number of raphe valves over 40μ long with hyaline terminal areas. The corresponding raphe-less valves have a very narrow transverse fascia, but there is no fascia on the shorter ones.

Østrup figures three raphe valves under the name A. hungarica var. andicola; all have the fascia expanding outwards on both sides and the two larger have hyaline terminal areas. The raphe-less valve figured by him under the same name has a very narrow transverse fascia similar to that on the largest raphe-less valves in the St. Cloud material. According to his description and figure the terminal fissures of the raphe are both turned in the same direction, but in the Sierra de Velasco and St. Cloud gatherings the long specimens with hyaline terminal areas, like the shorter ones without such areas, have the terminal fissures turned in opposite directions.

According to Hustedt's first (1911) description and figure of A. andicola, the terminal fissures are both bent in the same direction and the raphe-less valve has a narrow transverse fascia. In his later accounts (1930, 1933) the direction of the terminal fissures is neither mentioned nor shown in the figures, but the raphe-less valve is said to have a broad fascia widening outwards like that on the raphe valves. In a more recent paper, Hustedt (Abhandl. Naturwiss. Ver. Bremen 34: 246 (1957)) comments on the similarity of A. andicola to A. hungarica and on the sporadic occurrence of the former.

It thus appears that not only was Schizostauron andicola based on a large specimen of A. hungarica but also the various diatoms later identified with Cleve's by Østrup and Hustedt are post-auxosporic specimens of the same species. This would account
for their sporadic occurrence, their constant association with *A. hungarica*, and their comparative rarity in the gatherings in which they have been found.

Cleve-Euler maintains *A. hungarica* and *A. andicola* as separate species and comments on the discrepancies in the accounts of the terminal fissures. She also suggests that a specimen found fossil at Österbotten might be referred to *A. andicola* but belong to a distinct infraspecific taxon. Her description and figure are insufficient for positive identification but make it plain that the specimen in question does not belong to this species.


**Navicula granum** Schum. in Schr. Phys.-ökon. Ges. Königsb. 8: 59, t. 2 fig. 46 (1867).

**Stauroneis verbania** De Not. in Erb. Critt. Ital., Ser. 2: n. 434 (1871).

**Stauroneis tatrica** Gutw. in Sprawozd. Kom. Fizyjogr. 25: (24), t. I fig. 20 (1890).

**Schizostauron taticum** (Gutw.) De Toni in Nuova Notar. [1]: 196 (1890).

**Schizostauron verbanium** (De Not.) De Toni, Syll. Alg. 2: 225 (1891).


**Navicula pseudopopula** Krasske in Bot. Arch. 3: 197, fig. 4 (1923).—Cleve-Euler, tom. cit.: 187, fig. 891 (1953).

**Navicula pseudopopula** var. *aqueductae* Krasske, loc. cit., fig. 8 (1923).


**Navicula mutata** Krasske in Bot. Arch. 27: 354, fig. 16 (1929).

For description and figure, see Hustedt (1930, 1961).

A cosmopolitan freshwater species, and widespread in pleistocene fossil deposits.


**France** : Falaise, Brébisson (B.M. 18725 = Coll. Kutzing n. 1468).


**Scotland** : Lochend, near Edinburgh, 7 Mar. 1854, Gregory (B.M. 20507, 48023).


**Fossil** : Pleistocene :

**Scotland** : Knock, Isle of Mull, Duke of Argyll (B.M. 22320, isotype of Stauroneis rectangularis).
The outline of this species is very variable and there is quite a wide range in the density of its striaation. In consequence it is usually regarded as having many varieties (cf. Hustedt, 1930, 1961), or as consisting of more than one species (cf. Cleve-Euler, 1953). When a large number of populations are examined, however, the various forms are found so to intergrade that there seems little justification for the taxonomic recognition of them at any level.

In his protologue Kützing gives the locality of this species as "Lebend in süßem Wasser bei Nordhausen". The only specimens in his herbarium labelled Navicula pupula are the one from the River Main collected by A. Braun and the one from Falaise collected by Brébisson which are cited above. Both these came into his possession after the publication of the Bacillarien. Accordingly, he must either have failed to preserve the gathering in which he found the species or have found it in one of the gatherings from Nordhausen which are preserved in his herbarium but have failed to record the identification on the label. I have examined these gatherings and on his n. 58 I found small numbers of N. pupula as currently understood. These match his figure well, better than anything else present in any of his gatherings from Nordhausen. This gathering is labelled "Fragilaria corrugata Kg. Nordhausen" in Kützing's hand and is the only one of that species in his herbarium labelled with its name. In his protologue of Fragilaria corrugata Kützing (Kies. Bacill.: 45 (1844)) says "In Süßwassergräben unter verschiedenen andern Diatomeen bei Nordhausen".

Further confirmation that the current concept of N. pupula corresponds to Kützing's is provided by the two gatherings in his herbarium labelled with its name. Both these contain the species as now understood. The identification on the A. Braun specimen is in Kützing's own hand. That on the Brébisson specimen is written in ink by Brébisson, but other identifications have been added in pencil in Kützing's hand, and the words "Navicula Pupula Kg." have been underlined in pencil and the full stop after "Kg" converted into an exclamation mark by a pencil stroke, presumably by Kützing.

This species was independently described by Gregory in 1854 as Stauroneis rectangularis, and W. Smith in 1856 applied the name Navicula laevissima Kütz. to it, citing S. rectangularis as a synonym. W. Smith's Lewes gathering and Gregory's from Lochend, together with the original material of S. rectangularis, represent such of the material on which W. Smith's account of N. laevissima is based as is preserved in the British Museum Herbarium. Until 1880 most authors followed W. Smith and applied the name N. laevissima to this species. In 1860, however, Grunow suggested that N. pupula might be this species, and in 1880, after seeing "specimina authentica"¹, he stated firmly that this was so. At the same time he expressed doubts about the true identity of N. laevissima, and ever since then it

¹ At this time Grunow was collaborating with Van Heurck in the preparation of the latter's Synopsis des Diatomées, and Van Heurck had acquired at Eulenstein's death a duplicate set of Kützing's diatoms removed from the original packets by Eulenstein when the collection was in his hands (cf. Müller & Zaunick, Friedrich Traugott Kützing 1807-1893 Aufzeichnungen & Erinnerungen: 20 (1960)). The authentic material Grunow saw was therefore probably some of A. Braun's River Main gathering and certainly Brébisson's Falaise gathering, for his figure of the species is of a specimen from "Falaise, von Kützing selbst bestimmt".
has been treated as a doubtful species (cf. Hustedt in Pascher, Süssw.-Fl. Mitteleur. 10, ed. 2 : 279 (1930)). Its type, however, shows it to be the species normally known as *Navicula bacilliformis* Grun., for which it provides the correct name (see p. 90 below).

This species is the type of the genus *Sellaphora* Mereschk. (Ann. & Mag. Nat. Hist., Ser. 7, 9 : 186 (1902)). There is little doubt that it and the type of *Navicula* Bory belong to different genera, but until a comprehensive review of this group of genera can be undertaken, it seems best to retain it in its currently accepted position.

One of the names included by Hustedt (1961) in the synonymy of *Navicula pupula* is *Navicula borscowii* Mereschk. That combination has never been validly published; at the place referred to, Mereschkowsky described *Sellaphora borscowii* as a new species based on marine specimens from San Pedro, California, that lived in *Schizonema*-type tubes. There is nothing in his description or figure (Ann. & Mag. Nat. Hist., Ser. 7, 9 : 188, t. 4 figs. 6-10 (1902)) to suggest that it is this species.

As Mayer (Denkschr. Regensb. Bot. Ges. 21 : 168 (1940)) points out, Krasske’s original descriptions and figures of his *Navicula pseudopupula*, *N. aqueductae* and *N. mutata* do not show the characteristic terminal nodules of this species, nor, in the case of *N. mutata*, the laterally expanded central area. Hustedt’s figures in A. Schmidt’s *Atlas* (t. 396, figs. 10-14, 29-31 (1934)) of Krasske’s original material, however, show these features. Krasske attributes the figures of *Navicula pseudopupula* and *N. pseudopupula* var. *aqueductae* accompanying his original accounts of these taxa to Hustedt, so there is every reason for believing that Hustedt’s later figures are of the same taxa. He has explained (in Pascher, Süssw.-Fl. Mitteleur. 10, ed. 2 : 282 (1930); Internation. Rev. Hydrobiol. Hydrogr. 42 : 65 (1942)) that the original failure to see the characteristic features of these diatoms was due to the use of a mounting medium of too low a refractive index.

**Navicula laevissima** Kütz., Kies. Bacill.: 96, t. 21 fig. 14 (1844).


*Navicula fusticulus* Östr., Danske Diat.: 36, t. 1 fig. 19 (1910).


For description and figure, see Hustedt (1930 as *Navicula bacilliformis*, 1961 as *N. wittrockii*).

A cosmopolitan freshwater species, and widespread in pleistocene fossil deposits.

**Fossil**: *Pleistocene*:

ITALY: Santa Fiore (B.M. 18747, 18748 = Coll. Kützing n. 9b; B.M. 18820 = Coll. Kützing n. 911; isotypes).

This species is based on specimens that were found "fossil im Bergmehl von San Fiore". Among the specimens in the British Museum Herbarium labelled "Coll.
Kütz. Diat.” there are a number of packets labelled in EuleinStein’s hand with a species name, the locality “St. Fiore” and the number “911”. One of these is labelled “Navicula laevissima Kg.” and the slide n. B.M. 18820 was prepared from this material. In other cases where such packets occur, Kützing’s original packet with the same number is present under another species and bears the name of more than one species. No original packet of n. 911 is present and this number is too high for a packet that was in Kützing’s possession at the time when he wrote the Bacillarien. There is, however, a specimen labelled “St. Fiore Campylodiscus Eurania granulata Nav. binodis 9b” in Kützing’s hand, and this packet contains considerable quantities of the diatomite. It is clearly part of Kützing’s original sample of this fossil deposit. Comparison of the microscope slides made from the material in this packet with those made from the packets numbered 911 by EuleinStein shows that all were prepared from the same fossil sample. Whether Kützing received a second batch of it at some stage or whether EuleinStein mis-read Kützing’s “‘9b’ as ‘911’” (this is possible since Kützing’s figures are written very small) one cannot now tell. In this material the species under discussion here, i.e. that called Navicula bacilliformis by all authors from 1880 until 1961 and N. wittrockii by Hustedt in 1961, is not uncommon and is the only one matching Kützing’s description and figure. N. pupula also occurs, but much more rarely, and the specimens of it have not the gibbous centre mentioned in Kützing’s description (“medio leviter ventricosa”) and shown in his figure.

The name N. laevissima appears never to have been correctly applied by any subsequent author. W. Smith (Synops. Brit. Diat. 2 : 91 (1856)) used it for N. pupula and in this he was followed by a number of authors (cf. p. 88 above). Donkin (Nat. Hist. Brit. Diat.: 28, t. 5 fig. 2 (1871)), however, used it for a form which probably belongs to N. bacillum Ehrenb. In 1880 Grunow (K. Svensk. Vetensk.-Akad. Handl., Ny Följd, 17 (2) : 45 (1880)), who had seen authentic material of N. pupula but not of N. laevissima, gave an accurate account of N. pupula, but considered the identity of N. laevissima doubtful; he gave a description under the name but with a query, and further down the same page said that N. laevissima might be identical with N. ventricosa sensu Donkin (= Caloneis silicula var. ventricosa Cleve), and that the species he had described under the name N. laevissima should be given the new name N. pseudobacillum. At the same time he described N. bacilliformis as a new species and suggested that N. laevissima sensu Donkin might belong to it. In Van Heurck’s Synopsis, published later in the same year, Grunow was responsible for two figures on the same plate, one labelled N. pseudobacillum (t. 13 fig. 9) and the other N. laevissima (t. 13 fig. 13). According to Hustedt (in Pasch., Süssw.-Fl. Mitteleur. 10, ed. 2 : 280 (1930)), N. pseudobacillum is a synonym of N. bacillum Ehrenb., and both these figures in the Synopsis seem to represent that species.

Except for this uniting of N. bacillum and N. pseudobacillum, Grunow’s treatment of these species in the Arctischen Diatomeen has normally been followed until very recently; the name N. pupula has been correctly applied, the identity of N. laevissima has been regarded as doubtful, and the species under discussion has been
called *N. bacilliformis*. H. and M. Peragallo (Diat. Mar. France: 67, t. 8 fig. 25 (1897)), however, used the name *N. laevissima* for a marine form quite unrelated to any of the species to which it had previously been applied, or misapplied, and Pantocsek (Res. Wiss. Erforsch. Balatonsees 2 (2, 1, Anhang): 47, t. 5 fig. 112 (1902)) used the name in yet another sense.

In 1961 Hustedt called this species *N. wittrockii* (Lagerst.) Cleve-Euler since he considered that the type material of *Stauroneis wittrockii* Lagerst. was conspecific with the type material of *N. bacilliformis*, an opinion which seems to me to be justified by the original accounts of the two. Cleve-Euler herself, on the other hand, maintains that there are two species involved and that *N. wittrockii* is distinguished from *N. bacilliformis* by having straight striae.

**Navicula caucasica** Ross, nom. nov. (Fig. 38.)


Valves narrowly rhombic-lanceolate with obtuse, rounded apices, 47.5–60μ long, 12–15μ broad. Raphe slightly sinuous, somewhat oblique, central pores close, terminal fissures hooked, both turned in the same direction. Axial area rather narrow. Central area three-quarters of the breadth of the valve, expanded outwards. Terminal areas prominent and rather large. Striae radiate at the centre, convergent at the apices, somewhat curved, very finely punctate, 14–15 in 10μ; short striae opposite the central nodule of uneven length.

![Fig. 38. Navicula caucasica Ross (in B.M. 69176) × 1,000.](image)

Known from a single freshwater gathering from the Caucasus.


This species resembles *Stauroneis amphioxys* Greg. but the central area does not extend so far across the cell and widens outwards more markedly, and the striae are wider spaced, more strongly radiate at the centre, and convergent at the apices.
In spite of this resemblance, I place this species in *Navicula*, not *Stauroneis*, since the central area is not a stauros and the striae do not appear under the light microscope to have the structure typical of true *Stauroneis*.

*Stauroneis smithii* var. *sagitta* (Cleve) Hust. in Rabenh., Krypt.-Fl. Deutsch. 7 (2) : 811, fig. 1158 (1959).

_Pleurostauron sagitta_ Cleve in Cleve & Møller, Diatoms 5 : 6, n. 261 (1879), nom. nud.


*Stauroneis stefanssonii* Østr. in Rosenv. & Warm., Bot. Iceland 2 : 15, t. 2 fig. 18 (1918) ("Stefanssoni").

For description and figure, see Hustedt (loc. cit.).

From fresh and slightly brackish waters in northern Scandinavia and Iceland, and fossil from freshwater quaternary deposits in Sweden and Finland.

_Norway_ : Mouth of the Tana Elf (B.M. 13024 = Cleve & Møller, Diatoms n. 261, isotype).

In the *Synopsis of the Naviculoid Diatoms* Cleve includes *Stauroneis sagitta* in the subdivision *Schizostauron* of the *Naviculae microstigmatica*. The resemblance between the species to which this diatom is here referred and *Capartogramma* is discussed earlier in this paper (p. 53). It has been regarded as a distinct species by most authors, but Hustedt’s treatment of it as a variety of *S. smithii* seems justified. The division of the stauros on one or both sides in many specimens is the reason why Cleve referred it to *Schizostauron*, but this division of the stauros is comparable to that of a single tigillum sometimes found in *Capartogramma* and not to the possession of two diverging tigilla, which is the characteristic of that genus.
Stereo-pairs of electron micrographs: A, Capartogramma karstenii (Zanon) Ross (× 2,500); B, C. crucicula (Grun. ex Cleve) Ross (× 5,500); C, C. amphoroides Ross (× 2,500). Phot. K. Little.
A. *Capartogramma crucicula* (Grun. ex Cleve) Ross; stereo-pair of electron micrographs. \((\times 13,000.)\)  

B, C. *C. karstenii* (Zanon) Ross; electron micrographs. \((B \times 50,000; C \times 35,000.)\)  

Phot. K. Little.
ANGIOSPERMS OF THE CAMBRIDGE ANNOBON ISLAND EXPEDITION

A. W. EXELL

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY

LONDON: 1963
ANGIOSPERMS OF THE CAMBRIDGE ANNOBON ISLAND EXPEDITION

BY

A. W. EXELL

Pp. 93–118 ; Plates 3–12

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ANGIOSPERMS OF THE CAMBRIDGE
ANNOBON ISLAND EXPEDITION

By A. W. EXELL

The following is an account of the more interesting Angiospermae collected on the Cambridge Annobon Island Expedition 1959. The two collectors were Fenella A. Melville (now Mrs. Wrigley) and T. C. Wrigley.

I have included in the list all new records for Annobon and specimens of species already recorded for the island but meriting inclusion for one reason or another. It is particularly interesting to be able to record a number of gatherings of species described from Mildbraed’s 1911 collection of which the types (formerly in the Berlin Herbarium) have been destroyed. These have largely been identified ex descriptione: if correctly named they provide (allowing for the very small size of the island) topotypes of the species concerned. Photographs of three of the Mildbraed types and seven of the new topotypes are included in this account as illustrations. Except for the Orchidaceae (which are at Kew) all the specimens collected on the Cambridge Expedition are represented in the British Museum Herbarium, and all specimens cited in this account are in the British Museum Herbarium unless otherwise indicated.

In my statements of new records “the islands” means the three islands of Principe, S. Tomé and Annobon in the Gulf of Guinea. The four principal works which I have already published on the flora of these islands are: (1) Catalogue of the Vascular Plants of S. Tomé (with Principe and Annobon) (1944); (2) Supplement to the Catalogue of the Vascular Plants of S. Tomé (with Principe and Annobon) (1956); (3) Aditamento à Flora das Ilhas de São Tomé e do Principe (Confer. Internacion. Afr. Oc., Sess. 6, 3: 77–91) (1958), with A. Rozeira; (4) Additions to the Flora of S. Tomé and Principe (Bull. Inst. Franç. Afr. Noire 21, Sér. A, n. 2) (1959). They are abbreviated in this account as follows: (1) Exell, Cat.; (2) Exell, Suppl.; (3) Exell, Aditam.; (4) Exell, Addit. The third of these works was published without my seeing a proof and is marred by typographical errors. I have taken the opportunity to bring the nomenclature up to date as regards a few species listed in these works and to correct various errors which have been pointed out to me, but I have not troubled to correct the fairly obvious orthographical mistakes in the Aditamento. Taxa not recorded for Annobon are placed within square brackets.

I am indebted as usual to numerous colleagues at the British Museum (Natural History), the Royal Botanic Gardens, Kew, and other institutions; and more particularly to J. E. Dandy (general arrangement), Miss D. Hillcoat (Leguminosae), F. N. Hepper (Rubiaceae), J. Lewis (Loganiaceae), W. T. Stearn (Solanaceae, Piperaceae, Loranthaceae), J. Léonard (Euphorbiaceae), V. S. Summerhayes (Orchidaceae) and W. D. Clayton (Gramineae).
DILLENIACEAE

Tetracera alnifolia Willd.—Exell, Cat.: 100.

Annobon: S.E. of Santa Cruz, 450 m., forest on ridge, scabrid climber and scrambler, 7 Aug. 1959, Wrigley 249.

New record for Annobon.

ANNONACEAE

Annona muricata L.—Exell, Cat.: 101.

Annobon: Near Ambo, 27 m., open woodland, 20 July 1959, Wrigley 63.


Annona reticulata L.—Exell, Cat.: 101.

Annobon: Near Ambo, 27 m., and near Crater Lake, open woodland, 16 July 1959, Wrigley 42.


[CRUCIFERAE]


Nasturtium sinapis (Burm. f.) O. E. Schulz.—Exell, Suppl.: 10; Aditam.: 81.

Rorippa sinapis (Burm. f.) Ohwi & Hara.—Exell, Addit.: 450.

S. Tomé: Ribeira Peixe, Rozeira 236 (Herb. Porto Univ.). Diogo Vaz, Rozeira 869 (Herb. Porto Univ.).

This introduced species has previously been recorded from S. Tomé under the names Nasturtium sinapis and Rorippa sinapis. It is widely distributed in southeast Asia from Japan and China to India and Malaysia.

The name R. indica has been misapplied to another species, R. madagascariensis (DC.) Hara (tom. cit.: 198).]

CAPPARACEAE

Cleome rutidosperma DC., Prodr. i: 241 (1824).

Cleome ciliata Schumach.—Exell, Cat.: 105; Suppl.: 10.

Annobon: N.W. of the Island, 6 m., rocks and cassava plantations by sea, 11 July 1959, Melville 129.

De Candolle’s name replaces that of Schumacher. The species is recorded for Principe, S. Tomé and Annobon and is widespread in tropical Africa southwards as far as Northern Rhodesia.

PORTULACACEAE

Portulaca oleracea L.—Exell, Cat.: 110; Addit.: 450.

Annobon: Ambo, by the expedition’s houses, 15 m., sandy place by house, 21 July 1959, Melville 168.

New record for Annobon.
ANGIOSPERMS OF ANNOBON ISLAND

Talinum triangulare (Jacq.) Willd.—Exell, Cat.: 110; Suppl.: 11.
New record for Annobon. Introduced.

MALVACEAE

Sida rhombifolia L.—Exell, Cat.: 115.
Annobon: Near Capelle San Juan, 30 m., wayside in cultivated land, 10 Aug. 1959, Melville 258.
New record for Annobon.

Gossypium barbadense L.—Exell, Cat.: 119.
Annobon: Near Ambo, 9 m., pathside, 11 July 1959, Wrigley 12.
New record for Annobon. Introduced; presumably an escape from cultivation.

RUTACEAE

Citrus aurantifolia (Christm.) Swingle.—Exell, Cat.: 131.
Annobon: Near Ambo, 24 m., waste ground, 12 July 1959, Wrigley 25.

OCHNACEAE

Ochna quintasii (Tiegh.) Exell, Cat.: 132.
Ochna cf. gilgiana, Exell, Cat.: 132.
Annobon: Between Capelle San Juan and San Pedro, 45 m., steep wood, cliffs by sea, 11 Aug. 1959, Melville 260.
Recorded from Annobon by Mildbraed as O. cf. gilgiana. Also in S. Tomé and widespread in western tropical Africa, eastwards to Uganda and southwards to Angola.

MELIACEAE

Turraea glomeruliflora Harms.—Exell. Cat.: 136. (Plate 3.)
Annobon: Ridge west of Crater Lake, 360 m., open woodland; “small sepals; green petals; white filament tube with 10 stamens”; 18 July 1959, Wrigley 52.
Endemic to Annobon. Wrigley’s locality is quite near to that of the holotype, Mildbraed 6487 (Herb. Berlin, destroyed). A photograph of the holotype exists in the British Museum Herbarium and is reproduced in Plate 3.

CELASTRACEAE

Maytenus annobonensis (Loes. & Mildbr.) Exell, comb. nov. (Plate 4.)
ANGIOSPERMS OF ANNOBON ISLAND

Annobon: Ridge west of Crater Lake, 360 m., open woodland; “flower white; 3-merous fruit with 1 orange seed”; 18 July 1959, Wrigley 56.

Endemic to Annobon. This material was collected in almost the same locality as the holotype, Mildbraed 6541 (Herb. Berlin, destroyed), and the only doubt about the identification lies in the fact that the original specimen had neither flowers nor fruit so that here “ex descriptione” has little meaning. Actually this new gathering by Wrigley confirms the supposition that the species belongs to the genus Maytenus (Gymnosporia). It differs from M. monodii Exell (endemic to S. Tomé) by its dense ferrugineous pubescence on the young stems, being nearer in this respect to M. welwitschiana Exell & Mendonça (Angola) but with larger flowers than in the latter species and with a glabrous (or only minutely pubescent) capsule.

ANACARDIACEAE

Mangifera indica L.—Exell, Cat.: 145.

Annobon: Common tree, lower grassland and up to Crater Lake, regenerating very freely, 19 July 1959, Wrigley 61.

New record for Annobon. Introduced.

CONNARACEAE

Agelaea ovalis Schellenb.—Exell, Cat.: 148. (Plate 5.)

Annobon: Ambo, 90 m.; dry valley; “tree c. 30 ft.; fruit red and yellow with black and orange seed; flowers off-white (pinkish)”; 2 Aug. 1959, Melville 232.

Endemic to Annobon. Melville’s plant is almost certainly A. ovalis, of which the holotype, Mildbraed 6679 (Herb. Berlin), has been destroyed. It is, however, difficult to believe that the plant is a tree and I suspect an error in the collector’s note.

LEGUMINOSAE

Arachis hypogaea L.—Exell, Cat.: 155.

Annobon: Cultivated on a small scale during the wet season, 18 Aug. 1959, Wrigley 297, fruit only.

New record for Annobon. Introduced.

Desmodium ramosissimum G. Don.—Exell, Suppl.: 16.

Desmodium mauritianum sensu Exell, Cat.: 158.

Annobon: Path towards Pico do Fogo and Crater Lake, 90 m., pathside, 10 July 1959, Melville 105.

New record for Annobon.


Mucuna urens sensu Exell, Cat.: 160.

Annobon: Near Ambo, 24 m., climbing over trees, 14 July 1959, Wrigley 30.

Recorded for S. Tomé and Annobon as M. urens; widespread in tropical Africa and tropical America. Calabar Bean.
ANGIOSPERMS OF ANNOBON ISLAND


Clitoria alba G. Don, Gen. Syst. 2 : 215 (1832).
Vigna alba (G. Don) Planch. ex Baker f.—Exell, Cat.: 161.

ANNOBON: East path towards Crater Lake, 135 m., pathside and cassava plantation, running over rocks, 18 July 1959, Melville 162.
New record for Annobon. The species occurs also in S. Tomé and is widespread in tropical and subtropical regions.

CAJANUS CAJAN (L.) Millsp.—Exell, Cat.: 163.
ANNOBON: Near Ambo, 30 m., open grassland, 23 July 1959, Wrigley 76.
New record for Annobon. Introduced.

ERIOSEA GLOMERATUM (Guillem. & Perrott.) Hook. f. in Hook., Niger Fl.: 313 (1849).


ANNOBON: Near Ambo, 30 m., pathside, 17 July 1959, Wrigley 46.
New record of the genus Eriosema (DC.) Desv. for the islands. E. glomeratum is widespread in tropical Africa.

CAESALPINIA PULCHERRIMA (L.) Swartz.—Exell, Cat.: 165.
ANNOBON: Mission, Ambo, 15 m., garden, 4 Aug. 1959, Melville 233.

CASSIA OCCIDENTALIS L.—Exell, Cat.: 166.
ANNOBON: Path between Capelle San Juan and San Pedro, 60 m., pathside, 2 Aug. 1959, Wrigley 230.
New record for Annobon.


Cassia tora sensu Exell, Cat.: 167.

ANNOBON: Path between Capelle San Juan and San Pedro, 60 m., pathside, 2 Aug. 1959, Wrigley 230a.
New record for Annobon. The species occurs also in S. Tomé and is widespread in the tropics.
According to Brenan (tom. cit.: 248–252) C. tora L. is a different species which does not occur in West Africa.

CRASSULACEAE

KALANCHOE CRENATA (Andr.) Haw.—Exell, Cat.: 173 ; Suppl.: 19.
ANNOBON: Near shore near Ambo, 6 m., edge of dry river, 4 Aug. 1959, Wrigley 235.
New record for Annobon.
ANGIOSPERMS OF ANNOBON ISLAND

RHIZOPHORACEAE

Cassipourea annobonensis Mildbr. ex Alston.—Exell, Cat.: 174. (Plate 6.)

Annobon: Pico do Fogo on S.W. side, 360 m., edge of forest at base of Pico; "flowers 4-merous; tree 30 ft. (branches well spaced for climbing)"); 25 July 1959, Melville 190.

Endemic to Annobon. The locality is near to that of the holotype, Mildbraed 6511 (Herb. Berlin, destroyed). A photograph of the holotype exists in the British Museum Herbarium and is reproduced in Plate 6.

COMBRETACEAE

Terminalia catappa L.—Exell, Cat.: 175.

Annobon: Near Ambo, 24 m., planted; "the nuts are eaten"; 18 Aug. 1959, Wrigley 296.

New record for Annobon. Introduced. Indian Almond.

MELASTOMATACEAE

Tristemma oreothamnos Mildbr.—Exell, Cat.: 178. (Plate 7.)


Endemic to Annobon. The holotype of this species, Mildbraed 6677 (Herb. Berlin), has been destroyed; it was collected at a somewhat higher altitude on the neighbouring peak of Quioveo.

PUNICACEAE


New record of the genus Punica L. for Annobon. P. granatum, the Pomegranate, is a widely cultivated species of Asiatic origin.

CARICACEAE

Carica papaya L.—Exell, Cat.: 183.

Annobon: Crater Lake, 265 m., lakeside cultivation, 24 July 1959, Melville 182.

New record for Annobon. Introduced.

CUCURBITACEAE


Peponium bracteatum (Cogn.) Cogn.—Exell, Cat.: 184.

Described from S. Tomé as Peponia bracteata Cogn., but this is now referred by Jeffrey (loc. cit.) to Peponium vogelii, a species widely distributed in tropical Africa and extending into Natal.]

Adenopus breviflorus Benth.—Exell, Cat.: 184.


New record for Annobon.

Jeffrey (Kew Bull. 15 : 355 (1962)), in a new classification of the family Cucurbitaceae, includes Adenopus Benth. within the genus Lagenaria Ser.


Annobon: Ambo village, 9 m., cultivated; "fruit used as calabash"; 20 Aug. 1959, Melville 302.

New record for Annobon. Widespread and frequently cultivated in the tropics. Calabash, Bottle-gourd or White Pumpkin.

Luffa aegyptiaca Mill.—Exell, Cat.: 184.

Annobon: Ambo, near the expedition's houses, 24 m., climbing over top branches of Jatropha curcas, 12 July 1959, Melville 133. San Pedro, 15 m., village rubbish heap, 2 Aug. 1959, Wrigley 229.

New record for Annobon.


Jeffrey (tom. cit.: 352–354) has adjusted the nomenclature of this widely distributed palaeotropical species, which is recorded for S. Tomé. He adopts the generic name Diplocyclos (Endl.) Post & Kuntze.]


Melothria capillacea sensu Exell, Cat.: 185; Suppl.: 22.

Occurs in S. Tomé and on the mainland of western tropical Africa from Liberia to Gabon and Congo.

This and the following species belong to the palaeotropical genus Zehneria Endl. which is separated by Jeffrey (tom. cit.: 343) from the exclusively New World genus Melothria L.]
ANGIOSPERMS OF ANNOBON ISLAND


Melothria minutiflora sensu Exell, Cat.: 185.

Recorded from S. Tomé; widely distributed in the Old World tropics, extending into South Africa.]

ARALIACEAE

POLYSCIAS GUILFOYLEI (Bull) L. H. Bailey in Rhodora 18: 153 (1916).

Aralia guilfoylei Bull, Cat. 1873: 4 (1873).
Var. LACIINIATA L. H. Bailey, loc. cit. (1916).
Annobon: Capelle San Juan, 4.5 m., garden of Capelle, 14 Aug. 1959, Melville 281.
New record for the islands. Introduced; a cultivated plant of Polynesian origin.

RUBIACEAE

New record for Annobon. Introduced.

COFFEA LIBERICA Bull ex Hiern.—G. Taylor in Exell, Cat.: 208.
Annobon: Ridge west of Crater Lake, 360 m., open woodland, 18 July 1959, Wrigley 50.
New record for Annobon. Introduced.

BERTIERA ANNOBONENSIS G. Taylor.—G. Taylor in Exell, Cat.: 208. (Plate 8.)
Annobon: Near highest point of Crater, 480 m., forest; “undershrub, two specimens with white corolla, others fruit only”; 26 July 1959, Wrigley 93.
Endemic to Annobon. Wrigley 93 is topotypical material of Mildbraed 6502 (Herb. Berlin), one of the destroyed syntypes. The other syntype, Mildbraed 6760, came from Santa Mina.

UNCARIA AFRICANA G. Don, Gen. Syst. 3: 471 (1834).
Annobon: Pico Surcado and Monte Abecin, 570 m., forest climber, 11 Aug. 1959, Wrigley 304.
New record of the genus Uncaria Schreb. for the islands. This is the typical variety of U. africana, distributed on the mainland of West Africa from Portuguese Guinea eastwards and extending to Sudan, Uganda and Tanganyika.

[new page]

[GEOPHILA NEURODICTYON (K. Schum.) Hepper in Kew Bull. 16: 331 (1962).

Psychotria neurodictyon K. Schum.—G. Taylor in Exell, Cat.: 213.
Recorded from Principe.]
ANGIOSPERMS OF ANNOBON ISLAND

The generic name Geophila D. Don (non Bergeret) has been proposed for conservation over Carinta W. F. Wight, the name adopted by G. Taylor (in Exell, Suppl.: 25) for the three species previously listed by him (in Exell, Cat.: 217) under Geophila; cf. Taxon 9: 88 (1960).

Oldenlandia herbacea (L.) Roxb., Hort. Bengal.: II (1814).


Annobon: N.W. of the Island, 15 m., cassava plantation, II July 1959, Wrigley II.

New record for the islands. Widely distributed in the Old World tropics.

COMPOSITAE

Adenostemma perrottetii DC.—Exell, Cat.: 222; Suppl.: 26.

Annobon: South of Crater Lake, near higher point of Crater, 420 m., cultivated land, cassava plantations in the hills, 1 Aug. 1959, Melville 210.

New record for Annobon.

Mikania cordata (Burm. f.) B. L. Robinson.—Cannon in Exell, Suppl.: 27.

Mikania scandens sensu Exell, Cat.: 222.

Mikania sp., Cannon in Exell, Suppl.: 27.

Annobon: Near Ambo, 30 m., scrub, climber, 12 July 1959, Wrigley 27.

Previously recorded from Annobon as Mikania sp.


Dichrocephala bicolor (Roth) Schlecht.—Exell, Cat.: 223; Suppl.: 31.

The epithet integrifolia, though inapt, is the correct one for this widespread species which is recorded for S. Tomé.]

Synedrella nodiflora (L.) Gaertn.—Exell, Cat.: 226; Suppl.: 31.

Annobon: North shore of Crater Lake, 265 m., pathside, 24 July 1959, Wrigley 80.

New record for Annobon.


Melampodium ruderale Swartz, Fl. Ind. Occ. 3: 1372 (1806).

Annobon: Near Capelle San Juan, 30 m., wayside in cultivated land, 10 Aug. 1959, Melville 257.

New record of the genus Eleutheranthera Poit. ex Bosc for the islands. E. ruderalis is a pantropical weed.

CAMPANULACEAE

Cephalostigma perrottetii A. DC., Monogr. Campan.: 118 (1830).

Annobon: Pico do Fogo, 360 m., among rocks, 24 July 1959, Wrigley 90.

New record of the genus Cephalostigma A. DC. for the islands. C. perrottetii is widespread in tropical Africa and tropical South America.
ANGIOSPERMS OF ANNOBON ISLAND

APOCYNACEAE


Annobon: Ambo, near the Mission, 15 m., 2 Aug. 1959, Melville 220.

New record of the genus Allamanda L. for the islands. A. cathartica, native of tropical America, is widely cultivated in the tropics.

Catharanthus roseus (L.) G. Don.—Philipson in Exell, Cat.: 239.

Annobon: Ambo, 27 m., waste ground, 19 July 1959, Wrigley 58.

New record for Annobon. Introduced.

Plumeria rubra L.—Philipson in Exell, Cat.: 241.


New record for Annobon. Introduced.

ASCLEPIADACEAE

Asclepias curassavica L.—Exell, Cat.: 242; Suppl.: 34.

Annobon: Ambo, 180 m. S.W. of church, 22 m., cleared ground, 10 July 1959, Melville 102.

New record for Annobon. Introduced.

Loganiaceae

(By J. Lewis)


Var. congesta. (Plate 9.)


Lachnopylis annobonensis Mildbr.—Philipson in Exell, Cat.: 244.

Lachnopylis angolensis (Gilg) Philipson in Exell, Cat.: 245 (1944).

Annobon: Pico do Fogo, 2 m. and less below top of Pico, rocky mountainside, 12 Aug. 1959, Melville 277.

Widely distributed on the mountains of tropical Africa and extending into South Africa; previously recorded for Annobon under the name Lachnopylis annobonensis, of which Melville 277 is an exact topotype. The holotype of L. annobonensis, Mildbraed 6561 (Herb. Berlin), is destroyed, but there is an isotype in the British Museum Herbarium accompanied by a photograph of the holotype which is reproduced in Plate 9.

The opinions expressed by Bruce and Lewis (loc. cit.) and by Verdoorn (Bothalia 7: 14 (1958)) concerning the great variability and wide range of this species are...
confirmed by more recent workers in Floras concerning West and South Africa about to be published, and I have now no hesitation in including *N. angolensis* and *N. mannii* as well as *Lachnopylis annobonensis*. The Annobon plant is very clearly the common form of the species which has been known as *N. angolensis* on the neighbouring mainland. On S. Tomé, however, the species is represented by a plant which may be distinguished varietally.

[Var. *thomensis* (Philipson) J. Lewis, stat. nov.  
*Lachnopylis thomensis* Philipson in Exell, Cat.: 245 (1944).—Exell, Addit.: 462.  
Known from S. Tomé and Mount Kilimanjaro in Tanganyika.  
Specimens collected by Monod on the Pico in S. Tomé (*Monod 1954, 1989*) have unusually large elliptic leaves, about 15 cm. long and 6 cm. broad, bearing distinct traces of a white dendroid indumentum along the midrib and nerves beneath. However, they are exactly matched by a specimen collected by Haarer at a comparable altitude on Mount Kilimanjaro (*Herb. Kew*) which has always been accepted as *N. congesta*. The occurrence of *N. congesta* at similar altitudes on other mountains makes subspecific rank unsuitable for these variants, but their moderate distinctness justifies recognition at the varietal level.]

**GENTIANACEAE**


*Pladera decussata* Roxb., Hort. Bengal.: 10 (1814), *nom. nud.*  

**Annobon**: N.W. of the Island, 15 m., pathside, 11 July 1959, *Melville 137*.  
New record of the genus *Canscora* Lam. for the islands. *C. decussata* is widespread in the tropics of the Old World.


**Annobon**: N.W. of the Island, 15 m., cassava plantation, 11 July 1959, *Wrigley 9*.  
New record of the genus *Exacum* L. for the islands. *E. quinquenervium* is widely distributed in tropical Africa, Madagascar and the Mascarene Islands.

**CONVOLVULACEAE**


*Calonyction aculeatum* (L.) House.—Exell, Cat.: 249.  
**Annobon**: South of Crater Lake, 450 m., opening in forest, climbing on plants, 1 Aug. 1959, *Melville 207*.  
New record for Annobon.  
*Calonyction* Choisy is now included in *Ipomoea* L., and *C. aculeatum* takes the name *I. alba*.


**Annobon**: North of San Pedro, 420 m., clearings in forest, 21 Aug. 1959, *Melville 305*.  
New record for the islands. Widespread in tropical Africa.
Ipomoea mauritiana Jacq.—Exell, Addit.: 462.

Ipomoea digitata sensu Exell, Cat.: 250.

Annobon: Crater Lake, 265 m., lake edge, on Ficus and Elaeis, climber, 31 July 1959, Melville 206.
New record for Annobon.


Annobon: South of the Administrator’s house and just behind the expedition’s houses, 24 m., shady pathside, running over ground, 10 July 1959, Melville 103.
New record for the islands. Introduced; a widespread tropical species of American origin.

Solanaceae
(By W. T. Stearn)

Lycopersicon esculentum Mill.—Exell, Cat.: 252.

Var. cerasiforme (Dunal) Alef.—Exell, Cat.: 252.

Annobon: San Pedro, 3 m., sea shore, cultivated, 11 Aug. 1959, Melville 262.
New record for Annobon. Introduced.


Solanum duplosinuatum Klotzsch.—Exell, Cat.: 253.

Annobon: Between Pico do Fogo and San Pedro, 450 m., banana plantation, 26 July 1959, Wrigley 95.
New record for Annobon; recorded (with doubt) for Principe under the name S. duplosinuatum. Widespread in tropical Africa, extending into Natal.

Solanum nodiflorum Jacq., Collect. 2: 288 (1788).

Solanum nigrum sensu Exell, Cat.: 253; Suppl.: 36.

Annobon: Pico do Fogo, S.W. side, 390 m., bare soil between rocks, recently burnt, 25 July 1959, Melville 188.
Recorded for Principe, S. Tomé and Annobon under the name S. nigrum. Widespread in the tropics, where it has been much confused with the closely allied S. nigrum L.

Physalis angulata L.—Exell, Cat.: 254.

New record for Annobon. Probably introduced.


New record for the islands. Widespread in tropical Africa and also recorded for India and tropical America.

Capsicum annuum L.—Exell, Cat.: 254.


New record for Annobon. Cultivated.

Datura candida (Pers.) Safford.—Exell, Suppl.: 36.


New record for Annobon. Introduced; widely spread as a cultivated plant in tropical and subtropical countries.

Nicotiana tabacum L.—Exell, Cat.: 256.

Annobon: Ambo, 27 m., waste ground; “not (obviously) cultivated; not used”; 19 July 1959, Wrigley 59.

New record for Annobon. Introduced.

Scrophulariaceae

Lindernia diffusa (L.) Wettst.—Exell, Cat.: 256.

Var. diffusa.


New record for Annobon.

Var. pedunculata (Benth.) Skan.—Exell, Cat.: 256; Suppl.: 36.


New record for Annobon.


Alectra communis Hemsl.—Exell, Cat.: 257.

Annobon: Pico do Fogo, S.W. side, 390 m., burnt area, bare ground, 25 July 1959, Melville 189.

New record for Annobon. Recorded for Principe; widespread in tropical Africa, Madagascar, Mauritius and south-eastern Asia from India to Formosa and the Philippines.
ANGIOSPERMS OF ANNOBON ISLAND

ACANTHACEAE

Phaulopsis micrantha (Benth.) C. B. Clarke.—Exell, Cat.: 261.

Annobon: N.W. of the Island, 15 m., cassava plantation, 11 July 1959, Melville 120.

New record for Annobon.


Dianthera verticillata Forsk., Fl. Aegypt.-arab.: ciii, 9 (1775).

Dicliptera umbellata (Vahl) Juss.—Exell, Cat.: 263; Addit.: 463.

Annobon: Near Ambo and near Crater Lake, near streams, etc., 18 July 1959, Wrigley 49.

New record for Annobon. The species occurs in Principe and S. Tomé and is widespread in tropical Africa, extending into Arabia and India.

[VERBENACEAE]


Avicennia africana Beauv.—Exell, Cat.: 265.

The earliest publication of the combination A. germinans was in 1764 as given above. The species is recorded from S. Tomé; it occurs on the coasts of tropical America as well as West Africa.]

LABIATAE

Leonotis nepetifolia (L.) Ait. —G. Taylor in Exell, Cat.: 266.—Exell, Suppl.: 38.

Annobon: Ambo, by the expedition’s houses, 15 m., waste ground and common there; “natives dry and hang up to keep off mosquitoes”; 13 July 1959, Melville 141.

New record for Annobon.

Ocimum basilicum L.—G. Taylor in Exell, Cat.: 266.

Annobon: Ambo village, 15 m., pathside, 15 July 1959, Wrigley 40.

New record for Annobon.

NYCTAGINACEAE


Boerhavia diffusa sensu Exell, Cat.: 268 pro parte.

Principe: Without locality, Sept. 1853, Welwitsch 5391.


New records for Principe, S. Tomé and Annobon. Native of tropical America, now widespread in the tropics of both America and Africa.

Since the publication of my Catalogue in 1944 Meikle (loc. cit.) has distinguished two species within the West African material referred to *B. diffusa* L. Re-examination of the specimens in the British Museum Herbarium cited in the Catalogue shows that they all belong to *B. coccinea* as defined by Meikle.

**Boerhavia diffusa** L.—Exell, Cat.: 268 excl. parte.


Recorded for Annobon by Mildbraed, but the identity of his plant is now uncertain. The record for Principe, and at least some of the records for S. Tomé, belong to *B. coccinea* as indicated above under that species.

**Amaranthaceae**

**Amaranthus spinosus** L.—Exell, Cat.: 270.

**Annobon**: San Pedro, 3 m., pathside in village, 21 July 1959, *Melville 173*.

New record for Annobon.

**Amaranthus viridis** L.—Exell, Cat.: 270.

**Annobon**: N.W. corner of Crater Lake, 265 m., dry stream bed, 24 July 1959, *Melville 179*.

New record for Annobon.

**Achyranthes aspera** L.—Exell, Cat.: 270.

**Annobon**: Crater Lake, 270 m., forest paths, 25 July 1959, *Melville 192*.

New record for Annobon.

**Cyathula prostrata** (L.) Blume.—Exell, Cat.: 271.

**Annobon**: Path to Pico Surcado (Monte Santa Mina), 510 m., dense vegetation in mist-forest, 21 July 1959, *Melville 174*.

New record for Annobon.


*Telanthera maritima* (Mart.) Moq.—Exell, Cat.: 271 ; Aditam.: 86.


Recorded for Principe, S. Tomé and Annobon.

Keay and other recent authors include *Telanthera* R. Br. under *Alternanthera* Forsk.

ANGIOSPERMS OF ANNOBON ISLAND


The earliest publication of the combination A. sessilis appears to be that given above. The species is recorded for Principe, S. Tomé and Annonobon.

**Baseellaceae**

*Baseila alba* L.—Exell, Cat.: 274.

**Annonobon**: San Pedro and Ambo, 15 m., roof of houses, vine rooted in the ground; "used as pot-herb"; 21 July 1959, Wrigley 67.

New record for Annonobon. Probably introduced.

**Piperaceae**

(By W. T. Stearn)

*Peperomia hygrophila* Engler.—Exell, Cat.: 277.

*Peperomia annobonensis* Mildbr.—Exell, Cat.: 276.

**Annonobon**: Pico Surcado, 510 m., mist-forest, very abundant epiphyte, 21 July 1959, Wrigley 70.

*P. hygrophila* was based by Engler on specimens collected at 2,500–2,600 m. altitude on Cameroons Mountain, evidently in a moist habitat as the epithet implies; an isosyntype (*Preuss 805*) in the British Museum Herbarium represents a robust luxuriant individual with cuneate-based leaf-laminas 1.5–4 cm. broad and a flowering spike about 8 cm. long, these somewhat exceeding the dimensions given by Engler in his original description. *Exell 156* from virgin forest on S. Tomé approaches Preuss’s plant in luxuriance, having laminas 1–3.5 cm. broad, some cuneate, others almost rounded at the base, but with spikes 2.5–4.5 cm. long. Other specimens from S. Tomé bridge the gap between this and a small-leaved plant from the same island (*Monod 11744*) with laminas rounded or almost subcordate at the base and 0.5–1.4 cm. broad. In *Monod 12228* the lamina varies from almost circular with rounded base to narrowly obovate with narrowly cuneate base. The spike in S. Tomé material varies in length from about 8 cm. to 2 cm. I have examined the holotype of *P. annobonensis* (*Mildbraed 6532*) which is preserved at Berlin and which was collected on Annonobon in dry Steghanthus-Elaeis forest at 250–350 m. altitude. It differs from Wrigley’s mist-forest material in having mostly elliptic rather than mostly circular laminas, but both these Annonobon plants come well within the range of variation of *P. hygrophila* as manifested on S. Tomé and Cameroons Mountain.

**Lauraceae**

*Persea americana* Mill.—Exell, Cat.: 280.

**Annonobon**: S.W. of Crater Lake, 390 m., open forest, 5 Aug. 1959, Melville 239.


**Loranthaceae**

(By W. T. Stearn)

ANGIOSPERMS OF ANNOBON ISLAND

ANNOBON: Edge of forest near Pico do Fogo, 330 m., parasite on Ficus clarencensis, 24 July 1959, Wrigley 86.

New record for the islands. Also in Angola and Tanganyika.

The specimen, which has only unripe fruit, belongs to the small group of African species of Viscum with conspicuously flattened stems and the leaves reduced to scales. In the key to the tropical African species given by Sprague (tom. cit.: 394–395) it runs down to V. engleri, hitherto recorded only from Tanganyika; and it comes within the range of variation of this species as indicated by specimens from the Usambara Mountains (the locus classicus) and the Sagara Mountains. Specimens of what is evidently the same species collected by Gossweiler (n. 9884, Herb. Kew) in the Cuanza Sul region of Angola suggest that V. engleri may be widespread but sporadic in tropical Africa.

EUPHORBIACEAE


ANNOBON: Santa Cruz, 30 m. (also Ambo), planted by chapel, 8 Aug. 1959, Melville 269.

New record for the islands. Introduced; native of Mexico and Central America. Poinsettia.

[Cleistanthus libericus N. E. Br.—Exell, Cat.: 286.

In the Catalogue I listed this species from S. Tomé, but with a query. Dr. J. Léonard considers (and I agree) that the S. Tomé plant was correctly identified as C. libericus by Hutchinson.]

Thecacoris annobonae Pax & Hoffm.—Exell, Cat.: 287. (Plate 10.)

ANNOBON: Pico Surcado, 420 m., forest; “shiny leaves; very red wood; racemes of flowers with 5 stamens”; 21 July 1959, Wrigley 66. Near highest point of Crater, 480 m., forest, 26 July 1959, Wrigley 92.

Endemic to Annobon. This identification is probably correct but there is a slight element of doubt as the species was described from female inflorescences and fruit while Wrigley collected male inflorescences and fruit, so that his material can be compared only partly with the original description. T. annobonae was described as having “capsulae cocci pilosi”; the fruits of Wrigley 92 are nearly glabrous but have vestiges of an indumentum. Although there is a suggestion that there may be another species of Thecacoris on the island (Exell, Cat.: 288) Wrigley’s specimens nevertheless in all probability represent the species (T. annobonae) collected by Mildbraed on the rim of the North Crater at c. 500 m. altitude and said to be very common.


ANNOBON: East of Quiouveo (Pico del Centro), edge of clearing in forest, straggler, 1 Aug. 1959, Melville 212.

New record for the islands. Widespread in the Old World tropics; introduced into the West Indies.
Jatropha multifida L.—Exell, Cat.: 293; Suppl.: 42.

Annobon: Ambo, near the Post Office, 12 m., pathside, cultivated patch, 16 July 1959, Melville 156.

New record for Annobon. Introduced.

Codiaeum variegatum (L.) Blume.—Exell, Cat.: 296.

Annobon: Due south of Crater Lake, 420 m., forest near path to Quioveo, 1 Aug. 1959, Melville 208.

New record for Annobon. Introduced.

Discoclaoxylon pubescens (Pax & Hoffm.) Exell, stat. nov. (Plate II.)

Discoclaoxylon occidentale var. pubescens Pax & Hoffm. in Engler, Bot. Jahrb. 58, Beibl. 130: 39 (1923).—Exell, Cat.: 299.

Annobon: Highest point of Crater, 480 m., forest; "large leaves, 2/5 phyllotaxis; catkin-like inflorescence; 4-merous green flowers"; 26 July 1959, Wrigley 96.

Endemic to Annobon. There is little doubt that Wrigley’s plant is identical with D. occidentale var. pubescens, described from rather insufficient female material consisting of three syntypes: Mildbraed 6492, 6555 and 6751 (Herb. Berlin, destroyed). The male flowers in Wrigley’s material are considerably larger than those of D. occidentale (Muell. Arg.) Pax & Hoffm., measuring about 8 mm. in diameter when expanded. There are about five male flowers to each bract. They seem to expand one at a time and the pedicel is then 5–8 mm. long. There are 10–12 stamens. The leaves are similar to those of D. occidentale but are more hairy on the under surface, the petiole and the base of the midrib being tomentellous. I consider that these differences justify separate specific rank for the Annobon plant, and that D. occidentale is confined to S. Tomé.

Discoclaoxylon (originally Claoxylon sect. Discoclaoxylon Muell. Arg.) consists of a group of West African species geographically separated from Claoxylon A. Juss. and sufficiently distinct to warrant the generic rank given them by Pax and Hoffmann (in Engler, Pflanzenr. 4 (147, 7): 137 (1914)). Hutchinson and Dalziel (Fl. W. Trop. Afr. 1: 301 (1928)) reunited Discoclaoxylon with Claoxylon and this treatment was followed by Keay (in Hutch. & Dalziel, op. cit., ed. 2, 1: 401 (1958)). The main differences between the two genera, according to Pax and Hoffmann (tom. cit.: 76, 100, 137), are:

Claoxylon: extrastaminal disk none, but small glands usually present between the stamens; stamens 10–200 or more (very rarely fewer than 15).

Discoclaoxylon: extrastaminal disk urceolar, entire or lobulate; stamens 6–12. Claoxylon does not occur on the continent of Africa but is distributed from Madagascar and the Mascarene Islands eastwards through southern Asia to Australia and Polynesia.

The genus Discoclaoxylon now comprises four species: D. pedicellare (Muell. Arg.) Pax & Hoffm. (Fernando Po), D. occidentale (Muell. Arg.) Pax & Hoffm. (S. Tomé), D. pubescens (Pax & Hoffm.) Exell (Annobon) and D. hexandrum (Muell. Arg.) Pax
& Hoffm. (Fernando Po, Cameroons and Congo). The last-named species, which has (3-) 6-8 stamens (the others have 10-12) is the only one so far found on the mainland of Africa. When male and female flowers and fruits of all four are known their relationship may become clear, but it is already apparent that the distribution is "normal" with one West African species reaching Fernando Po, one endemic on that island, one on S. Tomé and a fourth on Annobon. The genus has not been recorded for Principe. It is one of the few "island genera" with more species on the islands than on the mainland (cf. Calvoa in the Melastomataceae which has about half its known species on the islands).

It seems desirable to typify the generic name Discoclaoxylon. Claoxylon sect. Discoclaoxylon Muell. Arg. (Flora 47: 437 (1864)) was founded on three species, C. pedicellare Muell. Arg., C. occidentale Muell. Arg. and C. hexandrum Muell. Arg., without indication of type; all three species were known only from male material. The position was unchanged when the section was later reviewed by its author (in DC., Prodr. 15 (2): 779 (1866)). When Pax and Hoffmann raised the section to generic rank as Discoclaoxylon the third species (D. hexandrum) had become known from the mainland of West Africa and female material had become available, so that quite a large part of their generic description (relating to ovary, capsule and seeds) came from this species, female material being still unknown in the other two species. It is also quite possible that D. pedicellare and D. occidentale are now extinct and complete material may never become available. Taking these points into consideration it seems best to select D. hexandrum as type of Discoclaoxylon.

**Acalypha annobonae** Pax & Hoffm.—Exell, Cat.: 299. (Plate 12.)

**Annobon**: Ridge west of Crater Lake, 360 m., open woodland; "female and male flowers on same shrub; low shrub 1-2 m."; 18 July 1959, Wrigley 55.

Endemic to Annobon. Wrigley's plant is practically a topotype. The holotype, Mildbraed 6538 (Herb. Berlin), has been destroyed.

**Ricinus communis** L.—Exell, Cat.: 301.

**Annobon**: Ambo village, 15 m., pathside, 15 July 1959, Wrigley 41.

New record for Annobon. Probably introduced.

**Moraceae**

**Artocarpus communis** J. R. & G. Forst.—G. Taylor in Exell, Cat.: 304.

**Annobon**: Near Ambo, 6 m., waste ground near sea, not seen to regenerate, 18 Aug. 1959, Wrigley 292.


*Artocarpus integer* sensu G. Taylor in Exell, Cat.: 304.

**Annobon**: Near highest point of Crater, 480 m. (also one sterile specimen on shore of Lake), forest, edge of clearing, 26 July 1959, Wrigley 91.
New record for Annobon; recorded for Principe and S. Tomé under the name *A. integer*. Introduced. Jack Fruit.

The name *A. integer* (Thunb.) Merr. applies to a different species (cf. Jarrett, tom. cit.: 329).

**URTICACEAE**

*Urera cameroonensis* Wedd.—G. Taylor in Exell, Cat.: 312.

**Annobon**: Common all over the Island in forest, forest scrambler, often forming lianes, 31 July 1959, Wrigley 223.

New record for Annobon.

**ORCHIDACEAE**

(By V. S. Summerhayes)


**Annobon**: South of Crater Lake and east of Quioveo (Pico del Centro), 450 m., humus below trees with locally sparse fern flora on ground, 1 Aug. 1959, *Melville 213* (Herb. Kew).

New record of the genus *Epipogium* R. Br. for the islands. *E. roseum* is widely but sporadically distributed in tropical Africa (Ghana, Cameroons, Fernando Po, Congo, Angola, Uganda), Indo-Malaysia, Australia and New Hebrides.

**Platylepis glandulosa** (Lindl.) Reichb. f.—Dandy in Exell, Cat.: 319.—Exell, Suppl.: 47.

**Annobon**: South of Santa Cruz (also Crater Lake, N.E. side), under forest, 24 July 1959, *Melville 184* (Herb. Kew).

New record for Annobon. The species extends from tropical Africa into Natal.


*Corymborkis welwitschii* (Reichb. f.) Kuntze.—Dandy in Exell, Cat.: 320.


New record for Annobon. The species is recorded for S. Tomé and is generally distributed in tropical Africa, extending into Natal and eastern Cape Province; it also occurs in Madagascar and Réunion.

**Liparis welwitschii** Reichb. f. in Flora 48 : 184 (1865).


New record for the islands. Also in Angola.
Polystachya Ridleyi Rolfe.—Dandy in Exell, Cat.: 323.

Annobon: South of Crater Lake, 510 m., epiphytic on Coffea trees in particular, 14 July 1959, Melville 154 (Herb. Kew).

New record for Annobon. Hitherto believed to be endemic to S. Tomé.


Bulbophyllum melanorrhachis Reichb. f., loc. cit. (1875), nom. syn.

Annobon: Ridge west of Crater Lake, 510 m., epiphyte, 14 July 1959, Wrigley 31 (Herb. Kew).

New record for the islands. Also on the mainland of West Africa from Guinea to Nigeria, Gabon and Congo.


Angraecum talbotii Rendle, Cat. Pl. Talbot: 108, t. 15 figs. 6, 7 (1913).

Annobon: Ridge west of Crater Lake, 510 m., epiphyte, 14 July 1959, Wrigley 33 (Herb. Kew).

New record of the genus Bolusiella Schlechter for the islands. B. talbotii occurs on the mainland of West Africa from Sierra Leone to Nigeria.

Amaryllidaceae


Annobon: Mission, Ambo, 15 m., garden, 4 Aug. 1959, Melville 234.

New record of the genus Hymenocallis Salisb. for the islands. H. littoralis is introduced into West Africa from tropical America.

Dioscoreaceae

Dioscorea alata L.—Dandy in Exell, Cat.: 344.—Exell, Suppl.: 49.

Annobon: Ambo, path to San Pedro, 24 m., cassava plantation, 22 Aug. 1959, Melville 308.

New record for Annobon. Introduced.

Dioscorea cayenensis Lam.—Dandy in Exell, Cat.: 345.—Exell, Suppl.: 49.

Annobon: Ambo, south of the Governor’s house, near footpath, 10 July 1959, Wrigley 2. South of Santa Cruz, 420 m., openings for cultivation, common, scrambling, 7 Aug. 1959, Wrigley 247.

New record for Annobon.

Dioscorea dumetorum (Kunth) Pax.—Dandy in Exell, Cat.: 345.—Exell, Suppl.: 49.
ANGIOSPERMS OF ANNOBON ISLAND

**Annobon:** South of Ambo, towards Pico do Fogo, 135 m., climber, 10 July 1959, Melville III. North of Santa Cruz, on coast path, 45 m., opening in forest, climber, 8 Aug. 1959, Wrigley 253.

New record for Annobon.

**LILIACEAE**

*Convallaria fruticosa* L., Herb. Amboin.: 16 (1754).

**Annobon:** Santa Cruz and near Quioveo, 420 m., forest near path, 17 July 1959, Wrigley 48.

New record of the genus *Convallaria* Commers. ex Juss. for the islands. *C. fruticosa* is a native of south-east Asia, introduced into tropical Africa and America.


**Annobon:** Ambo, near the Mission, 15 m., cultivated ground, 22 Aug. 1959, Wrigley 309.

New record for Annobon. Native of tropical Africa; introduced into other parts of the tropics. Species of *Sansevieria* (unnamed) have been introduced into S. Tomé (cf. Dandy in Exell, Cat.: 347) but none is reported from Principe.

**COMMELINACEAE**


*Buforrestia imperforata* C. B. Clarke.—Dandy in Exell, Cat.: 347.

The genus *Stanfieldiella* Brenan has recently been separated from *Buforrestia* C. B. Clarke (cf. Brenan, tom. cit.: 280). *S. imperforata* var. *imperforata* is recorded from Principe and S. Tomé.

**Commelina benghalensis** L., Sp. Pl. 1: 41 (1753).

**Annobon:** San Pedro, 15 m., streamside, 2 Aug. 1959, Wrigley 228.

New record for the islands. Widely distributed in tropical and subtropical regions of the Old World.

**ARACEAE**


**Annobon:** Above Crater Lake, 360-480 m., open woodland, probably planted, 16 July 1959, Wrigley 44.

New record of the American genus *Xanthosoma* Schott for Annobon. *X. sagittifolium* is introduced into tropical Africa from tropical America where it is cultivated for its edible tubers.
ANGIOSPERMS OF ANNOBON ISLAND

CYPERACEAE


Principina grandis Uitt.—Dandy in Exell, Cat.: 355.

Koyama (loc. cit.); in his recent new arrangement of the family Cyperaceae, has included Principina Uitt. in Hypolytrum Rich. Principina was previously regarded as a monotypic genus endemic to Principe.]


Remirea maritima Aubl.; non Cyperus maritimus Poir.—Dandy in Exell, Cat.: 356.—Exell, Aditam.: 87.


Recorded for Principe and Annobon, but not collected by the Cambridge Expedition.

Remirea Aubl. is included in the large genus Cyperus L. by Kern (loc. cit.) and by Koyama (Journ. Fac. Sci. Univ. Tokyo, Sect. 3, 8: 72 (1961)).

GRAMINEAE

(By W. D. Clayton)

Bambusa vulgaris Schrad. ex Wendl.—Dandy in Exell, Cat.: 365.

Annobon: Crater Lake, south side, 265 m., lakeside vegetation, near clearing in forest, 12 Aug. 1959, Melville 276.

New record for Annobon. Introduced.

Panicum brevifolium L.—Dandy in Exell, Cat.: 370.


New record for Annobon.

Oplismenus hirtellus (L.) Beauv.—Dandy in Exell, Cat.: 373.—Exell, Suppl.: 51.

Annobon: Path to Quioveo (Pico del Centro), just above north end of Crater Lake, 300 m., pathside in wood, 18 July 1959, Melville 163.

New record for Annobon.

Paspalum commersonii Lam.—Dandy in Exell, Cat.: 375.


New record for Annobon.

Paspalum conjugatum Berg.—Dandy in Exell, Cat.: 375.

Annobon: Near Ambo, 30 m., streamside, 12 July 1959, Wrigley 28.

New record for Annobon.

Anthephora cristata (Doell) Hack. ex De Wild. & Dur.—Exell, Suppl.: 52.

Annobon: N.E. coast near Ambo, 24 m., pathside in cassava plantation, 21 July 1959, Melville 171.

New record for Annobon.
**Beckeropsis laxior** W. D. Clayton, sp. nov.; affinis *B. nubica* (Hochst.) Fig. & De Not. sed differt ramulis laxioribus subglabris, spiculis acuminatis, glumis superioribus longioribus, lemmatibus spinuloso-hipsidulis. (Holotype in Herb. Kew from Nigeria: Summit of Orosun, Idanre Hills, *Keay FHI 22678.*)

*Beckeropsis nubica* sensu Dandy in Exell, Cat.: 378.

**Annobon:** S.W. side of Pico do Fogo, 390 m., bare soil after burning, 25 July 1959, *Melville 191.*

New record for Annobon. Also in S. Tomé and on the mainland of West Africa from Ghana to Cameroons.

**Pennisetum polystachion** (L.) Schult.—Dandy in Exell, Cat.: 378.—Exell, Aditam.: 89.

**Annobon:** Ambo, by the expedition’s houses, 15 m., waste ground, common, 13 July 1959, *Melville 139.*

New record for Annobon.

**Schizachyrium brevifolium** (Swartz) Nees ex Buse in Pl. Junghuhn.: 359 (1854).


**Annobon:** N.W. of the Island, 15 m., cassava plantation, 11 July 1959, *Melville 128.*

New record of the genus *Schizachyrium* Nees for the islands. *S. brevifolium* is widespread in the tropics.

**Cymbopogon citratus** (DC.) Stapf.—Dandy in Exell, Cat.: 380.

**Annobon:** Ambo, just north of the expedition’s houses, *fide* Melville (no specimen collected).

New record for Annobon. Introduced.

**Coix lacryma-jobi** L.—Dandy in Exell, Cat.: 381.

**Annobon:** Near Ambo, 24 m., streamside, 12 July 1959, *Wrigley 21.*

New record for Annobon. Introduced.
Turraea glomeruliflora Harms (Mildbraed 6487, holotype)
Maytenus annobonensis (Loes. & Mildbr.) Exell (Wrigley 56, topotype)
Agelaea ovalis Schellenb. (Melville 232, topotype)
Cassipourea annobonensis Mildbr. ex Alston (Mildbraed 6511, holotype)
Tristemma oreothamnos Mildbr. (Wrigley 65, topotype)
Bertiera annobonensis G. Taylor (Wrigley 93, topotype)
Nuxia congesta R. Br. ex Fresen. var. congesta (Mildbraed 6561, holotype of Lachnopylis annobonensis Mildbr.)
Thecacoris annobonae Pax & Hoffm. (Wrigley 92, topotype)
Discoclauxylon pubescens (Pax & Hoffm.) Exell (Wrigley 96, topotype)
Acalypha annobonae Pax & Hoffm. (Wrigley 55, topotype)
A REVISION OF THE GENUS
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P. W. BALL
AND
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BOTANY

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BY

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(University of Liverpool)

Pp. 119-172; 22 Text-figures; Plates 13-15

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), instituted in 1949, is issued in five series corresponding to the Departments of the Museum, and an Historical series.

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This paper is Vol. 3, No. 4 of the Botany series.
A REVISION OF THE GENUS PETRORHAGIA

By P. W. BALL and V. H. HEYWOOD

This revision was undertaken in connexion with the preparatory work for Flora Europaea. The genus Petrorhagia (Tunica auct.) had not been the subject of a recent survey and several interesting problems of generic circumscription required a solution.

The greater part of this study has been based on herbarium material from the institutions listed below. Several species are still known from only a few collections and the scope for field work in this genus is very wide.

Over fifty taxa within the genus have been described at specific level (under Tunica, Gypsophila, Dianthus, etc.). Twenty-five species are recognized in this revision.

Numerous taxonomic and distributional problems remain to be solved, especially in the eastern Mediterranean region where complex variation patterns are evident from the material it has been possible to examine. These patterns bear some resemblance to the kind described by Ehrendorfer (1958) as Fossil Hybrid Complexes in his studies on Galium sect. Jubogalium. Much further factual information is needed, however, before the possible evolutionary relationships of the species of Petrorhagia can be outlined.

The species and subspecies are delimited in this revision in a morphological-geographical sense (cf. Heywood, 1958).

We wish to acknowledge with gratitude the kindness of the Directors or Curators of the following Herbaria for allowing us to borrow or consult their material (the abbreviations are those used in the citation of specimens). Our thanks are due also to Mr. J. E. Dandy for his assistance with several points of nomenclature.

BM = British Museum (Natural History).
CGE = Botany School, University of Cambridge.
E = Royal Botanic Garden, Edinburgh.
FI = Herbarium Universitatis Florentinae, Florence.
K = Royal Botanic Gardens, Kew.
LIVU = Hartley Botanical Laboratories, University of Liverpool.
W = Naturhistorisches Museum, Vienna.
W-HAL = Halácsy Herbarium, Naturhistorisches Museum, Vienna.
W-RECH = Rechinger Herbarium, Naturhistorisches Museum, Vienna.

1Only a selection of material has been cited under Petrorhagia saxifraga, P. prolifera and P. velutina.
(1) **Habit and duration.**

All species of *Petrorhagia* are herbaceous—either annual or perennial, the latter often more or less caespitose and woody at the base, with non-flowering rosettes. Annual species occur in Sect. *Pseudotunica* subsect. *Creticae*, Sect. *Pseudogypsophila*, Sect. *Dianthella* and Sect. *Kohlrauschia*, while perennial species make up Sect. *Pseudotunica* subsect. *Illyricae* and Sect. *Petrorhagia*. The annual habit was one of the characters employed to separate *Kohlrauschia* as a genus from *Tunica* auct. but as noted elsewhere it is also found in other sections.

The stems range from simple, unbranched, through slightly branched to much branched.

(2) **Leaf venation.**

The number of veins in the leaves ranges from one to five. This number is usually constant for a species and throughout certain sections such as Sect. *Pseudotunica*. On the other hand the leaves in Sect. *Petrorhagia* have from one to five veins, variation even occurring within a single species.

(3) **Inflorescence.**

The inflorescence is extremely variable in the genus, although it is often constant within a section or subsection. The inflorescence is basically a dichasium, but in some species it is very condensed, so that the flowers are fasciculate, while in Sects. *Dianthella* and *Kohlrauschia* and Sect. *Petrorhagia* subsect. *Thessalae* a capitulum is formed with large outer bracts enclosing the rest of the inflorescence.

In addition to the bracts associated with branches of the inflorescence a few species always have two or more pairs of "epicalyx bracts" inserted just beneath the calyx of each flower and more or less enclosing it. These are most easily seen in *P. saxifraga*. In species with a fasciculate or capitate inflorescence it is not always possible to decide whether such epicalyx bracts are present or not. It must be emphasized that these structures are not epicalycine in nature since they do not form part of the calyx proper.

The consistency and colour of the bracts vary from membranous to coriaceous and from colourless to brown or purple, and the shape from lanceolate to suborbicular.

(4) **Calyx.**

The calyx is 5-toothed, and varies from obconic to cylindric in shape, and is usually thin and membranous. Each tooth has 1 or 3 (rarely more) veins associated with it, forming a costa of the calyx; there are 5 costae altogether. Between each pair of costae is a thin membranous, veinless commissure. In Sect. *Dianthella* the costae are very broad and often meet laterally so that the commissures are more or less absent (Figs. 19, 20).

The central vein of each costa is usually quite distinct but, in those species with 3 veins, the laterals are sometimes very weak and indistinct. The number of veins is sometimes constant within a section (e.g. Sect. *Kohlrauschia*), but may vary within a single species (e.g. *P. illyrica*).
There are two main types of calyx teeth in the genus. The first, found in Sects. *Pseudotunica*, *Pseudogypsophila* and *Dianthella* and in two species of Sect. *Petrorphagia*, has a strong central vein reaching the apex of the tooth and often forming a mucro. The second, found in Sect. *Kohlrauschia* and the rest of Sect. *Petrorphagia*, has all the veins disappearing beneath the apex of the tooth, the apex usually being obtuse. *P. fasciculata*, in Sect. *Petrorphagia*, is somewhat intermediate between these two types, with a central vein scarcely reaching the apex of a subacute tooth.

(5) Petals.

The petals of most species are linear- or oblong-oblong-oblanceolate with an entire rounded apex and without a distinct claw. Sect. *Kohlrauschia* is unusual in that the petals have a distinct long claw and usually an obcordate limb, although *P. glumacea* var. *glumacea* has a deltate limb with an irregularly toothed apex. However, the species of Sect. *Petrorphagia* subsect. *Thessalae* have more or less distinctly clawed petals, with a small elliptic-orbicular limb, while some species in Sect. *Petrorphagia* subsect. *Saxifragae* have obcordate petals which are not distinctly clawed. One or two species in other sections also have retuse or shortly 2-lobed petals while *P. hispidula* has 4-lobed petals.

(6) Seeds.

The seed structure is identical with that found in *Dianthus* and *Velezia* and it appears to be unique within the family. The embryo is straight and the seeds are dorsiventrally compressed usually with incurved or thickened margins, the hilum being situated in the centre of the concave surface. There is considerable variation within the genus but two main types can be recognized. One is found only in Sect. *Pseudotunica*, which has relatively large seeds (usually c. 2 mm. long or longer) which have thin margins. They are black when mature and almost smooth. The remaining sections have usually smaller seeds (0.8–1.5 mm. long) with distinctly thickened margins. They are dark or blackish-brown when mature, and distinctly reticulate or tuberculate or even papillose on the convex surface. In Sect. *Pseudotunica*, *P. lycica* and *P. candica* are somewhat intermediate between the two extremes.

(7) Cytology.

The following chromosome counts have been recorded in *Petrorphagia*:

**Sect. Petrorhagia**

*P. saxifraga*  \(2n = 60\)  cf. Löve & Löve (1961)

**Sect. Pseudogypsophila**

*P. alpina* subsp. *olympica*  \(2n = 30\)  cf. Darlington & Wylie (1955)

**Sect. Kohlrauschia**

*P. nanteuilii*  \(2n = 60\)  cf. Löve & Löve (1961); Ball & Heywood (1962)

*P. prolifera*  \(2n = 30\)  cf. Löve & Löve (1961); Ball & Heywood (1962)

*P. velutina*  \(2n = 30\)  cf. Darlington & Wylie (1955); Ball & Heywood (1962)
The number for *P. velutina* has been confirmed in material from Greece, and this also possesses the short chromosome noticed by Böcher et al. (1953) in material from Portugal. The difficulty of obtaining seed of most other species has prevented any further cytological study of the genus. The basic number is \( x = 15 \) as in *Dianthus*, but different from *Gypsophila* where according to Barkoudah (1962) it is \( x = 17 \) or 18. Polyploidy occurs in Sect. *Kohlrauschia*, cf. Böcher et al. (1953, 1955), Ball & Heywood (1962), and it may also occur in other parts of the genus, especially in the eastern Mediterranean region where a considerable degree of hybridization is occurring or has occurred in the past.

(8) *Experimental studies.*

Studies on the variation and physiological responses of samples of *P. prolifera*, *P. velutina* and *P. nanteuilii* grown from seed of various provenances have been made by Böcher et al. (1953, 1955).

(9) *Ecology.*

The evidence available from collectors' notes on herbarium labels, from Floras and from limited personal observations shows that most species of *Petrorhagia* grow in dry, sandy or calcareous habitats where there is little competition from other species. They may be found in sand, rocky debris, on rocks and cliffs, detritus, roadsides, walls, dry grassland, etc. *P. alpina* subsp. *olympica* frequently occurs in montane coniferous woodland, sometimes at the sides of streams, so it would appear that at least this subspecies prefers a relatively moist and shaded situation.

(10) *Geographical distribution.*

The genus occurs mainly in the eastern Mediterranean region and south-eastern Europe, extending west to Madeira and the Canaries (one species) and east to Pakistan and Kashmir (one species). A few species occur in North Africa. With the exception of *P. saxifraga*, *P. prolifera* and *P. nanteuilii*, the genus is absent from east, west, central and north Europe.

The greatest concentration of species occurs in Greece and Turkey with 12 and 9 species respectively. Eight species or subspecies are endemic to Greece and neighbouring Aegean islands, two to Crete, four to Turkey, one to Iran, one to Cyprus and three to North Africa.

There are four widespread species in the genus—*P. saxifraga*, which occurs throughout much of central and southern Europe and extends into south-west Asia; *P. prolifera*, which is distributed in central Europe and in the mountains of southern Europe, the Caucasus, northern Anatolia, and in those of western North Africa; *P. velutina*, which is widespread in the Mediterranean region; and *P. alpina*, which is found in the mountains of central and western Asia, extending to southern Bulgaria.

**Relationships and delimitation of *Petrorhagia* within the Silenoideae**

A survey of the relationships of *Gypsophila* and segregate genera and their distinction from *Tunica* (i.e. *Petrorhagia*) is given in Barkoudah's recent revision (1962). As noted there, Linnaeus included two species of *Tunica* in his treatments
of Gypsophila, possibly failing to distinguish between the two groups on account of the numerical basis of his Sexual System. Haller (Enum. Stirp. Helv. 1: 381 (1742); Hist. Stirp. Helv. 1: 39 (1768)) "made the boundaries between Gypsophila and Tunica sufficiently clear", as Barkoudah says, but in fact Haller was using the name Tunica in the sense of Dianthus.

Linnaeus (Sp. Pl., 1753) included two species of Petrorhagia in Dianthus—D. saxifragus (=P. saxifraga) and D. prolifer (=P. prolifera), and a further one in Gypsophila—G. rigida (=P. saxifraga var. glomerata). In 1759 (Syst. Nat., ed. 10) he transferred D. saxifragus to Gypsophila. Linnaeus (1763 and 1767) and Arduino (1764) described two further species (P. cretica and P. illyrica) under Saponaria. A number of other species were subsequently described under Gypsophila or Dianthus, but the genus Tunica was not recognized as independent until Mertens & Koch (1831) and Fischer & Meyer (1837) redefined it, at the same time misapplying the name. These latter authors included in Tunica all the species of Petrorhagia known at that time, except for those of Sect. Kohlruschia which were still retained in Dianthus. Kunth (1838) subsequently separated Kohlruschia from Dianthus as a distinct genus. Boissier in his Flora Orientalis reviewed all the known species and concluded that Kohlruschia was best united with Tunica and his view was followed by Bentham in Benth. & Hook., Gen. Pl. 1: 145 (1862), by Pax (in Engler & Prantl, Nat. Pflanzenfam. 3 (1b): 76 (1889)) and by Pax & Hoffmann (in Engler & Prantl, op. cit., ed. 2, 16c: 355 (1934)). Most modern European Floras, however, still recognize Kohlruschia and Tunica as distinct genera, but only one of these, Hayek (Prodr. Fl. Penins. Balcan. 1: 221–224 (1924)), treats of more than three or four species. This is an interesting example of the role of historical and local influences affecting taxonomic treatment.

As circumscribed in this revision Petrorhagia is more or less intermediate in most of the taxonomically significant characters between Dianthus and Gypsophila. It resembles Gypsophila in the following features:

(1) the calyx nearly always with membranous veinless commisses between the teeth;
(2) the calyx usually 5- or 15-veined;
(3) the flowers sometimes ebracteate;
(4) the petals usually not clawed;
(5) in inflorescence and general appearance (Sects. Pseudotunica and Pseudogypsophila).

In the following characters it resembles Dianthus:

(1) calyx rarely more or less without membranous commisses (Sect. Dianthella);
(2) calyx rarely 25- to 35-veined (Sect. Dianthella);
(3) flowers sometimes bracteate;
(4) petals sometimes clawed and with a broad limb (Sect. Kohlruschia);
(5) in inflorescence and general appearance (Sect. Kohlruschia);
(6) seed structure—seed compressed dorsiventrally with the embryo straight, lying lengthwise in the middle, not compressed laterally with the embryo curved and peripheral.
There is no doubt, however, of the much closer relationship on general grounds of *Petrorhagia* to *Dianthus* than to *Gypsophila*. Of the characters listed above only one, the seed structure, is constant and reliable. In all the features in which *Petrorhagia* resembles *Gypsophila* there is an intergradation with the opposing *Dianthus* character. Thus in characters (1) and (2) the membranous commissures are virtually absent in *P. pamphylica* while the same species has 5 or 7 veins to each costa. This species is linked to the rest of the genus through *P. peroninii*. In character (4) Sect. Kohrauschia has a distinct long claw with a broad limb, Sect. *Petrorhagia* subsect. Thessalae has a long, more or less distinct claw but a small limb, while in Sect. *Petrorhagia* subsect. Saxifragae some species (e.g. *P. graminea*) have petals with a broad limb but virtually no claw. There is thus almost a complete range from the *Gypsophila* type of petal found in Sects. *Pseudotunica*, *Pseudogypsophila*, *Dianthella* and part of Sect. *Petrorhagia* to the *Dianthus* type found in Sect. Kohrauschia.

Characters (3) and (5) are more complex. *Gypsophila* normally has a large, much-branched panicle with numerous small flowers, sometimes aggregated into small heads or fascicles. All the bracts are usually small and are only associated with branches of the inflorescence. *Dianthus*, on the other hand, usually has a little-branched inflorescence with the flowers solitary, fasciculate or capitate at the tips of the stems. It frequently has large brown scarious bracts surrounding solitary flowers or fascicles or capitula. Both situations are found in *Petrorhagia*. Sects. *Pseudotunica* and *Pseudogypsophila* and Sect. *Petrorhagia* subsect. *Saxifragae* closely resemble *Gypsophila*. However, *P. saxifraga* in Sect. *Petrorhagia* subsect. *Saxifragae* has bracts at the base of solitary flowers, and which are clearly not associated with branches of the inflorescence. The *Dianthus* situation is found in Sect. Kohrauschia which is almost unbranched with terminal heads of flowers surrounded by large brown scarious bracts. The remaining two groups, Sect. *Dianthella* and Sect. *Petrorhagia* subsect. Thessalae, are more or less intermediate between the two extremes. Sect. *Dianthella* has numerous brown or purplish scarious bracts surrounding one or a few flowers, although the stems are normally much branched. Sect. *Petrorhagia* subsect. Thessalae has little-branched stems with small terminal capitula. The bracts are usually relatively small and membranous except for a stout mid-vein, but in one species, *P. thessala*, they tend to be larger and broader with a broad brown scarious region.

It will be seen from this survey that a clear assessment of the affinities of the genus can only be obtained from the complex of characters referred to as the seed structure. Here there is no gradation with the *Gypsophila* type. Seed structure, in fact, distinguishes *Petrorhagia*, *Dianthus* and *Velezia* from all other genera of the subfamily Silenoideae. This fact lends strong support to the grouping of these three genera together into a distinct subtribe as is done by Bentham (in Benth. & Hook., Gen. Pl. 1: 142 (1862)) rather than to the arrangement of Pax (1889) and Pax & Hoffmann (1934), in which *Tunica* is placed with *Gypsophila* and *Dianthus*, and *Velezia* with *Saponaria* and *Vaccaria*.

The distinction between *Petrorhagia* (*Tunica*) and *Velezia* was discussed fully
by Davis (1957). The inclusion of Kohlrauschia within Petrorhagia does not substantially alter any of Davis's arguments or conclusions.

The characters by which Kohlrauschia, when treated as a separate genus, is usually separated from Petrorhagia (Tunica) are as follows:

1. annual;
2. inflorescence a capitulum;
3. petals with a long claw and a distinct, broad limb.

Annuals are found in three other sections of Petrorhagia while the unreliability of the remaining two characters has been discussed above. If Sect. Kohlrauschia is treated as a distinct genus, then there can be little justification for not treating Sects. Dianthella and Pseudotunica as distinct genera as well.

The expressions of the more important sectional characters throughout the genus are shown in the accompanying table. The sections are relatively distinct although the position of two species, P. kennedyae and P. phthiotica, is still not clear. This is discussed more fully under the species in question.
<table>
<thead>
<tr>
<th>Seeds</th>
<th>small, blackish-brown, tuberculate, with thickened margin</th>
<th>large, black, smooth, with thin margin</th>
<th>small, blackish-brown, reticulate-tuberculate, with thickened margin</th>
<th>small, blackish-brown, reticulate to papillose, with thickened margin</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inflorescence</td>
<td>paniculate, fasciculate or capitate</td>
<td>paniculate or fasciculate</td>
<td>paniculate</td>
<td>paniculate</td>
</tr>
<tr>
<td>Number of veins in the calyx</td>
<td>$1 \times 5$ or $3 \times 5$</td>
<td>$1 \times 5$ or $3 \times 5$</td>
<td>$1 \times 5$</td>
<td>$3 \times 5$ or $5-7 \times 5$</td>
</tr>
<tr>
<td>Bracts below calyx</td>
<td>present or absent</td>
<td>absent</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Petals</td>
<td>not clawed</td>
<td>not clawed</td>
<td>not clawed</td>
<td>clawed</td>
</tr>
<tr>
<td>Duration</td>
<td>perennial</td>
<td>annual</td>
<td>annual</td>
<td>annual</td>
</tr>
<tr>
<td>Section</td>
<td><em>Petrorhagia</em></td>
<td><em>Pseudotoma</em></td>
<td><em>Pseudopygospithila</em></td>
<td><em>Kohlrauschia</em></td>
</tr>
</tbody>
</table>

**PETRORHAGIA** (Ser.) Link


*Imperatia* Moench, Meth. Pl. : 60 (1794) ; non *Imperata* Cyr. (1792).


*Dianthus* sect. *Tunica* (Reichb.) Fenzl, loc. cit. (1840).


*Dianthella* Clauson ex Pomel, Mat. Fl. Atlant. : 9 (1860).


Type : *P. saxifraga* (L.) Link.

Annual or perennial herbs, sometimes with a woody stock. Leaves opposite, subulate to oblance, 1–3(-5)-veined, entire or the margin minutely serrulate. Inflorescence a dichasial cyme, with the flowers solitary, fasciculate, or capitate; bracteate or ebracteate, sometimes with decussate bracts surrounding the calyx (epicalyx bracts). Calyx obconic to cylindric, 5-toothed, each tooth with 1 or 3 (rarely up to 7) veins and usually with broad membranous veinless commissures between the teeth. Petals 5, clawed or not, the apex entire to bifid, rarely 4-lobed or irregularly toothed; without coronic scales. Stamens 10. Styles 2. Capsule opening by 4 apical teeth. Seeds numerous, dorsiventrally compressed, scutate; embryo excentric, straight.

The genus *Petrorhagia* as interpreted in this revision includes the species previously included by most authors in the genera *Tunica* and *Kohlrauschia*. A wide circumscription, similar to the one adopted here, was first used by Boissier, Fl. Or. 1 : 516–523 (1867).

The name *Tunica* has been attributed variously to Haller, Scopoli and Koch. It was in fact first validly published by Ludwig, Inst. Reg. Veg., ed. 2 : 129 (1757), as an illegitimate substitute for *Dianthus* L. (see Dandy, 1957). Haller (1768) and Scopoli (1772) also used *Tunica* as a replacement for *Dianthus*, all the species recognized by these authors being originally described by Linnaeus under *Dianthus*.

Mertens & Koch (1831) appear to have been the first authors to treat *Tunica* as a genus distinct from *Dianthus*. They recognized only one species, *T. saxifraga* (L.) Scop. Subsequent authors, e.g. Boissier (1867) and Williams (1890), followed Mertens & Koch’s misuse of the name *Tunica*, although Williams himself quite clearly states that *Tunica* of Scopoli is a replacement for *Dianthus*. Janchen (1963) likewise proposes acceptance of *Tunica* of Scopoli as emended by Koch, but even if this were possible the name would still be a later homonym of *Tunica* Ludwig, itself a synonym of *Dianthus*. Maire (1963) goes further and cites ‘‘*Tunica*’’ Boehm.
in Ludw. (1760), nom. abort., emend. Mert. et Koch (1831)" as a nomen conservandum, but as far as we are aware no such proposal has been made.

The typification of *Petrorrhagia* requires some consideration. Link placed under it four species, *P. glomerata*, *P. multicaulis*, *P. rigida* and *P. saxifraga*. *P. glomerata* is currently treated as a *Gypsophila*, the remaining species being referred to *Tunica* or *Kohlrnauschia*. It is therefore necessary to typify the name *Petrorrhagia* since Link himself indicated no type. Link's genus is based, by implication, on *Gypsophila* sect. *Petrorrhagia* Ser. in DC., Prodr. 1: 354 (1824). He did not directly cite Seringe or De Candolle, but his genus contains the same species as Seringe's section, except for *G. dianthoides*, which Seringe cited with a question mark. Accordingly we have to typify *Gypsophila* sect. *Petrorrhagia* Ser. The definition given by Seringe is "Calycis squamis scariosis 2–4 oppositis basi instructi". This agrees well with *G. saxifraga* which normally has 2 opposite pairs of bracts inserted just below the calyx and more or less completely enclosing it. Seringe again refers to these bracts in the description of this species, and a further point, which clearly indicates that Seringe regarded it as typical, is that "petorrhagia" is a simple translation into Greek of "saxifraga". The typification of *Petrorrhagia* by *P. saxifraga* was proposed by Britton & Brown (Ill. Fl. N. U.S. & Can., ed. 2, 2: 72 (1913)) and there seems no good reason to reject it.

Dandy (1957), unaware of the previous typification by Britton & Brown, proposed *Gypsophila glomerata* as the type of Sect. *Petrorrhagia* Ser. and consequently of Link's generic name. In *G. glomerata* there is sometimes a pair of opposite bracts towards the base of the pedicel of the lateral flowers of a partial dichasium, but they are always clearly separated from the base of the calyx by a length of pedicel, and the central flowers never have such bracts. This interpretation of the structure of *G. glomerata* agrees with the inflorescence diagram given by Barkoudah (1962) in fig. 1 of his revision of *Gypsophila*. In our view the bract situation in *G. saxifraga* agrees better with Seringe's definition than does that of *G. glomerata*. Barkoudah, apparently following Dandy, gives *Petrorrhagia* as a synonym of *Gypsophila*. This according to our view is not correct, except in so far as *P. glomerata* is concerned.

**Key to the Species**

Bracts enclosing the calyx; inflorescence often capitate-fasciculate:

Petals with a long distinct claw and a broad obcordate or obdeltate limb, pink or purplish; largest bracts usually at least 4 mm. broad:

Seeds not more than 1.3 mm. long, papillose; leaf sheaths at least twice as long as broad    24. *P. velutina*

Seeds at least 1.3 mm. long, reticulate to tuberculate; leaf sheaths not more than twice as long as broad:

Petal-limb crenate or lacinate; seeds 1.7–2.2 mm. long, almost smooth or sparsely tuberculate    25. *P. glumacea*

Petal-limb obcordate; seeds 1.3–1.8 mm. long, reticulate or tuberculate:

Seeds reticulate    22. *P. prolifera*
Seeds tuberculate:
Outermost bracts of the head mucronate (western Europe and western
North Africa) . . . . . . 23. P. nanteuilii
Outermost bracts obtuse (Balkan peninsula) . . 25. P. glumacea
Petals not distinctly clawed or if clawed then with a small elliptic limb, white or
pink; largest bracts usually less than 4 mm. broad:
Leaves 3-veined; annual, rarely perennial:
Bracts 1-veined; perennial . . . . . . 12. P. fasciculata
Bracts 3- to many-veined; annual:
Costae of calyx 5- to 7-veined; seeds 1.6-2 mm. long, 1.2-1.7 mm. broad .
Costae of calyx 3-veined; seeds 1.1-1.2 mm. long, 0.7-0.9 mm. broad .
Leaves 1-veined or obscurely veined; perennial:
Flowers solitary or fasciculate; bracts and epicalyx bracts distinctly shorter
than the calyx; stems usually much branched:
Stems glandular-pubescent at least at the base; calyx teeth more or less
triangular, acute or subobtuse . . . . . 12. P. fasciculata
Stems eglandular; calyx teeth oblong, obtuse . . 13. P. saxifraga
Flowers capitate; bracts more or less completely enclosing the calyx:
Calyx teeth more or less triangular, acute (Crete) 19. P. dianthoides
Calyx teeth oblong, obtuse:
Petals white with pink or purple veins; outer bracts brown-scarious
with white-membranous margin . . . . 16. P. thessala
Petals white without coloured veins; outer bracts almost entirely
white-membranous:
Stems glabrous or papillose-scarbid at the base; largest bracts
1.5-2.5 mm. broad; petals 5.5-8 mm. long, pale-red on the lower
surface . . . . . . . . . 18. P. macra
Stems pubescent at the base; largest bracts 0.7-1.3 mm. broad; petals
8-9 mm. long, not red on the lower surface . 17. P. cyrenaica
No bracts enclosing the calyx; flowers solitary, rarely a few fasciculate:
Petals emarginate, retuse or 4-lobed at the apex:
Petals 4-lobed . . . . . . . . . . . . . 8. P. hispidula
Petals emarginate or retuse:
Calyx teeth oblong, obtuse; petals usually pink or reddish, or white or
yellow with pink or purple veins:
Basal leaves 8-20 mm. long; petals 1.8-2.5 mm. broad, obcordate, pink,
reddish or white . . . . . . . 14. P. graminea
Basal leaves 4-8 mm. long; petals 0.8-1 mm. broad, pale yellow with
purple veins . . . . . . . . . . . . . 15. P. rhiphaea
Calyx teeth triangular-oblong, more or less acute or mucronate; petals
white, sometimes with pink veins:
Costae of calyx 3-veined (the lateral veins sometimes weak near the apex);
seeds c. 1.5 mm. long, black, smooth . . . 4. *P. candica*
Costae of calyx 1-veined; seeds c. 1 mm. long, blackish-brown, more or less
  tuberculatc . . . . . . . . . 12. *P. fasciculata*

Petals entire:

Annual, without non-flowering rosettes:
Costae of calyx 3-veined; seeds 2–3.5 mm. long, smooth, with thin margin:
  Calyx glabrous; petals included in the calyx or rarely shortly exserted;
    seeds 2–2.8 mm. long . . . . . . . 6. *P. cretica*
  Calyx densely glandular-pubescent; petals distinctly exserted from the
calyx; seeds 2.7–3.5 mm. long . . . . 7. *P. arabica*
Costae of calyx 1-veined; seeds less than 2 mm. long, reticulate-tuberculatc,
  with thickened margin:
  Stem glabrous; petals 3.5–6 mm. long, entire . . . . 9. *P. alpina*
  Stem viscid-glandular at the apex; petals 6–8.5 mm. long, bifid
    10. *P. kennedyae*

Perennial, more or less caespitose and woody at the base, with non-flowering
rosettes:
Costae of calyx 3-veined:
  Lower leaves 15–30 mm. long; petals often purple-spotted at the base;
    seeds 1.8–2.1 mm. long, 1–1.3 mm. broad . . 3. *P. armerioides*
  Lower leaves 10–15 mm. long; petals purple-veined on the lower surface;
    seeds 1.5 mm. long, 0.5 mm. broad . . . . . . . . 5. *P. lycica*
Costae of calyx 1-veined:
  Petals pink; seeds blackish-brown, reticulate-tuberculatc
    11. *P. phthiotica*
Petals white or yellow; seeds black, smooth:
  Stem densely glandular-pubescent throughout, or glabrous in the lower
  part, rarely completely glabrous; petals white or pale yellow;
    anthers usually purple . . . . . . . 1. *P. illyrica*
  Stem densely glandular-pubescent at the base, usually glabrous in the
  upper part; petals yellow; anthers white . . . . . . . . . 2. *P. ochrolenca*

Sect. i. *Pseudotunica* (Fenzl) Ball & Heywood

*Petrorhagia* sect. *Pseudotunica* (Fenzl) Ball & Heywood, comb. nov.

*Tunica* sect. *Pseudosaponaria* A. Braun in Flora 26 : 384 (1843), nom. illegit.
*Tunica* sect. *Gypsophiloides* Boiss., Fl. Or. 1 : 519 (1867); non *T.* sect. *Gypsophiloides*
  Griseb. (1843).


Type (lectotype): *Tunica illyrica* (Ard.) Fisch. & Meyer (=*P. illyrica* (Ard.)
Ball & Heywood).
Annual or perennial. Leaves 3-veined. Epicalyx bracts absent. Petals not clawed. Seeds large, black, smooth, with thin margin.

Subsect. a. *Illyricae* Ball & Heywood

*Petrorhagia* subsect. *Illyricae* Ball & Heywood, subsect. nov.; subsectio typica sectionis *Pseudotunicae*, continens species perennes, seminibus 1.5-2.3 mm. longis. Type: *P. illyrica* (Ard.) Ball & Heywood.

Perennial. Seeds 1.5-2.3 mm. long.

1. *Petrorhagia illyrica* (Ard.) Ball & Heywood, comb. nov.


Stem up to 40 cm. high, much branched, densely glandular-pubescent to glabrous. Lower leaves 10-30 mm. long, linear-subulate to linear-oblong, 3-veined. Inflorescence lax or subfastigate. Calyx 3.5-6(-6.5) mm. long, glabrous to densely glandular-pubescent; costae 1- or sub-3-veined; teeth obtuse and mucronate to acuminate. Petals 5.5-10 mm. long, oblong-spathulate, entire, white, rarely pale-yellow, spotted with purple at the base, sometimes with pink veins on the back. Anthers usually purple. Seeds 1.7-2.3 mm. long, 0.9-1.3 mm. broad, margin not thickened.

Distribution: Balkan peninsula, southern Italy (Calabria), Sicily, western North Africa.

1a. *Petrorhagia illyrica* subsp. *illyrica*. (Fig. 1.)

Stem more or less densely glandular-pubescent throughout. Calyx 3.5-5.5 mm. long, densely glandular-pubescent; costae 1-veined. Petals 6-8 mm. long.


Crete: Asprovunna (Levka Ori), 21-22 July 1893, Baldacci 107 (BM; W-HAL). Lasithi, 1899, Baldacci 293 (BM) (? locality correct).

The sheet of *Saponaria illyrica* in the Linnaean Herbarium has two distinct specimens both of which are somewhat anomalous. One is labelled “Ard.” and since it agrees with Arduino’s description and plate it may be regarded as at least
an isotype. It has extremely long pedicels (10–15 mm.), small calyx (c. 4 mm.) with 1-nerved costae, and is densely pubescent throughout. It most closely resembles plants from Sterea Ellas and neighbouring regions of Greece, although the pedicels are exceptionally long.

For discussion of the specimens from Crete see p. 142.

Figs. 1–4. 1, Petrorhagia illyrica (Ard.) Ball & Heywood subsp. illyrica. 2, P. illyrica subsp. haynaldiana (Janka) Ball & Heywood. 3, P. illyrica subsp. taygetea (Boiss.) Ball & Heywood. 4, P. ochroleuca (Smith) Ball & Heywood. a, calyx; b, petal. (All × 5.)

1b. Petrorhagia illyrica subsp. haynaldiana (Janka) Ball & Heywood, comb. nov. (Fig. 2; Plate 13 A.)

Tunica illyrica auct. ital.; non Fisch. & Meyer.
Tunica cretica auct. ital.; non Fisch. & Meyer.
Tunica ochroleuca auct. ital.; non Fisch. & Meyer.
Tunica angustifolia auct. ital.; non Briq.
Tunica compressa auct. ital.; non Fisch. & Meyer.
Stem glabrous in the lower part, or sometimes completely glabrous. Calyx (4·5–5)–6 mm. long, usually glabrous; costae 1-veined. Petals 7–10 mm. long.


**ROMANIA**: Verciorova, Portam ferream, Degen, *Fl. Austro-Hung.* 2863 (BM; K; W-HAL; W-RECH). Inter pagos Verciorova et Gurovoie, 23 July 1887, 10 July 1887, 10 July 1895, *Degen* 19 (BM; E; K; W-HAL); 1887, *F. W. Schultz* 2420 (BM; K). Infra Orsova, 28 June 1870, *Janka* (K; W-HAL; isotypes).


This subspecies is difficult to separate from subsp. *illyrica*. The populations in northern Greece and Macedonia cannot be satisfactorily placed under either subspecies, although here they are included in subsp. *haynaldiana* on the basis of the larger flowers and the stem often glabrous at the base. The populations in Italy and Sicily are similar and are also included here on the generally more robust habit, larger flowers, longer pedicels and the lower part of the stem sometimes glabrous. *Tunica cretica*, *T. ochroleuca*, *T. compressa* and *T. armerioides*, etc. of Italian authors are only minor variants of this subspecies.

**1c. Petrhorhagia illyrica** subsp. *angustifolia* (Poir.) Ball & Heywood, comb. nov.


*Gypsophila compressa* Desf., *Fl. Atlant.* 1: 343 (1798).


*Dianthella compressa* (Desf.) *Pomel, Mat. Fl. Atlant.* 9 (1860).


Indumentum variable, stems usually densely pubescent throughout or glabrous in the lower part. Pedicels strongly compressed (usually more or less terete in all
other subspecies). Calyx 5·5–8 mm. long; costae 1–veined, rarely 3-veined. Petals 8–11 mm. long.


Tunisia: Djebel Zaghouan, 9 July 1854, Krilik (K).

Libya: Garian, 16 Nov. 1948, Johnson 5A (BM); 18 May 1952, Guichard KG/LIB/403 (BM); 24 May 1939, Sandwith 2758 (K). Suani Bin Adem, 10 Nov. 1952, Guichard KG/LIB/5 (BM). Benghazi, Grotta di Lete, 1 Apr. 1939, Sandwith 2221 (K).

A variable subspecies with a range of variation parallel to that found in subspecies illyrica and haynaldiana and in P. armerioides. It can be separated only with some difficulty from subsp. haynaldiana as the reliability of the pedicel character is uncertain.

1d. _Petrorhagia illyrica_ subsp. _taygetea_ (Boiss.) Ball & Heywood, stat. nov. (Fig. 3.)

_Tunica illyrica_ var. _taygetea_ Boiss., Fl. Or. 1: 521 (1867).


Stem more or less densely glandular-pubescent throughout. Calyx 3·5–5 mm. long; costae more or less 3-veined, the lateral veins often very weak. Petals 5·5–7·5 mm. long.


This taxon has had a somewhat disturbed history. It was first distributed by Heldreich as _Tunica cretica_ but Boissier described it as a new variety of _T. illyrica._
Halácsy, *Conspiculus Florae Graecae*, again considered this plant to be identical with *T. cretica*, and appears to have been followed by later authors. Recently Davis showed that the name *T. cretica* had been misapplied by all authors since Fischer & Meyer, and that the Cretan plant required a new name. Unfortunately, Davis followed the majority of authors in regarding Taygetean plants as being identical with Cretan plants.

We cannot agree with Heldreich, Halácsy or later authors that these two populations are identical or even that they should be referred to the same species. If the venation of the calyx is ignored, the Cretan plant still differs from *P. illyrica* and the Taygetean populations by a number of characters and appears to be one of the more distinct species in this critical group (for further discussion see under *P. candica*, p. 141). Here the Taygetean population is regarded as a subspecies of *P. illyrica*, showing some affinity with *P. candica* (cf. the smaller flowers, the feebly 3-veined calyx costae, and the longer pedicels) but clearly distinct from this latter species.

Subsp. *taygetea* forms a fairly distinct unit within *P. illyrica*. It is most readily recognized by the venation of the calyx costae but similar venation occurs in plants of typical *P. illyrica* in Attiki. The other characters are statistical rather than absolute differences, so these Taygetean plants are considered to represent a subspecies rather than a separate species.

2. *Petrorhagia ochroleuca* (Smith) Ball & Heywood, comb. nov.  (Fig. 4.)


Stem up to 30 cm. high, usually much branched, glabrous except for the lowest internodes which are shortly and densely glandular-pubescent, sometimes the middle and upper parts of the stem sparsely glandular-pubescent (plants from Evvoia). Lower leaves 10–25 mm. long, linear, 3-veined. Inflorescence lax; pedicels 4–14 mm. long. Calyx 4.5–5.5 mm. long, glabrous or rarely sparsely glandular; costae 1-veined, sometimes with very feeble lateral veins; teeth acute or acuminate. Petals 5–7 mm. long, linear-oblong, entire, pale-yellow, purplish at the base. Anthers white. Seeds 1.8–2 mm. long, 0.9–1.1 mm. broad, margin not thickened.

Distribution: South-eastern Greece.

Greece: Attiki: Hymettus, Heldreich (BM; E; K; W-HAL); Spruner (K); Halácsy (E; W-HAL). Hymettus, versus Pankrati, 13–14 June 1932, Rechinger fil. 1855 (W-RECH). Parnes, 18 June 1878, Heldreich (W-HAL); 18 July 1911, Tunta 1278 (W-HAL). Parnes, Karavola, 29 June 1930, Guiol 1271 (BM). Evvoia: Inter Psachna et Achmet Aga, 27 May 1955, Rechinger fil. 16509 (W). Limni, 28 May 1955, Rechinger fil. 16675 (W) (ad *P. armerioidem* trans.).

*P. ochroleuca* is very similar to *P. illyrica* and is only doubtfully retained as a distinct species. It can be recognized by a combination of characters (indumentum, flower and anther colour, pedicel length), none of which on its own serves reliably to
distinguish this species from *P. illyrica*. The material collected recently by Rechinger from Evvoia serves only to emphasize the doubtful status of *P. ochroleuca*.

3. **Petrorhagia armerioides** (Ser.) Ball & Heywood, comb. nov.

*Gypsophila armerioides* Ser. in DC., Prodr. 1 : 353 (1824).


Stem up to 30 cm. high, densely glandular-pubescent at the base and apex, usually glabrous in the middle, but sometimes glandular-pubescent throughout (plants from Greek mainland). Lower leaves 15–30 mm. long, linear or linear-oblong, 3-veined. Inflorescence fastigiate or lax with pedicels 1–5 (–9) mm. long. Calyx 4–6 (–6.5) mm. long, densely glandular-pubescent; costae strongly 3-veined; teeth triangular-mucronate or acuminate. Petals 6–8 (–9) mm. long, oblong-spathulate, white, often purple-spotted at the base. Anthers purplish. Seeds 1.8–2.1 mm. long, 1–1.3 mm. broad, margin not thickened.

Distribution: South-eastern Greece, Aegean Islands, ? north-western Turkey.

3a. *Petrorhagia armerioides* var. *armerioides*. (Fig. 5.)


Inflorescence dense, fastigiate; pedicels usually 1–5 mm. long.


3b. *Petrorhagia armerioides* var. *laxa* (Bornm. & Rech.) Ball & Heywood, comb. nov.


Inflorescence lax; pedicels 3–9 mm. long.

REVISION OF THE GENUS PETRORHAGIA


Figs. 5–8. 5, Petrorhagia armerioides (Ser.) Ball & Heywood var. armerioides. 6, P. candida Ball & Heywood. 7, P. lycica (P. H. Davis) Ball & Heywood. 8, P. cretica (L.) Ball & Heywood. a, calyx; b, petal. (All × 5.)

P. armerioides is quite distinct in the Aegean Islands, being distinguished by the 3-veined calyx costae, the indumentum, and the usually short pedicels and dense inflorescence. However, on the mainland of Greece and Evvoia intermediates between this species and P. illyrica or P. ochroleuca, or between all three species, seem to occur fairly frequently. Nearly all the plants from these areas are to some extent intermediate as they are usually pubescent throughout the length of the stem. Plants with lax inflorescence and with feeble lateral veins on the calyx costae also occur occasionally (e.g. prope Athena, Reliquiae Orphanideae). It seems desirable that these populations should be studied in considerable detail, but this must await further extensive collections particularly in Evvoia and Andros and other islands off
the coast of Attiki. When such material is available it may be found necessary to regard *P. armerioloides* and *P. ochroleuca* as subspecies of *P. illyrica*.

The variety which occurs in Chios and Samos is rather unusual, although it appears to differ from typical Aegean plants only in the lax inflorescence. It should not be confused with the long-pedicelled plants occurring on the mainland of Greece and Evvoia which are intermediates between this species and *P. ochroleuca* or *P. illyrica*.

4. *Petrorhagia candica* Ball & Heywood, sp. nov.; inflorescentia laxa pauciflora absque bracteis epicalycinis, calycis costis 3-venosis, petalis emarginatis retussive albis subtus roseo-venosis, seminibus nigris laevibus c. 1.5 mm. longis, facile distinguetur. (Fig. 6.)


Stem up to 20 cm. high, simple or little branched, glabrous or sparsely glandular-pubescent. Lower leaves 10–20 mm. long, linear-subulate, 3-veined. Inflorescence lax, few (1–8)-flowered; pedicels (4–)6–20 mm. long. Calyx (3–)3.5–4.5 mm. long, glabrous or sparsely glandular-pubescent; costae 3-veined, the lateral veins sometimes weak; teeth acute or obtuse-mucronate. Petals 4.5–7 mm. long, oblong-spashulate, retuse or emarginate, white with pink veins on the lower surface. Seeds (slightly immature) c. 1.5 mm. long.

**Distribution:** Crete.


As recently pointed out by Davis (1957), *Saponaria cretica* L. is the species described by Fischer and Meyer as *Tunica pachygona* and not the plant commonly called *T. cretica*.

Unfortunately we cannot agree with Halácsy (Consp. Fl. Graec. 1 : 194 (1900)) or Davis that *Tunica cretica* auct. is identical with *T. illyrica* var. *taygetea* or that they can be included within the same species, so it is necessary to treat this Cretan plant as a new species.

*P. candica* can be readily recognized by the emarginate or retuse petals, the 3-veined calyx costae, longer pedicels and relatively sparse indumentum. The cauline leaves tend to be shorter and there are more pairs per unit length than in other species of this section. This, combined with a lesser degree of branching, gives the plant a strict appearance not found elsewhere in the section.
With some justification Davis minimizes the importance of 3-veined calyx costae, but his statement that "botanists seem to have been hypnotised into seeing them [3-veined costae] in T. cretica auct." is not correct. Nor is his statement that Rechinger in *Flora Aegeae* keys out *T. cretica* auct. as having 1-veined costae. The lateral veins are sometimes feeble, but never completely absent.

All the material seen from Crete has proved to be *P. candica* while all "*Tunica cretica*" from other areas is referable to other species. The only exception to this is *Baldacci, Iter Creticum* 107, which seems to be *P. illyrica* subsp. *illyrica*. The plants from this collection are all rather small and the three sheets seen are all very similar, so that there seems little likelihood of an error. Further investigation at this locality is desirable. A second collection by Baldacci, *Iter Creticum Alterum* 293, is probably wrongly labelled.

5. *Petrothagia lycica* (P. H. Davis) Ball & Heywood, comb. nov. (Fig. 7; Plate 13 b.)


Stem 10–20 cm. high, branched in the upper part, densely glandular-pubescent. Lower leaves 10–15 mm. long, linear to linear-spathulate, 3-veined. Inflorescence lax, the pedicels 3–18 mm. long. Calyx 5–6.5 mm. long, glabrous or sparsely glandular-pubescent on the costae; costae 3-veined; teeth triangular, acuminate to acute-mucronate. Petals 7–9 mm. long, oblong-spathulate, white, purple-veined on the lower surface. Seeds 1.5 mm. long, 0.5 mm. broad, brown, minutely papillose.

Distribution: Turkey (western Anatolia).

**Turkey**: Mugla, Fethiye, Baba Dağ above Akbel yayla, 30 July 1947, *Davis i3675* (E, holotype; K). Minara, 31 July 1947, *Davis i3709* (BM; E; K).

This recently described species does not seem to be very closely related to any of the other species in this section. Its seeds are more or less intermediate between the two types found in the genus, but appear to be most similar to those of *P. candica*. In other characters it resembles *P. armerioides* var. *laxa* and *P. ochroleuca*, but even so it seems to be a quite distinct species. For further discussion see Davis (1957).

Subsect. b. Creticae Ball & Heywood

*Petrothagia* subsect. *Creticae* Ball & Heywood, subsect. nov.; a subsectione *Illyricis* differt habitu annuo, seminibus majoribus 2–3.5 mm. longis.

Type: *P. cretica* (L.) Ball & Heywood.

Annual. Seeds 2–3.5 mm. long.

6. *Petrothagia cretica* (L.) Ball & Heywood, comb. nov. (Fig. 8.)


*Gypsophila pachygon* (Fisch. & Meyer) D. Dietr., Synops. Pl. 2 : 1543 (1849).

Stem up to 40 cm. high, much branched, densely glandular-pubescent, viscid. Lower leaves 8–25 mm. long, oblong, subobtuse, more or less 3-veined. Inflorescence lax; pedicels 4.5–20(–30) mm. long, glabrous or rarely glandular-pubescent. Calyx 6–10.5 mm. long, glabrous; intercostal membranes 0.9–1.4 mm. broad. Petals included in the calyx or rarely shortly exserted, linear-spathulate, entire, white, sometimes reddish on the lower surface. Seeds 2–2.8 mm. long, 1.3–1.9 mm. broad.

Distribution: South-western Asia, Greece.

Greece: Thessalia: Kalampaka, 27 July 1896, Sintenis 1223 (E; K).


Iran: Azna, 12 June 1937, Köie 1378 (W).

For discussion of the nomenclature of this species see Davis (1957). The type of Saponaria cretica is undoubtedly this species (see p. 141).

7. Petrorhagia arabica (Boiss.) Ball & Heywood, comb. nov. (Fig. 9.)
Tunica pachygyona var. hirtituba F. N. Williams in Journ. of Bot. 28 : 199 (1890).
Stem up to 30 cm. high, much branched, glandular-pubescent, viscid. Lower leaves 15–30 mm. long, linear-oblung, subobtuse, more or less 3-veined. Inflorescence lax, with pedicels 3–30 mm. long, densely glandular-pubescent. Calyx 6·5–9 mm. long, densely glandular-pubescent; intercostal membranes 0·7–1·1 mm. broad. Petals 9–12 mm. long, distinctly longer than the sepals, linear-spathulate, entire, white. Seeds 2·7–3·5 mm. long, 1·6–2 mm. broad.

**Fig. 9–12.**

9, *Petrorhagia arabica* (Boiss.) Ball & Heywood. 10, *P. hispidula* (Boiss. & Heldr.) Ball & Heywood. 11, *P. alpina* (Habl.) Ball & Heywood subsp. *alpina*. 12, *P. kennedyae* (Jacks. & Turrill) Ball & Heywood. a, calyx; b, petal. (All × 5.)

Distribution: Israel and Jordan.

This species generally appears to be distinct from *P. cretica*. It can be distinguished by the usually much larger seeds, the pubescent calyx with comparatively narrow intercostal membranes, and the petals always distinctly longer than the sepals. *P. cretica* rarely has the calyx very slightly glandular at the base and more frequently has the petals slightly longer than the sepals. The frequency with which these apparent intermediates occur is uncertain, but if they should prove to be widespread in Syria, Israel and Jordan then *P. arabica* should perhaps be regarded as a subspecies of *P. cretica*. However, from the sparse material seen these two species appear to be distinct in this area, although there has undoubtedly been some confusion between them.

8. **Petrorhagia hispidula** (Boiss. & Heldr.) Ball & Heywood, comb. nov. (Fig.10.)


Stem up to 30 cm. high, much branched, glandular-pubescent, viscid. Lower leaves 10–25 mm. long, linear-oblong, linear or linear-subulate, more or less 3-veined. Inflorescence lax, with pedicels 4–15 mm. long, densely glandular-pubescent. Calyx 5.5–7 mm. long, pubescent or subglabrous; intercostal membranes 0.4–0.7 mm. broad. Petals 5.5–8 mm. long, included in the calyx or slightly exserted, linear-spathulate, 4-lobed, white. Seeds 1.8–2.2 mm. long, 1.2–1.7 mm. broad.

Distribution: Turkey (southern Anatolia).


Sect. 2. **Pseudogypsophila** (A. Braun) Ball & Heywood

*Petrorhagia* sect. **Pseudogypsophila** (A. Braun) Ball & Heywood, comb. nov.


*Tunica* sect. **Pseudogypsophila** A. Braun in Flora 26 : 384 (1843).

*Tunica* sect. **Leptopleura** (Jaub. & Spach) Boiss., Fl. Or. 1 : 521 (1867).

Type: *Tunica stricta* (Ledeb.) Fisch. & Meyer (=*P. alpina* (Habl.) Ball & Heywood).


9. **Petrorhagia alpina** (Habl.) Ball & Heywood, comb. nov.

*Gypsophila alpina* Habl., Neue Nord. Beitr. 4 : 57 (1783); in S. G. Gmel., Reise Russl. 4 : 178 (1784).


Stem up to 40 cm. high, erect, much branched, glabrous. Basal leaves rosulate,
5–30 mm. long, 1–4(-7) mm. broad, oblong- to linear-spathulate, acute or obtuse; cauline leaves linear, acute, 1-veined. Calyx 2·5–4·5(-5·5) mm. long, glabrous, green; teeth shortly triangular-acute or obtuse-mucronate. Petals (3–)3·5–6 mm. long, linear-oblong, entire, white. Seeds 0·7–1·2 mm. long, 0·4–0·7(-0·9) mm. broad, ovate-oblong.

Distribution: Mountains of western and central Asia, eastwards to the western Himalaya; southern Bulgaria.

9a. *Petrorhagia alpina* subsp. *alpina*. (Fig. 11.)

Leaves oblong-spathulate. Inflorescence strict; pedicels 0·5–12(-20) mm. long, erect.


9b. *Petrorhagia alpina* subsp. *olympica* (Boiss.) Ball & Heywood, stat. nov. (Plate 13 c.)
Leaves linear-spathulate. Inflorescence spreading; pedicels (0.5–)3–30 mm. long, patent.

**Bulgaria**: In pinetis m. Pirin ad Suchodol, 14 July 1929, *Stojanoff, Stefanoff & Georgieff* (K).


Bobrov (1958) has recently shown that *Gypsophila alpina* Habl. is identical with *Tunica stricta* (Ledebr.) Fisch. & Meyer. Hablizl’s epithet is therefore the earliest for the species.

Boissier listed a number of characters by which *Tunica olympica* could be distinguished from *T. stricta* (spreading panicle, longer slender pedicels, smaller obovate seeds). Our investigations have shown that these characters are not very satisfactory. The seeds of both taxa appear to be identical, while there is such a wide range in pedicle length, even on the same plant, that this can only be used on a statistical basis. The difference in the inflorescence, although reasonably satisfactory, is not always reliable, and there seems to be some intergradation in northern, central and eastern Turkey. We therefore treat *T. olympica* as a subspecies of *P. alpina*.

10. *Petrorhagia kennedyae* (Jacks. & Turrill) Ball & Heywood, comb. nov. (Fig. 12; Plate 13 d.)

Stem 5–30 cm. high, erect, usually branched from the base, shortly glandular-hispid at the base, glabrous or glabrescent in the middle, glandular and viscid at the apex. Basal leaves up to 12 mm. long and 4 mm. broad, oblong-elliptic, obtuse; cauline leaves 5–15 mm. long, 0.5–2 mm. broad, 3-veined, linear, acute. Inflorescence lax, many-flowered; pedicels 5–25 mm. long, spreading. Calyx 4.5–6.5 mm. long, glandular-viscid, the costae often reddish or purplish; teeth broadly triangular-acute or obtuse-mucronate. Petals 6–8.5 mm. long, linear-spathulate, white, usually reddish on the lower surface, bifid. Seeds 1.3–1.6 mm. long, 0.6–0.8 mm. broad, oblong.

Distribution: Cyprus.

Cyprus: Troodos mountains, 17 July 1880, Sintenis & Rigo 764 (BM; CGE; K; W-HAL); 20–25 June 1912, Haradjian 467 (K). Platres, 18 June 1938, Kennedy 1037 (K, holotype). Mesopotamus, 21 June 1939, Lindburg (K); on dry igneous slopes in Pinus forest, 1200 m., 16 May 1941, Davis 3450 (E; K). Krigos, Potamos, 20 June 1938, Kennedy 1038 (K). Stevros (Paphos), 1200 m., 3 July 1940, Davis 1759 (E; K). Rondhklas valley between Pano and Kykko, 450–600 m., 8 May 1941, Davis 3385 (E; K). Above Alithenon, Merton 2408 (K).

This species appears to have been first collected as long ago as 1880 by Sintenis and Rigo, but was not recognized until 1938 when Jackson & Turrill published a description; soon afterwards Rechinger described it independently.

The relationships of this species are somewhat uncertain. Jackson & Turrill placed it in Tunica sect. Pachypleura, primarily because of its superficial resemblance to P. cretica (Tunica pachygona). It resembles that species in its annual habit, glandular indumentum and comparatively large flowers, but differs in the one-veined calyx costae and the small, blackish-brown scutate seeds. These differences are here considered to be of major taxonomic significance and indicate that this species should be placed in Sect. Pseudogypsophila together with P. alpina, which is also an annual species. However, P. kennedyae is quite distinct from P. alpina, and can be distinguished by a series of characters (e.g. indumentum, larger flowers, bifid petals, etc.).

Sect. 3. Petrorhagia

Petrorhagia sect. Petrorhagia; sectio typica generis.

Tunica sect. Pseudodianthus A. Braun in Flora 26 : 384 (1843), nom. illegit.
Tunica sect. Eutunica Boiss., Fl. Or. 1 : 518 (1867), nom. illegit.
Tunica sect. Tunicastrum F. N. Williams in Journ. of Bot. 28 : 194 (1890), nom. illegit.

Type: P. saxifraga (L.) Link.

Perennial. Leaves 1-veined (rarely up to 5-veined). Flowers with or without epicalyx bracts. Petals not abruptly clawed. Seeds blackish-brown, tuberculate, with thickened margin.

Subsect. a. Saxifragae Ball & Heywood

Petrorhagia subsect. Saxifragae Ball & Heywood, subsect. nov.; sectio typica
sectionis *Petrorhagiae*, continens species caulibus valde ramosis, floribus solitariis vel fasciculatis, bracteis lanceolatis vel ovatis.

Type: *P. saxifraga* (L.) Link.

Stems much branched. Flowers solitary or fasciculate; bracts and epicalyx bracts (when present) lanceolate or ovate, membranous, 1-veined.

II. *Petrorhagia phthiotica* (Boiss. & Heldr.) Ball & Heywood, comb. nov. (Fig. 13; Plate 14 A.)

*Tunica phthiotica* Boiss. & Heldr. in Boiss., Fl. Or., Suppl.: 82 (1888).


Stems 3–20 cm. high, sparsely glandular-pubescent or subglabrous. Lower leaves 3–8 mm. long, 1–3-veined. Inflorescence lax; epicalyx absent. Calyx 3–5 mm. long, glabrous; costae 1-veined; teeth broadly triangular to very obtuse, mucronate. Petals 4–6.5 mm. long, 0.5–1 mm. broad, oblong-spathulate, entire, pink. Seeds 1.2–1.6 mm. long, 0.55–0.75 mm. broad.


Distribution: South-eastern Greece (Oiti); very doubtful in north Peloponnisos.

The relationships of this species are somewhat uncertain, although it is perhaps nearest to *P. fasciculata*. However, *P. phthiotica* also shows some resemblance to *P. alpina* and it may represent a link between Sects. *Petrorhagia* and *Pseudogypsophila*. It was originally placed in his *Tunica* sect. *Gypsophiloides* by Boissier, but the very different seed type, in addition to a number of secondary characters, clearly distinguishes it from the other members of that group, which we place under *Petrorhagia* sect. *Pseudotunica*. It is difficult to understand why Hayek regarded it as only a variety of *Tunica ochroleuca*, but this may have been due to the paucity of material, and the failure to recognize the importance of the seed characters. Apart from the seeds, *P. phthiotica* can easily be distinguished from *P. ochroleuca* by the smaller pink or purplish flowers, the broad triangular mucronate calyx teeth, and the different indumentum (cf. Davis, 1957).

*P. phthiotica* differs from other members of Sect. *Petrorhagia* in a number of characters, the significance of which is somewhat uncertain. The distinctive calyx teeth, glabrous calyx, entire petals, complete absence of fasciculation of flowers, and the sparse patent-glandular hairs are the more obvious differences, and these may well prove to be more indicative of relationships than the perennial habit, the very narrow leaves, and the pink flowers.

12. *Petrorhagia fasciculata* (Marg. & Reut.) Ball & Heywood, comb. nov. (Fig. 14.)


Stems 5–30 cm. high, glandular-pubescent, sometimes glabrous above. Lower leaves 6–30 mm. long, 0·5–1·8 mm. broad, usually 1-veined, rarely up to 5-veined. Inflorescence branched; flowers usually fasciculate and bracteate, rarely solitary and then ebracteate. Calyx 2·5–5·5 mm. long, shortly or sparsely hirsute or glandular; costae 1-veined; teeth acute or subobtuse. Petals 3·5–6 mm. long, linear-spathulate, retuse, white or pale-yellow. Seeds 0·8–1 mm. long, 0·6–0·7 mm. broad.

Distribution: Western Greece and Ionian Islands.


This species appears to be a reasonably distinct member of Sect. *Petrorhagia* and can be recognized by the white or pale-yellow, usually fasciculate flowers, the smaller calyx with more or less acute teeth and one-veined costae, and the patent, glandular hairs (sometimes even on the calyx). These last two characters are shared with *P. phthiotica* and this to some extent supports the view that *P. phthiotica* should be placed in this section. However, *P. fasciculata* has a number of important features in common with the other members of the section (e.g. the fasciculation
of the flowers, the white hirtulose calyx indumentum, the more or less oblong calyx teeth, and the very narrow linear leaves) so that there can be no grounds for regarding it as separate.

It should be noted that plants of *P. fasciculata* sometimes occur with all the flowers solitary, which are then ebracteate.


*Dianthus saxifragus* L., Sp. Pl. 1: 413 (1753).
*Dianthus filiformis* Lam., Fl. Franc. 2: 537 (1778), *nom. illegit.*
*Imperatia filiformis* Moench, Meth. Pl.: 60 (1794), *nom. illegit.*
*Petrorhagia multicaulis* (Poir.) Link, loc. cit. (1831).
*Tunica bicolor* Jord. & Fourr., loc. cit. (1866).
*Tunica xerophila* Jord. & Fourr., loc. cit. (1866).
*Tunica ciliata* Dulac, Fl. Déc. Haut.-Pyrén.: 260 (1867), *nom. illegit.*
*Tunica arenicola* (Dufour) F. N. Williams in Journ. of Bot. 28: 194 (1890).
*Kohlrauschia saxifraga* (L.) Dandy in Watsonia 4: 42 (1957).

Stems 5–45 cm. high, glabrous, shortly papillose or scabrid-pubescent. Lower leaves 5–25 mm. long, 0·4–1·5 (2·5) mm. broad, 1-veined. Inflorescence lax or fasciculate; flowers usually with 4 epicalyx bracts. Calyx 3–6 (7) mm. long, glabrous or occasionally sparsely pubescent; costae 1-veined with 2 weak lateral veins; teeth oblong, obtuse. Petals 4·5–10 mm. long, 1·2–3 (4) mm. broad, the limb obcordate, white or pink. Seeds 0·9–1·6 mm. long, 0·6–1·1 mm. broad.

Distribution: Central and southern Europe and south-western Asia.

13a. **Petrorhagia saxifraga** var. *saxifraga*. (Fig. 15 ; Plate 14 b.)

Lower leaves 0·4–1·5 mm. broad. Flowers solitary. Calyx 3–6 mm. long.


3 June 1873 (FI). *Alpes-Maritimes*: Menton, Dec. 1866, Joad (E); Rechinger fil. 1507 (W-RECH); Nov. 1920, Lester-Garland (K).

**Corsica**: Evisa, 13 June 1884, Reverchon (BM; E; FI; K; W-HAL). Pentes du Pigno, à Bastia, 2–13 June 1867, Mabille 21b (BM; CGE; E; FI; K). Vizzavona, July 1907, Martelli (FI). Ragliano, 26 Sept. 1854, Revelière 43 (BM).

**Germany**: München, Spitzel 393 (BM; CGE; E; K). Prope Riesenfeld, 1 Aug. 1883, Woerlein (LIVU).


**Czechoslovakia**: Slovakia austr.-occid., prope Plavecký Čtvrtok, 20 June 1929, Domin & Krajina 35 (CGE; K).

**Hungary**: Fehér, Fehérvarcsurgó, 28 June 1923, Fl. Hung. 836 (BM; E; K). Tolna, ad stationem Tolnanemeti, 8 July 1922, Pillich (BM; K). Szontagh, Odenburg (Sopron), 1861, Semproni (K).

**Romania**: Verciorova, 5 June 1887, Degen 20 (E; K; W-HAL). Băile Herculane, June 1907, Schneider 1215 (BM; K). Gura Vaii, June 1881, Grecescu (W-HAL). Kudijévar, 19 June 1875, Tauscher (E).


SARDINIA: Sadali, 24 July 1898, Martelli (FI). Terranora Pousania, 16 June 1899, Martelli (FI).

SICILY: Enna, Sept. 1841, Parlatore (FI). Palermo, May 1905, Ross 515 (BM; E; FI). Madonie a Quacedda, June 1840, Parlatore (FI). Ins. Favigna, 5 May 1855, Huet (BM; CGE; FI; K). Sorrentino, July 1845, Sorrentino (FI).


BULGARIA: Near Rila, 2 Aug. 1926, Turrill 1541b (K); 2 Aug. 1926, Stojanoff & Stefano off (BM). Causovo, June 1908, Stribrny (BM).


TURKEY: Bosphore, Ancher-Eloy 553 (BM; K). Tokat, Niksar-Karakus, 5 Sept. 1954, Davis 24898 (E). Trabzon, Maçka, 10 July 1934, Balls 1626 (E;
K). Giresun, Tandere-Yavuzkenal, near Karinca, 13 Aug. 1952, Davis 20709 (BM ; E ; K). Rize, June 1866, René de Parquet (BM). Katahor, 7 July 1933, Balls 474 (E ; K).


IRAN: Twenty-five miles west of Zorab, 14 June 1929, Cowan & Darlington (K). Mazanderan, Kudjur, inter Sanus et Kindj, 9–11 Aug. 1948, Rechinger fil. 6570 (BM ; K).

Introduced and naturalized:


13b. *Petrorhagia saxifraga* var. *glomerata* (Ten.) Ball & Heywood, comb. nov.


Very similar to var. *saxifraga* but flowers fasciculate.


SICILY: Palermo, June 1904, Ross 516 (E ; Fl); 1893, Gasparini (BM ; CGE). Etna, 1844, Tornabene (Fl). Baida, 1848, Tineo (Fl). Madonie, 1848, Tineo (Fl).


ALBANIA: Durrës, 30 Aug. 1935, Alston & Sandwith 2740 (BM ; K).

13c. *Petrorhagia saxifraga* var. *gasparinii* (Guss.) Ball & Heywood, comb. nov.


Stems procumbent var. with numerous rosettes of leaves. Lower leaves 1–2.5 mm. broad, oblong. Flowers solitary. Calyx 4.5–7 mm. long. Petals 7–10 mm. long.

SICILY: Messina, June 1866, Sequenza 81 (Fl); Nicotra 21 (W-HAL). Isnello, 1848, Tineo (Fl). Madonie, 1866, Pasquale (Fl).

This very widespread species shows comparatively little variation throughout
its range. There is a certain amount of intergradation with *P. graminea* in Peloponnisos and besides the typical variety there are the two varieties described above, which occur mainly in Italy and Sicily.

Var. *glomerata* is characterized by the fasciculation of the flowers and this seems to occur sporadically throughout the range of the species. However, in Italy and Sicily it is much more frequent, and there tends to be a greater degree of fasciculation. *Gypsophila rigida* L. appears to be identical with this variety. Var. *gasperinii* presents a different problem. This variety appears to be confined to Sicily, and perhaps southern Italy. If it were not for this very restricted distribution var. *gasperinii* would probably be regarded as no more than an abnormal growth form, but in the present circumstances a field investigation seems to be desirable to determine its true status. It is not at all clear whether var. *glomerata* or var. *gasperinii* occur in discrete populations at all, but what evidence is available suggests that they may not.

Numerous other varieties have been described, but it seems doubtful whether any of them deserve taxonomic recognition.

14. *Petrorhagia graminea* (Smith) Ball & Heywood, comb. nov. (Fig. 16.)


*Tunica graminea* (Smith) Boiss., Diagn. Pl. Or. Nov. 2 (8): 60 (1849); Fl. Or. 1: 519 (1867).

Caespitose, usually very woody at the base with dense rosettes of leaves; flowering stems up to 40 cm. high, shortly and densely pubescent, sometimes glabrous above. Basal leaves 8–20 mm. long, 0.5–0.9 mm. broad. Inflorescence usually lax, sometimes with a few flowers fastigiate; epicalyx absent. Calyx 3.5–5.5 mm. long, densely pubescent, sometimes with the teeth subglabrous; costae 1-veined with 2 obscure lateral veins; teeth oblong, obtuse. Petals 5–10 mm. long, the limb 1.8–2.5 mm. broad, obcordate, pink, reddish, or white becoming pink. Seeds 1.1–1.5 mm. long, 0.8–0.9 mm. broad.

Distribution: Southern Greece (Peloponnisos).


This species, normally without epicalyx, appears to be very closely related to *P. saxifraga*. A number of collections from the Peloponnisos are intermediate between the two species, but it is not clear whether these represent occasional hybrid swarms or geographically intermediate populations. Only an extensive investigation in the area concerned is likely to provide a solution to this problem.

Bossier placed this species in his *Tunica* sect. *Gypsophiloides*, but the evidence of intergradation with *P. saxifraga* quite clearly supports the transfer to *Petrorhagia* sect. *Petrorhagia*. The seed characters, the white-hirtulose, oblong obtuse calyx teeth, and the occasional fasciculation of the flowers also support this.

*Tunica rhiphaea* Pau & Font Quer in Font Quer, Iter Marocc. 1929 : n. 147 (1930) ; in Cavanillesia 3 : 77 (1930).

Stems 5–15 cm. high, glabrous in the lower part, glandular-pubescent at the apex. Basal leaves 4–8 mm. long, 0·4–0·7 mm. broad, linear with obtuse apex. Inflorescence lax; epicalyx absent. Calyx 2·5–4·5 mm. long, glandular-pubescent; costae feebly 3-veined; teeth ovate to oblong, obtuse. Petals 4–7 mm. long, the limb 0·8–1·1 mm. broad, linear-oblong, retuse, pale-yellow with purple veins. Seeds (immature) 0·8–1·2 mm. long, 0·7–0·9 mm. broad.

Distribution: Spanish Morocco.

SPANISH MOROCCO: In rupibus schistosis supra oppidum Mahzen dictum (Ktama), ad 1,350 m., 29 June 1929, *Font Quer* 147 (BM, isotype).

This species is very similar to *P. graminea* and may eventually prove to be identical with it, or perhaps a subspecies. It is kept distinct here owing to the paucity of the material, and further collections are necessary before any definite conclusions can be reached. The main differences are the smaller flowers with pale-yellow, purple-veined (not pink, reddish or white becoming pink), much narrower petals, and the shorter leaves.

Subsect. b. *Thessalae* Ball & Heywood

*Petrorhagia* subsect. *Thessalae* Ball & Heywood, subsect. nov.; a subsectione *Saxifragis* differt caulibus simplicibus vel sparse ramosis, floribus capitatis, bracteis late ovatis vel suborbicularibus.

Type: *P. thessala* (Boiss.) Ball & Heywood.

Stems simple or with few branches. Flowers capitate; bracts broadly ovate or suborbicular, membranous and 1-veined to brown-scarious and many-veined.

16. *Petrorhagia thessala* (Boiss.) Ball & Heywood, comb. nov.  (Fig. 17.)


Stems 10–35 cm. high, simple or slightly branched above, shortly papillose-pubescent at least at the base. Leaves up to 15 mm. long, linear. Heads up to 10-flowered; outer bracts 6–many, the largest 6–10 mm. long, 2·5–4 mm. broad, about equalling the flowers, ovate, brown-scarious with white-membranous margin, rarely 5–7 mm. long, 1·5–2 mm. wide, ovate-lanceolate, and almost completely membranous except for the vein. Calyx 5·5–7 mm. long, glabrous or papillose with oblong, obtuse teeth. Petals 6·5–8 mm. long, linear-spathulate, entire, retuse or rarely crenate, white with pink or purple veins. Seeds 1·8–2·3 mm. long, 1·3–1·7 mm. broad.
Distribution: Greece; doubtfully in southern Jugoslavia.


This species has a somewhat disjunct distribution, its main centre being Olimbos and neighbouring mountains, with apparently small populations on Parnis Oros, and scattered localities in Macedonia and Thrace.

The plants from Tochotai (Oktchilar) differ somewhat from the rest of the species. The bracts of the inflorescence are smaller and almost completely hyaline. They approach P. macra and P. cyrenaica in this character, but otherwise resemble typical P. thesala.

Records from Jugoslavia have not been confirmed, the specimens seen proving to be Petrorhagia saxifraga. However, the distribution in Greece is such that the species will probably be found to occur in both southern Jugoslavia and Bulgaria.

Figs. 17, 18. 17, Petrorhagia thesala (Boiss.) Ball & Heywood. 18, P. dianthoides (Smith) Ball & Heywood. a, calyx; b, petal; c, epicalyx bract or the largest bract from a head. (All × 5.)
17. *Petrorhagia cyrenaica* (Durand & Barratte) Ball & Heywood, sp. nov.


Stems 5–30 cm. high, glaucous, glabrous or papillose-scabrid at the base. Leaves up to 15 mm. long, linear to setaceous. Heads 1–3-flowered; outer bracts numerous, the largest 4–8 mm. long, 1·5–2·5 mm. broad, shorter than the flowers, ovate-lanceolate, white-membranous with brown-scarious veins. Calyx 4·5–6 mm. long, slightly and sparingly pubescent with oblong, obtuse teeth. Petals 5·5–8 mm. long, linear-spathulate, ?entire, white, pale-red on the lower surface. Seeds (immature) 1·3–1·5 mm. long, 1·1 mm. broad.

Distribution: Libya.


Very little material of this species has been seen, but it appears to be distinguishable from *P. thessala* by its fewer-flowered heads with smaller flowers, and smaller almost entirely membranous bracts. Also, in the material seen, the calyx has always been sparingly pubescent, although a glabrous variant has been described by Pampanini (Arch. Bot. Forli 12 : 24 (1936)).

18. *Petrorhagia macra* (Boiss. & Hausskn.) Ball & Heywood, comb. nov.


*Tunica gracilis* F. N. Williams in Journ. of Bot. 28 : 196 (1890).

Stems 25–40 cm. high, slightly branched above, pubescent at the base, glabrous elsewhere. Leaves up to 10 mm. long, oblong-linear to subulate. Heads 1–5-flowered; outer bracts 4–many, the largest 3·5–5 mm. long, 0·7–1·3 mm. broad, triangular-lanceolate to ovate, acuminate, white-membranous with a brown-scarious vein. Calyx 5·5–8 mm. long, sparsely pubescent with more or less oblong-obtuse teeth. Petals 8–9 mm. long, linear-spathulate, entire, white. Seeds not known.

Distribution: Iran (Kurdistan).

Iran: Monte Shahu, 1867, *Haussknecht* (K, isotype, also holotype of *Tunica gracilis*).

Very similar to *P. thessala* and *P. cyrenaica*. *Tunica gracilis* was described from isotype material of *T. macra*. The specimen closely fits the description of *T. macra*, and there does not seem to be any reason why it should be regarded as a distinct species.

19. *Petrorhagia dianthoides* (Smith) Ball & Heywood, comb. nov. (Fig. 18.)


Stems up to 40 cm. high, simple or slightly branched above, glabrous. Leaves up
to 20 mm. long, linear to subulate. Heads 1-6(8)-flowered; outer bracts 4-many, the largest 4.5-10 mm. long, 1-2.5 mm. broad, lanceolate to ovate-lanceolate, white-membranous except for the brown-scarious vein. Calyx 5-7 mm. long, pubescent, with triangular-lanceolate, more or less acute teeth. Petals 6-10 mm. long, oblong-spathulate, entire, white with red veins. Seeds (immature) 1-1.3 mm. long, 0.8-0.9 mm. broad.

Distribution: Crete.


This species appears to be one of the most distinct in the section.

Sect. 4. Dianthella (Boiss.) Ball & Heywood

Petrorhagia sect. Dianthella (Boiss.) Ball & Heywood, comb. nov.


Type: Tunica pamphylica Boiss. & Balansa (= P. pamphylica (Boiss. & Balansa) Ball & Heywood).

Annual. Leaves 3-veined. Flowers solitary or subcapitate; bracts ovate, brown- or purplish-scarious, 3-many-veined. Calyx costae 3-7-veined. Petals not clawed. Seeds small, blackish-brown, reticulate-tuberculate, with thickened margin.

20. Petrorhagia pamphylica (Boiss. & Balansa) Ball & Heywood, comb. nov. (Fig. 19.)


Stems 10-35 cm. high, pseudodichotomously branched from the base, glabrous. Cauline leaves up to 16 mm. long, 1 mm. broad, linear, 3-5-veined. Flowers solitary; epicalyx bracts 6-12, 3-4 mm. long, shorter than the calyx, oblong to ovate, acute, brown- or purplish-scarious with white-membranous margin and with 5-many thick veins. Calyx 5-7 mm. long; costae very broad, 6-7-veined, the commisural membranes almost absent; teeth 0.8-1.1 mm. broad, lanceolate-acuminate. Petals 7-9 mm. long, the limb c. 0.5 mm. broad, linear-spathulate, obtuse, entire, pale-pink. Seeds 1.6-2 mm. long, 1.2-1.7 mm. broad.

Distribution: Turkey (southern Anatolia).

Turkey: Antalya, near Gebiz, stony hillside, 1,000 m., 22 July 1949, Davis 15478 (BM; E; K).

21. Petrorhagia peroninii (Boiss.) Ball & Heywood, comb. nov. (Fig. 20; Plate 14 c.)

Tunica peroninii Boiss., Fl. Or., Suppl.: 81 (1888) ("Peronini").
Stems 15–30 cm. high, pseudodichotomously branched from the base, pruinose-papillose. Cauline leaves 8–20 mm. long, c. 1 mm. broad, linear, 3-veined. Flowers solitary or subcapitate; bracts and epicalyx bracts 6–many, up to 5–7.5 mm. long, exceeding the calyx, lanceolate, brown- or purplish-scarious with white-membranous margin, papillose, 3(–5)-veined. Calyx 5–7 mm. long; costae 3-veined, with a narrow but distinct commissural membrane; teeth 0.4–0.7 mm. broad, oblong-lanceolate. Petals 5.5–8.5 mm. long, the limb c. 0.5 mm. broad, linear-spathulate, obtuse, entire, white, sometimes purplish on the lower surface. Seeds 1.1–1.2 mm. long, 0.7–0.9 mm. broad.

Distribution: Turkey (southern Anatolia).

Turkey: Prov. Mersin, Dist. Anamur, montagne ouest d’Anamour, June 1872, Peronin 5 (BM; K; isotypes). Between Ferhenk and Anamur, rocky metamorphic hills, 50 m., 19 Aug. 1949, Davis 16329 (BM; E; K).

These two rare species, as already mentioned (p.126), appear in some respects to form a link between Petrorhagia and Dianthus.

Sect. 5. Kohlruschia (Kunth) Ball & Heywood

Petrorhagia sect. Kohlruschia (Kunth) Ball & Heywood, comb. nov.


Type: Kohlruschia prolifera (L.) Kunth (= P. prolifera (L.) Ball & Heywood).

Annual. Leaves 3-veined. Flowers capitate; bracts very broad, orbicular-ovate or suborbicular, brown-scarious, many-veined. Petals distinctly clawed. Seeds small, blackish-brown, reticulate to papillose, with thickened margin.
22. *Petrorhagia prolifera* (L.) Ball & Heywood, comb. nov.  (Plate 15 A.)

*Dianthus diminutus* L., op. cit., ed. 2, 1: 587 (1762).
*Caryophyllus aridus* Moench, Meth. Pl.: 59 (1794), nom. illegit.

Stems up to 50 cm. high, usually simple, glabrous or scabrid. Cauline leaves up to 40 mm. long and 2 mm. broad, linear-oblong, 3-veined; sheath 1-2.5 mm. long, about as long as broad. Largest bracts of head 6-12 mm. long, 3-7(-8) mm. broad, usually obtuse. Calyx 10-13 mm. long; costae 3-veined; teeth oblong, obtuse. Petals 10-14 mm. long, the limb 2-3.5 mm. wide, obcordate, pink or purplish. Seeds 1.3-1.9 mm. long, 0.8-1.1 mm. broad, reticulate.

Distribution: Central Europe, mountains of southern Europe, Caucasus (northern Anatolia), mountains of western North Africa.


**POLAND:** Krappilk (Schlesien), 19 July 1899, *Ziesché* (E).


ITALY: Basilicata: Pignola, 8 June 1924, Gaviolo (FI). Gruppo del Pollino,


Corsica : Bastia, 28 Sept. 1880, Chubern (FI). Bastelica, 20 June 1878, Reverchon (K).


Belgium : Mariembourg, 23 June 1935, Mosserony (K).


Turkey: Adana, Feke, Sencan Deresi between Gürümze and Süphandere, 1 July 1952, Davis 19603 (K). Adapazari, Arifiye, 1 July 1962, Davis 36281 (E).

Introduced:


The typification and relationships of this species are discussed by Ball & Heywood (1962).

23. *Petrorhagia nanteuilii* (Burnat) Ball & Heywood, comb. nov. (Fig. 21; Plate 15 B.)


*Kohlrauschia nanteuilii* (Burnat) Ball & Heywood in Watsonia 5 : 115 (1962).

Very similar to *P. prolifera* but the stems sometimes pubescent in the middle; leaf sheaths 1–3.5 mm. long, sometimes up to twice as long as broad; seeds tuberculate.

Distribution: Western Europe and western North Africa.


Corsica: Près Bastia, 17 June 1881, Chubern (FI).

Sardinia: Isola Maddalena, June 1893, Vaccari (FI).

![Figures 21 and 22](image)

Figs. 21, 22. 21, Petrorhagia nanteuilii (Burnat) Ball & Heywood. 22, P. glumacea (Bory & Chaub.) Ball & Heywood var. glumacea. a, calyx; b, petal; c, epicalyx bract or the largest bract from a head. (All × 5.)


Morocco: Tichka l’Agadal, 10 June 1936, Balls 2766 (BM; K). Amizmiz, 17 June 1936, Balls 2851 (BM; K).

Madeira: Madeira, Lindley (K); July 1862, Clarke (K). Funchal, 27 Mar. 1949, Sledge (BM). Bay E. of Pont Gorda, 27 Apr. 1924, Riley (K).


For full discussion of the separation of this species from P. proliferata see Ball & Heywood (1962).

24. *Petrorhagia velutina* (Guss.) Ball & Heywood, comb. nov. (Plate 15 c.)

*Gypsophila velutina* (Guss.) D. Dietr., Synops. Pl. 2: 1542 (1840).
*Kohlrauschia velutina* (Guss.) Reichb., Ic. Fl. Germ. & Helv. 4: 43 (1844).

Stems up to 50 cm. high, usually simple, usually with crowded glandular hairs on the middle internodes, rarely almost glabrous. Cauline leaves up to 35 mm. long and 2 mm. broad, linear-oblong, 3-veined; sheath 3–7(-8) mm. long, at least twice as long as broad. Largest bracts of head 7–12 mm. long, 4.5–8.5 mm. broad, mucronate. Calyx 8–14 mm. long; costae 3-veined; teeth oblong, obtuse. Petals 11–16 mm. long, the limb 1.2–2.5 mm. broad, obcordate, sometimes bifid, pink or purplish. Seeds 1–1.3 mm. long, 0.7–0.8 mm. broad, strongly tuberculate or papillose.

Distribution: Mediterranean region.


France: Alpes-Maritimes: Près Nice, 7 May 1861, Bourgeau (FI). Esteril, 7 May 1889, Bonafous & Vidal (K).


Italy: Liguria: Pizzo, Apr.–May, Ricca (FI). Emilia: Bologna, Monti


JUGOSLAVIA: Hrvatska: Pola (Pula), 7 June 1874, Freyn (FI). Promontore (Istria), 23 May 1898, Marchesetti (FI). Fasana, 10 June 1909, Korb (W).

ALBANIA: Sarande, 3 June 1933, Alston & Sandwith 1372 (BM; K). Levani, 23 Apr. 1918, Schneider (W). Ljusme, 1 May 1918, Schneider (W).

BULGARIA: S. of Varna, 20 May 1925, Gilliat-Smith 1134 (K).


Libya : Between Cyrene (Shahhat) and Apollonia (Marsa Susa), 4 Apr. 1939, Sandwith 2350 (K).


Introduced :

HAWAII: Waimea, S. Kohala, 25 May 1938, Hosaka 2110 (K).


25. *Petrorhagia glumacea* (Bory & Chaub.) Ball & Heywood, comb. nov.


Stems up to 50 cm. high, usually simple, glabrous or scabrid. Cauline leaves up to 40 mm. long and 2 mm. broad, linear-oblong, 3-veined; sheath 1–2 mm. long, usually shorter than broad. Largest bracts of head 12–18 mm. long, 8–12 mm. broad, obtuse. Calyx (9–)10–13 mm. long; costae 3-veined; teeth oblong, obtuse. Petals 12–18 mm. long, the limb 3–6 mm. broad, very variable in shape, pink or purplish. Seeds 1·5–2·2 mm. long, 1·2–1·7 mm. broad, almost smooth to tuberculate.

Distribution: Balkan peninsula.

25a. *Petrorhagia glumacea* var. *glumacea*. (Fig. 22; Plate 15 D.)

Petal limb obdeltate, crenate to laciniate at the apex. Seeds 1·7–2·2 mm. long, 1·4–1·7 mm. broad, almost smooth or slightly tuberculate.


Petal limb obcordate, usually entire. Seeds 1·5–1·8 mm. long, 1·2–1·5 mm. broad, tuberculate.


Turkey: Muratli, 20 June 1890, Degen (K).


Introduced:

Italy: Trentino: Prope Povo et Roncegno, July 1899, Murr in Dörfler, Herb. Norm. 4011 (BM ; E).

This is a somewhat variable species which has been confused with P. prolifera in the central and northern Balkan peninsula. All the Bulgarian specimens seen and many of those from Jugoslavia and northern Greece are undoubtedly P. prolifera.

The status of the two varieties recognized is still not clear as it has not been possible to determine the extent of the correlation between the petal and seed characters. Most specimens are either in flower and without mature seeds or in fruit and without petals. Large almost smooth seeds occur only in Peloponnisos and southern Sterea Ellas while small tuberculate seeds occur in all areas except Peloponnisos. The petal type of var. glumacea is largely restricted to Peloponnisos, but intermediate types occur occasionally almost throughout the range of var. obcordata. A further difficulty is that in many specimens the petals are badly pressed owing to the bulkiness of the head so that it is difficult to see the precise shape and tooting of the petal limb.

From this discussion it will be clear that there is the possibility that the two varieties recognized may eventually be treated as subspecies. However, the evidence available at the present is so inconclusive and unsatisfactory that it is impossible to justify raising them to this rank.

_Insufficiently known species_


"_T. glaberrima nigrescenti-viridis_ perennis basi suffrutescens multicaulis, caulibus
filiformibus rectis vel ascendentibus ad nodos superiores sæpè geniculatis simplicibus unifloris raritæ ramulo auctis nigrantisibus asperulis, foliis parvis angustæ lineari-triquetrifis crassiusculis obtusiusculis supræ sulcatis subtus carinatis margine scabridis strictis internodio 3–4 plò brevirioribus basi breviter connatis, bracteis 8–10 calyci subæquilongis lanceolatis acutissimis subpungentibus praeter nervum rubrum crassum angustè albo-membranaceis, calyce oblongo campanulato brevissimè puderulo tubo enervi albido dentibus tubo triplò brevirioribus oblongis nigrantisibus albo-marginatis, petalis angustè linearibus obtusis ungue nudo laminà pallidè roseà breviter exsertà, capsula. . .

"Hab. in rupibus Syriæ borealis ponè urbem Antiochiam sitis ubi specimena paucæ Junio 1846 legi.


The above is a transcription of Boissier’s protologue.

Tristram (Survey of Western Palestine, Flora & Fauna : 240 (1884)) also records this species from northern Lebanon, but he does not give any further information. No material has been seen and no additional records have been traced. Even the most recent description (Post, 1932) is clearly based entirely on Boissier’s data.

The description suggests that this species is nearest to Petrorhagia sect. Petrorhagia subsect. Thessalæ, all the species of which are rare and local late-flowering perennials. Geographically it would form a link between the Balkan and North late-flowering species, and P. macra from Kurdistan.

Excluded species


SPECIAL LITERATURE


MARINE ALGAE OF GOUGH ISLAND

BY

YVONNE M. CHAMBERLAIN

Pp. 173–232; 80 Text-figures; Plates 16–19

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY

LONDON: 1965
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MARINE ALGAE OF GOUGH ISLAND

By YVONNE M. CHAMBERLAIN

(Mrs. Butler.)

The material reported on in this paper was collected by Dr. N. M. Wace during the stay of the Gough Island Scientific Survey on Gough Island from 13 November 1955 to 13 May 1956, and is now in the British Museum Herbarium. The collections were made on only a few days during this summer period and the species included here undoubtedly represent only a few of those present on the island. However, as Dr. Wace is an ecologist, he collected particularly those species which dominated the littoral and sub-littoral zones; I think therefore that all the zone-forming species are included here together with the most abundant associated littoral species. Only two or three attempts at dredging were made and these were unfortunately fruitless; none, therefore, of the smaller sub-littoral species, notably the Delesseriaceae, which undoubtedly grow round Gough Island, is included in the collections.

Acknowledgements

I am indebted to Dr. Wace for making the collections, which were well preserved and clearly labelled, also to him and Dr. M. W. Holdgate (the invertebrate zoologist of the expedition) for much helpful discussion on the littoral ecology of the island, and to Mr. J. J. van der Merwe who collected some more Blidingia and Enteromorpha when he stayed on Gough Island after the return of the Survey and thus helped to clarify some taxonomic and ecological problems.

I worked on the material while I was a member of the staff of the British Museum (Natural History) and I am grateful to Mrs. F. L. Balfour-Browne, Mr. J. E. Dandy and Mr. R. Ross for general, editorial and nomenclatural help; to Dr. W. T. Stearn who wrote the latin diagnoses of new species; and to Mr. D. W. Cooper who made sections of the Corallinaceae.

For general taxonomic guidance I am indebted to Dr. P. S. Dixon and to Mme. Marie Lemoine, with whom I was able to discuss the Corallinaceae when I visited the Muséum National d’Histoire Naturelle, Paris. Several of the species were sent to taxonomists expert in particular groups and their help is acknowledged in the appropriate places.

Finally, I would like to thank the Directors of the following Institutions for permission to examine herbarium material: Royal Botanic Gardens, Kew; Bolus Herbarium, Cape Town; Herbarium of the University of California; Rijksherbarium, Leyden; Muséum National d’Histoire Naturelle, Paris; and Dr. Egil Baardseth, who presented a duplicate collection of his Tristan da Cunha algae to the British Museum.
GEography of Gough Island

Gough Island (Figs. 1, 2) is an outlier of the Tristan da Cunha group of islands situated near the southern end of the mid-Atlantic ridge. It lies 370 km. S.S.E. of Tristan da Cunha, more than 3,000 km. from South America to the west and 2,400 km. from South Africa to the north-east. The island lies in the West Wind Drift and within the zone of sub-antarctic, cold-temperate water (Knox, 1960, p. 578) but may occasionally be influenced by the cold-temperate mixed water derived from the Brazil current. Gough Island lies between the Antarctic and Sub-tropical Convergences (Knox, 1960, p. 582) but is closer to the latter, which is here at, or somewhat to the south of, Tristan da Cunha.
Fig. 2. Sketch map of Gough Island to show localities where marine algae were collected.

LITTORAL ecology of Gough Island

It is intended to publish a paper on the littoral ecology of Gough Island and only the main features will be summarized here.

The entire island is very exposed in comparison with continental shores so that the terms sheltered, moderately exposed, etc., are relative only to conditions on the island. On the moderately exposed shore at Dell Rocks Beach the zonation is:

- **Upper supra-littoral**: Lichina sp.
- **Lower supra-littoral**: Porphyra tristanensis, Verrucaria sp.
- **Upper littoral**: Blidingia minima in crannies and sheltered places. *Iridaea laminarioides* where more exposed. *Enteromorpha bulbosa*.
- **Mid littoral**: *Iridaea laminarioides* gradually giving way to *Rhodoglossum revolutum*.
- **Lower littoral**: *Iridaea laminarioides* and *Rhodoglossum revolutum* succeeded by *Durvillaea antarctica* and *Melobesiaeae*.
- **Sub-littoral**: The *Durvillaea-Melobesiaeae* zone extends down into the sub-littoral and below this *Macrocystis pyrifera* is dominant.
Plate 16A shows the shore at Isolda Rock which is somewhat more exposed than Dell Rocks Beach. Light-coloured Melobesieae can be seen on the left, a dark band of *Iridaea laminarioides* in the centre and plants of *Durvillaea antarctica* on the right.

On the more sheltered Midshipman Rock, the mid littoral is dominated by a band of *Ralfsia* sp., below which is a band of Melobesieae and Corallina officinalis. West Point Reefs is the most exposed locality; here *Iridaea laminarioides* and *Rhodoglossum revolutum* zones are absent and the mid littoral is dominated by a band of white Melobesieae succeeded by a band of *Polysiphonia howei* (probably) and other Rhodomelaceae. *Macrocystis pyrifera* is also absent on very exposed shores.

Among the most common plants occurring in littoral rock pools throughout the island are: Corallina officinalis, Dermatolithon nodulosum, *Iridaea undulosa*, Scytosiphon lomentaria and Codium fragile.

The algal zonation on Gough Island is typical of the sub-antarctic pattern (Skottsberg, 1941; Knox, 1960, p. 601). It differs markedly from that of Tristan da Cunha, which has more in common with a South African shore. This corresponds with the fact that Gough Island is well south of the Sub-tropical Convergence while Tristan da Cunha is at its mean position. Very little is known about the east coast shore of South America at about the same latitude as Gough Island, but it is probable that further investigations will show that it has a zonation pattern similar to that of Gough Island. Further south, Tierra del Fuego and the Falkland Islands have a zonation pattern similar to that of Gough Island but with a greater number of typical antarctic species.

**Localities and habitats, with species present**

(Entries in brackets relate to algae that have not been identified at species level and are not included in the Systematic List.)


Outer Dell Rocks. 18 Feb. 1956. From mid-tide level to 2 m. below low-tide level. *G.I.S.S. 1510*. *Durvillaea antarctica*. 


Midshipman Rock. 18 Feb. 1956. Mid-littoral zone, on shiny olive-green deposit. *G.I.S.S. 1515, 1517, 1518. [Ralfsia], Corallina officinalis, Centroceras clavulatum, Microcladia alternata, [Delesseriaceae], Herposiphonia paniculata, Polystiphonia howei*.


**Phytogeography**

The elements of which the Gough Island marine algal flora is composed are:

<table>
<thead>
<tr>
<th>Type</th>
<th>Number of Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cosmopolitan</td>
<td>19</td>
</tr>
<tr>
<td>General southern hemisphere</td>
<td>4</td>
</tr>
<tr>
<td>Southern cold-temperate</td>
<td>6</td>
</tr>
<tr>
<td>North and south Atlantic</td>
<td>3</td>
</tr>
<tr>
<td>Tristan da Cunha group endemics</td>
<td>6</td>
</tr>
<tr>
<td>Endemic</td>
<td>2</td>
</tr>
</tbody>
</table>

This list is necessarily incomplete and inaccurate for two reasons. The first is that, compared with, for example, the angiosperms, relatively little is known about the distribution of marine algae and, until fairly recently, authors have made little attempt to relate the flora of the area on which they were working to that of other areas. Secondly, there is at present a very wide variation of opinion among algal taxonomists as to what constitutes a species. In the past, a large number of new species have been described without regard to seasonal, ecological or geographical variation, and also without reference to previous literature on or collections from the same area. On the whole, present-day phycologists regard species in the widest sense, as entities which are liable to great variation according to the external conditions mentioned above. I agree with this concept, and this may account for the large number of cosmopolitan and widely distributed species in the list.
It is a well-known fact, however, that isolated islands usually have relatively high numbers of two groups of species in their flora, cosmopolitan species and endemic species, so that the list may be only an exaggeration of the true picture. Of the second group, the endemic species, two species so far known only from Gough Island are described, and as these are in the Corallinaceae, which is a very difficult and often ignored family, it is probable that they will later be found elsewhere. On the other hand, endemic species are more likely to be found among the smaller, less conspicuous species. As previously explained, the collector concentrated on the dominant species and many possible endemics have no doubt so far escaped notice. There were some more possibly new species in the collection but the material was too scanty, in my opinion, to merit their description as such.

There are some rather surprising absences from Gough Island, most notably Hildenbrandia lecannellieri and Adenocystis utricularis. Sub-littoral members of the Delesseriaceae and of Desmarestia are also missing from the collection, probably because of the difficulties of dredging. Two littoral members of the Delesseriaceae were collected but I was unable to identify them further than that they are probably species of Nitophyllum. The Hildenbrandia and Adenocystis may have been missed, but Dr. Holdgate, who has seen many southern cold-temperate shores, is fairly sure that they were not at any of the localities visited by the Survey.

In conclusion, on present evidence it is not possible to make many generalizations about the Gough Island marine algal flora. It does however represent a typical sub-antarctic zonation pattern and the high number of endemic species (to the Tristan da Cunha group) is typical of isolated localities.

**Systematic List**

**CYANOPHYTA**

**CHAMAESIPHONACEAE**


Cosmopolitan.

This species occurred as an epiphyte on Calothrix crustacea and Rhizoclonium ambiguum. When Dr. Drouet discussed the identification of the Gough Island Cyanophyta with me, he commented that the only difference between this and the next species is that this is an epiphyte and *E. deusta* is a lithophyte.


1 Dr. Francis Drouet of the Academy of Natural Sciences of Philadelphia kindly identified the *Cyanophyta*. 

Cosmopolitan.

The growth form of the specimens of this plant from Gough Island is the cushion type. It grows on rocks in the upper littoral zone where it forms a film, usually in association with other *Cyanophyta*. *Calothrix crustacea* is its most frequent associate.

**RIVULARIACEAE**


Cosmopolitan.

*C. crustacea* is the most common blue-green alga collected on Gough Island. It grows in pools and on rocks in the upper littoral and spray zones of several localities, where it forms a film mixed with *Entophysalis deusta* and *Lyngbya confervoides*. It often bears epiphytes such as *Plectonema calothrichoides* and *Entophysalis conferta*. From the available information, there is no indication that the *Cyanophyta* are ever the dominants of a littoral zone on Gough Island, although they are certainly a noticeable feature of the upper littoral zone on the Midshipman Rock. Baardseth (1941, p. 133) records *Cyanophyta* as forming a dense covering of rocks in the *Porphyra* zone on the exposed rocks of Tristan da Cunha and they frequently occur as the dominant or sub-dominant algal community at this shore level in other parts of the world. Skottsberg (1941) did not mention the *Cyanophyta* in his analysis of antarctic and sub-antarctic algal communities.

**OSCILLATORIACEAE**


Cosmopolitan.

Collected from the Midshipman Rock where it grew with *Calothrix crustacea* and *Entophysalis deusta* as a film on rock submerged in an upper-littoral rock pool.


Cosmopolitan.

This species was found growing with *Phormidium submembranaceum* on the Midshipman Rock.
Only a small amount of this alga was collected; it came from the upper littoral zone on the Midshipman Rock where it was growing mixed with Oscillatoria nigroviridis forming a film on the rocks.
Growing as an epiphyte on Calothrix crustacea.

CHLOROPHYTA
ULVACEAE
Ulva intestinalis var. nana Sommerfelt, Suppl. Fl. Lapp.: 186 (1826).
This plant grew abundantly in the upper and mid littoral zones at Dell Rocks Beach and occurred both in sheltered rock crevices and in pools. It was also collected from Capsize Sands. It formed a low, bright-green turf which at times dominated the shore community. This species is found throughout the world in the upper littoral zone of the sea-shore and quite often dominates parts of this zone (cf. T. A. & A. Stephenson, 1954, p. 38).
The Gough Island material consists of minute plants rarely more than 1 cm. high. Numerous fronds grow from a flattened basal part (Fig. 3); the fronds are tubular,
the tubes being closed when young but open at the top when older. Some of the older plants are twisted while others are swollen at the top. The cells seen in surface view are irregular in shape and arrangement (Fig. 4); they have thick walls and a large single pyrenoid. The cells measure up to 7 µ in diameter but are mostly about 3–5 µ. In transverse section (Fig. 5) the cells are elongated and measure about 3–4 µ × 8–9 µ, and the whole section is about 15–18 µ deep. The inner wall is thick and may measure up to 8 µ deep.

Numerous forms and varieties of *Blidingia minima* have been described, under the various names given in synonymy above, according to the size and shape of the fronds, the thickness of the cell walls and the nature of the basal part. The Gough Island material is most like the descriptions of *Enteromorpha gunniana* (e.g. that of Sjöstedt), but Womersley, who has seen Agardh’s type material, does not think it sufficiently distinct to merit specific separation from the rest of the complex.

Dr. Carl Bliding kindly confirmed the identification of this species.

**Enteromorpha bulbusa** (Suhr) Montagne in Gaudich., Voy. Monde La Bonîte, Bot. 1: 3 (1846).—De Toni, Syll. Alg. 1: 127 (1889). (Figs. 6–8.)

*Solenia bulbusa* Suhr in Flora 22: 72, t. 4 fig. 46 (1839).

*Enteromorpha africana* Kütz., Phyc. Gen.: 300 (1843); Tab. Phyc. 6: 14, t. 40 fig. 2 (1856).

*Enteromorpha hookeriana* Kütz., Sp. Alg.: 480 (1849); Tab. Phyc. 6: 13, t. 40 fig. 2 (1856).


South America, Falkland Islands, South Africa, Crozet Islands, Kerguelen Island, Australia, New Zealand, Chatham Islands, Antarctica, ? Japan.
Collections of *E. bulbosa* were made at the very exposed West Point Reefs where it was growing in penguin-fouled rock pools in the spray zone, at Dell Rocks Beach where it grew on littoral rocks, and at Capsize Sands. The green band recorded as being present on other parts of the island was probably dominated by this species and *Blidingia minima*.

The largest plants of this species collected from Gough Island (Fig. 6) are 6 cm. high and up to 5 mm. wide, but most of the plants are smaller than this. Both branched and unbranched plants were collected; when branches are present they are long and very similar to the main axis, as is characteristic of this species, and not noticeably smaller than the main axis as in many other species of *Enteromorpha*. The thallus is tubular and compressed, the branches and axis are usually open at the top and often torn. The branches and main axis taper downwards to a terete base and some specimens still have the warty basal part by which they had been attached to the rocks. Many of the tubes are perforated (Fig. 6) by an amphipod; this animal apparently lives in the tubes of *E. bulbosa* and many specimens of it were found *in situ*.

When seen in surface view (Fig. 7) the cells are irregularly arranged, are up to 15μ in diameter, and have rounded corners. There is one fairly large pyrenoid per cell. In transverse section (Fig. 8) the cells are rectangular and measure about 25μ tall × 12μ wide. The inner and outer membranes of the tube are fairly thick.
and the section measures about 30 µ deep altogether. The plants are grass-green in colour and tend to be darker at the base of the axis and branches than in the upper parts, a feature mentioned by von Suhr.

The Gough Island plants agree well with von Suhr’s description, with Montagne’s material in the herbarium of the Muséum National d’Histoire Naturelle, Paris, and with Kützing’s figures of *E. africana* and *E. hookeriana*, both considered by De Toni to be *E. bulbosa*.

*E. bulbosa* is a common plant of the sub-antarctic littoral; according to Skottsberg (1941, p. 56) it forms a widespread community on shores with a loose, mobile substrate such as sand, and frequently occurs also in other associations such as littoral pools. *E. bulbosa* has been recorded from the antarctic (cf. Hariot, 1907, p. 3, and Gain, 1912, p. 26) and from warmer parts such as South Africa (Levring, 1938, p. 5), New Zealand (Chapman, 1956, p. 411) and Australia (Womersley, 1956, p. 351), but it is on sub-antarctic shores that it grows most prolifically.

The identification of this species was confirmed by Dr. Bliding.

**Ulva lactuca** L., Sp. Pl. 2: 1163 (1753). (Figs. 9–12.)


Cosmopolitan.

This plant was very common on rocks and in pools in the upper littoral zone of the Gough Island shores.

![Image](https://example.com/image.jpg)

**Figs.** 9–12. *Ulva lactuca* L.: 9, blade margin; 10, surface view of frond; 11, transverse section of frond; 12, transverse section of stipe, semi-diagrammatic.

The material collected from Gough Island varies considerably in size and shape. All the specimens have a somewhat fleshy stipe from which the blades expand; the blades are sometimes entire but more often divided—sometimes right down to
the holdfast. The blade margins (Fig. 9) vary from smooth to crenulate or fimbriate, all types of margin sometimes occurring on one plant. Although there is considerable variation in external appearance, the microscopic structure of the plants is remarkably constant. In the upper parts of the plants the cells are irregularly arranged, somewhat rounded and up to 20µ in diameter in surface view (Fig. 10). In section the blade is 60–70µ thick (Fig. 11), the two rows of cells are separated by a hyphal layer and the cells are rather rounded and not more than one and a half times as high as they are wide. The stipe in section (Fig. 12) is much thicker than the blade and has a wide central region of hyphae.

This material undoubtedly corresponds to what has been generally accepted as Ulva lactuca L.—an extremely common plant which grows throughout the world. Papenfuss (1960, pp. 303–305) has investigated Linnaeus's material of U. lactuca and his concept of the genus Ulva. As a result of this investigation, Papenfuss concluded that the genus which Linnaeus really had in mind was that now known as Enteromorpha Link and proposed that the generic name Ulva should be conserved in the sense of Thuret and all subsequent authors; this proposal has now been accepted, and I am here using the name in that sense.

CLADOPHORACEAE

Rhizoclonium ambiguum (Hook. & Harv.) Kütz., Sp. Alg.: 387 (1849). (Figs. 13–15.)


Rhizoclonium africanum Kütz., Tab. Phyc. 3: 21, t. 67 fig. 2 (1853).


Rama novae-zelandiae (J. G. Agardh) V. J. Chapman in Trans. R. Soc. New Zeal. 80: 56, fig. 11 (1952).

Standoff Rock, on less-exposed part of the rock above the Corallina zone, 18 Feb. 1956, G.I.S.S. 1526. Window Pool, on walls of small shallow cave beside pool, 12 Apr. 1956, G.I.S.S. 1557.

Wide distribution in the Southern Hemisphere and the tropics; recorded from as far north as Florida.

A small quantity of this species was found in the Bostrychium on Standoff Rock; it occurred in greater quantity in a shallow cave beside Window Pool. The latter habitat compares with the grottos mentioned by Taylor.

The plants consist of sparingly branched filaments (Figs. 13–15), the cells of which measure 60–90µ wide and up to 150µ long. The cell walls are thick and lamellated. Rhizoidal outgrowths are quite frequent and they usually terminate in a digitate hapteron which often attaches itself to other filaments of the plant. The cell contents do not show much structure, but prominent, dark, parietal bodies are present, which are waste products. A few sporangia are present but the nature of the spores cannot be determined in this preserved material.

The Gough Island plants are very similar to the type material in the Kew Herbarium and the isotype material in the British Museum Herbarium. Stockmayer was of the opinion that Kützing's *Rhizoclonium hookeri* and *R. africanum* were to be referred to the same species; this view is now generally accepted. The type of *R. hookeri* is a specimen collected by J. D. Hooker on Kerguelen Island at the same time.
as he collected his *Conferva ambiguum* but which he labelled *C. linum*. There is an isotype of *R. hookeri* in the British Museum Herbarium which in all ways exactly resembles *R. ambiguum*. This species is often called *R. hookeri* by modern authors, but if, as most authors agree, that species and *R. ambiguum* are to be united, the latter name is correct because the publication of its basionym antedates that of *R. hookeri*.

The characteristic features of *R. ambiguum* are its sparse branching—most species of *Rhizoclonium* are unbranched—and the filament width, which ranges from 40 µ to 100 µ. It is usually found in marine habitats but is also recorded from brackish and fresh water (Taylor, loc. cit.). The type specimen was marine, although Kützing incorrectly stated that it came from fresh water. In 1952 Chapman erected a new genus, *Rama*, which differed from *Rhizoclonium* only in being sparingly branched; to this genus he transferred *Lychaete novae-zelandiae*. Chapman said that *Rama* was similar to *Spongomorpha*. However, as the branching in *Rama* is dichotomous (Figs. 13, 15) as opposed to the characteristic lateral branching of *Spongomorpha*, they are not really very similar. In 1956 Chapman repeated his description of *Rama novae-zelandiae* and treated *Rhizoclonium hookeri*, which he described as being unbranched and 47–70 µ wide, as a separate species, retaining it in the genus *Rhizoclonium*. In Bornet & Thuret’s herbarium (in the Muséum National d’Histoire Naturelle, Paris) there is an isotype of *Lychaete novae-zelandiae* collected by Berggren at Warrington, New Zealand. This plant is sparingly branched and has rhizoids, the cell walls are thick and lamellated, and the filaments measure 60–80 µ wide. It closely resembles the type material of *R. ambiguum*. In my view, *Rama novae-zelandiae* as well as *Rhizoclonium hookeri* should be united with *R. ambiguum*. This species is characterizedly branched, but this feature alone does not seem sufficient basis for generic separation and I have retained it in the genus *Rhizoclonium*.


*Rhizoclonium riparium* var. validum (Hansg.) De Toni, Syll. Alg. i : 279 (1889).


Standoff Rock, on less-exposed part of the rock above the *Corallina* zone, 18 Feb. 1956, G.I.S.S. 1526.

Probably cosmopolitan.

This alga was collected from the upper littoral zone of Standoff Rock, where it formed part of the Bostrychietum together with *Bostrychia mixta*, *Rhizoclonium ambiguum* and *Spongomorpha* sp. The plant consists of filaments (Figs. 16–18)

1 The publication date of L. W. Dillwyn’s *A Synopsis of the British Confervae* is cited by many authors as 1809. In fact it was published in fascicles issued from 1802 to 1809 and for nearly all species the precise date of publication is printed on the plate.
which measure 30–37μ wide with cells whose length is less than to two and a half times more than their width depending on how recently they have divided. The cell walls are lamellated and fairly thick. The filaments are unbranched but rhizoids are present which terminate in slightly digitate haptera (Figs. 16, 17). Cytological details are not discernible as the cell contents have shrunk. Growth takes place by intercalary cell division and all stages of this process can be seen in the material (Figs. 16, 18).

No previous record of the occurrence of *R. riparium* forma *validum* as a member of a *Bostrychia mixta* community has been found but *R. riparium* has often been recorded and some of the records probably refer to this forma. In the British Museum Herbarium there is a specimen of this plant from the spray zone of the shore at Knysna, South Africa, which has some *Bostrychia mixta* with it. This material was collected by Boodle and annotated by E. S. Barton but was not included by her in her lists of Cape algae. The spray zone is the usual habitat of this particular Bostrychietum (cf. Post, 1959, p. 498). Also in the British Museum Herbarium there is material of *R. riparium* forma *validum* from Kerguelen Island collected on the “Erebus” and “Terror” Expedition and labelled *Conferva tortuosa* ß *perreptans* in J. D. Hooker’s handwriting. Joly’s record (1957, p. 59) of *R. riparium* from Brazil probably refers to forma *validum* since he records the filaments as being 35–40μ wide.
The name *Rhizolonium riparium* forma *validum* is usually cited as having been published by Foslie in Wittrock & Nordstedt, Alg. Aq. Dulc. Exsicc. : n. 624 (1884), but the printed label of this number, which was included in Fasc. 14, reads:

624. *Rhizolonium riparium* (Roth) Harv.

*Forma valida*, crassit. cell. 26–36μ, altit. ½ minore–2½ plo majore.

. . . . . [Habitat].

*M. Foslie.*

The second line is clearly a comment on the characteristics of this particular specimen and not the last part of the name of a new taxon followed by a diagnosis. This view is confirmed by the list of new taxa in Fasc. 1–20 of the work (Wittrock & Nordstedt, Alg. Aq. Dulc. Exsicc. 21: 16 (1889)) where the entry under n. 624 has the same form as the printed label, whereas on the next page there appears:

944. *Rh.* hieroglyphicum (Ag.) Kütz. f. calida (Kütz.) Wittr.

It may well be that, when communicating the specimen to Wittrock and Nordstedt, Foslie intended that it should be treated as a new forma, for in 1890 he treats the name *Rhizolonium riparium* forma *validum* as having been published by them on n. 624 of their set of exsiccata, but this does not alter the fact that they did not do so.

The epithet *validum* was first validly published for an infraspecific taxon in *Rhizolonium riparium* by Hansgirg in his *Prodromus der Algenflora von Böhmen*, the taxon being based on the specimen issued by Wittrock & Nordstedt. Hansgirg nowhere states the rank to which he assigns the infraspecific taxa which he designates with roman letters, but it is clear from the way in which his work is set out that it is higher than variety, designated by Greek letters thus: “var. β)”, and they must therefore presumably be treated as subspecies. Hansgirg’s attribution of the name to Foslie is based on a mistake and its authorship cannot therefore be cited as “Foslie ex Hansgirg”; there is no evidence that Foslie ever regarded this taxon as having a rank higher than forma. De Toni reduced Hansgirg’s *R. riparium* b) *validum* to the rank of a variety in 1889. Although Foslie in 1890 makes no reference to Hansgirg or De Toni, he cites the same type and his name must be treated as an alteration of rank.

This taxon is quite clearly delimited. It consists of plants of the *Rhizolonium* type with unbranched filaments 28–45μ wide but mostly in the 30–35μ range. The cells are longer than wide unless they have divided very recently and usually have fairly thick walls, although wall thickness depends to some extent on external conditions. There has been much confusion as to what the taxon should be called and in the first place the difference between *Conferva tortuosa* Dillw. and *C. tortuosa* sensu J. G. Agardh (Alg. Medit. Adr.: 12 (1842), non Dillw.) had to be established. This was done in 1939 by Chapman, who included them in *Rhizolonium tortuosum* (Dillw.) Kütz. and *Chaetomorpha capillaris* (Kütz.) Börg. respectively. He included *R. riparium* forma *validum* as a synonym of *R. tortuosum*. Subsequently, Chapman transferred *R. tortuosum* to *Lola* A. & G. Hamel. This genus, as described by A. & G. Hamel (1929, p. 1094), is distinguished from *Rhizolonium* by the possession of numerous parietal, not few axial, nuclei; and from *Chaetomorpha* by having heterogamous as opposed to isogamous sexual reproduction. The Hamels also said
that *Lola* was unbranched and only rarely had rhizoids. Chapman seems to have transferred *R. tortuosum* to *Lola* only because it was unbranched as he gives no details about either its cytology or reproduction. In view of the great variability of branching throughout the *Cladophorales*, I do not think this reason enough to transfer the plant to another genus. In 1931 (p. 25) G. Hamel included in the genus *Lola* the species *Conferva implexa* Harv. and quoted *R. tortuosum* Kütz. as a synonym of this. He said that it had 8–18 nuclei but made no comments on the reproduction. *R. tortuosum* is quite distinct from *C. implexa* and I do not think it is possible to take this statement as evidence of the cytological structure of *R. tortuosum*.

In 1955 Koster published a very careful and exhaustive review of the genus *Rhizoclonium* in the Netherlands. In this she included *R. riparium* forma *validum*. Whilst agreeing with Chapman that this was the same taxon as *R. tortuosum*, she considered that its separation from *R. riparium* was untenable. In forma *validum* she included all plants, with or without rhizoids, with filaments 28–40μ wide and in forma *riparium* plants, with or without rhizoids, with filaments 17–33μ wide. Examination of Dillwyn material (not type) of *Conferva tortuosa* and Wittrock & Nordstedt’s n. 624 on which *R. tortuosum* forma *validum* is based, both in the British Museum Herbarium, confirmed that they agree with this concept. The Dillwyn specimen of *C. tortuosa* is without rhizoids and has filaments 35–40μ wide, Wittrock & Nordstedt’s material has many rhizoids and the filaments are about 30μ wide. I have not been able to make observations on the nuclei of any of the specimens I have examined as this was not found to be possible on pressed or formalin-preserved material.

Sinha (1958) published the results of a cytological investigation on this and other species of the *Cladophorales*. Included in his results were the following chromosome counts:

<table>
<thead>
<tr>
<th>Species</th>
<th>mitosis</th>
<th>meiosis</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>R. riparium</em> (marine)</td>
<td>2n = 36</td>
<td>n = 18</td>
</tr>
<tr>
<td><em>R. riparium</em> (brackish and freshwater)</td>
<td>2n = 36</td>
<td></td>
</tr>
<tr>
<td><em>R. riparium</em> forma <em>validum</em> (brackish)</td>
<td>2n = 24</td>
<td></td>
</tr>
<tr>
<td><em>R. riparium</em> forma <em>validum</em> (marine)</td>
<td>2n = 24</td>
<td></td>
</tr>
<tr>
<td><em>R. tortuosum</em> (marine)</td>
<td>2n = 24</td>
<td></td>
</tr>
</tbody>
</table>

He then wrote: “There is cytological support for Stockmayer’s view that *R. riparium* f. *validum* is a synonym of *R. tortuosum* and that *R. riparium* is a distinct species whether found in marine, freshwater or brackish situations”.

In view of all the evidence outlined above, I am in no doubt that *Conferva tortuosa* and *R. riparium* forma *validum* are synonymous and I am also in agreement with Koster in retaining this forma in the species *R. riparium*.


South Africa, Tristan da Cunha, New Zealand, Pondicherry, Bermuda.

*C. radiosa* grew very abundantly on Church Rock where it dominated the lower littoral zone of the rock and extended into the sub-littoral on the sheer southern face. It was also collected from the sub-littoral zone at Window Rock. Baardseth recorded it from littoral pools and from the sub-littoral zone on Tristan da Cunha.

Figs. 19–21. *Cladophora radiosa* (Suhr) De Toni: 19, terminal branching; 20, terminal branching of specimen from Cape of Good Hope labelled *C. pellucida* by Harvey; 21, habit of Gough Island plant.
The plant grows in dense, erect clumps up to 9 cm. high, which consist of numerous branched fronds. From the base of the fronds downward-growing rhizoids are produced which interweave and form a mat on the rock. The lowermost cell of the frond is very large, measuring up to 40 mm. long × 0.45 mm. wide with thick, lamellated walls up to 70μ thick. The plants (Fig. 21) branch from about two-thirds of the way up; the main branches are dichotomous and the secondary ones (Fig. 19) are dichotomous or trichotomous. The blunt apical cells measure from 700μ to 1,300μ in length and from 200μ to 330μ in width, the shorter ones tending to be the widest. The upper cells measure up to 2,000μ long × 200–330μ wide and the walls are about 45μ thick. There is a tendency for the cells to be somewhat swollen at the cross walls and more particularly at the dichotomies. An occasional swollen, barrel-like cell is present, but there are not enough of these to make them a characteristic feature of the plant.

The nomenclature and taxonomy of this little-known species of Cladophora have become somewhat confused. Barton pointed out that Conserva radiosa and Cladophora catenifera are both the same taxon, and Papenfuss has confirmed this. Papenfuss also attributes the combination Cladophora radiosa to Kützing. However, although Kützing in the Species Algarum included this species under the general heading of Cladophora, he put it in Species Inquirendae at the end of the genus and retained the generic name Conserva for it. The first author to call the plant Cladophora radiosa was therefore De Toni.

The species is characterized by the very long basal cell, the rhizoidal base and the dichotomous to trichotomous nature of the branching. It bears some resemblance to C. prolifera (Roth) Kütz. but is much less wiry; also that species, when pressed, is green whereas C. radiosa is brown. The type specimen of C. catenifera is a specimen from the Cape of Good Hope collected by Harvey and sent to Kützing as C. pellucida. There are two isotypes of C. catenifera in the British Museum Herbarium (Fig. 20) with which the Gough Island material agrees quite well. The main difference lies in the rather longer upper cells of the Harvey material. The relative shortness of the cells of the Gough Island plant may be due to the extremely severe conditions of the locality. Baardseth points out that the apparently barrel-like shape of the cells of C. catenifera as illustrated by Kützing was probably due to the preservation; it was certainly not a noticeable feature of the Harvey material in the British Museum Herbarium after it had been soaked and gently warmed in a weak detergent solution.

Chapman (1956, p. 446) recorded this species from New Zealand and pointed out its similarity to C. feredayi Harv. Chapman gives no cell measurements and his drawing is not clear enough to enable comparison of the New Zealand material with material from other localities.


Europe, North America, Brazil.
Plants of this species grew in abundance attached to the base of *Corallina* plants in littoral rock pools on Íselda Rock. The plants (Fig. 22) are up to 5 cm. high and are fairly stiff; they are composed of long, straight, branching filaments. Branching (Figs. 23, 24) is mainly dichotomous but sometimes trichotomous, particularly in the lower parts of the plant; there is thus no single main axis. The angle between the branches is always acute and the plants are not spreading. At the dichotomies, the basal cells of the branches coalesce (Fig. 24), a characteristic of this species. Growth is mainly intercalary. The apical cells are obtuse (Fig. 24) and measure 200–350 (–500) μ long × 60–90 μ wide. Cells in the

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**Figs. 22–25.** *Cladophora rupestris* (L.) Kütz.: 22, habit of plant; 23, terminal branching; 24, detail of branching and apex, *a* = apical cell; 25, sporangia.
upper branches measure 300–700μ long × up to 200μ wide and cells in the lowermost part of the plant measure up to 1,050μ long × 150μ wide. All the cells have the characteristically very thick, lamellated wall (Fig. 25) up to 45μ thick the structure of which has been investigated by Frei & Preston (1961). The material was reproducing (Fig. 25), and spores escaping through a pore in the cell wall can be seen. In this preserved material it is not possible to determine the type of spore.

Mr. C. van den Hoek, who kindly determined the material, said that had it come from Europe he would have had no hesitation in naming it C. rupesiris but that it might be better to give it this name only tentatively in view of the geographical isolation of the locality from the main area of distribution. There have been various records of this species from the Southern Hemisphere, but the only reliable one is probably that of Joly (1957, p. 57) from Brazil. J. D. Hooker (1845–47, p. 495) and Dickie (1876, p. 47) recorded the species from Kerguelen, but the material on which these reports are based (in the Kew and British Museum Herbaria respectively) is all Spongomorpha sp. There are several records of C. rupesiris from South Africa but these have also been re-identified as other taxa: for example, Hohenacker, Meeresalg. 465 and Tyson, Alg. Exsicc. Austro-Afr. 13 have both been identified by Papenfuss as C. capensis. Hariot (1889, p. 18) recorded the species from Fuegia, but I was not able to find the specimen on which this record was based in the Herbarium of the Muséum National d’Histoire Naturelle, Paris. On present knowledge, therefore, it seems that the distribution of C. rupesiris in the southern hemisphere is restricted to the Atlantic Ocean.

CODIACEAE


Cosmopolitan.

This species was common in littoral rock pools on Gough Island and was collected from West Point Reefs and Slaughtered Seal Bay. The material collected consists of large, robust plants up to 30 cm. tall with branches up to 2 cm. broad. The branching is irregular; it is mostly dichotomous but sometimes numerous small branches are given off over a very small area or sections of branch present a warty appearance. The utricles are mucronate, and sporangia are present in G.I.S.S. 1506.

Although the species C. fragile is so widespread, Silva has distinguished a number of subspecies each of which has a fairly restricted distribution. As he has not finished his work on the species from the South Atlantic, it is not possible to say which subspecies the Gough Island material represents.

1 Dr. P. C. Silva is at present working on Codium from the South Atlantic and is including the Gough Island material in his survey.


Church Rock, dominant over considerable areas of shaded vertical rock face, 5 Mar. 1956, _G.I.S.S._ 1532, 1535.

Distribution not certain, probably chiefly Atlantic.

This species was collected from Church Rock where it was growing on a shaded, vertical rock face. The specimens agree well with Baardseth’s description of the plants from Tristan da Cunha.

**PHAEOPHYTA**

**ECTOCARPACEAE**


Slaughtered Seal Bay, below 15 cm. in rock pools, 22 Dec. 1955, _G.I.S.S._ 1506.

Europe, Canary Islands, Tristan da Cunha.

The plant was found growing in tufts on _Codium fragile_ in rock pools at Slaughtered Seal Bay. The tufts are about 2 cm. high and have a rhizoidal base, the filaments of which weave in among the _Codium_ utricles and anchor the tufts firmly. Kuckuck described two sorts of tuft in European material and the Gough Island plants resemble his northern form in being rather compact and having a dense “kernel” of branched filaments where most of the reproductive bodies are found surrounded by an outer fringe of unbranched, lightly pigmented filaments.

The erect filaments are branched, ribbon-like and 40–50μ wide. These dimensions are similar to those given by Baardseth for the Tristan da Cunha material and by Børgeisen for that from the Canary Islands but are rather smaller than in the European specimens described by Kuckuck as being about 70μ wide. The meristems are intercalary except in some young side branches (Fig. 26), which are still entirely meristematic. The meristems and branches occur in the lower two-thirds of the tufts and beyond this region the filaments extend into long, scantily pigmented hairs. Branching is irregular; many branches arise from the growth of the stalk cell of old sporangia (Fig. 27). The branches are initially at right-angles to the filaments which bear them, but gradually the lower wall of the basal cell elongates more than the upper wall and the angle thus becomes acute.

The plants were reproducing abundantly; both unilocular and plurilocular sporangia are present. Both types of sporangium can be seen in a single tuft, but the two types are not found on the same filament, a condition illustrated by Kuckuck (loc. cit., figs. 9, 10).
Unilocular sporangia have only been recorded once previously: by Kuckuck on material from Rovigno (now Rovinj) on the Adriatic coast. In the Gough Island plants these sporangia (Figs. 28–31) are globose, and mature ones have a diameter of about 50µ. With very few exceptions the sporangia have a one-celled stalk, but occasional two-celled stalks (Fig. 29) are present. Sometimes a new sporangium develops inside the ruptured wall of an old one (Fig. 30). Unilocular sporangia are usually borne laterally on the filaments but occasionally they develop terminally on young side branches. No unilocular sporangia containing ripe...
spores were found, and it was accordingly not possible to ascertain how they developed and were liberated. These unilocular sporangia differ somewhat from those described by Kuckuck as being sessile and 70–90 μ high × 50–70 μ wide. Kuckuck also described a second type of unilocular sporangium. This type was stalked, globose and about 70 μ in diameter, and was thus more like the Gough Island sporangia; it differed however in being found characteristically on the same filament with plurilocular sporangia.

The plurilocular sporangia (Figs. 32, 33) are nearly always stalked and lateral but occasional sessile or terminal ones are seen. They are solid-looking, ovoid bodies and mature ones measure up to 80 μ wide × 100 μ long; this is very similar in size and shape to those described by Kuckuck, Bornet and others. The spores differentiate in the sporangium and are liberated by the rupture of the apex of the sporangium (Fig. 33). Plurilocular sporangia also grow inside the ruptured wall of old sporangia.

Many liberated spores are present in the material (Fig. 34); several had germinated and others had developed into the few-celled plantlet stage on the surface of the filaments. It is also common to find spores germinating while still inside the sporangia. These features were also commented on by Bornet.

The Gough Island plants therefore agree closely with this species as it is known from other parts of the world. Dr. P. Kornmann, who kindly confirmed the identification, remarked on this close similarity.

Baardsseth’s record of this species from Tristan da Cunha was the first from the Southern Hemisphere but the species is well known from Europe and the Canary Islands. Good descriptions of the plant have been given by Bornet, Børjesen and Kuckuck.


A small quantity of this plant was found growing as an epiphyte on *Codium fragile* in rock pools at Slaughtered Seal Bay; it was intermingled with the much more abundant growth of *Feldmannia globifera*. The soft, feathery plants are up to 2.5 cm. tall and show the characteristic opposite branching (Fig. 35) of the species and the cortication of the lower part of the main axis by downward-growing rhizoids (Fig. 36). The main axis and branches measure 40–70 μ wide, which is rather narrow for this species (cf. up to 100 μ given by Kuckuck) and the material generally is in rather poor condition. The cells are barrel-shaped and in most cells the contents have disintegrated; in some, however, the typical discoid chromatophores can be clearly seen. The meristematic regions (Fig. 35) are intercalary
and in these parts the cells are wider than long. In the more mature parts, the cells are more elongated, especially in the branch apices where they are also very lightly pigmented. The apices are not prolonged into long hairs as they often are in this species, but are very like those illustrated by Sauvageau.

Sessile sporangia are present on the upper sides of the side branches (Fig. 35). The young sporangia are quite clearly divided and plurilocular; although divisions are not apparent in the mature sporangia, they are almost certainly all plurilocular. The apparent absence of cell walls is probably due to the generally poor state of preservation of the material. The sporangia are ovoid and mature ones measure 40–60µ wide × 60–80µ long; this is within the usual size range for this species.


Ectocarpus virescens Thur. ex Sauvageau in Journ. de Bot. 10: 124, figs. 1–7 (1896).—Hamel, Phéophyc. France : 29, fig. 7 (1931).

Figs. 37–41. Giffordia mitchelliae (Harv.) Hamel: 37, rhizoidal base of plant; 38, branching, m = meristematic region; 39, detail of cell contents, d = discoid chromatophore, n = nucleus; 40, plurilocular sporangium; 41, dehisced plurilocular sporangium, m = meiospore.
Dell Rocks Beach, occasional in sheltered places between boulders and in shallow pools, 12 Apr. 1956, G.I.S.S. 1558.

Widely distributed in warm and temperate waters.

This species was found growing on rocks in shallow pools and in sheltered places between boulders at Dell Rocks Beach. The plants are about 5 cm. tall and soft and feathery like the form from sheltered places on Tristan da Cunha reported by Baardseth. The base of the plant is rhizoidal (Fig. 37) and the upper part richly and irregularly branched (Fig. 38); the side branches are sometimes secund as shown in the figure, but this is not a pronounced feature of the plant. The main axes measure up to 40μ wide with cells up to twice as long as wide. The cells have discoid chromatophores (Fig. 39). Meristematic regions occur at the base of the side branches (Fig. 38); these branches usually taper somewhat towards the apex but the apical cells are always obtuse.

Plurilocular sporangia are present (Figs. 40, 41); these are usually sessile and lateral on side branches but are occasionally found on the main axis or terminally on young side branches. The sporangia are elongated with rather a blunt apex; they vary considerably in size, the largest measured being 120μ x 30μ. The loculi are about 6-7μ high x 7-8μ wide and thus correspond (like the ones described by Baardseth from Tristan da Cunha) to the meiospore loculi of Sauvageau (tom. cit.: 114).

SPHACELARIACEAE


Fig. 42. Sphacelaria furcigera Kütz. : branching, propagule on left.
Slaughtered Seal Bay, below 15 cm. in rock pools, 22 Dec. 1955, G.I.S.S. 1506. Widely distributed in warm, temperate and colder waters.

This species was found growing as an epiphyte on Codium fragile in rock pools at Slaughtered Seal Bay. The plant is firmly anchored to the host by means of rhizoids which weave in among the Codium utricles and form knotted masses at intervals. Reinke shows the rhizoids of S. furcigera actually penetrating the tissue of the Sargassum on which it is growing, but the nature of the Codium thallus is such that the Sphacelaria cannot penetrate its tissues. The plants measure up to 12 mm. high; the upper parts are sparingly branched (Fig. 42) and hairless; the filaments measure 20–40\(\mu\) wide, which accords well with the dimensions given by Reinke and Irvine; the plants also bear a close resemblance to the figures of Kützing. Sporangia are absent but occasional bi-radiate propagules are present (Fig. 42), the appearance of which does not differ markedly from ordinary side branches.

Some of the material was sent to Dr. Irvine who confirmed the identification and commented as follows: “I could find no well-developed propagules, though a few showed clear signs of developing two arms only. The young propagules appear to be second or even third generation from the base and there is no sign of hairs either on the propagules or elsewhere. The general dimensions, mode of branching, number of longitudinal divisions of segments (1–3) and form of propagules seem right for S. furcigera; the lack of hairs is probably unimportant as in general I have found that their presence is very variable, apparently depending on the temperature, at least to some extent, i.e. the higher the temperature the more hairs. The only point that does worry me a little is the presence here and there of quite distinct little holdfasts like those of S. pennata; in general though, the axes spring from dispersed rhizoids as is usual in this species. There are also very occasional secondary transverse divisions, but I do not really think that this is of much significance.”

Skottsberg recorded the species from Tierra del Fuego and the Falkland Islands.

PUNCTARIACEAE


Ulva sinuosa Roth, Catalect. Bot. 3: 327, t. 12 (1806).


Probably cosmopolitan.

This species was collected only once from Gough Island, where it grew quite abundantly on rocks of the lower littoral zone of the Midshipman Rock. The plants form brown, warty, gelatinous cushions which are up to 1 cm. thick (Plate 16 b).
In section (Figs. 43–45) the plant body consists of an outer layer, one or two cells deep, of more or less cubic cells up to about 12\(\mu\) in diameter, which are usually pigmented. Inside this cortex is the medulla, consisting of colourless, irregular cells which increase in size towards the centre. The middle of the thallus is hollow. Pigmented hairs are present; these grow fairly deeply embedded in the thallus (Fig. 45) in cryptostomata and are about 7\(\mu\) in diameter. Plurilocular sporangia were found over much of the surface of the thallus; the sporangia (Figs. 43, 44) arise from the outer cells of the cortex and consist of sixteen cells in two rows of eight. Mature sporangia measure up to 40\(\mu\) high \(\times\) 8\(\mu\) wide. Paraphyses are present between some of the sporangia; they are large and somewhat clavate and measure about 50\(\mu\) \(\times\) 15\(\mu\). The cortex and medulla together are about 160\(\mu\) thick.

![Diagram of Colpomenia sinuosa](image)

**Figs. 43–45.** *Colpomenia sinuosa* (Roth) Derb. & Solier: 43, vertical section through thallus, \(p\) = paraphysis, \(ms\) = mature sporangium; 44, vertical section through thallus, \(p\) = paraphysis, \(ys\) = young sporangium; 45, vertical section through thallus, \(h\) = hair, \(c\) = cryptostoma.

The type form of *C. sinuosa* is a balloon-like, hollow ball. Several varieties have however been described which closely resemble the tuberculate Gough Island plant. Saunders (tom. cit.: 164) described a new species, *C. tuberculata*, which was subsequently reduced to *C. sinuosa* forma *tuberculata* by Setchell & Gardner (tom. cit.: 541). This forma is extremely like the Gough Island plant in external form but differs in microscopic detail. The cortex is about four cells deep and the sporangia, which measure up to 25\(\mu\) tall, have cells in a single row, not a double row. The
Gough Island plant also strongly resembles *Iyengaria stellata* (Børg.) Børg. (1939, p. 92) externally, although it is smaller than that species (which includes *Colpomenia capensis* Levring (1938, p. 20)) in both macroscopic and microscopic detail. The generic status of *Iyengaria* is rather dubious as it is separated from *Colpomenia* only by the absence of paraphyses among the plurilocular sporangia and an allegedly somewhat different growth process in the thallus. Re-investigation of *Iyengaria* is needed; meanwhile the Gough Island plant would seem to differ from it in the possession of sporangial paraphyses.

In conclusion, I think that this alga comes within the generally accepted variation range of *C. sinuosa*, and while it does not externally resemble the type form of this species, it is yet not sufficiently like any of the described varieties to be referred to one of them. Tuberculate forms of *C. sinuosa* have been mentioned by various authors and of particular interest is that described and illustrated by Joly (1957, p. 84, t. 4 fig. 3 b) from Brazil, which appears to be very similar, macroscopically, to the Gough Island plant. Unfortunately, Joly does not give an account of the microscopic structure and further comparison is thus impossible.


Cosmopolitan.

Of the four collections of this plant made on Gough Island, two (*1519* and *1536*) are of the form which Setchell & Gardner designate as *cylindricus minor* and the other two are of that which they call *typicus*. The plants of the latter come from the mid and lower shore while the others are from pools, often bird-fouled, on the upper shore. Baardseth recorded both forms from Tristan da Cunha.

**LESSONIACEAE**


*Fucus pyriferus* L., Mant. Pl. Alt.: 311 (1771).


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*MARINE ALGAE OF GOUGH ISLAND*
Circum-subantarctic between latitudes 40° S. and 60° S.; west coast of South America as far north as Peru; west coast of North America.

Two collections of *Macrocystis pyrifera* were brought back from Gough Island including an intact holdfast and an apical frond with the leaflets joined together terminally. The holdfast (Fig. 46) shows the dichotomous haptera typical of this species. The pear-shaped air bladders (Fig. 47) at the base of the leaflets are also a characteristic feature.

Plants of this species formed a band round Gough Island from about 18 to about 55 m. immediately below the *Durvillaea* band; it was absent only from the very exposed part of the western end of the island.

**DURVILLAEACEAE**


*Durvillaea utilis* Bory in D’Urville, Fl. II. Malouines : 17, 22 (Dec. 1825¹) (reimpr. in Mém. Soc. Linn. Par. 4 : 589, 594 (Jan. 1826¹)), *nom. invalid.*

¹ For these dates see under *Iridaea undulosa*, p. 224.

Outer Dell Rocks, dominant from mid-tide level to 2 m. below low-tide level on immobile rocks, occasional in deep rock pools, 18 Feb. 1956, G.I.S.S. 1510.

Sub-antarctic Islands, South America, New Zealand.

This species dominated the lower littoral and sub-littoral zones of the Gough Island shores. Two collections were made, one of young plants showing the shield-like attachment organ and divided, leathery frond; the other a fragment of a mature frond showing the spongy, honeycomb texture. The young plants had no reproductive organs but the mature frond bore female conceptacles. The plants grew to an immense size with fronds up to 3 m. long and holdfasts at least 7.5 cm. thick.

**D. antarctica** is a very characteristic species of the sub-antarctic sub-littoral; its distribution is mapped by Knox (1960, p. 589). It does not grow as far north as Tristan da Cunha in the Atlantic.

In the prefatory part of the Flore des Iles Malouines, D’Urville gives an account of the general appearance of an alga and concludes: "M. Chamisso l’avait très-bien décrit sous le nom de Fucus antarcticus; mais M. Bory y a reconnu le type d’un genre nouveau, et a jugé à propos de l’appeler Durvillaea utiliz." In the list of species, compiled, as far as the cryptogams were concerned, by Bory, the entry relating to this species reads: "27. Durvillaea utilis. Bory. Porro. Le Gentil (Voyage, tome II, pl. 3.) Fucus antarcticus. Chamisso (Voyage pitt. de Choris.) Laminaria porroidea. Lamour. (Dict. class. hist. nat. art. Géographie botanique)."

"Porra" of Le Gentil is a vernacular name and the botanical name provided for the species in his work is a "pre-Linnaean" one: *Fucus ramis ex tuberculo rotundo exientibus, foliis planis, profunde crenatis, pediculatis, pediculis uno versus dispositis* (Le Gentil de la Galaisière, Voy. Mers Inde 2 : 215, t. 3 (1781)). The name *Laminaria porroidea* was never validly published, although Lamouroux (Dict. Sci. Nat. 25 : 189 (1822)) had published *Laminaria porra*, based on Le Gentil’s "Porra".

In his full account of *Durvillaea* in the Voyage... Coquille, Bory points out that D’Urville’s account was based primarily on a different alga, *Laminaria Buccinalis* (L.) Lamour. (= *Ecklonia maxima* (Osb.) Papenf.), and that Le Gentil’s "Porra" also was not *Durvillaea* but probably *Macrocystis*. He states, however, that Lamouroux had imperfect specimens of *Durvillaea* from Valparaiso in his herbarium labelled *Laminaria porroidea*.

The generic name *Durvillaea*, and hence the specific name *D. utilis*, is not validly published in the Flore des Iles Malouines. D’Urville’s remarks can scarcely be treated as a description. Even if they could, they would be a description of the species already described as *Fucus antarcticus* by Chamisso, and neither they nor Chamisso’s original description can be regarded as a descriptio generica-specifica, for the genus, though monotypic, is not founded on a new species.

1 For this date see under *Iridaeae undulosa*, p. 224
When the generic and specific names were validly published by Bory in the *Dictionnaire Classique*, he again cited *Fucus antarcticus* as a synonym of *Durvillaea utilis*, the epithet of which is consequently superfluous and illegitimate. In this, and throughout his works, Bory spelled the generic name *Durvillaea*, indicating that he intentionally latinized D'Urville's name as "Durvillaeus". The "correction" to "*Durvillea*", the form usually adopted, cannot therefore be justified under Art. 73 of the International Code.

**RHODOPHYTA**

**BANGIACEAE**


Only one collection of this species was made and that was from the supra-littoral zone of Standoff Rock where the *Bangia* was growing with *Porphyra tristanensis*, *Hildenbrandia* sp. and *Verrucaria* sp.—a very characteristic supra-littoral community. Although it was not recorded or collected from any other part of Gough Island, it is a rather inconspicuous plant when growing and probably occurs elsewhere on the island.


9 : 36, figs. 14, 15 f (1941). (Figs. 48–51.)


Tristan da Cunha group of islands.

*P. tristanensis* is the dominant plant of the Gough Island supra-littoral, where it forms a zone together with a lichen, *Verrucaria* sp.

Some of the material was sent to Miss J. M. Graves who has studied South African *Porphyra*. I am grateful to her for drawing Figs. 48–50 and for the following description and comparison with *P. capensis* Kütz. :

"The specimens correspond quite well with *P. capensis* as that species is found in moderately warm water (e.g. False Bay, Cape). The holdfast has the typically umbilicate form. In section [Fig. 48] the vegetative cells appear to have one chromatophore. The cells are not so markedly elongate as are those of typical *P. capensis* but I think they fall within the variation range. The protoplasts have unfortunately shrunken away from the cell walls which makes measurement of the cell dimensions a little difficult, but as far as I can make out, the vegetative cells are from 15–25μ wide x 50–60μ long as seen in transverse section. The ratio length/breadth therefore varies from 2 : 1 to 4 : 1. The majority of the cells measured are about three times as high as broad as is the case in warm-water *P. capensis*. A
Figs. 48–51. *Porphyra tristanensis* Baards.: 48, transverse section through thallus, vegetative cells; 49, surface view of thallus, c = carpospores; 50, transverse section through thallus of *G.I.S.S. 1513*, c = carpospores; 51, transverse section through thallus of *G.I.S.S. 1503*, c = carpospores.

Comparison of measurements of *P. capensis* and the Gough Island plants can be seen in the following table:

<table>
<thead>
<tr>
<th></th>
<th>Length of vegetative cells in transverse section</th>
<th>Width of vegetative cells in transverse section</th>
<th>Thickness of thallus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cold-water <em>P. capensis</em></td>
<td>100–135μ</td>
<td>12–26μ</td>
<td>130–180μ</td>
</tr>
<tr>
<td>Warm-water <em>P. capensis</em></td>
<td>47–68μ</td>
<td>11–19μ</td>
<td>70–80μ</td>
</tr>
<tr>
<td>Gough Island <em>G.I.S.S. 1513</em></td>
<td>50–60μ</td>
<td>15–25μ</td>
<td>up to 90μ</td>
</tr>
</tbody>
</table>
"The plants are all carposporophytic. The number and arrangement of carpospores in the parent cell is similar to that in warm-water *P. capensis*. There is a total of sixteen carpospores per cell and these appear as two rows of four cells each [Fig. 50] in transverse section. The arrangement in surface view [Fig. 49] is somewhat more irregular than in *P. capensis*. The distribution of the fertile area on the thallus—an irregular marginal zone which is slightly broader at the distal end than at the sides—corresponds well with *P. capensis*.

"To sum up, I would say that the available material corresponds quite well with warm-water *P. capensis*."

I myself thoroughly investigated the plants in *G.I.S.S.* 1503 and found them to agree with Miss Graves's description of *G.I.S.S.* 1513 as to the vegetative characters. In this material also, only carposporophytic plants are present and in these plants there are often up to 32 carpospores per parent cell (Fig. 51); this also comes within the variation range of *P. capensis* (see Isaac, 1957).

The taxonomy of the genus *Porphyra* is extremely confused; with such a simple structure, the number of characters is small and there seems to be considerable overlapping between species. Workers on European members of the genus are gradually elucidating the taxonomy by studying the appearance and development of living plants and it seems that only by doing this in conjunction with careful study of type material will it be possible to define specific limits within the genus. Unfortunately in this case only preserved material is available for study and all the plants are female. The plants are thus probably dioecious but it may be that it is a monoecious species in which the spermatia have not yet developed. I think there is little doubt, however, that this species is the same as that described by Baardseth from Tristan da Cunha and that this is probably the same as *P. capensis* from South Africa.

Levring (1953, p. 464, and 1956, p. 410) published accounts of *Porphyra* in Australia and New Zealand and found that, of the two lithophytic species, *P. umbilicalis* J. G. Agardh was dioecious with usually 8 carpospores per parent cell while *P. columbina* Montagne was monoecious with 32 carpospores per parent cell. Other workers, however, consider that *P. umbilicalis* can be either monoecious or dioecious and this probably also applies to *P. columbina* as it does to *P. capensis*. It seems, therefore, best to call the Gough Island plants *P. tristanensis* until the relationship between this and other southern cold-temperate species has been elucidated by the study of living material of them all.

**Gelidiaceae**

*Gelidium regulare* Baards. in Res. Norw. Sci. Exped. Tristan da Cunha 9: 52, figs. 23, 24 A (1941). (Fig. 52.)


*G. regulare* was found in littoral rock pools at Slaughtered Seal Bay; it was growing with *Corallina officinalis*, *Dermatolithon nodulosum*, *Lithothamnium lamellatum* and *Centroceras clavulatum*. 

The plants (Fig. 52) measure up to 6 cm. tall. They show the distinct main axis and abundant, tripinnate branching described by Baardseth. Tetrasporangia are present. Baardseth pointed out that this species is very similar to the European species *G. latifolium* (Grev.) Born. & Thur., but until more is known of the distribution and variation range of that species it seems best to give the South Atlantic plants a different name.

![Diagram of *Gelidium regulare*](image)

**Fig. 52.** *Gelidium regulare* Baards.: habit of plant, *t* = tetraropangia.

**CORALLINACEAE**

*Coralina officinalis* L., Syst. Nat., ed. 10, i : 805 (1758). (Figs. 53, 54.)


All Northern and Southern Hemisphere temperate seas, arctic, antarctic.

*C. officinalis* was very common on the shores of Gough Island; it grew in littoral rock pools, and in two places, Standoff Rock and the Midshipman Rock, it formed a zone on the rocks at mid-tide level.

The plants (Fig. 53) are small, seldom exceeding 4 cm. in height. They have a very pronounced main axis bearing densely crowded, slender, pinnate branches which often branch again. The intergenicula of the main axis and first-order branches are flattened, the second-order branches are usually thread-like and terete. Reproductive conceptacles (Fig. 54) are abundant; they are globose with an apical pore and are occasionally antenniferous. In longitudinal section the cells of the intergenicula are seen to be in horizontal rows all of much the same height; the cells measure about 60–70μ high × 7–9μ wide and form lateral synapses. Each geniculum is composed of a single row of long cells with thick walls. The plants are frequently covered with epiphytes, *Herposiphonia paniculata* being the most common one.
C. officinalis has frequently been recorded from southern cold and temperate waters, but in only one case (Skottsberg, 1923, p. 67) has the material been described and this material is obviously different from the Gough Island plants. The Gough Island plants differ from the type form of C. officinalis in their small size and very dense branching but I am of the opinion that they come within the variation range of this species. Dr. Levring, to whom I sent some material, said that it closely resembled his material from Chile and he thought that it should be included in C. officinalis (see Levring, 1960, p. 40).

In the collections in the herbaria of the British Museum, Kew and the Muséum National d'Histoire Naturelle, Paris, there are a few specimens which much resemble the Gough Island material of C. officinalis and these specimens are variously identified as C. officinalis, C. cuvieri and C. chilensis. The distinctions between these three and other species, such as C. vancouveriensis, are far from clear and it seems best to refer the Gough Island plants to C. officinalis.

**Corallina goughensis** Y. M. Chamberlain, sp. nov. (Figs. 55–60; Plate 16 c.)

*Planta usque ad 4 cm. alta, frondibus numerosis erectis e crusta basali ortis, per duos longitudinalis trientes inferiores simplicibus intergeniculis teretibus, per trientem superioriorem dichotome vel corymbose ramosis intergeniculis compressis. Intergeniculorum cellae dispositae in strata horizontalia extremam partem versus deorsum curtata ita corticem formantia; cellae medianae 35–70μ longae, 6–8μ latae, synapsibus lateralis umbilicis bene evolutis. Genicula unizonalia; cellae usque ad 250μ longae. Conceptacula tetrasporica terminalia, in sinu inter ramulos duos posita, poris apicalibus. Tetrasporae zonatim divisa, c. 160μ longae, 60μ latae.*

Isolda Rock, very abundant in lower-littoral rock pools, 6 Mar. 1956, G.I.S.S. 1547 (holotype).

Not known elsewhere.

Plant up to 4 cm. tall with numerous fronds springing from a basal crust. Lower two-thirds of plant unbranched with terete intergenicula; upper third branched dichotomously or corymbose with flattened intergenicula. Cells of intergenicula (Fig. 56) in horizontal rows curving out at the sides to form a cortex. Central cells 35–70μ long × 6–8μ wide, lateral synapses (Fig. 56) very pronounced. Genicula unizonal (Figs. 57, 58), cells up to 250μ long. Tetrasporic conceptacles (Fig. 59) present in the angles of the branches, pores apical. Tetraspores (Fig. 60) zonately divided, about 160μ long × 60μ wide.

This plant was found growing in littoral rock pools at Isolda Rock where it was very abundant. Externally, the plant (Plate 16 c; Fig. 55) is characterized by its dichotomous-corymbose branching, internally by the very striking lateral synapses between the intergenicular cells (Fig. 56) which appear colourless in an otherwise stained section.

It was very difficult to decide in which genus this plant should be included. In the most recent survey of the articulated Corallinaceae, Manza (1937, 1940) divides the species with only terminal conceptacles into the genera Corallina, Jania,
**Arthrocardia** and *Duthiea* 1. With the exception of *Duthiea*, which is characterized by having lateral conceptacle pores, the genera are distinguished by their branching; on this basis this plant should be classified as a *Jania*. However, in the *Corallinaceae* the branching even in a single plant is liable to be extremely variable, and Suneson (1943, p. 48) has pointed out that there are even forms of *Corallina officinalis* which are dichotomous. Most authors distinguish *Corallina* from *Jania* by the length of the geniculate cells, which are at least twice as long as the intergeniculate cells in *Corallina*, and are about the same length as the intergeniculate cells in *Jania*. On this basis I have classified this plant as a *Corallina*. The material is somewhat similar to *Jania digitata* Manza but the intergenicula are more flattened in *C. goughensis* and the upper branches are less regularly dichotomous than those of *J. digitata*.

**Dermatolithon nodulosum** Y. M. Chamberlain, sp. nov. (Figs. 61–65; Plate 17.)

*Planta* horizontaliter crustaceo-expansa, in statu vivo rosea, ad 2 cm. crassa, nodulos calcarios permutlos confertim ferens. *Crusta basalis* ad 700μ crassa, plerumque in vaginam circa nodulos producta, constata e strato supremo simplici cellulis epithallinis parvis planis, stratis medianis pluris horizontalibus cellulis perithallinis ad 50μ longis et 10μ latis, strato infimo simplici cellulis hypothallinis obliquis ad 80μ longis et 10μ latis. *Noduli* e perithallo bene evoluto cellulis ad 100μ longis et 15μ latis constati. *Cellulae perithallinae et hypothallinae* omnes synapsibus secundariis lateralis apicem cellulae versus munitae. *Conceptacula* tetrasporangii in perithallo praesentia, plerumque supra superficiem crustae eminentia, desuper visa circulaire, diametro interno ad 250μ metiendi, ad 150μ alta. *Tetrasporae* zonatim divisae.


Not known elsewhere.

Plant (Plate 17 A) pink when living, up to 2 cm. thick, bearing nodules (Plate 17 B; Fig. 61). Basal crust (Fig. 63) up to 700μ thick, composed of a single layer of small flat epithallial cells, horizontal layers of perithallial cells measuring up to 50μ long × 10μ wide and a single layer of oblique hypothallial cells measuring up to 80μ long × 10μ wide. Nodules (Figs. 61, 62, 64) composed of a much-developed perithallus with cells 100μ long × 15μ wide. All perithallial and hypothallial cells have secondary, lateral synapses which occur towards the top of the cell. Basal crust often extending to form a sleeve round the nodules (Fig. 62). Tetrasporic conceptacles (Figs. 62, 65) present in perithallus, usually projecting a little above the surface. Conceptacles circular in surface view, in section having a diameter up to 250μ and being up to 150μ deep. Tetrasporangia zonately divided.

1 This name, *Duthiea* Manza (1937), is a later homonym of *Duthiea* Hack. (1895) (Gramineae).
D. nodulosum was very abundant on the shores of Gough Island; its conspicuous pink crusts grew on the margins of deep rock pools and over the rock surface of shallow pools; occasionally it grew on the open rocks.

The size and habit of this plant are unusual for a Dermatolithon, most species of which have a very thin thallus and are epiphytic or epizoic. Two other species, D. hapalidioides (Crouan) Foslie and D. papillosum (Zanard.) Foslie, have been recorded as growing on rocks in temperate waters although both are more commonly epiphytic or epizoic. D. nodulosum is similar to these species in microscopic...
structure but is a very much larger plant and has coarser nodules. The other two species have so far only been recorded from the European and North African coasts (Hamel & Lemoine, 1952, pp. 61, 63).

In young plants, only the basal crust is present. The epithallial and outer perithallial cells (Fig. 63) of this crust have homogeneous, rather dense contents, the inner perithallial cells become vacuolated and the hypothallial cells are also vacuolated. The nodules are composed almost entirely of horizontal rows of large perithallial cells (Figs. 61, 64), which are almost devoid of contents and form numerous secondary lateral synapses with the cells round them. What little remains of the cell contents usually collects round the primary pit connexions and secondary synapses.

Only tetrasporangial conceptacles were found. These have one central pore (Plate 17 c; Fig. 65). The tetraspores are usually divided zonately into four but bispores are also present. The conceptacles do not cave in after the spores have been shed and many empty ones can be seen buried in the older parts of the perithallus (Plate 17 c).

LITHOTHAMNIUM NEGLECTUM (Foslie) Foslie in Deutsch. Südpol.-Exped. 1901-03 8 : 207 (1908) ; Contrib. Monogr. Lithothamnia, ed. Printz : 43, t. 9 figs. 1-4 (1929).—Lemoine in 2me Expedit. Antarct. Franç. 1908-10, Melobésiées : 14 (1913) ; apud Cotton in Journ. Linn. Soc. Lond., Bot. 43 : 196, t. 9 fig. 2, t. 10 figs. 3-6 (1915) ; in K. Svensk. Vetenskapsakad. Handl., Ny Följd, 61 (4) ; 12 (1920). (Fig. 66 ; Plate 18.)


Antarctic and sub-antarctic.

Two collections (G.I.S.S. 1507, 1548) of this species come from rock pools at Slaughtered Seal Bay and Isolda Rock respectively. These plants are rather similar both macroscopically and microscopically. They have leaf-like pink thalli (Plate 18 A) with concentric markings. The thallus (Fig. 66) is up to about 400μ thick ; it has a single layer of epithallial cells, below which is the perithallus. The perithallial cells run vertically below the epithallus and measure up to 10μ wide × 17μ long ; they run horizontally in the middle of the thallus and curve downwards below to the hypothallus, the cells of which measure up to 50μ long × 7μ wide. Tetrasporic conceptacles (Plate 18 c) occur in the perithallus ; these measure up to 300μ wide × 200μ deep and open through numerous pores. The tetraspores are zonately divided and measure up to 145μ long × 70μ wide.

The third collection (G.I.S.S. 1553) comes from Isolda Rock where, together with Lithophyllum sp., the plant formed a conspicuous band on the rocks in the upper mid-littoral zone. This plant (Plate 18 b) was white when growing, probably due to bleaching in its exposed position. A similar band was reported to occur in other
parts of the island but no other collection from it was made. This plant is smaller than the preceding ones both microscopically and macroscopically and it probably represents Foslie’s *L. neglectum* forma *fragile* (1908, p. 208).

The two forms are well illustrated in Foslie’s photographs (1929, t. 9) of the species, *G.I.S.S. 1553* resembling Foslie’s figs. 1–3 and *G.I.S.S. 1507* and *1548* his fig. 4.

**GIGARTINACEAE**


¹ For the dates of the natural history parts of the *Voyage ... Coquille* see Sherborn & Woodward in Ann. & Mag. Nat. Hist., Ser. 7, 7 : 392 (1901).


Widespread in southern South America, Falkland Islands, Kerguelen, Crozet Islands, Auckland Island, ? North America.

I. laminarioides was one of the most common littoral algae on Gough Island. On moderately sheltered boulder beaches it formed a conspicuous mid-littoral zone of bright orange-brown which was bounded above by a Blidingia zone and below often merged into a Rhodoglossum zone. It has been recorded as a dominant littoral plant in other regions, such as Chile (Levring, 1960) and Kerguelen and the Crozet Islands (Levring, 1944).

The Gough Island plants (Figs. 67, 68) grow from communal, fairly thin basal crusts which spread over the rocks, each crust giving rise to numerous erect fronds. According to Dr. Holdgate, the smaller, orange-brown plants grew in the more exposed places while larger plants, which were usually more violet in colour, came from the sheltered channels and crannies between the boulders. The material collected measures up to 20 cm. long but is mostly under 9 cm. ; plants from more sheltered places undoubtedly grew longer than this, however. All the plants have a small, terete stipe above the basal crust; above the stipe is a strongly channelled apophysis from which develops the smooth-edged blade which typically has a cuneate base. Only one small piece of the material was found to be fertile ; this (Fig. 68) has tetrasporangia along one side of the edge of the blade. In transverse section (Fig. 69) the blade can be seen to consist of a central medulla of widely spaced, very thin and elongated cells ; towards the edge the cells become shorter and fatter and interweave more noticeably ; finally filaments of up to five, small, oblong cells are produced which lie at right-angles to the surface of the thallus and form a densely packed cortex. The tetrasporangia develop in the medulla ; the intercalary development of the tetrads of spores can be seen when they are young (Fig. 70) and ripe tetrads measure up to about 35μ in diameter (Fig. 69).

Various species of Iridaea occur in great abundance on rocky sub-antarctic shores. The fact that small samples of Iridaea from this area have frequently been collected and often identified without reference to previous collections has resulted in a confused picture of the taxonomy of the genus. Setchell & Gardner in their 1937 paper made the first real attempt since Bory's account in the Voyage . . . Coquille to sort out the taxonomy of the South American species, and their conclusions have been accepted by most subsequent authors. Setchell & Gardner also changed the name of the genus to Iridophycus since Iridaea Bory is a later

Homonym. *Iridophycus* has not been generally accepted, however, and *Iridaea* Bory has been conserved. There is an error in the entry referring to it in the list of *nomina generica conservanda* (Internation. Code Bot. Nomencl. Montreal 1959: 205 (1961)); this reads: "*Iridaea* Bory, Dict. Class. Hist. Nat. 9: 15. 1826". On
the page cited Bory used the spelling *Iridia*, on the next page *Iridea* twice and *Iridaea* twice, and on p. 192 of the same volume *Iridaea*; in his other publications Bory always used the spelling *Iridaea*.

Among the species of *Iridaea* described by Bory is *I. laminarioides*, the type material of which was collected at Concepcion, Chile, by D'Urville during the voyage of "La Coquille". Setchell & Gardner (1937, pp. 202, 206) considered that the type material—the smaller and larger plants of which Bory thought to be juvenile and adult stages of the same species—represented two separate species. They called the adult plants (Bory, 1827, t. 11 fig. 1 D, E) *Iridophycus laminarioides* and the so-called juvenile plants (fig. 1 A, B, C) *I. boryanum*. This last species they considered to be the same as Kützing's *Iridaea heterococca* but did not give it that name because in their opinion the name was based on a monstrosity, the type material carrying a blue-green epiphyte mistaken by Kützing for reproductive organs of the *Iridaea*. Various authors (e.g. Skottsberg and Levring in his 1960 paper) have used Setchell & Gardner's classification of the genus but both Skottsberg and Levring pointed out that the separation of the two species is unsatisfactory since many intermediate forms occur. I had the opportunity of examining Bory's type material of *I. laminarioides* in the herbarium of the Muséum National d'Histoire Naturelle, Paris, and I have also studied much other herbarium material of *Iridaea* in the Paris, British Museum and Kew Herbaria. In my opinion, Bory's type material does represent two species but I think that the plants on which Bory's fig. 1 A, B, C and D were based are all the same species, D perhaps being from a more sheltered position on the shore, and that E (which has a ciliate margin) is a different species. As the fragment of E drawn by Bory represents all the material there is, I do not think it is possible to decide what species it is. *I. laminarioides* is a very variable species, but whilst the blade and apophysis may sometimes have irregular outgrowths, they are never regularly ciliate like Bory's fig. 1 E. The small form (Bory's A, B and C), with which most of the Gough Island material agrees very closely, usually dries to a shade of brown if pressed when fresh while the larger form (D) is often more red or purple. As far as I could see when I examined the type material, the lower left-hand blade of D is in fact a separate plant and was never part of the main frond as shown by Bory; the angle it makes with the main frond looks most unnatural in the drawing too.

The distinctive features of *I. laminarioides* are the very short stipe, the pronounced apophysis which is channelled and has a smooth edge, and a blade with a cuneate base and a smooth edge; the blade may or may not be divided. I also think that the fronds usually arise from a communal basal crust; certainly those in the Gough Island material did so and much of the herbarium material I examined appeared to show this too; unfortunately it was usually impossible to make sure about this since dried material of *Iridaea* disintegrates very quickly when soaked out. This feature of the communal basal crust has been used by Setchell & Gardner (1937, p. 211) as one of the diagnostic characters of another of their new species, *Iridophycus caespitipes*. Skottsberg (1941, p. 82) commented on and published a drawing of this species and said how similar the erect fronds are to those of *Iridaea*.
Iridophycus caespitipes is probably only a form of Iridaea laminarioides and the more pronounced development of the basal crust could well be a response to the very exposed habitats from which it has been collected.

While working on the Iridaea laminarioides group of species, I made sections of the blade of a considerable number of herbarium specimens. I found a wide range of variation in the tissues, the cells in some being much more densely packed than they were in others. In the filaments of the cortex, there was a variation both in the number of cells in the filaments and in the size and shape of the cells. Some of the variation may have been due to the method of pressing the specimens and I could not see that there was any significant correlation between the detailed microscopic structure of the blade and the external appearance of the plant. The observations of Setchell & Gardner as to the microscopic characteristics of their various species seem to have been based on a rather small sample in each case. The appearance of the cross-section of a blade from Bory’s type specimen of I. laminarioides (Fig. 71) was rather different in the cortical region from the Gough Island material (Fig. 69) but I do not think the difference is great enough to warrant specific separation of the two plants. The only plant of Iridophycus caespitipes that I have been able to examine is the fragment in the Kew Herbarium collected in the Falkland Islands by Mrs. Vallentin and sent to Setchell & Gardner by Cotton as Iridaea cordata (Setchell & Gardner, 1937, p. 212). The specimen is so incomplete that it gives no idea of the external characteristics of the species, but in cross-section the cortical cells of the blade are very considerably larger than those of all the other material which I sectioned. For this reason I have not included Iridophycus caespitipes as a synonym of Iridaea laminarioides.

It is quite clear that, before the taxonomy of Iridaea can be satisfactorily worked out, much more work will have to be done with fresh material and field observations made by phycologists. Until this has been done, I think it is difficult to be sure whether the North American plants which are called I. laminarioides really belong to the same taxon as the South American ones, and also to sort out the relationship between I. laminarioides and other very similar species such as I. micans Bory and I. obovata Kütz.


Iridaea ciliata Kütz., Sp. Alg.: 726 (1849) ; Tab. Phyc. 17 : 4, t. 10 (1867).—Baards. in

1 I am indebted to M. R. Délèpine for a photocopy of this paper.


Southern South America, Falkland Islands, Tristan da Cunha.

*Iridaea undulosa* occurred quite frequently on the shores of Gough Island; it was most often found in littoral rock pools but was also collected from the *Cladophora radiosa* zone just above and below mid-tide level on the sheer southern face of

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**Figs. 72, 73.** *Iridaea undulosa* Bory: 72, habit of plant, *a* = apophysis, *e* = emergences, *b* = blade, *t* = tetrasporangia; 73, transverse section of blade, *c* = cortex, *m* = medulla, *t* = tetrad of spores.
Church Rock. The plants collected measure up to 17 cm. tall \times 12 \text{ cm. wide} (Fig. 72), are more or less ovate in shape and are of a deep, purple-red colour and a rather leathery texture when alive. The apophysis is flat or very slightly channelled and always bears obvious emergences; it is unbranched but occasionally the emergences are large enough to look like young plants. The base of the blade is cuneate to reniform and the margin is, in most cases, ciliate; in some younger plants it is smooth. Many of the plants are tetrasporic but no sexual reproductive organs were found. In section (Fig. 73) the blade can be seen to have the usual \textit{Iridaea} structure; the long, thin cells of the medulla are widely scattered and the cortex consists of three-celled filaments of fairly large cells. The very wide spacing of the cells may be more apparent than real; the plants are extremely gelatinous and when sectioned the gelatinous substance immediately swells so much that it pushes the cells apart. Tetrads of spores develop in sporangia in the medulla in an intercalary manner characteristic of this genus.

Setchell & Gardner (1937, pp. 215–222) divided the South American species of \textit{Iridaea} with ciliate margins and unbranched apophyses into three species, the specific delimitations depending upon whether the base of the blade was cuneate to reniform or cordate. Skottsberg (1941, pp. 85–88) considered that these interspecific boundaries were untenable and that the three species should be treated as forming one taxon, a view which I share. The distribution seems to be limited to the Atlantic and Pacific coasts of South America and some South Atlantic Islands.

The question of whether the name \textit{Iridaea undulosa} was validly published in D'Urville's \textit{Flore des Iles Malouines} is not easy to decide. That work as a separate publication certainly antedates the ninth volume of the \textit{Dictionnaire Classique d'Histoire Naturelle}, and so also probably does the sixth part of the fourth volume of the \textit{Mémoires de la Société Linnéenne de Paris}, in which it was also printed.\(^1\)

In the \textit{Flore des Iles Malouines} there is a general but not a botanical description of \textit{Iridaea micans} in the prefatory part by D'Urville, and in the list of species, for the cryptogamic part of which Bory was responsible, there is:

   Cap. (fide Gaud.).
   \textit{b. I. papillosa}.

Nowhere in this work is there an indication that \textit{Iridaea} is a new genus, unless this can be read into the statement: "L'éclat de ses couleurs lui a valu le nom d'\textit{Iridaea micans}".

\(^1\) Flore des Iles Malouines. Title-page dated 1825; not noticed in the Bibl. France; received at weekly meeting of Paris Academy of Sciences on 9 January 1826 (Proc.-Verb. Acad. Sci. Par. 8 : 332 (1918)); therefore presumably December 1825.
   Mém. Soc. Linn. Par. 4 (6). Cover dated Jan. 1826; not noticed in Bibl. France but notices of other numbers suggest that it ran close to schedule; not received by Paris Academy of Sciences; date on cover (Jan. 1826) probably correct.
However, Bory’s article headed “Iridée, Iridée” in the ninth volume of the *Dictionnaire Classique*, which appeared only a few weeks later, begins “Le genre ainsi désigné par Stackhouse, ne pouvant être conservé selon Lamouroux, nous adoptons ce nom pour un genre nouveau de Fucacées”.* The species he describes in this article include *I. micans* but not *I. undulosa*. In his fuller treatment of the genus in the *Voyage . . . Coquille*, he treats *I. undulosa*, and *I. crispa*, described in the *Dictionnaire Classique*, as synonyms of the new and superfluous name *I. augustinae*.

Unless *Iridae micans* and *I. undulosa* are regarded as having been published in the *Flore des Iles Malouines* as species of the genus *Iridée* Stackh., they are not validly published there. The spelling of the generic name in the part of that work for which Bory was responsible differs from Stackhouse’s, and we know from Bory’s subsequent publications that a different genus was intended. However, in deciding whether a name is validly published in a particular publication, matter published later cannot be taken into account. The decision on the place of valid publication of these two names therefore turns on the answer to the question: had neither vol. 9 of the *Dictionnaire Classique* nor the *Voyage . . . Coquille* been published, would *Iridéea* in the *Flore des Iles Malouines* have been considered as a mis-spelling of *Iridéea* Stackh. or as the name of a new genus for which no definition was provided? The definitions of the species in the *Flore des Iles Malouines* are inconsistent with membership of a genus defined thus: “*Iridéea*. Fronde cartilaginea, tereti; ramosissima, pinnata: ramis oppositis, supra decompositis, capillaribus . . . Fructificatio incognita.” (Stackhouse, *Ner. Brit.*, ed. 2: ix (1816)). They would nevertheless at the time have been regarded as belonging to the same group of algae as *Iridéea* Stackh., and their names must therefore be regarded as having been validly published as names of new species of that genus. Their subsequent transfer to *Iridéea* Bory cannot be regarded as the making of new combinations, and hence there is the anomalous situation that these two correct names were validly published earlier than was the name of the genus which forms their first part.

**Rhodoglossum revolutum** Baards. in Res. Norw. Sci. Exped. Tristan da Cunha: 78, figs. 39 c, 40 e, 41 d (1941). (Figs. 74–77.)


Tristan da Cunha (Inaccessible Island).

*R. revolutum* was a common plant of the Gough Island littoral. It grew on rocks and in pools in the mid-littoral and in some cases, particularly on rather less exposed beaches such as Dell Rocks Beach, it formed a zone below the *Iridéea laminarioioides* zone. The only previous record of this species is its original gathering from the
littoral zone of Inaccessible Island. Baardseth gives no indication of its abundance there, but as the species is not mentioned in the ecological section of Baardseth’s work it can be assumed that it was not present in any great quantity and certainly did not dominate a zone as it did in places on Gough Island. It would seem therefore that this is a plant of very restricted distribution which attains its maximum development on Gough Island.

The plants (Fig. 74) consist of a spreading basal crust from which arise erect fronds in all stages of development. The fronds are fleshy and of a dark reddish-brown colour; the lower half of most plants is entire; above this the plants usually branch dichotomously up to four or five times but occasional unbranched plants are present. The margins of the fronds are entire and frequently inrolled. The fronds measure up to 6 or 7 cm. high and are extremely gelatinous, which causes them to shrink excessively when pressed. Baardseth describes the plants as being 2 or 3 cm. high, but this measurement must have been based on dried material; the isotypes in the British Museum Herbarium measured up to 3 cm. on the herbarium sheet, but one specimen which was 2 cm. high when dry expanded to 3.5 cm. when soaked in water. The Gough Island plants measure up to 1 cm. across but are usually about 5 mm.; Baardseth recorded 4–8 mm. for the width. In section the fronds are flat except at the very bottom where they are terete. The frond is composed of a cortical region of filaments of small elongate cells at

Figs. 74–77. *Rhodoglossum revolutum* Baards.: 74, habit of plant; 75, transverse section through blade, *m* = medulla, *c* = cortex; 76, transverse section through blade with tetraspore mother cells (*tmc*), *c* = cortex; 77, mature tetrad of spores.
right-angles to the surface of the thallus and an inner medulla of long, thin branching cells which anastomose with one another (Fig. 75).

Female and asexual reproductive organs are present. The carposporophytes develop on the concave surface of the upper parts of the thallus; when mature they form a protuberance on the surface of the thallus and in section are seen to be surrounded by a pericarp, as shown in Baardsøth's drawing (his fig. 41 b). The tetrasporangia are also developed on the concave side of the upper thallus and can be seen as dark patches. They do not protrude from the thallus. The spore mother cells develop in accessory filaments (Fig. 76) from the lower cells of the cortex. When mature (Fig. 77), the tetrads of spores measure up to 35μ in diameter.

Baardsøth commented at length on his reasons for including this species in the genus *Rhodoglossum* and the generally unsatisfactory distinctions between the genera *Rhodoglossum*, *Gigartina* and *Iridaea*.

**Ceramiaceae**


*Ceramium clavulatum* Agardh in Kunth, Synops. Pl.: 2 (1822).


Widely distributed in warm and temperate waters.

This plant was found frequently on Gough Island intertwined with other algae.


A small quantity of this species was found growing as an epiphyte on *Corallina officinalis* at the Midshipman Rock. Female and tetrasporic plants are present and agree well with Baardsøth's description and material.

**Rhodomelaceae**


Standoff Rock, on less–exposed part of the rock above the *Corallina* zone, 18 Feb. 1956, *G.I.S.S. 1526*.

Southern circumpolar temperate and cold waters, Japan, China.

*B. mixta* is a very common plant of southern shores where it frequently dominates a community at or above high-tidemark, especially in places where there is a certain amount of freshwater seepage. On Gough Island it was found only at Standoff Rock, where it grew mixed with *Rhizoclonium ambiguum*, *R. riparium* forma *validum*
and Spongomerpha sp. Dr. Erika Post kindly confirmed the identification of this plant.


Tristan da Cunha group of islands.

![Image of Herposiphonia paniculata](image)

**Figs. 78, 79.** *Herposiphonia paniculata* Baards.: 78, ventral view of plant, r = rhizoid, s = short branch, l = long branch; 79, tetrasporic branchlet.

*H. paniculata* was a frequent epiphyte on *Corallina officinalis*. The plants (Fig. 78) measure up to 2.5 cm. high. The main axis consists of a central cell surrounded by 12–14 pericentral cells each about two to three times as long as wide. Each segment of the main axis gives off a branch; on every fourth segment are alternating, ventral, long branches which repeat the structure of the main axis; on the intervening segments are simple branches up to 27 segments long and 100 μ wide. This organization is characteristic of the genus. Tetrasporic (Fig. 79) and carposporophytic plants are present; the mature cystocarps on the latter grow laterally on the simple branches and measure up to 350 μ wide × 500 μ long. The tetraspores are borne in branchlets of the compound branches.

The Gough Island material agrees well with that described by Baardseth, who points out that this plant may later prove to be within the variation range of one of the other species of *Herposiphonia* with sexual organs occurring laterally on the branchlets. In habit, the plants closely resemble the North American species...
H. grandis Kylin and H. rigida N. L. Gardn., but they have consistently more pericentral cells than either of these species.

Lophurella sp. (Fig. 80.)

Church Rock, occasional amongst Cladophora radiosa on vertical rock face, 5 Mar. 1956, G.I.S.S. 1533.

It is unfortunately impossible to identify the species of this material with certainty as the plants are incomplete, the ultimate branches being absent. However, as the genus is predominantly sub-antarctic and antarctic, its presence on Gough Island is of interest. The wiry plants (Fig. 80) measure up to 5 cm. high and arise from a creeping, rhizomatous base. Tetraspores are present. The plants belong to one of two species, L. hookerana (J. G. Agardh) Falkenb. or L. patula (Hook. & Harv.) De Toni, but, without the terminal branchlets, it is impossible to say which.


West Point Reefs, pools below spray zone, 6 Mar. 1956, G.I.S.S. 1541.

Tristan da Cunha group of islands.

The Gough Island material of this species was found growing as an epiphyte on Codium fragile in rock pools at West Point Reefs.

The material agrees exactly both with Baardseth's description of the type and with isotype material in the British Museum Herbarium except in the size of the
spermatangial branchlets. In the Gough Island material these are 140–180μ long whereas Baardseth describes them as being about 75μ long. However, when I measured the spermatangial branchlets in the isotype material, I found that these were of the same order of size as those in the Gough Island plants; it seems therefore that Baardseth must have been measuring young branchlets.


Atlantic and Caribbean from North Carolina to Brazil, Tristan da Cunha, Pacific from Panama to Colombia.

*P. howei* was collected from Midshipman Rock and from Isolda Rock, where it grew in a low, brown turf on lower littoral rocks; on Isolda Rock it actually dominated a zone below *Iridaea laminarioides* and above *Durvillaea antarctica*. A similar zone above the *Durvillaea* zone was reported on West Point Reefs and was probably dominated by *P. howei*, but no collection was made.

The plants from Isolda Rock (Plate 19 A) measure about 1 cm. high and have the habit of a *Lophosiphonia* with well-developed prostrate shoots, which have rhizoids below and erect, sparingly branched filaments above. From the structure of the apices of the prostrate shoots it can be clearly seen, however, that this plant belongs to the genus *Polysiphonia* and not *Lophosiphonia*; the branches develop exogenously on all sides of the shoot and the dorsiventral habit is due to the fact that the branches on the lower surface abort and rhizoids develop from the pericentral cells on the lower side. The rhizoids are long, thin-walled, cut off from the pericentral cell which produces them, and they end in a well-developed hapteron. The erect shoots are strongly recurved at their apices and the apices bear dichotomously branched trichoblasts. The filaments have 8–13, mostly 10–11, pericentral cells; the segments of the basal filaments measure about 130μ wide × 150μ long, those of the erect filaments 70–100μ wide × 55–85μ long. The erect filaments branch rarely when sterile but more abundantly when tetrasporic. Tetraspores are produced in the upper branches in somewhat spiral series; there is one tetraspore per segment. This material is in close agreement with Hollenberg's and Taylor's descriptions of the species both in morphology and habitat. The plants from the Midshipman Rock are very similar but have somewhat longer segments; those of the prostrate shoots are 100–140μ wide × 140–170μ long. I do not think there is any doubt however that they belong to the same species. The plants recorded by Baardseth from the Tristan da Cunha group of islands as *Polysiphonia* sp. are also *P. howei*. 


Standoff Rock, on less-exposed part of the rock above the Corallina zone, 18 Feb. 1956, G.I.S.S. 1526.

Widespread in the Pacific Ocean, Australia, New Zealand.

This species was collected from Standoff Rock, where it formed part of a dense turf together with Polysiphonia sp. The plants (Plate 19 B) are rather flaccid and seldom measure more than 1.5 cm. high. They are composed of a prominent, prostrate basal filament which gives off rhizoids mainly from its lower surface and erect filaments mainly from its upper surface; sometimes the positions are reversed. The rhizoids are long and end in frilly haptera; their contents are a continuation of those of the parent pericentral cell. The filaments are ecorticate and have four pericentral cells throughout. The basal segments measure 140–250μ long × c. 140μ wide in the older parts and 70–90μ long × c. 125μ wide nearer the apex. The erect filaments have segments 70–120μ long × 110μ wide and these, in their upper parts, give off side branches with noticeably much shorter segments measuring 30–55μ long × 70μ wide. Branching is quite frequent and in tetrasporic filaments it is abundant. Tetraspores are borne in the side branches and there is one per segment. Branching is endogenous; no trichoblasts were seen.

The Gough Island plants agree well with isotype material in the British Museum Herbarium and with Queensland material named by Dr. Cribb.

SPECIAL LITERATURE


A. The shore at Isolda Rock. B. *Colpomenia sinuosa* (Roth) Derb. & Solier, habit of plant \((\times 2)\). C. *Corallina goughensis* Y. M. Chamberlain, habit of plant \((\times 2)\).
Dermatolithon nodulosum Y. M. Chamberlain. A. Habit of plant \( (\times \frac{3}{2}) \). B. Detail of nodules \( (\times 11) \). C. Transverse section through nodule with tetrasporic conceptacles.
THE CEYLON SPECIES OF ASPLENIUM

W. A. SLEDGE

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Pp. 233-277; 3 Text-figures; Plate 20

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THE CEYLON SPECIES OF *ASPLENIUM*

*By W. A. SLEDGE*

Asplenium is the largest genus of ferns in Ceylon. Many of the species are well defined and easy to recognize; others are highly polymorphic. No preliminary discussion of the former group is required. The taxonomic, nomenclatural and distributional points which arise in connexion with some of them are discussed under the appropriate species. As regards the more polymorphic species my aim has been to define the limits of their variability without assigning names to the diverse forms which they comprehend. As this procedure has led in some cases to the referring of rather heterogeneous assemblages of seemingly different plants to single species, some discussion of the problems involved and some justification of the method adopted are required.

In recent years a rapidly growing body of research work has demonstrated the existence of cytological complexities in numerous genera of ferns. Asplenium is notable for the wide range of polyploidy shown within the genus and many hybrids have been described. Chromosome counts have been made (Manton & Sledge in Phil. Trans. R. Soc. Lond., Ser. B, 238: 127-185 (1954)) of about half the Ceylon species of Asplenium and these have established the presence there of diploid, triploid, tetraploid, octoploid and dodecaploid plants. More than one grade of polyploidy exists within some species and clear cytological evidence of hybridity was obtained in one of the stock plants examined. Having regard to the necessarily limited number of plants investigated in a project designed to explore the cytology of the fern flora of Ceylon in general and not aimed at any one genus in particular, it is more than likely that hybrids are frequent and that apogamy and other grades of polyploidy exist both within unworked species and within species at present known only from counts based on single plants. While most of the species appear to be tetraploid, *A. affine* is represented by octoploid and dodecaploid races. Three plants of *A. aethiopicum* were also found to be octoploid in Ceylon. In Africa tetraploid, octoploid and dodecaploid races of *A. aethiopicum* are known to occur and the morphology of tetraploid plants is closely similar to that of some Ceylon plants.

Illustrations are given in our paper (Manton & Sledge, loc. cit., fig. 17) of fronds from octoploid and dodecaploid plants of *A. affine*. The differences displayed would be sufficient to warrant taxonomic distinction if all plants agreed either with the one or the other; but in fact a series of intermediate forms exists such that no useful separation or subdivision can be drawn. A dodecaploid race is most likely to have involved the participation of some other species in its origin, and it would be expected that some character or characters could be found whereby the two races might be distinguished. Such hereditable differences might well be found if large
suites of living plants were assembled and kept under constant observation, but the taxonomic difficulty in such species as *A. affine* and *A. aethiopicum* lies in the fact that both show great inherent plasticity and the range of phenotypic modification produced by this plasticity is closely paralleled and overlapped by the range of variation produced by genotypic diversity.

Evidence of this inherent plasticity is shown in the accompanying silhouettes (Figs. 1, 2) which show fertile fronds taken from wild specimens of *A. aethiopicum* and *A. affine* and fronds taken from the same rhizomes after cultivation at Kew for

![Silhouettes of fronds](image)

**Fig. 1. Asplenium aethiopicum** (Burm. f.) Becherer. The left-hand frond from a wild plant (*P.222*) collected in Ceylon in 1951; the right-hand frond taken from the same rhizome after one year in cultivation at Kew. Both × ¼.

one year and five years respectively. Apart from the size, the variable characters include degree of pinnation and shape of pinnules in both species, the presence or absence of proliferating buds on the rhachis in *A. affine* (absent in the frond taken from the wild plant but present on that produced in cultivation, both on the main rhachis and on the pinna rhachides, though too small to show in the silhouette), and the degree of development of scales on the rhachis and pinnae of *A. aethiopicum* (densely woolly-scaly in the frond taken from the wild plants but very sparsely scaly in the frond produced in cultivation). The differences in gross morphology between the two fronds of each pair considerably exceed those which have served, sometimes rightly and sometimes wrongly, to distinguish between species.
The crucial point in the taxonomic treatment of such polymorphic macrospecies is that discontinuity of variation must determine the limits of species. The lower limit to the degree of morphological difference that can be accepted as providing a specific distinction is that by which a competent taxonomist can with certainty discriminate between two groups. But there is no upper limit to the morphological variability that can be admitted within a species if not accompanied by at least some degree of reproductive isolation. That some species are larger and more polymorphic than others is an inescapable fact.

Fig. 2. *Asplenium affine* Swartz. The left-hand frond from a wild plant (P.52) collected in Ceylon in 1951; the right-hand frond taken from the same rhizome after five years in cultivation at Kew. Both × ½.

The evidence supplied by these two plants is alone sufficient to show that the great differences displayed are of no value for taxonomic purposes. Where so wide a response to age and environment is shown by individual plants, it is clearly impossible without full-scale cytotaxonomic investigations to define the taxa present within each macrospecies; and, indeed, even then it is by no means impossible that the phenotypic expression of genetic differences may be too much at the mercy of environmental influence for it to be of any taxonomic value, since it may well be impossible to assess differences with confidence in a dried specimen or even in the majority of living specimens. Most taxonomists feel dissatisfied at leaving unnamed a series of grossly divergent morphological types; but where the pattern of variation
is so continuous, with many variables and little or no correlation, the division of the species into a series of subspecific units, designed to cover the range of variation in such a way that they will be recognizable to some one other than the author who establishes them, is practicable only for a limited number of specimens since the boundaries between such units must be purely arbitrary. To assign Latin names to such arbitrary divisions is not only worthless: it is potentially harmful in that later taxonomists, impressed by the great apparent difference of a specimen to which some infraspecific rank has been given, may raise it to independent specific status and in so doing create a binomial which divorces it from the species to which it properly belongs.

I have discussed elsewhere (Kew Bull. 15: 401 (1962)) the taxonomy of *A. affine* and shown that the supposedly distinct species to which the name *A. spathulinum* has been widely applied is a clear case of two names covering a single species, since the distinctions were based on variable, non-correlated characters. The most extreme variant, which I distinguished as a forma, had been treated by Hooker (Sp. Fil. 3: 169 (1860)) as typical *A. affine*. Owing to acceptance of a tradition concerning the different geographical ranges of the two supposed species, the application of the names *A. affine* and *A. spathulinum* as accorded to most specimens in herbaria is determined usually by the provenance of the specimen concerned rather than by its morphological characters. The fact that the species *A. affine* is now known from cytological evidence to be an unresolved species complex affords no justification whatever for the perpetuation of a name originally given to a form embraced within its own known amplitude of variation. In the case of *A. aethiopicum* I have named no variants, though earlier botanists sometimes gave specific rank to one of its Ceylon forms, to which they incorrectly applied the name *A. laserpitii-folium*. A detailed cytogenetic investigation of the African forms of *A. aethiopicum* is at present being pursued by Mr. A. F. Braithwaite and his findings may be expected to throw some light on the taxonomy of this species as represented in Ceylon.

I have referred only to *A. affine* and *A. aethiopicum* in this discussion since for them direct evidence of plasticity can be supplied. But the same considerations apply to other polymorphic species, of which *A. erectum* and *A. falcatum* are examples. Only a brief reference to these species need be made here since they are fully discussed later on. In the case of *A. erectum*, species, varieties and forms have been founded on variations in pinna form which I consider of no taxonomic significance. Such taxa have frequently been described by authors with no knowledge of the living plants or the range of variation displayed in wild populations, their differences being more a reflection of the limited numbers of herbarium specimens which were available for study than an expression of valid taxonomic distinctions. Selected examples might be taken from any large population of *A. erectum* in Ceylon that would display considerable range in frond and pinna shape and would cover forms to which some authors have assigned independent rank. Such differences I consider examples of intraspecific variation of a fluctuating nature. In the case of *A. falcatum*, plants with bipinnate fronds are of frequent occurrence in Ceylon and these have been confused in the past with other species. No evidence is available
to show if such plants are able, like Diplazium dilatatum, to produce both simply pinnate or bipinnate fronds according to age or environmental conditions, or whether they are fixed varieties. They are, however, so widely different in appearance from the usual simply pinnate condition that nomenclatural recognition is here very desirable as a means of referring such plants to their correct species.

Thwaites (Enum. Pl. Zeyl.: 383 (1864)) recognized twenty species of Asplenium. As with all Ceylon ferns, his arrangement closely followed Hooker's account in the Species Filicum, both in the matter of classification and nomenclature. Beddome's account of the genus in his Handbook to the Ferns of British India, Ceylon and the Malay Peninsula (1883) hardly differs, such changes as are made largely following those introduced in the Synopsis Filicum. Little detailed attention has since been paid to Ceylon ferns. The twenty-two species enumerated in Willis's Catalogue of the Plants of Ceylon (1911) represent a revised list compiled from Christensen's Index Filicum.

In the following account I recognize twenty-five species. A. macrophyllum, which was listed by Beddome and Willis, I am unable to maintain as a distinct species in Ceylon whatever its status elsewhere. One of the four additional species, A. inaequilaterale, was recognized by Beddome under the name A. lunulatum var. trapeziforme. A. obscurum and A. pellucidum have not previously been recorded from Ceylon and one new species, A. disjunctum, is described.

Most of the Ceylon species of Asplenium are montane plants, commonly growing on rocks and trees in jungle and forest, or as ground species. The only species common in the lowlands are A. nidus and A. falcatum. Two species, A. pellucidum and A. nitidum, are known from Ceylon only from single specimens in herbaria.

The most widely distributed of the Ceylon species of Asplenium is A. aethiopicum which, in one or other of its many forms, is found in tropical America, Africa, Asia, Australia and Polynesia. A. formosum and A. inaequilaterale also grow in tropical America and Africa but in Asia are confined to peninsular India and Ceylon. Species which range eastwards only from Ceylon and India are A. ensiforme, A. cheilosorum, A. indicum, A. nitidum, A. decorum and A. tenerum. Of these the second, third, fifth and sixth reach the Philippine Islands. The following widely distributed species range both westwards to Africa or the Mascarene Islands and eastwards to the Philippines or Polynesia: A. nidus, A. normale, A. unilaterale, A. obscurum (Madagascar to China), A. erectum, A. tenerum, A. pellucidum, A. falcatum, A. affine and A. varians.

Of the species with more restricted ranges, A. zenkeranum, A. decrescens and A. serricula are confined to Ceylon and South India, the last-named species also occurring in the Philippine Islands. A. gardneri is known only from Ceylon and Sumatra. A. longipes and A. disjunctum are endemic to Ceylon. Apart from the two endemics, A. gardneri and A. decorum are the only other Ceylon species of Asplenium which are not also found in India.

My grateful thanks are due to the Directors and Curators of the following herbaria
for access to, or for the loan of, specimens in their charge. Abbreviations used in the citation of specimens are those adopted in the *Index Herbariorum*.

BM = British Museum (Natural History), London.
CGE = Botany School, University of Cambridge.
E = Royal Botanic Garden, Edinburgh.
G = Conservatoire et Jardin Botaniques, Geneva.
GL = Department of Botany, University of Glasgow.
K = Royal Botanic Gardens, Kew.
PDA = Department of Agriculture, Peradeniya.
SING = Botanic Gardens, Singapore.
US = United States National Museum (Department of Botany), Smithsonian Institution, Washington, DC.
W = Naturhistorisches Museum, Vienna.

In the citation of specimens the numbered ones distributed by Thwaites have been listed first since sets of these specimens are to be found in many herbaria and the numbers have been widely quoted. Statements as to localities where these plants were collected rarely accompany the specimens and the data which have been pencilled on many of the sheets in the Peradeniya collection are indicative of localities whence the species had been recorded rather than of localities where the actual specimens on the sheets were collected. Since errors of identification occur, the localities are not therefore always reliable. Earlier sets of specimens were distributed by Gardner and of these the Cambridge sheets bear his own annotations giving name, place of origin and date of collection. Other gatherings by Gardner bear numbers only.

**ASPLENIUM** L.

**Key to the Species**

Fronds simple:
- Veins connected by a marginal strand; fronds large ........................................... 1. *A. nidus*
- Veins free; fronds small to medium-sized ................................................................. 2. *A. ensiforme*

Fronds pinnate, bipinnate or tripinnate:
- Fronds simply pinnate:
  - Pinnae 1–2 cm. long; stipes black and polished; rhizome short, fronds tufted:
    - Upper margin of pinnae deeply cut ........................................................................ 3. *A. formosum*
    - Upper margin of pinnae crenate or dentate ......................................................... 4. *A. normale*
  - Pinnae more than 2 cm. long:
    - Stipe black and polished; rhizome creeping:
      - Upper margin of pinnae deeply cut, sori confined to the lobes ......................... 5. *A. cheilosorum*
    - Upper margin of pinnae serrate, sori not on the lobes ...................................... 6. *A. unilaterale*
  - Stipe green or, if dark, not glossy and polished:
    - Pinnae dimidiate, the lower side cut away to the costa; rhizome long-creeping ........ 7. *A. obscurum*
Pinnae subequal-sided or the lower side cuneate, or if dimidiate then rhizome erect:
Rhizome short, fronds tufted:
Pinnae up to 5 cm. long:
   Fronds decrescent . . . 8. A. erectum
   Fronds not decrescent:
      Veins forked:
         Stipe and rhachis scaly . . . 18. A. indicum
         Stipe and rhachis not scaly . . 9. A. inaequilaterale
      Veins simple (except for lowermost acroscopic ones):
         Pinnae toothed . . . 10. A. tenerum
         Pinnae cut to the costa into linear lobes . 25. A. decorum
Pinnae more than 5 cm. long:
   Fronds decrescent . . . 11. A. pellucidum
   Fronds not decrescent:
      Fronds gemmiparous . . . 12. A. zenkeranum
      Fronds not gemmiparous:
         Stipe green:
            Pinnae 0.5–2 cm. broad, widest at the middle 13. A. serricula
            Pinnae 2–4 cm. broad, widest near the base 14. A. longipes
            Stipe black . . . 17a. A. falcatum var. falcatum
      Rhizome creeping, fronds more or less distant:
         Fronds gemmiparous ; sori diverging . . . 15. A. gardneri
         Fronds not gemmiparous ; sori parallel with the costa 16. A. decrescens
Fronds bipinnate or tripinnate:
   Pinnules ovate, spathulate or narrowly rhomboid, lobed or dentate but not divided into narrow segments:
   Medium to large ferns ; texture of frond firm:
      Stipe and rhachis quite glabrous . . . 19. A. nitidum
      Stipe and rhachis scaly:
         Veins very close ; fronds not gemmiparous:
            Stipe and rhachis (at least when young) woolly with hair-pointed scales ; rhizome creeping . . . 20. A. aethiopicum
            Stipe and rhachis not woolly-scyal ; rhizome short, fronds tufted 17b. A. falcatum var. bipinnatum
   Veins spaced ; fronds often gemmiparous . . . 21. A. affine
   Small fern ; texture of frond thin, herbaceous . . . 22. A. varians
Pinnules linear, 1–2 mm. broad, or divided into narrow segments:
   Fronds gemmiparous:
      Fronds bipinnate-tripinnatifid . . . 23. A. disjunctum
      Fronds tripinnate-quadrripinnatifid . . . 24. A. tenuifolium
      Fronds not gemmiparous ; pinnules linear . . . 25. A. decorum


Rhizome stout, erect, apex clothed with lanceolate, attenuate, brown scales bordered by filamentous appendages. *Fronds tufted, in a rosette, simple, variable in length and breadth, commonly 100 x 10 cm. but often larger or sometimes smaller, base narrowed into a short stipe, apex acute or acuminate, margins entire, costa prominently raised beneath; veins simple or once, sometimes twice, forked, uniting to form a continuous intramarginal vein; texture stiff, subcoriaceous. Sori narrow, extending from the costa 1/2-3 the way to the margin. Spores plano-convex, 33-39 x 24-27μ, with an undulate perispore wing and Anastomosing surface folds.*


Common in the low country up to 300 m. and ascending to 750 m.; usually epiphytic but sometimes terrestrial.

Tropics of the Old World.


Rhizome short, suberect, bearing narrow, attenuate, dark-brown scales at its apex and at the base of the stipes. *Fronds tufted, 15-35 x 1-3 cm., entire, narrowly oblong or elliptic, narrowed at the base into a stipe 1-2 cm. long, gradually acuminate above, margins entire or slightly repand, both surfaces glabrous save for a few filiform scales on the lower part of the midrib beneath; veins immersed, mostly once forked, free; texture stiff, subcoriaceous. Sori spreading along the veins from near the costa nearly to the margin. Spores reniform, 42-48 x 24-30μ, with a wide undulate perispore wing and Anastomosing surface folds.*


On rocks and trees in forests above 1,000 m.
Ceylon, South India, Himalaya from Punjab to Assam, south China, Burma, Thailand, Indochina.


Rhizome short, erect, scaly at the apex, scales linear, entire, black with brown margins. *Stipes* 1–5 cm. long, *dark-purple to black*, naked, *polished*; *rhachis* of the same colour with a very narrow wing on each side which is continuous to the base of the *stipe*. Lamina simply pinnate, up to 30 cm. long, 2 cm. wide, with 30–40 or more pairs of pinnae, the lower ones reduced in size; pinnae subsessile, horizontal, dimidiate, upper base truncate to broadly cuneate, about half of the lower side cut away, *upper margin and distal part of lower margin deeply incised*, the proximal lobes mostly bifid; *veins* immersed, forked or simple; texture firm-herbaceous. *Sori* short, oblique, 1–3 per pinna and usually confined to the lower side of the costa. Spores light-brown, 33–36 × 24μ, plano-convex with a perispore wing and surface folds.


On rocks by streams in forests up to 1,000 m.; confined to the eastern and northern edge of the central massif.

Tropical America from Mexico to Peru, West Indies, tropical Africa, Portuguese East Africa, Madagascar, Ceylon, South India (Nilgiri, Palni and Anaimalai Hills).

This is one of a group of ferns confined, in Ceylon, to the transitional region between the wet and dry zones fringing the eastern and northern edges of the central mountain massif. *Athyrium hohenackeranum* and *Anisocampium cumingianum* are other species which show the same distribution.

*Asplenium formosum* has a similar distribution to *A. inaequilaterale*, ranging from tropical America eastwards across Africa but reaching Asia only in peninsular India and Ceylon.


*Asplenium multifidum* Wall., Numer. List. : 8, n. 207 (1829), nom. nud.

*Asplenium opacum* Kunze in Linnaea 24 : 261 (1851).

*Asplenium pavonicum* Brackenr. in U.S. Expl. Exped. Wilkes : 150, t. 20 fig. 1 (1854).


*Rhizome erect*, the apex clothed with narrow brown scales. *Stipes* numerous, tufted, 3–15 cm. long, *wiry, polished, dark-chestnut to purple-black*; *rhachis* glossy like the stipe, grooved above. Lamina pinnate, up to 30 cm. long, 2–4 cm. broad,
linear-oblong with numerous (15–45) pairs of close-placed, sessile, patent pinnae, and sometimes proliferous from a bud formed distally on the rhachis, upper pinnae reduced in size, the lowermost scarcely reduced, often deflexed; pinnae 0.75–2 × 0.5–0.75 cm., dimidiate, obtuse, upper base truncate, more or less parallel to the rhachis, slightly auricled with the auricle sharply angled at the tip, lower base very obliquely cuneate forming a more or less horizontal line \( \frac{1}{3} \) the length of the pinna, upper margin and apex crenate-dentate, both surfaces glabrous; one or more veins above the costa forked, those below the costa simple; texture stiff-herbaceous. Sori short, variable in number, often one on the auricle and 2–3 others obliquely placed above the costa and 1–2 below and more or less parallel with the lower margin. Spores plano-convex, 30–36 × 24–27µ, with a rather broad perispore wing and anastomosing surface folds.


Common in forests above 1,200 m.

Tropical East Africa and Madagascar, Mauritius, Ceylon, South India, Himalaya from Nepal to Assam, south China, Formosa, Indochina, Malaya, Sumatra, Java, Borneo, Philippines, New Guinea, Hawaii.

*A. normale* is like *A. erectum* in appearance but is distinguished by the dark, glossy, polished stipe and rhachis. In *A. erectum* the stipe and rhachis may be grey or dark-coloured but are never glossy and polished, and a slender green wing borders each side of the groove on the upper surface of the rhachis. The margins of the pinnae are more shallowly incised in *A. normale*, and the auricles (often weakly developed) are sharply angled at the tip.
I have examined the type specimen of Blume's *A. minus* from Java. It is the same as *A. normale* and has been so identified by Rosenstock.

Kunze admitted to not having seen examples of Don's species when he described *A. opacum*. There is an authentic example of the latter at Kew. It differs only in its somewhat larger and broader pinnae, and is matched by some Ceylon forms.


Rhizome creeping, clothed with narrow, dark, tapering, acute scales. *Stipes* up to 20 cm. long, dark-purple, polished, scaly at the base, otherwise glabrous; *rhachis* of the same colour, naked, glossy. Lamina up to 35 cm. long, 4–5 cm. broad, linear in outline with numerous (up to 40 or more) pairs of pinnae, the lower ones very shortly stalked; *pinnae* 2–3 × 0.5–0.8 cm., *dimidiate* with nearly the whole of the lower margin cut away, upper base broadly cuneate to truncate, upper margin and extremity of lower margin lobed, the lobes mostly bifid; veins once forked, the two branches passing one to each tooth of a lobe; texture thin, membranous. *Sori* short, confined to the lobes and mostly to the distal fork only of each lobe; indusium thin, brown. Spores reniform to plano-convex, 42–51 × 30–33µ, with a rather broad perispore wing and many reticulately anastomosing surface folds.


In wet forests above 900 m.

Ceylon, North and South India, south China, Burma, Indochina, Malaya, Borneo, Philippines, Formosa, Japan.


*Asplenium emarginatodentatum* Zenker apud Kunze in Linnaea 24 : 263 (1851).

Rhizome creeping, slender, scaly at the apex, scales narrow, brown, margins entire. *Stipes* 10–20 cm. long, dark-castaneous to black, glossy, naked; *rhachis* of the same
colour, shining, grooved above with a narrow green wing on each side of the groove. Lamina simply pinnate, very variable in size, $15-35 \times 5-12$ cm., narrowly or broadly oblong or oblong-lanceolate, the lowermost pinnae not or only slightly reduced in size, often somewhat reflexed; pinnae in $15-30$ pairs, very shortly stalked, patent, dimidiate, commonly $2-3 \times 0.5$ cm., sometimes up to $7 \times 1.5$ cm., upper base truncate more or less parallel to the rhachis, lower side cut down to the costa to a third to half or more the length of the pinna, apex blunt or acute, upper margin and distal part of lower margin dentate; veins mostly once forked, continuous to the apex of the teeth; texture thin, herbaceous. Sori occupying the middle part of the veins and on the acroscopic fork, sometimes confined to the distal half of the pinnae. Spores dark, with a rather broad finely toothed perispore wing and many Anastomosing surface folds.

6a. *Asplenium unilaterale* var. *unilaterale*.

Pinnale small, 2–4 $\times 0.5$ cm. or a little larger.


6b. *Asplenium unilaterale* var. *majus* (C. Chr.) Sledge, stat. nov.


*Asplenium unilaterale* forma *majus* C. Chr. in Bernice P. Bishop Mus. Bull. 177 : 67 (1943).

Pinnale large, $5-7 \times 1-1.5$ cm. or still larger.


On wet rocks by streams and on wet banks; common in forests, 500–2,000 m.

Tropical Africa from Ghana, Fernando Po and Cameroons eastwards to Madagascar, Mascarenes, Seychelles, Ceylon, North and South India, Thailand, Indochina, Malaya, Indonesia and New Guinea, northwards to China and Japan, Philippines, Polynesia and Hawaii.

The two extremes of size look very different. The smaller one matches Lamarck’s *A. unilaterale*, the type sheet of which carries two fronds, in one of which the largest pinnae are 2.5 cm. and in the other 4.5 cm. long. Larger plants match *Cuming 110* from Luzon, the type of *A. excisum* C. Presl, in which the largest pinnae are $6 \times 1.5$ cm. in the Kew specimen and up to 10 cm. long in the British Museum specimen. Some North Indian specimens have pinnae reaching 10 cm. in length.
Copeland (Bernice P. Bishop Mus. Bull. 59 : 61 (1929)) treated *A. excisum* as merely a large form of *A. unilaterale*; and Christensen (Bernice P. Bishop Mus. Bull. 177: 67 (1943)) recognized two forms of *A. unilaterale*, equating *A. excisum* with his forma *majus* and stating that "intermediate forms are found in Samoa as well as in the wide area where this species occurs". Holttum (Fl. Malaya 2 : 439 (1954)) gives specific rank to *A. excisum* whilst admitting it to be "very closely related to *A. unilaterale*", the typical form of which occurs in the same locality in Malaya as *A. excisum*. He also refers to some large specimens growing amongst smaller ones of *A. unilaterale* "which seem intermediate between *A. unilaterale* and *A. excisum". Beddome's illustration (Ferns S. Ind.: t. 132 (1864)) represents such an intermediate form; the largest pinnae on the specimen are 5 × 1 cm. Several of the sori on this gathering are allantidioid as correctly depicted in the plate.

I can find no significant difference between small and large plants and as both appear to be coexistent throughout the range of *A. unilaterale* I prefer to regard them as variants of one species. Wall (Cat. Ferns Indig. Ceyl. : Table, 4 (1873)) also states that the extreme forms are connected by intermediates and that the large forms grow in "wet swampy spots". I cannot confirm that size difference is simply an expression of habitat difference but a Ceylon plant with large pinnae produced still larger ones (7–8 cm. long) in cultivation at Kew.


*Asplenium erosodentatum* Blume, tom. cit. : 182 (1828).


Rhizome creeping. *Stipes* to 20 cm. long, grey-green; *rhachis of the same colour*. Lamina simply pinnate, 30–40 × 7–10 cm., oblong or oblong-lanceolate, with 25–35 pairs of shortly stalked spreading, falciform and dimidiate pinnae; pinnae 4–6 × 1 cm., upper base broadly cuneate to truncate, lower base cut down to the costa to nearly half the length of the pinna, apex acute, margins serrate-dentate, often doubly serrate above; veins mostly once forked, continuous to the apex of the teeth; texture herbaceous. Sori short, about equidistant from costa and margin. Spores dark, with a broad perispore wing with toothed edge and with anastomosing surface folds.


In wet mountain forests; not common.

Malawi, Madagascar, Ceylon, South India (Nilgiri and Palni Hills), North India, South China, Burma, Thailand, Indochina, Java.

The dull greyish-green stipe and rhachis serve to separate this readily from *A. unilaterale* var. *majus*, in which the stipe and rhachis are dark-chestnut to black and glossy, though in the latter the narrow green wings which extend downwards from the pinnae on either side of the grooved upper surface of the rhachis may give a green appearance when viewed above to a rhachis which in the same frond is dark and glossy when seen from below. In other respects *A. obscurum* differs little from
A. unilaterale var. majus, but the latter seems to be at one end of a range of forms connecting it with A. unilaterale var. unilaterale, in which the pinnae are small. A. obscurum apparently shows no such range of variation. Two of Wall’s specimens of A. obscurum in Herb. Glasgow University have many completely allantodioid sori with indusia fixed on both sides of the sori and bursting dorsally. As noted above, the same condition has been observed in A. unilaterale.

Christensen was the first to record this species from Madagascar, whence he cites specimens which “agree perfectly with Javanese ones”, and the Ceylon specimens quoted above agree with those so named by Christensen.


Asplenium pyramidatum Desv. in Mém. Soc. Linn. Par. 6 : 271 (1827).
Asplenium sphenolobium Zenker ex Kunze, loc. cit. (1851), nom. syn.
Asplenium brasiliense sensu Bedd., Ferns S. Ind. : 45, t. 135 (1864); non Raddi.
Asplenium lunulatum var. erectum (Bory ex Willd.) Sim, Ferns S. Afr., ed. 2 : 145 (1915).

Rhizome erect, scaly at the apex, scales narrow, acute, dark-brown. Fronds tufted, 15—50 cm. long. Stipes 1—10 cm., glabrous or nearly so, grey or dark-coloured, not glossy; rhachis naked, grooved above with a very narrow green wing on each side of the groove. Lamina 10—40 × 2—4 cm., linear-elliptic with 25—40 pairs of sub-sessile, patent pinnae, the lower and upper ones gradually reduced in size and the lower ones commonly deflexed with the lowestmost often reduced to auricles; pinnae 1—2 × 0:5 cm., trapezoid-lanceolate, upper base truncate, more or less auricled, lower base exciso-cuneate, the edges bluntly inciso-crenate throughout, lowermost pinnae sometimes auricled on both sides; basal acrostichal veins forked, the rest simple; texture herbaceous. Sori short, oblong, not reaching the margin or costa, usually absent from the auricles. Spores plano-convex, 24—30 × 18—21 μ, with an undulate perispore wing and irregular surface folds.


Frequent in forests in the mountains above 1,200 m.

Tropical and South Africa, Mascarene Islands, Ceylon, South India, Java, Timor, Samoa, Hawaii.

Earlier writers followed Baker (in Hooker & Baker's Synopsis Filicum) in using the name Asplenium lunulatum for Ceylon plants. Swartz first used this name (Synops. Fil.: 80 (1866)) to replace the illegitimate name A. falcatum Thunb. (non Lam.), which was based on material from the Cape of Good Hope. But as Hooker long ago pointed out (Sp. Fil. 3: 128 (1860)) the plant was unknown to Swartz and "no authentic specimen nor any authentic intelligible description exists". As currently interpreted, A. lunulatum (sensu stricto) is considered to be an exclusively South African plant.

Several Nilgiri gatherings made by Schmid were named A. lunulatum var. sphenolobium by Kunze, the varietal epithet having been previously used by Zenker as the epithet of a manuscript specific name. In the same work Kunze described A. camptorhachis from another Nilgiri gathering, Schmid 123. The former name was later reduced to synonymy and the latter treated as a form or (e.g. in Beddome's Handbook to the Ferns of British India) a variety of A. lunulatum until Hieronymus (Hedwigia 60: 210–266 (1919); op. cit. 61: 4–39 (1919)) segregated a number of species previously referred to A. lunulatum and A. erectum. He used the name A. sphenolobium for Ceylon plants, specimens from Java, Samoa and Hawaii being referred to the same species. When first publishing the name A. sphenolobium in 1910, Hieronymus attributed it to "Zenker apud Kunze", but it had previously only been published in synonymy and his was its first valid publication as a specific name. Hieronymus considered that A. camptorhachis was probably a mountain form or variety of A. sphenolobium.

I have examined Schmid 96, cited by Kunze as A. lunulatum var. sphenolobium, and Schmid 123, the type of A. camptorhachis, both in the Botanisches Museum, Berlin, and I agree with Hieronymus that the former is identical with Ceylon plants. The sheet of Schmid 123 carries a single small specimen, which incidentally shows no
sign of buds on the rhachis though Kunze described it as "saepe gemmifera". This sheet has been annotated by Hieronymus "A. sphenolobium var. camptorhachis (Kze.) Hieron." and I agree with him in referring the specimen to A. sphenolobium, though in so plastic a species I do not consider the differences merit even varietal distinction. The specimens quoted by Hieronymus from Java, Samoa and Hawaii, and others from the same regions, are inseparable from South Indian and Ceylon plants.

Skottsberg (Medd. Göteborg. Bot. Trädg. 15: 59–67 (1942)) has discussed the taxonomy of A. lunulatum and its allies at length. Many names are involved but probably few valid taxa. Large suites of specimens from Ceylon display considerably greater variation in pinna form than Hieronymus or Skottsberg allow but I am convinced that all belong to a single variable species. Sometimes the auricle is free almost or quite to the base, when the pinna agrees with Skottsberg's illustration (tom. cit.: 66, fig. 87) of A. macraei forma subbipinnatum (Hilleb.) Skotts., or with Tardieu-Blot's illustration (in Humbert, Fl. Madag., Polypod. 1: 221, fig. 30 (6) (1958)) of A. erectum var. zeyheri; but all pinnae on the same rootstock are not uniform and I do not think these variations are of any real taxonomic significance. Specimens from tropical Africa named A. lunulatum var. serratodentatum Rosenstock and A. quintasii Gandog. I am unable to distinguish from Ceylon plants, and Skottsberg (tom. cit.: 67) also says of South Indian plants that "much the same form is spread over Tropical Africa".

It is quite evident from Skottsberg's thorough and critical comparisons and his series of drawings of scales, spores and pinnae of plants from Hawaii, South India, Ceylon and Africa, that any taxonomic categories proposed within such a series must have purely arbitrary boundaries. His discussion fully supports his conclusion (tom. cit.: 65) that "I cannot give these segregates a higher rank than forma. All are connected by intermediate specimens and to some extent the shape and cutting of corresponding pinnae varies in the same plant". Christensen (Bernice P. Bishop Mus. Bull. 25: 26 (1925)) had earlier stated that he was "nearly convinced" that A. macraei (which Hieronymus had treated as a distinct species) and A. sphenolobium were "forms of a single species" and, as a result of his detailed comparisons, Skottsberg (tom. cit.: 62) concludes "I cannot see how a line can be drawn between Hawaiian sphenolobium and macraei". He therefore reduces the former to a forma of the latter, regretting that the rules of priority require the adoption of a specific epithet originally given to the most extreme bipinnate form of the species, which appears to be confined to Hawaii, whilst the commoner, simply pinnate form with dentate or lobed pinnae ranges from there to tropical Africa.

Skottsberg, however, has little to say about A. erectum (sensu stricto). The name is constantly coupled with A. lunulatum in his discussion and he did not examine the type or authentic examples. A. erectum was described from specimens collected by Bory in Bourbon (i.e. Réunion) and was later regarded as either a synonym or variety of A. lunulatum until Hieronymus reinstated it. Hieronymus says it is closer to

1 Tardieu-Blot attributes this name to "(Pappe & Rawson) Alston & Schelpe in Journ. S. Afr. bot., XVIII (1952), 161" but the combination was actually made first by T. Moore (Index Fil.: 127 (1859)).
A. sphenolobium than to A. lunulatum, differing in its longer scales with different cell net, in its wider fronds and in the more deeply serrate pinnae. As regards the longer scales—up to 5 mm. in A. erectum—Skottsberg points out that Hieronymus's A. sphenolobium var. diplaziosorum has scales 5 mm. long, so the distinction can scarcely rank as of specific value; and one has only to look at Skottsberg's series of illustrations (tom. cit.: 61, figs. 36–61) of rhizome scales from plants ranging from Hawaii to Africa to see how impracticable it is to draw even an approximate boundary between the examples figured on the basis of size, cell shape or wall thickness; indeed Hieronymus himself admits (Hedwigia 60: 227) that the scales vary in this respect in Indian plants, whilst Skottsberg states that "the thickness of the cell walls may vary even in the same specimen". As regards the reputedly wider fronds and different depth of serration of the pinnae in A. erectum, I find no appreciable difference in either respect between the type specimen of A. erectum and other Réunion specimens at Kew and many examples of Ceylon and Indian plants. One of the characters given in Willdenow’s original description was the presence of auricles on both sides of the lower pinnae in A. erectum and this is evident in the type specimen. But in Réunion plants at Kew, as stated by Hooker, only "some specimens" show an auricle both above and below; moreover a frond of the type specimen of A. pyramidatum Desv. (equated by Hieronymus and Christensen with A. erectum) is without auricles on the lower sides of the basal pinnae. No valid distinction remains therefore whereby A. erectum may be distinguished from A. sphenolobium.

Christensen was evidently not convinced of the soundness of Hieronymus's conclusions for in his Pteridophytes of Madagascar (1932) he did not follow him in the treatment of A. lunulatum (sensu lato) but adopted Sim's arrangement in placing A. erectum as a variety under A. lunulatum, the form with auricles on both sides of the pinna being described as A. lunulatum var. erectum subvar. subbiauritum. Later (Index Fil., Suppl. 3: 32 (1934)) he cited A. erectum as a South African fern without mention of the Mascarene Islands whence the type was described, and in his Pteridophytes of Tristan da Cunha (Res. Norw. Sci. Exped. Tristan da Cunha 1 (6): 13 (1940)) he gave specific rank to A. erectum and so identified plants from the Tristan da Cunha group of islands as he could "not find any good character by which most specimens from the islands may be distinguished from A. erectum".

The type specimen of A. erectum is in the Willdenow Herbarium at Berlin. There is a photograph of it in the British Museum Herbarium (see Plate 20) and two sheets from "Herb. Mus. Paris. Ile Bourbon" in Hooker's collection at Kew. Though neither of these sheets has the collector's name inscribed on the label, the specimens on one or both sheets are presumably from Bory's collection as in Hooker's citation of specimens (Sp. Fil. 3: 127 (1860)) he says "I... confine myself to specimens in my own herbarium", the first citation being "Bourbon Bory. Herb. Mus. Paris in Herb. Nostr." These and other examples from Réunion and the other Mascarene Islands are, to me, indistinguishable from Ceylon plants.

It has always been recognized that the South African plant regarded as the true A. lunulatum is very close to A. erectum, but many South African specimens named
A. lunulatum have considerably less incised pinnae and the illustration in Sim (Ferns S. Afr., ed. 2 : t. 47 a, b (1915)) of A. lunulatum var. lunulatum shows a frond with pinnae much more nearly entire than in Ceylon and South Indian plants. I do not know if there are consistent differences in scale and spore characters between African plants corresponding with Sim’s A. lunulatum var. lunulatum and Asiatic plants, but as the former are similar to, rather than identical with, Ceylon and Indian plants I am not disposed to unite them. I conclude therefore that Asplenium erectum is the correct name for Ceylon plants.


Asplenium brachyotus Kunze in Linnaea 10 : 512 (1836).
Asplenium trapeziforme sensu Bedd., Ferns S. Ind. : 45, t. 134 (1864); non Roxb.
Asplenium lunulatum var. trapeziforme Bedd., Handb. Ferns Brit. Ind. : 148 (1883) pro parte; non A. trapeziforme Roxb.

Rhizome erect, scaly at the apex, scales linear, tapering, entire, dark-brown-black, 3-5 mm. long. Fronds tufted, 20-40 cm. long, rarely more. Stipes 8-16 cm. long, grey, sparsely and minutely hairy. Lamina up to 25 cm. long, 4-8 cm. broad, oblong-lanceolate, terminating in a lobed apex, simply pinnate with 15-20 pairs of shortly stalked pinnae, the lowermost not reduced; pinnae 2.5-5 x 1 cm., trapezoid-lanceolate, dimidiate, upper base truncate and more or less parallel to the rhachis, lower margin obliquely cut away to 1/3 or more of the length of the pinna, apex acute or subacute, both margins crenate-dentate, glabrous above and beneath; veins forked, not continuous to the apex of the teeth; texture herbaceous. Sori on the anterior forks of the veins forming a row on each side of the costa but not touching the costa and falling well short of the margin. Spores plano-convex, 30-33 x 21-24 μ, with a perispore forming a median wing and anastomosing surface folds.


On damp ground in mountain forests, 600-1,900 m.

South America, tropical and South Africa, Madagascar, Réunion, Ceylon, South India (Nilgiri, Palni and Anaimalai Hills, Bombay).

A. inaequilaterale has been confused with A. unilaterale and A. obscurum to which its fronds bear the closest resemblance. It differs from both these species in its erect
rhizomes bearing tufted fronds, the stipes and rhachides of which are not, as in *A. unilaterale*, dark-purple-black and polished. In *A. inaequilaterale* no separate pinnae are formed in the uppermost part of the frond, which terminates in a lobed apex; whereas in *A. unilaterale* and *A. obscurum* the distal pinnae decrease regularly in size but remain discrete to the apex of the frond. In *A. inaequilaterale* the lamina on the lower margins of the pinnae is obliquely cuneate, meeting the costa near its base, whereas in *A. unilaterale* and *A. obscurum* the lower margins of the pinnae are cut down to the costa for a considerable distance from the base. The lateral veins of the pinnae run to the tips of the marginal teeth in *A. unilaterale* and *A. obscurum*; in *A. inaequilaterale* the veins fall short of the margin.

Specimens from Réunion, whence the type was described, are a good match for Ceylon and South Indian plants.

Roxburgh's *A. trapeziforme*, described from the "Malay Islands", is not the same plant. It also has an erect rhizome but photographs in the British Museum Herbarium of the type specimen, including enlargements of the pinnae, clearly show the veins running to the extremities of the marginal teeth. The fronds are also pinnate to the end, not terminating in a distal, lobed, pinna-like extremity.


Rhizome erect, clothed at the apex with lanceolate, acute, dark-coloured scales. Stipes tufted, green, up to 20 cm. long, scaly when young, becoming glabrescent. Lamina 15–30 × 4–8 cm., oblong-lanceolate, simply pinnate with 10–25 pairs of spreading pinnae, the lower ones not or scarcely reduced, the upper ones suddenly reduced, the frond terminating in a narrow, winged prolongation, 2–3 cm. long, bearing simple oblique lobes; pinnae 2–5 cm. long, 6–15 mm. broad, shortly stalked, oblong-lanceolate, upper base more or less truncate, often subauriculate, lower base narrowly cuneate, margins with regular, oblique, blunt teeth, apex usually bluntly rounded, sometimes acute, both surfaces glabrous or with a few minute, appressed, pale-brown, irregular scales on the veins beneath; costa raised above, veins all simple save the basal one on the acrosopic side which is forked once or twice; texture firm-herbaceous. Sori not reaching either the costa or the margin; indusium pale. Spores light-brown, plano-convex, 42–48 × 27–33 μ, with a winged perispore and a few surface folds.

THE CEYLON SPECIES OF ASPLENIUM


In mountain forests, 1,200–2,100 m.

Seychelles, Ceylon, South India, Burma, Thailand, Indochina, Malaya, Java, Borneo, Philippines, New Guinea, Polynesia.

Ceylon plants agree closely with examples from Polynesia, whence the type was described. Mettenius’s variety terminans was described from material of Gardner’s from Ceylon, said to differ in its more coriaceous fronds, which were paler beneath, and in its longer pinnae. It was evidently founded on a single gathering and represents no more than a minor state or form. I am unable to see any significant difference between Gardner’s specimens at Kew or other Ceylon plants and those from elsewhere.

II. *Asplenium pellucidum* Lam. in Encycl. Méth., Bot. 2: 305 (1786).


Rhizome short-creeping, clothed with subulate, black, hair-like scales. Fronds 60–90 cm. long, 10 cm. or more broad. Stipes and rhachides dark, grooved above, fibrillose with black, hair-like scales. Lamina simply pinnate, narrowed above and below with 60 or more pairs of pinnae; pinnae horizontal, the lower ones gradually reduced to short auricle-like appendages, sessile, up to 6 × 1 cm., linear-oblong, apex acute, broadly cuneate or truncate and *auricled at the upper base, narrowly cuneate at the lower base*, margins serrate; veins once or twice forked, the costa grooved above, hairy below when young; texture chartaceous to subcoriaceous, dark-brown when dry. Sori on the acrosopic branches of the veins forming two oblique rows extending from the costa and falling short of the margin; indusium firm, brown.

Ceylon: Near Galle (PDA).

Habitat in Ceylon unknown.

Madagascar, Mascarene Islands, Ceylon, Sikkim, Burma, Indochina, Malaya, Sumatra, Java, Borneo, Philippines, New Guinea.

The distribution of *A. pellucidum* is consistent with its occurrence in Ceylon but the single frond in the Peradeniya collection, added since Thwaites’s time, is the only specimen I have seen.


Rhizome sub repent, clothed with lanceolate, acute, brown scales with paler fimbriate margins. Stipes grey-green, up to 30 cm. long, grooved above and bearing narrow, brown, fimbriate scales; rhachis similarly grooved and scaly. Lamina oblong-lanceolate, 30–70 × 10–20 cm., *imparipinnate* with 7–20 pairs of distant
pinnae and a terminal pinna bearing a scaly bud on the costa; pinnae normally 5–10 × 1.5–2.5 cm., sometimes to 15 × 3 cm., stalked, lanceolate, oblong-lanceolate or ligulate, apex acute, upper base rounded, lower base cuneate, margins crenate or subentire, costa raised above, upper surface naked, lower surface usually with a few appressed, laciniate, ferrugineous scales; veins once or twice forked; texture firm, chartaceous. Sori forming two oblique rows between the costa and the margin; indusium pale, broad. Spores plano-convex to ellipsoid, 42–50 × 30–40 μ, with a rather broad undulate perispore wing and a few surface folds.


In moist forests of the Central Province, 1,200–2,100 m.

Ceylon, South India (Nilgiri and Palni Hills).

The proliferous terminal pinna in this species is usually contracted suddenly to the costa at the point where the large scaly bud is formed, and the costa is then prolonged and develops an irregular lamina. Very occasionally fronds may continue apical growth more or less indefinitely without forming a terminal pinna.


Asplenium coriaceum Bory in Bélangier, Voy. Ind.-or., Bot. 2: 46 (1833); non A. coriaceum Desv. (1827).

Rhizome oblique, subrepetent, scaly at the apex, scales linear, tapering, 6 × 1 mm., walls brown, margins paler, fimbriate. Fronds tufted, 25–50 cm. long. Stipes green, up to 20 cm. long, scaly at the base, naked above. Lamina imparipinnate, pale-glaucous-green, up to 30 × 15 cm., sometimes more, with 3–10 pinnae on each side of the rhachis and a terminal pinna resembling the lateral ones; pinnae shortly stalked, linear or elliptic-oblong, 7–15 cm. long, about 1 cm. (rarely 2 cm.) broad, widest at or near the middle, narrowing gradually to the base, apex long-acuminate, margins coarsely serrate, glabrous on both surfaces or with a few laciniate pale-brown scales beneath, costa raised above; veins simple or once forked; texture coriaceous or subcoriaceous. Sori 0.5–1 cm. long, extending from near the costa but falling short of the margin; indusium pale, whitish. Spores reniform to plano-convex, 42–48 × 27–39 μ, with a winged perispore and surface folds.

CEYLON: Thwaites C.P. 1010 in part (BM; E; G; K; PDA)—data pencilled on PDA sheets: Nuwara Eliya, 1847 and Feb. 1857, Gardner; Matale, 1849, Gardner). Hantane Range, on trees in forest, Oct. 1844, Gardner 1070 bis (CGE).

On trees and rocks in mountain forests; infrequent.

Ceylon, South India, Philippines.

Fée described this species from Ceylon specimens—"Gardner no. 30"—and his reference to the rigid texture and pallid green colour clearly indicate that his plant was the same as that which Hooker later described as A. wightianum. Its differences from A. longipes are referred to under that species. South Indian specimens are identical with those from Ceylon. It appears to be more widely distributed in Ceylon than A. longipes but at lower elevations.

A Philippine specimen at Kew seems identical with Ceylon plants. Copeland included A. serricula (as A. wightianum) in his Polypodiaceae of the Philippine Islands (1905) but he omits it in his Fern Flora of the Philippines (1960).

14. Asplenium longipes Fée, Mém. Fam. Fouq. 5: 195 (1852); op. cit. 7: 49, t. 16 fig. 3 (1857).


Asplenium vulcanicum sensu T. Moore, Index Fil.: 178 (1860) pro parte, quoad specimen.

Zeyl.; non Blume.—Hook. & Baker, Synops. Fil.: 201 (1867) pro parte.

Rhizome obliquely erect, scaly at the apex, scales tapering, 7-8 x 1-1.5 mm., walls brown, margins paler, fimbriate. Fronds tufted, 30-60 cm. or more long. Stipes green, up to 30 cm. long, scaly when young, becoming naked or almost so with age. Lamina imparipinnate, green, up to 40 x 15 cm., with 4-8 pinnae on each side of the rhachis and a terminal pinna resembling the lateral ones; pinnae petiolate, lanceolate, 7-12 cm. long, about 2-2.5 cm. (rarely 3.5 cm.) broad, widest near the base, superior base rounded to broadly cuneate, inferior base more obliquely cuneate, apex acuminate, margins coarsely serrate, glabrous on both surfaces or with a few small brown scales beneath, costa raised above; veins simple or once forked; texture firmly herbaceous. Sori up to 1.5 cm. long, extending from the costa to near the margin; indusium whitish. Spores plano-convex, 36-42 x 24-27µ, with a winged perispore and surface folds.


On trees and rocks in forests; common about Nuwara Eliya but not recorded from elsewhere.

Endemic.

This species was described from Ceylon plants gathered by Walker. Féé’s description of the pinnae as ovate-lanceolate and his illustration leave no doubt that this is the plant which Hooker redescribed, again from specimens of Walker’s, as A. walkeræae. It is closely related to A. serricula but differs in its thinner texture, greener fronds and in its pinnae being broadest near the base with the acrosopic margin broadly cuneate or even rounded. In A. serricula the fronds are whitish-green or glaucous-green and subcoriaceous in texture and the pinnae are narrowly oblong or elliptic-oblong, broadest at or near the middle and tapering at both ends. In A. longipes the pinnae are normally 2–2.5 cm. wide in the widest part and still wider in robust specimens, whereas in A. serricula they are normally 1 cm. wide, occasionally reaching 2 cm. in large specimens. As correctly described by Hooker, diplazioid sori sometimes occur in A. longipes.

Thwaites (Enum. Pl. Zeyl.: 383 (1864)) considered the two to be connected by intermediate forms and hence untenable as separate species. Wall (Cat. Ferns Indig. Ceyl.: 4 (1873)), whose field knowledge of Ceylon ferns was both extensive and accurate, expressed precisely the opposite view. My own experience leads me to agree with Wall; and nearly all herbarium specimens can be readily assigned to one or the other species. Moreover, if A. longipes were merely a variant of A. serricula with broad pinnae it might well be expected to accompany that species in South India, whereas all specimens from there match Ceylon examples of A. serricula and none approaches A. longipes.

Hooker considered the Ceylon plant “undoubtedly quite distinct” from A. vulcanicum Blume, but Moore (Index Fil.: 178 (1860)) and Baker (Hook. & Baker, Synops. Fil.: 201 (1867)) included it in that species. I have examined the type specimen of A. vulcanicum from Java and concur with Hooker’s view. It differs in the fronds being proliferous from a bud borne distally on the rhachis and in the oblong or oblong-lanceolate, cuneate-based pinnae, the margins of which are subentire except towards their serratâ apices. In A. longipes the fronds are never proliferous and the margins of the lanceolate pinnae are coarsely serrate throughout. The non-proliferous A. salignum Blume of Malaya and Java is also much less coarsely serrate and has fewer pinnae—its fronds vary from simple to pinnate with 3–4 pairs of pinnae—than Ceylon plants. The type sheet of this has all the fronds on three complete specimens either simple or trifoliolâte. A specimen in the British Museum
Herbarium from Java, collected by Horsfield and named A. walkeræ, has coarsely toothed pinnae as in A. longipes but differs from that in being proliferous.

A. longipes is common in the forests of the Nuwara Eliya district but I have not met with it elsewhere. Where localities are cited on herbarium sheets, they are all in this district.


Asplenium tenerum sensu Thw., op. cit.: 383 (1864); non Forst. f.

Rhizome creeping, clothed at the apex with short, ovate, blackish scales 1 mm. long. Fronds 20–50 cm. long. Stipites green, darkening with age, 5–15 cm. long, terete on the back, channelled above, scaly at the base, elsewhere, like the rhachis, with scattered short, broad, dark-brown scales with peltate bases and often with irregularly dentate margins. Lamina oblong-lanceolate, simply pinnate, 10–30 or more cm. long, 5–10 (15) cm. broad, green when dry, with 8–15 (20) pairs of pinnae, the lowermost not or scarcely reduced, terminating in an apical pinna similar to the lateral ones and gemmiparous from the upper base of one of the distal pinnae; pinnae 3–6 (8) cm. long, 1–1.5 cm. broad near the base, shortly stalked, patent or ascending, not imbricating, upper base broadly cuneate or truncate, lower base narrowly cuneate, lanceolate, acute, margins toothed, glabrous above, sparsely scaly about the base beneath and often with a few minute scales on the veins; veins immersed, forked, well spaced, not striate above; texture firm-herbaceous. Sori up to 1 cm. long, spreading along the veins from near the costa and falling short of the margin. Spores plano-convex, 36–42 × 24–27μ, with a perispore forming a rather broad irregular undulate wing and a few surface folds.


On rocks and trees in forests, especially in the Southern Province.

Ceylon, Sumatra.

Hooker included A. gardneri partly under A. caudatum Forst. f. and partly under A. macrophyllum Swartz. Beddome considered it “probably only a variety” of the latter (Handb. Ferns Brit. Ind.: 151 (1883)). But it is a quite distinct species not, in my opinion, closely related to the A. falcatum group. From the least-divided forms of A. falcatum it differs in its creeping rhizome with much smaller and blunter scales, in its gemmiparous fronds of a more supple and pliable texture, in the veins
of the pinnae being immersed and not forming striations above and also being far fewer and more widely spaced than in that species and hence in having fewer sori to the pinna, usually five or six on each side of the costa as against three or four times that number in _A. falcatum_. From the creeping _A. decrescens_ it is at once distinguished by its sori not forming parallel rows close to the costa and by its gemmiparous habit.

I have only met with this species in the Sinha Raja forest and Wall cites it only from the Southern Province. Gardner collected it at Nuwara Eliya but I have seen no other gatherings from that much-botanized area. Teschemacher’s specimens from Sumatra quoted by Hooker under _A. macrophyllum_ are identical with Ceylon plants but the Khasi Hills plants referred by C. B. Clarke to _A. gardneri_ are specifically distinct (_A. khasianum_ Sledge in Kew Bull. 15 : 397 (1962)).

16. _Asplenium decrescens_ Kunze in Linnaea 24 : 261 (1851).


_Rhizome long-creeping_, clothed with narrow, finely pointed, very dark-coloured, imbricating scales 5 mm. long. Fronds 30–60 cm. long. Stipes 5–30 cm. long, deep purplish-brown, scaly at first, becoming almost or completely glabrous save at the base; rhachis grooved above, usually with scattered, filiform, brown scales or more rarely almost glabrous. Lamina oblong-lanceolate, up to 30 cm. or more long, with 10–20 pairs of shortly stalked pinnae, the lowermost slightly reduced, the uppermost gradually reduced and merging into the lobed apex; pinnae 5–10 cm. long and 1 cm. broad near the base, lower base narrowly cuneate, upper base broadly cuneate or rounded, narrowed gradually to the acuminate apex, both edges more or less deeply lobed, the lobes oblique and sharply toothed, becoming simply serrate distally, striate above and dark-olive-brown when dry, under surface with brown, filiform scales on the veins; _veins numerous, crowded_, forked; texture chartaceous. _Sori_ situated on the vein branches nearest the costa, at first somewhat imbricating and diverging but _becoming confluent with age to form two parallel rows close to the costa_ but with a few flabellately arranged sori on the basal lobes. Spores plano-convex, 36–42 × 24–27 μ, with a perispore forming an undulate wing and a few surface folds.

On rocks and trees in the higher parts of the interior, 1,300–2,200 m.

Ceylon, South India (Nilgiri and Palni Hills).

Kunze described this species from specimens collected by Schmid in the Nilgiri Hills. One of the two gatherings which he quotes, *Herb. Koch n. 122*, is in the Berlin Botanical Museum. I have examined this sheet and have no doubt that the specimens belong to the same species as the Ceylon plants which have long passed under the name *A. caudatum* Forst. f. One of the specimens is complete with rhizome and shows the creeping habit. The fronds on this plant and a separate larger frond mounted on the same sheet show the characteristic arrangement of the sori, which are elongated close to and more or less parallel with the costae of the pinnae. The type specimen represents a considerably smaller form with more entire pinnae than is commonly met with in this species, but both in size and lobing of the pinnae *A. decrescens* is a variable species and the original specimens may well represent high-altitude or precociously fertile examples. Kunze's choice of specific epithet was both inappropriate and inexplicable since his description states that the fronds are not decrescent.

Hooker (Sp. Fil. 3: 152 (1860)) was responsible for referring the Ceylon plant to Forster's *A. caudatum*. Forster (Florul. Ins. Austr. Prodr.: 80 (1786)) does not state where his *A. caudatum* was collected but according to Schkuhr (Krypt. Gew.: 72, t. 77 (1809)) it came from the Friendly Islands. The type specimen at Göttingen labelled "*Asplenium caudatum* Forst. prod. no. 432. In ins. Maris pacifici leg. Forster" consists of a portion of a pinnate frond about 12 cm. long with pinnae about 4 cm. long, pinnatifid about half-way to the costa with serrate lobes and with diverging sori. Schkuhr's illustration depicts the form of the pinnae and arcuate, diverging sori, some reaching almost to the frond margin, very well. Yet Hooker (loc. cit.), although referring to this illustration as "faithful", describes the sori as "almost parallel with and near the costa", a statement which was no doubt responsible for the confusion surrounding the application of this name by Beddome, Thwaites and others who relied largely on Hooker's work. Most specimens labelled *A. caudatum* from south-east Asia and the Pacific Islands are easily distinguished from Ceylon plants by the cutting of the pinnae and especially by the stipe and rhachis which are more profusely clothed with black, clathrate scales with long hair-points.

Ceylon plants have also been referred to *A. contiguum* Kaulf. by Moore and Beddome, and this identification is certainly to be preferred to Hooker's. Kaulfuss's species was described from Hawaii and some specimens from there are very like *A. decrescens*. Authentic specimens, however, are not available for study and Hawaiian plants labelled *A. contiguum* are decidedly diverse. A Kew specimen so identified by Christensen differs from the Ceylon plant in its less-cut pinnae which are glabrous beneath. The Philippine *A. lepturus* J. Smith ex C. Presl, which Christensen (Index Fil.: 118 (1905)) cites as a synonym of Kaulfuss's species and to
which Moore (Index Fil.: 121 (1859)) and Hooker (Sp. Fil. 3 : 156 (1860)) gave varietal rank also under \textit{A. contiguum} Kaulf., is another closely related taxon. This was based on \textit{Cumina} 211 from Luzon, the specimens of which at Kew and the British Museum differ from the Ceylon plant in their more caudate pinnae, glabrous beneath and with more diverging sori. Ceylon and Nilgiri plants fall between these species and the African \textit{A. friesiorum} C. Chr., which differs in its broader-based, thinner-walled, brown, shining and iridescent scales, and in the position of its sori which are all strictly costal.

Skottsberg (Medd. Göteb. Bot. Trädg. 15 : 97 (1942)) discussed the relationships of Hawaiian, Philippine, Ceylon-South Indian and African plants and concluded that all are conspecific with \textit{A. contiguum} although he cited differences (tom. cit.: 103) in the scale and spore characters both of the African and Ceylon-South Indian plants and these are listed in his table (tom. cit.: 82) as varieties—unnamed—of \textit{A. contiguum}. The African \textit{A. friesiorum} seems to me to merit the specific separation which all later authors have upheld and I prefer to use the name \textit{A. contiguum} for Hawaiian and Pacific Island plants and to retain Kunze's name for Ceylon plants, which are certainly identical with those from South India.

\textit{A. decrescens} is readily distinguished from \textit{A. falcatum}, which it most closely resembles, by the position of its sori which lie close to and parallel with the costa of the pinna, and by its long-creeping rhizome. The two species are also quite distinct in their distribution in Ceylon, \textit{A. falcatum} being a fern of low elevations (I have not met with it above 675 m.) whereas \textit{A. decrescens} grows only in the higher mountains of the interior, above 1,300 m.


\textit{Asplenium adiantoides} (L.) C. Chr., Index Fil. : 99 (1905) ; non \textit{A. adiantoides} Lam. (1786).—Holtl., Fl. Malaya 2 : 431 (1954).

\textit{Rhizome oblique or short-creeping with close-set stipes}, clothed with narrow, pointed, dark scales 5 mm. long. Fronds 30–90 cm. long. Stipes up to 30 cm. long, dark-purple to black with spreading scales at the base and smaller, appressed, deciduous scales with more or less stellately lobed bases above; rhachis grooved above with scattered, dark-brown, irregularly lobed scales. Lamina oblong-lanceolate, simply pinnate or bipinnate, up to 40 cm. long or sometimes more, with 5–15 pairs of shortly stalked pinnae, the lowermost not reduced, terminating in an apical pinna similar to the lateral ones and often with one or two long ascending pinna-like lobes at its base; pinnae lanceolate, 5–15 cm. long, 2 cm. broad near the base, the lower base more or less excised, the upper base broadly cuneate or rounded, narrowed gradually from near the base to the acuminate, serrate apex, margins serrate, incised, pinnatifid or pinnately divided, glabrous and striate above, under surface with some laciniate scales near the base of the pinna and often on the veins; \textit{veins numerous, crowded, forked; texture subcoriaceous. Sori linear-elargate, spreading along the veins from the costa to near the margin. Spores plano-convex, 30–36 × 21\mu}, with a peri-
spore forming a median undulate wing and irregular anastomosing thickened ridges on the surface.

17a. *Asplenium falcatum* var. *falcatum*.

Fronds pinnate; margins of pinnae serrate or shallowly to deeply incised with toothed lobes.


17b. *Asplenium falcatum* var. *bipinnatum* Sledge, var. nov.


*Asplenium praemorsum* var. *latum* sensu T. Moore, Index Fil. : 156 (1859) pro parte; non Desv.

*Asplenium spathulinum* sensu Bedd., *Ferns S. Ind.* : 75, t. 226 (1864); non J. Smith ex Hook.

Frondes bipinnatae; pinnaulae infimae pinnarum inferiorum et mediarum breviter stipitatae vel subsessiles, rhomboideae, basi cuneatae, margine versus apicem acutum serrata alicuando margine tenui vel profunde incisae, plerumque 1·5–3 cm. longae, in exemplis magnis usque ad 6 cm. longae, cum apice attenuato; pinnaulae mediae in basin posteriore decurrentes, superiores connatae in apicem pinnae serratum sensim mutatae; pinnae supremae fere ut in var. *falcato*, rarius pinnaeae vel pinnatifidae.

On rocks and trees at low or moderate elevations.

Madagascar, Mascarenes, Ceylon, India, south China, Malaya, Indonesia, Philippines, Polynesia, Australia, New Zealand.

Linnaeus based his description of Trichomanes adiantoides on a Ceylon specimen collected by Hermann. The specimen is in the British Museum Herbarium (Herb. Hermann, vol. 3, fol. 47). He also cited synonyms from Plukenet and Burman. Lamarck based his Asplenium falcatum on specimens from Mauritius and included the Burman synonym, and his is the correct name for this species since A. adiantoides (L.) C. Chr., which has been widely employed for it, is an illegitimate combination as Lamarck had used the name A. adiantoides for another species.

A. falcatum is widespread in tropical Asia and, in its typical form, is easily recognized. It varies much in the size and form of the pinnae, the margins of which may be subentire, serrate, irregularly incised, pinnatifid or pinnately divided. Clarke (Trans. Linn. Soc. Lond., Ser. 2, Bot. 1: 480 (1886)) states that the fronds are “sometimes pinnatifid nearly to the midrib” and Skottsberg (Medd. Göteb. Bot. Trädg. 15: 78-102 (1942)), who made a detailed study of variation in this and allied species but who evidently saw little material from Ceylon, describes and illustrates the most extreme form as being no more than pinnatifidate. Other descriptions do not allow even this degree of lobing and none recognizes the existence of bipinnate forms, though Compton (Journ. Linn. Soc. Lond., Bot. 45: 446 (1922)) under A. adiantoides described a tripinnate variety from New Caledonia. Yet in Ceylon fully bipinnate forms are not uncommon and a very instructive series of specimens in the Kew Herbarium, collected by Wall, illustrates the wide range in form which A. falcatum may assume from simply pinnate examples with serrate pinnae through those with lobed and pinnatifid pinnae to fully bipinnate forms. Several of the Peradeniya sheets have been labelled by Thwaites “Aspl. falcatum forma composita” and Baker has annotated one of Wall’s sheets at Kew “A. falcatum bipinnate variety” though he never published a description. Some Ceylon plants transitional between normal A. falcatum and the var. bipinnatum agree with Skottsberg’s illustration (tom. cit. : 79, fig. 211) of A. falcatum var. sectum (Hilleb.) Skottsbg.

Although bipinnate forms of A. falcatum appear to be much more frequent in Ceylon than elsewhere, they are not confined to Ceylon. Some specimens from South India are identical with Ceylon plants of var. bipinnatum, and A. mysorensis Roth, described from Madras, consists at least in part of bipinnate fronds of A. falcatum. Holttum (Fl. Malaya 2 : 432 (1954)) refers to a Malayan specimen with deeply dissected pinnae and a specimen at Kew from the same region (Bukit Ketri, Perlis, 5 Feb. 1904, Matthew) is bipinnate. I have not seen the bipinnate variety from any other region.

The middle and lower pinnae of fronds of A. falcatum var. bipinnatum look so different from var. falcatum as to be scarcely recognizable as the same species. But the distal end of the frond usually shows a transition to undivided pinnae of the
normal type. Where, as is occasionally the case, the frond is bipinnate throughout, all resemblance to the typical form is lost. Failure to recognize the relationship between bipinnate fronds and the simply pinnate condition has led to confusion with other species. The Ceylon specimen which Beddome described and illustrated (Ferns S. Ind.: 75, t. 226 (1864)) as *A. spathulinum* from a specimen sent to him under that name by Thwaites, is an example of *A. falcatum* var. *bipinnatum*. It shows well the transition to the var. *falcatum* type of pinna in the distal part of the frond. Ferguson (Ceyl. Ferns: 26–27 (1880)) was well aware from field experience of the range of variation in the fronds of this species and he correctly identified Beddome’s illustration as being bipinnate *A. falcatum*, though he was incorrect in also referring Beddome’s preceding illustration (Tom. cit.: t. 225) to the same species. Moore’s *A. praemorsum* var. *latum* includes bipinnate *A. falcatum* as well as *A. aethiopicum* and Macrae’s Ceylon specimen, included by Presl in his *Tarachia furcata* var. *platyphylla*, is also *A. falcatum* var. *bipinnatum*.

Var. *bipinnatum* almost certainly covers a genetically heterogeneous group, for the occurrence of large spherical spores or of abortive sporangia in some gatherings is indicative of apogamous and hybrid strains, but such plants are not separable morphologically from others having plano-convex spores similar to, though larger than, those of var. *falcatum*.

The altitudinal range in Ceylon of *A. falcatum* is markedly different from that of *A. aethiopicum* and *A. affine*, the two species with which the bipinnate variety has most frequently been confounded. *A. falcatum* is a lowland fern whereas the other two are ferns of high elevations. The highest altitude at which I have collected any form of *A. falcatum* in Ceylon is 675 m., though Thwaites cites 4,000 ft. (1,200 m.) on the label of a Kew specimen of the bipinnate variety, and the same altitude is ascribed to an Indian specimen of *A. falcatum* var. *bipinnatum* also at Kew, collected by Beddome at Coorg. *A. aethiopicum* and *A. affine* are both confined, in Ceylon, to forests in the higher mountains of the interior. The former I have collected only between 1,500 and 2,025 m. and the latter between 1,200 and 2,040 m.

18. *Asplenium indicum* Sledge, nom. nov.

*Asplenium planicaule* Wall., Numer. List: 8, n. 189 (1829), nom. nud.

*Asplenium falcatum* var. *abruptum* Kunze in Linnaea 24: 260 (1851).


*Asplenium laciniatum* sensu Bedd., Handb. Ferns Brit. Ind.: 154 (1883) pro parte; non D. Don.

Rhizome short, erect, apex clothed with dark-brown to black, narrow, tapering scales. *Stipes* grey-green, up to 12 cm. long, *scaly when young, as is the rhachis*, with linear-lanceolate, entire-margined, brown scales, becoming glabrous or almost so with age. Lamina linear-oblong, up to 30 cm. long, 3–6 cm. broad, simply pinnate with 12–20 pairs of pinnae, apex acuminate; *pinnae shortly petiolate*, (i–) 2–4 cm. long and nearly 1 cm. broad in the widest part, *dimidiate-ovate*, acute, *superior base
broadly cuneate, subauriculate, inferior base narrowly cuneate and entire to \(\frac{1}{2}\) or more the length from the base, the rest of the pinna above and below irregularly and shallowly lobed with dentate margins; veins close, once or twice forked; texture stiff, subcoriaceous. Sori linear-elongate, spreading along the veins from near the costa but falling short of the margin. Spores reniform to plano-convex, 30–45 × 24–30\(\mu\), with a narrow perispore wing and surfaces rugose with thickened anastomosing ridges.


On rocks and trees in forests above 1,000 m.; not common.

Réunion (teste Hieronymus), Ceylon, South India (Malabar mountains), Himalaya from Kumaun to Assam (Khasi and Lushai Hills), China (Yunnan), Burma, Thailand, Indochina, Philippines, Japan (as var.).

Ceylon specimens match Wallich 189, the type of A. planicaule Wall. ex Mett., which name, however, is a later homonym and has to be replaced. Hieronymus (loc. cit.) has discussed this and the related species A. laciniatum, to which it had been reduced as a variety by Christensen (Index Fil. : 126 (1905)), who did not, however, give it a varietal name.

A. indicum suggests a small form of A. falcatum with greatly shortened pinnae and green stipes which are scaly when young. The texture and close venation of the pinnae are similar to those of A. falcatum, to which it appears to be related though, as Hooker (Sp. Fil. 3 : 163 (1860)) rightly said, no transitional specimens occur which might be considered as a passage to that species. A. indicum moreover is a mountain species whereas A. falcatum is a fern of low altitudes, and the geographical ranges of the two species do not coincide.


Rhizome short-creeping with clustered stipes, apex clothed with narrow, purple-brown, wavy-edged, thin-walled, glossy scales up to 2 cm. long. Stipes stout, dark coloured, glabrous; rhachis similar, grooved above. Lamina up to 100 × 30 cm., ovate to deltoid-ovate in outline, bipinnate, lowest pinnae not, or scarcely, reduced; largest pinnae to 15 × 8 cm. or more with up to 8 pairs of free pinnules below the
lobed apex, *pinnules* variable in size and outline, sometimes short (about 2 cm. long) and broad, rounded above and with serrate margins, or triangular and narrowed to an acute apex, up to 7 cm. long and deeply lobed at the base with the broadly rounded acroscopic lobe almost or quite free to the base, *pinnules* of upper *pinnae* smaller with broadly cuneate to truncate upper base and narrowly cuneate lower base, all *striate and shining above, glabrous on both surfaces*; *veins very numerous and closely placed*, in the larger *pinnules* springing from a fairly distinct costa; texture firm. Sori elongate, extending from near the midrib but falling short of the margin. Spores "with a wing of narrow to moderate width".

**Ceylon**: "Ceylon", Mrs. Walker (K).

In lowland forests.

Ceylon, South India, Himalaya from Nepal to Assam, Malaya, Sumatra, Java, Borneo.

The scales of *A. nitidum* are larger, lighter in colour and have thinner walls than those of *A. aethiopicum* and *A. falcatum*; their edges are wavy and the surfaces often more or less iridescent, as in the African *A. frieziorum*. The dark rhachis and completely glabrous fronds, sometimes with a sheen on the upper surface, are distinctive. It varies greatly in size. In the single Ceylon example at Kew the largest *pinnules* are $14 \times 8$ cm., the largest *pinnules* $5 \times 2$ cm., narrowly triangular in outline, *pinnatifid* at the base, dentate above and with acute apices. The specimen matches closely *Cuming 376* from Malacca, which Hooker correctly cited as typical of the species; this gathering is the type of *A. spathulinum* Kunze, who stated erroneously that it came from the Philippines. Holttum uses the name *A. glaucophyllum* Alderw. van Rosenb. for this species, citing *A. nitidum* "sensu Tardieu-Blot et Ching" as a synonym, but as Tardieu-Blot & Ching's description was based on the type specimens in the Riksmuseum, Stockholm, which are illustrated in their paper, their sense is surely also the original sense.

The specimens on which Swartz based his description of *A. nitidum* were collected by Rottler at Tranquebar in Madras. The species might therefore be expected to occur elsewhere in South India and Ceylon. But the specimen from Travancore in Beddome's collection at Kew, from which the drawing was made for Plate 149 of his *Ferns of Southern India*, is the only gathering, other than Rottler's specimens, that I have seen from southern India, and the specimen and illustration, though correctly referred to *A. nitidum*, do not represent a characteristic frond. There are no specimens from South India or Ceylon in the British Museum collection. Mrs. Walker's specimen in the Kew Herbarium, collected a century and a quarter ago, is the only example I have seen from Ceylon. There is no specimen in the Peradeniya herbarium. It is evident, therefore, that *A. nitidum* must be a very rare species in both South India and Ceylon. It is also probable that it is still rarer now than

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1 There is some doubt as to the provenance of the Kew specimen of *A. nitidum* despite the geographical probability of its authenticity. Four other ferns in Hooker's collection, labelled simply "Ceylon", viz. *Ctenopteris fuscata* Kunze, *Drynaria sparssora* (Desv.) T. Moore, *Dryopteris khasiana* C. Chr. and *Pyroosia acrostichoides* (Forst. f.) Ching, are similarly unrepresented in the herbarium at Peradeniya and no other Ceylon gatherings are known. It may well be that all were sent to Hooker from plants grown in the Peradeniya Botanic Garden.
formerly, for it grows in forests at low elevations and these have been much reduced in extent during the last century.

Thwaites and other Ceylon botanists were unacquainted with *A. nitidum* and the specimens so named by them are *A. affine*, though Thwaites’s “forma magis composita. An *A. laserpiifolium...*C.P. 3801” quoted under *A. nitidum* (Enum. Pl. Zeyl. : 384 (1864)) is a large dissected form of *A. aethiopicum*. The fern Beddome named *A. laserpiifolium* Lam. in his *Ferns of Southern India* (t. 225) and later, in the *Handbook*, referred to *A. nitidum*, is also a form of *A. aethiopicum*.


*Asplenium laserpiifolium* sensu Bedd., Ferns S. Ind.: 75, t. 225 (1864); non Lam.

*Rhizome creeping*, clothed with *linear-lanceolate, dark-brown, glossy, hair-pointed scales* 5 mm. long. *Fronds commonly 30–60 cm.*, sometimes 1 m. high. *Stipes* up to 30 or more cm. long, purplish-black, usually more or less thickly clothed, as are the *rhachides and young fronds, with ferrugineous, hair-pointed, decidual scales* intermixed with copious, *slender, woolly, hair-like scales*, but sometimes with few scales more or less restricted to the base of the pinnae or practically glabrous. Lamina bipinnate, 15–45 or more cm. long, 5–20 cm. broad, *linear-lanceolate to ovate-lanceolate with 12–25 pairs of shortly stalked, patent pinnae, the lowermost somewhat reduced, the upper ones merging into the lobed apex; pinnae 2–10 cm. long, 1–2.5 cm. wide near the base, acute or sometimes caudate, lower pinnules rhomboid or subspathulate, base cuneate, apex truncate, rounded or acuminate, split into two or three oblong, incised lobes with serrate apices; median and distal pinnules broadly adnate, oblong with irregularly toothed apices; glabrous or almost so above, usually scaly or hairy beneath on the veins but sometimes glabrous; veins close, flabellate, forked, giving a striate appearance to the upper surface of the pinnules; texture subcoriaceous. *Sori* linear, 0.5–1 cm. long. *Spores* plane-convex, (39–) 41–45 (–48) × 24–27 (–30) μ, with a perispore forming a median, undulate wing and irregular, anastomosing, thickened ridges on the surface.


In mountain forests above 1,500 m.

Tropical America, Africa from the Cape to Ethiopia and Madeira, Mascarene Islands, Ceylon, South India, Java, Australia, New Caledonia, Hawaii.

This is a polymorphic species which varies much in size and degree of dissection of the frond and in the degree to which the scaly clothing of the frond axis and pinnae is developed. The fronds may be narrow in outline in tall as well as dwarf plants, or they may be broad. In forms with narrow fronds the pinnae are either deeply pinnatifid or pinnate; wider-froned plants have pinnate pinnae, the pinnules being deeply pinnatifid or again pinnate. The pinnules may be closely or laxly arranged on the pinna rhachis and may be narrow, the narrowness in dried specimens often being accentuated by their revolute margins, or broad and flat.

The copious, ferrugineous, woolly, hair-like scales on the stipes and rhachides, and often on the under sides of the pinnules, are normally characteristic and facilitate identification. But forms occur in Ceylon, and elsewhere, in which these are absent on mature fronds and such forms are more likely to be confused with other species. Loss of scales is only partly due to age for fully mature fronds may remain woolly whilst small immature fronds on other plants may be almost glabrous. Both in the matter of indumentum and in frond form A. aethiopicum is undoubtedly a plastic species. The silhouettes (Fig. 1) show fronds taken from the same rootstock in successive years, the smaller frond being taken from the wild plant when collected, the larger from the same rootstock after cultivation for one year at Kew. Apart from the difference in size and dissection, the hair-like scales are almost confined to the regions of the pinna bases in the larger frond. More extreme examples from Ceylon of such large plants devoid of woolly indumentum have been referred to A. laserpitiifolium Lam. Beddome's illustration (Ferns S. Ind.: t. 225 (1864), as A. laserpitiifolium), drawn from a Ceylon specimen of C.P. 3801, shows such an extreme form and it is hardly surprising that it should have been referred to another species. The drawing shows an apparently glabrous plant, though there are in fact some narrow scales with attenuated toothed apices on the specimen, which is preserved at Kew. The spore measurements of similar plants moreover agree with those of A. aethiopicum. Some Nilgiri gatherings agree closely with such Ceylon
plants in the form and cutting of the fronds, but the presence on them of many of the characteristic hair-scales has facilitated correct identification, whilst their absence on some Ceylon plants led Beddome, Thwaites and others to assign these to another species.

Bipinnate forms of *A. aethiopicum* with broad, shallowly lobed pinnules and without hair-like scales bear a close resemblance to bipinnate forms of *A. falcatum*. Beddome’s illustration (Ferns S. Ind. : t. 144 (1864)) represents such a form and should be compared with his illustration (tom. cit. : t. 226 (1864), as *A. spathuliformis*) which represents *A. falcatum* var. *bipinnatum*. The pinnae in the distal parts of the frond, showing transitions in the one case to those typical of simply pinnate *A. falcatum*, together with the larger spores and the more strongly creeping rhizome with its narrow, hair-pointed scales in *A. aethiopicum*, afford means of separation. The great variation displayed by *A. aethiopicum* is due partly to environmental and partly to genetical factors. The specimen figured (Fig. 1) is known to be an octoploid and other grades of polyploidy may well occur in Ceylon as tetraploid and dodecaploid races are known from Africa. The large dissected form figured by Beddome as *A. laserpitiifolium* is similar to the African tetraploid. Some of my Ceylon gatherings have abortive sporangia and may be of hybrid origin. A valid subdivision can only be based on experimental studies, for any attempt to describe a series of subordinate taxa to cover the wide range of variation in Ceylon would be impracticable in view of the known fact that a wide morphological response to changes in growth conditions or age may occur within an individual plant.

21. *Asplenium affine* Swartz in Schrad., Journ. Bot. 1800 (2) : 56 (1801).—Sledge in Kew Bull. 15 : 401, fig. 2 (1962). (Fig. 2.)

*Asplenium spathuliformis* J. Smith ex Hook., Sp. Fil. 3 : 170 (1860), nom. illegit., pro parte, quoad specim. ex Luzon, Borneo et Ceylon; non *A. spathuliformis* Kunze (1848).

Rhizome short-creeping, clothed with narrow, attenuate, dark-brown scales. Stipes 10–20 cm. long (up to 40 cm. in forma *majus*), dark-coloured, sparsely scaly when young, becoming glabrous or nearly so; rhachis similar, grooved above. *Lamina bipinnate*, 15–30 × 5–15 cm. (tripinnate at the base and up to 80 × 30 cm. in forma *majus*), lanceolate to oblance-ovate in outline, *often proliferous from buds borne distally on the rhachis*; pinnules 10–20 on each side, lanceolate to ovate, acute, the upper ones merging into the lobed apex; largest pinnules up to 8 × 3 cm., bearing 1–5 pairs of spathulate or broadly ovate pinnules below the lobed apex; *pinnules usually blunt and rounded with toothed apices*—more rarely subacute—and *often auriculate on the anterior margin*, the largest 1–2 cm. long, entire or shallowly lobed or sometimes with the anterior auricle free almost to the base; surfaces glabrous or with a few narrow scales on the rhachides beneath; *veins forked, not crowded*, basal acroscopic pinnules showing 5–18 ultimate vein endings according to size; texture chartaceous. Sori elongate, falling short of the margin. Spores reniform to plano-convex, 36–57 × 24–30 μ, with a conspicuous undulate perispore wing and anastomosing surface folds.
21 (i). *Asplenium affine* forma *affine*.

Fronds of moderate size, 30–60 × 10–15 cm., lanceolate; pinnae up to 8 cm. long, bearing 1–5 pairs of spathulate or broadly ovate pinnules with rounded, toothed apices and often auriculate on the anterior margin; largest pinnules 1–2 cm. long, entire or shallowly lobed or sometimes with the anterior auricles free almost to the base.


21 (ii). *Asplenium affine* forma *majus* Sledge in Kew Bull. 15 : 408, fig. 3 (1962).


*Asplenium nitidum* sensu Bedd., Ferns S. Ind.: 50, t. 148 (1864) non Swartz.

*Asplenium cuneatum* var. *affine* Baker, Fl. Maurit. & Seych.: 489 (1877) pro parte; non *A. affine* Swartz.

Fronds large, up to 1 m. long and 30 cm. wide, broadly lanceolate; pinnae more attenuate or even caudate, up to 18 cm. long with 8–9 pairs of ovate-acute pinnatifid or pinnate pinnules with toothed margins, the largest 3–4 (–5) cm. long.


21 (iii). *Asplenium affine* forma *tenuisectum* Sledge, forma nov.

Pinnulae angustae circa 2 mm. latae, eae basales acrosopicae profunde pinnatifidae vel pinnatae cum segmentis angustis.
CEYLON: Thwaites C.P. 3801 in part (PDA, holotype).

Common in forests above 1,200 m.

Madagascar, Mascarene Islands, Seychelles, Ceylon, South India, Hainan, Thailand, Cambodia, Malay, Sumatra, Borneo, Philippines, New Guinea, New Hebrides, Fiji.

A. affine was described from a Mauritius specimen which I consider inseparable from Ceylon plants. Plants from the Seychelles so identified by Christensen are certainly identical with Ceylon specimens. A similar specimen, Cuming 210 from the Philippines, was named A. spathulinum by John Smith but was not described. Hooker validated this name by description and A. spathulinum J. Smith ex Hook. has been widely used for supposedly distinct plants from south-east Asia. In my paper on A. affine and A. spathulinum (Kew Bull. 15: 401–410 (1962)) I cited Cuming 210 as the holotype of the latter name. But as Mr. C. V. Morton has pointed out (in litt.) Hooker's description was drawn from several collections including the type collection of A. insiticium Brackenr. which is cited as a synonym. As this had already been validly described, A. spathulinum J. Smith ex Hook. is synonymous with, and a superfluous renaming of, the Hawaiian A. insiticium Brackenr. Moreover, A. spathulinum J. Smith ex Hook. is in any case a later homonym of A. spathulinum Kunze (Bot. Zeit. 6: 524 (1848)) and is therefore doubly illegitimate. Kunze's species was based on Cuming 376 from Malacca (not the Philippines as stated by Kunze and Metteni.us). Mettenius (Abhandl. Senckenb. Naturforsch. Ges. 3: 204 (1859)), Hooker (Sp. Fil. 3: 173 (1860)) and Tardieu-Blot & Ching (Notul. Syst. 5: 148 (1936)) all refer Cuming 376 to A. nitidum Swartz and the sheet of this number at the British Museum bears out their identification.

In my paper referred to above I have shown that A. affine Swartz and A. spathulinum auct. cannot be maintained as separate species. A. affine is a very variable species and fronds taken from the same rhizome before and after cultivation (see Fig. 2) display considerably greater differences than those by which it has been customary to distinguish it from A. spathulinum auct. Wild specimens are frequently met with similar to the large-fronded form which I have distinguished as A. affine forma majus, and these have often been assigned to different species. It was on such a robust form that Hooker based his description and figures of A. affine, considering it—not unnaturally—to be specifically distinct from Smith's Philippine A. spathulinum. So arose the belief that two species exist, one in the Mascarene Islands and one in the south-eastern Asia and the islands beyond; a belief which has been upheld by recent writers, though specimens available in herbaria give no support to this view. A. affine forma tenuisectum also merits recognition as an extreme variant, for its narrow pinnules are so different in appearance from those of typical A. affine that the relationship is not obvious. Octoploid and dodecaploid races of A. affine exist in Ceylon but apart from the greater average spore size in the latter they do not appear to be characterized by any constant morphological differences which will serve to separate two taxa.

Thwaites and other Ceylon botanists were unacquainted with the true A. nitidum and used this name for plants of A. affine. Specimens of A. affine were distributed by Thwaites, C.P. 1008, as A. nitidum. His A. spathulinum was partly A. falcatum
var. bipinnatum and partly a form of A. aethiopicum. A specimen of A. falcatum var. bipinnatum sent by Thwaites to Beddome as A. spathulinum is figured over the latter name on plate 226 of his Forns of Southern India. Later, in his Handbook, Beddome referred this illustration to A. affine, adding the comment "probably taken from a specimen of furcatum and not from affine as represented at Kew". He thus gave it three different names and erroneously in each case. Ferguson also referred specimens of A. affine to A. nitidum and used the name A. affine for specimens of A. falcatum var. bipinnatum. The fern figured by Beddome on plate 148 of his Forns of Southern India as A. nitidum represents A. affine forma majus and should be compared with those figured by Hooker (Sp. Fil. 3 : t. 202 (1860)) and Sledge (Kew Bull. 15 : 407, fig. 3 (1962)). There is no representation of typical A. affine in Beddome's illustrations but silhouettes of fronds from six different plants are shown in my paper (tom. cit. : 404, fig. 2) together with a silhouette (tom. cit. : 402, fig. 1) of the type specimen.

Despite the confusion which has surrounded the use of the names A. affine and A. nitidum in Ceylon, the former is a well-marked species quite distinct from members of the A. falcatum-A. aethiopicum-A. nitidum group. In A. affine the fronds are often proliferous from a bud arising on the distal part of the rhachis. Normally the bluntly rounded, broadly ovate to spathulate pinnules of A. affine are distinctive, although all four species are subject to considerable variation as regards degree of dissection of the frond. The veins in the pinnules of A. affine, however, are always relatively few in number and fairly widely spaced, basal acroscopic pinnules usually showing from 5 to 18 ultimate vein endings according to size. In A. falcatum var. bipinnatum, A. aethiopicum and A. nitidum the veins are repeatedly forked and much more closely spaced, comparable figures for basal acroscopic pinnules being 20−50 and sometimes in large specimens of A. nitidum exceeding 100. A. affine is also a fern of mountain forests whereas A. nitidum, of which I have seen only a single specimen from Ceylon, and A. falcatum var. bipinnatum are both lowland plants.


Rhizome erect, clothed at the apex with linear, hair-pointed, dark-chestnut scales. Fronds tufted, up to 20 cm. long and 1.5−4.5 cm. broad, oblong-lanceolate, the lower pinnae not much reduced. Stipules green, with filiform scales when young, glabrescent. Pinnæ 8−12 on each side, 1−3cm. long, pinnae or deeply pinnatifid, obtuse; pinnules few, rounded with acutely toothed outer edges and cuneate bases, glabrous above and beneath like the slender green rhachis; texture thin, herbaceous; veins forked. Sori 2−4 on each pinnule; indusium pale, membranous, entire. Spores plano-convex, 27−30 × 21−24μ, with a perispore forming a reticulate network of surface folds.

Ceylon: Thwaites C.P. 3139 (BM ; E ; GH ; K ; PDA)—data cited on PDA sheet: Uva, Apr. 1854). Hakgala, 1,500 m., Aug. 1881 (PDA). Ramboda, Wall in
**The Ceylon Species of Asplenium**


In crevices of walls and under rocks in the elevated parts of the interior, 900–1,600 m.

South Africa, Ceylon, India, China, Japan, Hawaii.

This is a small fern superficially resembling *Athyrium hohenackerianum* more than any other Ceylon species of *Asplenium*.

### 23. *Asplenium disjunctum* Sledge, sp. nov. (Fig. 3.)

*Rhizoma erectum*, apice paleis lineari-lanceolatis acutis integris atrofuscis c. 3 mm. longis vestitum. Frondes fasciculatae, usque ad 20 cm. longae, 5 cm. latae. Stipites 4–8 cm. longi, griseo-virides vel brunnescentes, juventute, ut rhachides, squamulis patentibus angustis acutis brunneis instructi, denique denudati; *rhachis* sursum sulcata, *in parte superiore* sed infra apicem gemmam nigro-squamulosam proliferantem gerens. Lamina ambitu anguste oblongo-lanceolata, *bipinnata*, *tripinnatifida*, *segmentis angustatis* 1–2 mm. *latis*, pinnis circa 10-jugis, infra apicem simpliciter pinnata, inimis vix brevioribus, marginibus pinnarum saepe in sicco revolutis; pinnae breviter petiolatae, 1 cm. inter se remotae, ad 3 × 1.5 cm., ambitu ovatae; pinnulae 2–4 utroque latere, infra apicem pinnatifidae, basales pinnarum inferiorum et mediatorum profunde pinnatifidae, segmentis angustis integrisque, supra glabre, infra squamulis paucis fusco-cellulis basi lacerato-fimbriatis apice longe attenuatis praesertim juxta basin pinnarum conspersae; venae in segmentis semel vel bis furcatae, in sicco supra manifestae; textura firmiter herbacea. *Sori in extrema parte venarum ad apicem segmentorum attingentes*. Sporae plano-convexae, 33–36 × 24 μ, perisporeo juga spissata et anastomosantia formanti.


Eastern side of the island at low elevations.

Endemic.

This is the fern referred to by Beddome (Suppl. Ferns Brit. Ind. : 31 (1892)) as probably an abnormal variety of "*Asplenium furcatum*". He probably saw only the single very indifferent specimen which is preserved in his collection at Kew. There is in my opinion no relationship with that species or with any other Ceylon species. Its finely cut, proliferous fronds give it some superficial resemblance to *A. tenuifolium*; but in *A. tenuifolium* the larger tripinnate-quadrripinnatifid, glabrous fronds are membranous in texture, light-green in colour with green stipules and rhachides, and the ultimate segments are sharp-pointed with solitary immersed veins which terminate well below the tips of the segments.

*A. disjunctum* seems to me to be most closely allied to *A. elmeri* Christ, which was described from the Philippines and has since been found in Borneo. From this it
Fig. 3. *Asplenium disjunctum* Sledge (holotype).  
*a*, whole plant;  
*b*, frond tip with gemma;  
*c*, underside of pinnule;  
*d*, rhizome scale;  
*e*, spore.
differs in facies and in the position of the sori, which are always situated at the ends of the segments. The pinnules are narrower, less markedly cuneate and more sharply incised, the narrowness of the pinnules and their segments being accentuated by the tendency for their margins to be revolute in the dried specimens, a tendency which is not apparent in specimens of A. elmeri. The latter species is known only from wet forests on high mountains in Luzon (Mt. Benguet) and Borneo (Mt. Kinabalu) at altitudes of 1,500–4,000 m. Both the stations for the Ceylon species are at low elevations on the eastern, dry side of the island.

The name refers to the separate and distant stations, 50 miles (80 km.) apart, whence the two localized gatherings were made. That from Mandagala in the Eastern Province is far removed from any other station whence I have seen collections.


Rhizome oblique, paleaceous with narrow, finely pointed, dark-brown scales. Fronds tufted, tripinnate or quadripinnate, normally 30–40 × 6–12 cm., sometimes larger, lanceolate or oblong-lanceolate, the lowermost pinnae slightly reduced. Stipe and rachis slender, grooved above, glabrous or with a few hairs. Lamina green, 10–30 cm. long, with 10–15 pairs of alternate, stalked, patent pinnae, the lower ones 5–7 cm. long, lanceolate, bipinnate to tripinnate, proliferous from scaly buds in the upper part, ultimate segments narrowed below and with acute to mucronate tips, apices of the frond and primary pinnae pinnatifid with linear segments; glabrous above and beneath; veins solitary, central, terminating well below the apices; texture thinly herbaceous. Sori 1–2 to a segment; indusium pale, membranous, entire. Spores reniform to plano-convex, 30–36 × 21–27 μ, with a perispore forming a broad undulate wing and many anastomosing surface folds.


On rocks by streams about Nuwara Eliya.

Ceylon, South India, North India from Nepal to Assam, west China (Yunnan), Thailand, Indochina, Formosa.

This is a very distinct species on account of its finely dissected fronds. Hooker, Beddome and Clarke do not refer to the proliferous habit though many Indian specimens show small scaly buds, often dormant. In Ceylon specimens the fronds invariably bear buds, often two or three on each frond, which arise in the groove at or close to the junction of the pinna rachis and first acrosopic pinnule.

*Aspleniun belangeri* Bory in Bélanger, Voy. Ind.-or., Bot. 2: 51 (1833).


*Asplenium veitchianum* T. Moore, Index Fil.: xlix (1857), 176 (1860).


Rhizome erect, scaly at the apex, scales ovate-acute, black with paler, brown edges. Fronds tufted, up to 30 cm. long. Stipes green, up to 10 cm. long, scaly below with narrow, dark, clathrate scales which are often jagged at the base, intermixed with and replaced higher on the stipe and on the under side of the rhachis and pinnae by scattered, pale-brown, appressed, irregularly laciniate to stellate-squamulose scales. *Lamina pale-green*, up to 20 cm. long, rarely more, 4–6 cm. broad, oblong-lanceolate to ovate in outline, apex acute or sometimes caudate, bipinnate; midrib of rhachis raised above and bordered by narrow lateral wings; *pinnae 2–5 cm. long*, linear-oblong cut down regularly into numerous (up to 12 pairs) linear, straight or somewhat falcate segments 1 mm. broad, the posterior margins decurrent to form a narrow wing to the *pinna rhachis*, the lowest acroscopic segment bifurcate, the rest simple and traversed by a single central vein; texture somewhat fleshy. Sori one to each segment on the anterior margin; indusium whitish, not reflexed at maturity. Spores light-brown, plano-convex, 39–42 × 24–27 μ, with a perispore wing and surface folds.


Epiphytic in wet forest in the south, especially (?) exclusively) the Sinha Raja forest. Ceylon, Indochina, Malaya, Sumatra, Java, Borneo, Celebes, New Guinea, Philippines.

Ceylon plants were referred by Hooker to *A. prolongatum* Hook. and were so named by Thwaites. They differ however in several respects. They lack the remarkably attenuated apical prolongation of the rhachis, they never bear a terminal bud, the shape of the frond is oblong-lanceolate to ovate, not linear-oblong, the pinnae are sparingly furfuraceous or stellate-squamulose beneath and their divisions are shorter but more numerous, and the basal scales are not so long or attenuated. Beddome’s illustration (Handb. Ferns Brit. Ind.: 162, fig. 79 (1883), as *A. rufiforme*) which represents typical *A. prolongatum* well illustrates the difference between this species and *A. decorum*. Sometimes the apex of the frond is drawn out or caudate, but it then bears simple, oblique and distant lobes and lacks the sudden transition from pinnae to long naked extensions bearing terminal bud s which are so characteristic of *A. prolongatum*. The qualification in Hooker’s statement (Sec. Cent. Ferns: sub t. 42 (1861)) that “Nearly every one exhibits the remarkable prolongation of the rachis, rooting at the apex” was evidently inserted to cover the few Ceylon specimens which were seen by him, as all the other gatherings he quoted (and
THE CEYLON SPECIES OF _ASPLENIUM_ 277

many subsequent gatherings correctly referred to this species) are quite consistent in this character. Christensen evidently doubted that the Ceylon plant was identical with _A. prolongatum_ as he excluded Ceylon from the distribution of that species as given in the third supplement to the _Index Filicum_.

The African _A. rutifolium_ (Berg.) Kunze, with which Ceylon plants were at one time identified, differs in its ovate or lanceolate pinnae, the basal acroscopic pinnules of which, and often the basiscopic ones also, are enlarged and pinnate.

The epithet _belangeri_ which has been widely used for this species is not available as _A. belangeri_ (Bory) Kunze is a later homonym of _A. belangeri_ Bory (= _A. longissimum_ Blume). Moore pointed this out long ago (Index Fil: xlix (1857), 176 (1860)) and substituted the epithet _veitchianum_. But Kunze had already described _A. decorum_, based on a plant from Java (Zollinger 1260), which he considered specifically distinct from his _A. belangeri_. The differences on which it was founded however are trivial and all recent workers have agreed in recognizing only one dareoid species in Malaysia, under which _A. decorum_ has been cited as a synonym.

This species requires further study. Whilst I am sure that the Ceylon population cannot be included under _A. prolongatum_ Hook., I am by no means sure that it is identical with Malaysian _A. decorum_. Plants from Malaya and Indonesia are mostly considerably larger than those from Ceylon and have more regularly divided pinnae; but the frond apex is the same in both and although Malaysian plants frequently produce buds they are not invariably proliferous as in _A. prolongatum_.

_A. decorum_ has often been regarded as a variety or form of _A. tenerum_ differing only in its deeply and regularly pinnatifid pinnae. Although Holttum regards it as a distinct species, he considers it closely related to _A. tenerum_, with which it frequently grows in Malaya. In Ceylon, however, it is geographically separated from _A. tenerum_, which is confined to the mountainous region of the interior, _A. decorum_ occurring only in the south of the island, and at lower elevations.
Asplenium erectum Willd. (Bory 70, holotype.)
INDEX TO VOLUME 3

The page numbers of the principal references and the new taxonomic names are printed in **bold-face** type, synonyms in *italics*. Names of infraspecific taxa are indexed only when they are new or are synonyms.

Acalypha annobonae .......................... 113
       *Acanthaceae* .......................... 108
       *Achyranthes andicola* ................. 85
       subsp. *lorenziana* .................. 81
       var. *subquadrata* .................. 82
       *baldjickii* .......................... 82
       *danica* .............................. 76
       var. *maxima* .......................... 72
       *fimbriata* .............................. 72
       *heteropis* ............................ 72
       *hungarica* ............................ 84
       *lorenziana* ............................ 77, 82
       *lyrata* ............................... 70
       *manifera* .............................. 72
       *reichardtiana* ....................... 70
       *stroemi* ............................... 72
       *vassaryi* .............................. 72
       *Achnanthidium baldjickii* ............ 81
       *hungaricum* ............................ 84
       *neglectum* ............................. 84
       *Achyranthes aspera* .................. 109
       *Actinoneis lorenziana* ............... 82
       *Adenopus breviflorus* ............... 101
       *Adenostemma perrottetii* ............. 103
       *Agelacia ovalis* ................. .......................... 98
       *Aghardia adhaerens* ................. 197
       *Alectra communis* .................. 107
       sessilibra .................................. 107
       *Allamanda cathartica* ............. 104
       *Alternanthera maritima* .......... 109
       sessilis .................................. 109
       *Amaranthaceae* ...................... 109
       *Amaranthus spinosus* .......... 109
       viridis .................................. 109
       *Amaryllidaceae* ...................... 115
       *Anacardiaceae* ....................... 98
       *Andropogon brevifolius* ............ 118
       *Angiosperms of the Cambridge Annobon Island Expedition* .... 93-118
       *Angraecum talbotii* ............. 115
       *Annona muricata* .................... 96
       reticulata .................................. 96
       *Annonaceae* ............................. 96
       *Antheophora cristata* ............. 117

       *Anthocodium fragile* ............. 196
       *Apocynaceae* ......................... 104
       *Araceae* ................................ 116
       *Arachis hypogaea* ................ 98
       *Aralia guilfoylei* ................. 102
       *Araliaceae* ......................... 102
       *Artocarpus communis* ............ 113
       heterophyllus .......................... 113
       *integer* ................................ 113
       *Arun sagittifolium* ............... 116
       *Asclepiadaceae* ..................... 104
       *Asclepias curassavica* ............ 104
       *Aspplenium, The Ceylon species of* 233-277
       *Asplenium* .............................. 240
       *adiantoides* ......................... 261, 267
       *aethiopicum* ......................... 267
       *affine* ................................. 269
       forma *tenuisectum* .................. 270
       *affine* ................................. 270
       *belangeri* .............................. 276
       *brachyotus* ............................ 252
       *brasilense* ............................. 248
       *camptorhachis* ..................... 248
       *caudatum* ............................... 258, 259
       *cheilosorum* ........................... 245
       *contiguum* .............................. 250
       *coriaceum* .............................. 255
       *cristatum* .............................. 247
       *eunetum var. affine* ............. 270
       decorum .................................. 276
       decrescens .............................. 259
       *disjunctum* ............................. 273
       *elongatum* .............................. 253
       *emarginatodentatum* ............. 245
       *ensiforme* .............................. 242
       *erectum* ................................. 248
       *erosodontatum* ....................... 247
       *erythrocaulon* ....................... 245
       *excisum* ................................. 249
       *falcatum* ............................... 261
       *var. abbreviatum* .................... 264
       *var. bipinnatum* ...................... 262
       *formosum* ............................... 243
       *furcatum* ............................... 267
       *gardneri* ................................. 258
       *glaucophyllum* ....................... 265
       *heterocarpum* ......................... 245
       *hirtum* ................................. 254
### Asplenium—contd.

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>inequilaterale</td>
<td>252</td>
</tr>
<tr>
<td>indicum</td>
<td>264</td>
</tr>
<tr>
<td>insigne</td>
<td>264</td>
</tr>
<tr>
<td>laciniatum</td>
<td>264</td>
</tr>
<tr>
<td>laetum</td>
<td>245</td>
</tr>
<tr>
<td>laserpitifolium</td>
<td>267</td>
</tr>
<tr>
<td>longipes</td>
<td>256</td>
</tr>
<tr>
<td>lunulatum</td>
<td>248</td>
</tr>
<tr>
<td>var. camplotrhachis</td>
<td>248</td>
</tr>
<tr>
<td>var. erectum</td>
<td>248</td>
</tr>
<tr>
<td>var. sphenolobium</td>
<td>248</td>
</tr>
<tr>
<td>var. trapeziforme</td>
<td>252</td>
</tr>
<tr>
<td>macraceri forma sphenolobium</td>
<td>248</td>
</tr>
<tr>
<td>macrophyllum</td>
<td>258</td>
</tr>
<tr>
<td>minus</td>
<td>243</td>
</tr>
<tr>
<td>multijugum</td>
<td>243</td>
</tr>
<tr>
<td>mysorensense</td>
<td>262</td>
</tr>
<tr>
<td>nidus</td>
<td>242</td>
</tr>
<tr>
<td>nitidum</td>
<td>265</td>
</tr>
<tr>
<td>nitidum</td>
<td>270</td>
</tr>
<tr>
<td>normale</td>
<td>243</td>
</tr>
<tr>
<td>obscurnum</td>
<td>247</td>
</tr>
<tr>
<td>opacum</td>
<td>243</td>
</tr>
<tr>
<td>pavonicum</td>
<td>243</td>
</tr>
<tr>
<td>pellucidum</td>
<td>254</td>
</tr>
<tr>
<td>persistifolium var. latifolium</td>
<td>254</td>
</tr>
<tr>
<td>planicaule</td>
<td>264</td>
</tr>
<tr>
<td>praemorsum</td>
<td>267</td>
</tr>
<tr>
<td>var. latum</td>
<td>262</td>
</tr>
<tr>
<td>prolongatum</td>
<td>276</td>
</tr>
<tr>
<td>pyramidalum</td>
<td>248</td>
</tr>
<tr>
<td>resectum</td>
<td>245</td>
</tr>
<tr>
<td>serricula</td>
<td>255</td>
</tr>
<tr>
<td>serriforme</td>
<td>247</td>
</tr>
<tr>
<td>spathulatum</td>
<td>262, 265, 269</td>
</tr>
<tr>
<td>sphenolobium</td>
<td>248</td>
</tr>
<tr>
<td>tenerum</td>
<td>253</td>
</tr>
<tr>
<td>var. terminans</td>
<td>253</td>
</tr>
<tr>
<td>tenerum</td>
<td>258</td>
</tr>
<tr>
<td>tenuifolium</td>
<td>275</td>
</tr>
<tr>
<td>trapeziforme</td>
<td>252</td>
</tr>
<tr>
<td>unilaterale</td>
<td>245</td>
</tr>
<tr>
<td>forma majus</td>
<td>246</td>
</tr>
<tr>
<td>var. majus</td>
<td>246</td>
</tr>
<tr>
<td>varians</td>
<td>272</td>
</tr>
<tr>
<td>weichiorum</td>
<td>276</td>
</tr>
<tr>
<td>vulcanicum</td>
<td>256</td>
</tr>
<tr>
<td>walkerae</td>
<td>256</td>
</tr>
<tr>
<td>wightianum</td>
<td>255</td>
</tr>
<tr>
<td>zenkeranum</td>
<td>254</td>
</tr>
<tr>
<td>Avicennia africana</td>
<td>108</td>
</tr>
<tr>
<td>germinans</td>
<td>108</td>
</tr>
</tbody>
</table>

### Beetneropsis laxior

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>luxia</td>
<td>117</td>
</tr>
</tbody>
</table>

### Bertiera annobonensis

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ingenta</td>
<td>109</td>
</tr>
</tbody>
</table>

### Blidingia minima

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>minimina</td>
<td>180, 183</td>
</tr>
</tbody>
</table>

### Boehava cocinea

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>diffusa</td>
<td>109</td>
</tr>
<tr>
<td>diffusa</td>
<td>108</td>
</tr>
</tbody>
</table>

### Bolusia talbotii

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bostrichia mixta</td>
<td>179, 227</td>
</tr>
</tbody>
</table>

### Bryonia palmata

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>scabra</td>
<td>102</td>
</tr>
</tbody>
</table>

### Bryonopis laciniosa

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buchenavia and Ramatella, A revision of the genera</td>
<td>1-46</td>
</tr>
</tbody>
</table>

### Buchenavia

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>acuminata</td>
<td>29</td>
</tr>
<tr>
<td>callistachya</td>
<td>20</td>
</tr>
<tr>
<td>capitata</td>
<td>12</td>
</tr>
<tr>
<td>congesta</td>
<td>36</td>
</tr>
<tr>
<td>corrugata</td>
<td>19</td>
</tr>
<tr>
<td>discolor</td>
<td>26</td>
</tr>
<tr>
<td>fanshawe</td>
<td>29</td>
</tr>
<tr>
<td>fluminensis</td>
<td>38</td>
</tr>
<tr>
<td>gracilis</td>
<td>37</td>
</tr>
<tr>
<td>grandis</td>
<td>35</td>
</tr>
<tr>
<td>huberi</td>
<td>34</td>
</tr>
<tr>
<td>kleinii</td>
<td>14</td>
</tr>
<tr>
<td>longibracteata</td>
<td>33</td>
</tr>
<tr>
<td>macahensis</td>
<td>37</td>
</tr>
<tr>
<td>macrophylla</td>
<td>32</td>
</tr>
<tr>
<td>megalophylla</td>
<td>26</td>
</tr>
<tr>
<td>ochroprumna</td>
<td>16</td>
</tr>
<tr>
<td>oxycarpa</td>
<td>24</td>
</tr>
<tr>
<td>oxycarpa</td>
<td>21</td>
</tr>
<tr>
<td>pallidovirens</td>
<td>27</td>
</tr>
<tr>
<td>parvifolia</td>
<td>13</td>
</tr>
<tr>
<td>ptariensis</td>
<td>12</td>
</tr>
<tr>
<td>pterocarpa</td>
<td>23</td>
</tr>
<tr>
<td>pulcherrima</td>
<td>33</td>
</tr>
<tr>
<td>puncta</td>
<td>17</td>
</tr>
<tr>
<td>reticulata</td>
<td>17</td>
</tr>
<tr>
<td>sericocarpa</td>
<td>15</td>
</tr>
<tr>
<td>stellae</td>
<td>32</td>
</tr>
<tr>
<td>suavecolens</td>
<td>21</td>
</tr>
<tr>
<td>tomentosa</td>
<td>19</td>
</tr>
<tr>
<td>vaupesana</td>
<td>12</td>
</tr>
<tr>
<td>viridiflora</td>
<td>28</td>
</tr>
<tr>
<td>Buckelisia maritima</td>
<td>109</td>
</tr>
<tr>
<td>Buclida angustifolia</td>
<td>12</td>
</tr>
<tr>
<td>capitata</td>
<td>12</td>
</tr>
<tr>
<td>Buforestia imperforata</td>
<td>116</td>
</tr>
<tr>
<td>Bulbophyllum melanolorrhachis</td>
<td>115</td>
</tr>
</tbody>
</table>

### Caesalpinia pulcherrima

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cajanis cajan</td>
<td>99</td>
</tr>
</tbody>
</table>

### Calonycetum aculeatum

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calothrix crustacea</td>
<td>179, 182</td>
</tr>
</tbody>
</table>

### Campalocaliae

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Campanulaceae</td>
<td>103</td>
</tr>
</tbody>
</table>

### Canscora decussata

<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>105</td>
<td></td>
</tr>
</tbody>
</table>
INDEX

Capartogramma, The diatom genus, and the identity of Schizostauron 47–92

Capartogramma 50

amphoroides 64

cruciula 59

jeani 55

karstenii 54

rhombicum 58

CAPRARACEAE 96

Capiscum annum 107

Carica papaya 100

CARICACEAE 100

Carposphyllum aridus 161

Cassia obtusifolia 99

occidentalis 99

tora 90

Cassipourea annobonensis 100

Catharanthus roseus 104

CELASTRACEAE 97

Centroceras clavatum 178, 179, 180, 227

Cephalostigma perrottetii 103

CERAMICACEAE 227

Ceranium clavatum 227

Cecylion species of Asplenium, The 233–277

CHAMAESPONACEAE 181

Chamberlain, Yvonne M. 173–232

CHLOROPHYTA 180, 181

Chorda lomentaria 205

Citrus aurantifolia 97

Cladophora catenifera 192

radiosa 179, 192

rupestris 179, 194

CLADOPHORACEAE 187

Clayton, W. D. 117–118

Cleistanthus libericus 111

CLEOMACEAE 96

Cleome ciliata 111

rutidosperma 96

Clitoria alba 99

Coc cocchlioris deusta 181

Coconeis beltmeyeri 69

danica 77

delitaca 69

diaphana var. β 69

dirupta 69

flexella 69

hungarica 85

CODIACEAE 196

Codium variagatum 112

Codium adhaerens 179, 197

fragile 178, 196

Coffeea libérica 102

Coix lacryma-jobi 118

Colpomenia sinuosa 179, 203

COMBRETACEAE 100

Commelina benghalensis 116

Commelinaeaceae 116

COMPOSITAE 103

Conservaria ambiguous 187

fuscopurpurea 208

granulosa 199

Confervae—contd.

radiosa 192

rupestris 194

tortuosa 189

CONNARACEAE 98

Convallaria fruticosa 116

Convolvulaceae 105

Convolvulus nil 106

Corallina goughensis 179, 213

officinalis 178, 179, 180, 211

CORALLINACEAE 211

Cordyline fruticosa 116

Corymborkis corymbosa 114

wikitschii 114

CRASSULACEAE 99

CRUCIFERAEE 96

Cucurbita lagenaria 101

sicaria 101

CUCURBITACEAE 100

CYANOPHYTA 181

Cyathula prostrata 109

Cymbopogon citratus 118

CYPERACEAE 117

Cyperus pedunculatus 117

Darea belangeri 276

Datura candida 107

DELESSERTIEAE 179

Dermatolithon nodulorum 178, 179, 180, 215

Desmodium mauritianum 98

ramossimum 98

Diandellia 129

compressa 136

DIANTHERA 108

DIANTHERA VERTICILLATA 129, 160

DIANTHUS sect. KOHLRAUSCHIA 129, 132

sect. Pseudotunica 129

sect. Tunica 160

subgen. Proliferastrum 161

diminutus 151

filiformis 151

glumaceus 169

nanteuilli 164

obcordatus 169

prolier 161

rectacaulis 145

saxifragus 151

velutinus 166

Dichrocephala bicolor 103

integrifolia 103

Dichiptera umbellata 108

verticillata 108

DILLENIACEAE 96

Dimeregramma baldjiickii 81

Dioscorea alata 115

cayennensis 115

dumetorum 115

Dioscoreaceae 115

Diploptera palmatus 101

Diporochna quintasii 97
<table>
<thead>
<tr>
<th>Common Name</th>
<th>Page Numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discoclauxylon occidentale var. pubescens</td>
<td>112</td>
</tr>
<tr>
<td>pubescens</td>
<td>112</td>
</tr>
<tr>
<td>Dolichos unguiculatus</td>
<td>99</td>
</tr>
<tr>
<td>Durvillaea antarctica</td>
<td>178, 206</td>
</tr>
<tr>
<td>utilis</td>
<td>206, 207</td>
</tr>
<tr>
<td>Durvillaeaceae</td>
<td>206</td>
</tr>
<tr>
<td>Ectocarpaceae</td>
<td>197</td>
</tr>
<tr>
<td>Ectocarpus globifer</td>
<td>197</td>
</tr>
<tr>
<td>granulosus</td>
<td>199</td>
</tr>
<tr>
<td>mitchelliae</td>
<td>201</td>
</tr>
<tr>
<td>virescens</td>
<td>201</td>
</tr>
<tr>
<td>Eleutheranthera ruderalis</td>
<td>103</td>
</tr>
<tr>
<td>Enteromorpha africana</td>
<td>184</td>
</tr>
<tr>
<td>bulbosa</td>
<td>179, 180, 184</td>
</tr>
<tr>
<td>gunniana</td>
<td>183</td>
</tr>
<tr>
<td>hookeriana</td>
<td>184</td>
</tr>
<tr>
<td>micrococcus</td>
<td>183</td>
</tr>
<tr>
<td>minima</td>
<td>183</td>
</tr>
<tr>
<td>nana</td>
<td>183</td>
</tr>
<tr>
<td>Entophysalis conferta</td>
<td>179, 180, 181</td>
</tr>
<tr>
<td>deusta</td>
<td>179, 181</td>
</tr>
<tr>
<td>Epipogium roseum</td>
<td>114</td>
</tr>
<tr>
<td>Eriosema glomeratum</td>
<td>99</td>
</tr>
<tr>
<td>Euphorbia pulcherrima</td>
<td>111</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>111</td>
</tr>
<tr>
<td>Exacum quinquevernum</td>
<td>105</td>
</tr>
<tr>
<td>Exell, A.W.</td>
<td>93–118</td>
</tr>
<tr>
<td>Exell, A. W., and C. A. Stace</td>
<td>1–46</td>
</tr>
<tr>
<td>Feldmannia globifera</td>
<td>178, 197</td>
</tr>
<tr>
<td>Fiedleria</td>
<td>129</td>
</tr>
<tr>
<td>illyrica</td>
<td>133</td>
</tr>
<tr>
<td>Fucus antarcticus</td>
<td>206</td>
</tr>
<tr>
<td>pyriferus</td>
<td>205</td>
</tr>
<tr>
<td>Gelidiaceae</td>
<td>210</td>
</tr>
<tr>
<td>Gelidium regulare</td>
<td>178, 210</td>
</tr>
<tr>
<td>sp.</td>
<td>178</td>
</tr>
<tr>
<td>Gentianaceae</td>
<td>105</td>
</tr>
<tr>
<td>Geophila neurodictyon</td>
<td>102</td>
</tr>
<tr>
<td>Gerardia sessilflora</td>
<td>107</td>
</tr>
<tr>
<td>Gifforia granulosa</td>
<td>178, 199</td>
</tr>
<tr>
<td>mitchelliae</td>
<td>180, 201</td>
</tr>
<tr>
<td>Gigartinae</td>
<td>218</td>
</tr>
<tr>
<td>Gossypium barbadense</td>
<td>97</td>
</tr>
<tr>
<td>Gough Island, Marine algae of</td>
<td>173–232</td>
</tr>
<tr>
<td>Gramineae</td>
<td>117</td>
</tr>
<tr>
<td>Gymnosporia annobonensis</td>
<td>97</td>
</tr>
<tr>
<td>Gypsophila sect. Petrorhagia</td>
<td>129</td>
</tr>
<tr>
<td>sect. Tunicastrum</td>
<td>132</td>
</tr>
<tr>
<td>subgen. Tunicia</td>
<td>129</td>
</tr>
<tr>
<td>alpina</td>
<td>145</td>
</tr>
<tr>
<td>arenicola</td>
<td>151</td>
</tr>
<tr>
<td>armerioides</td>
<td>139</td>
</tr>
<tr>
<td>compressa</td>
<td>136</td>
</tr>
<tr>
<td>cretica</td>
<td>141, 142</td>
</tr>
<tr>
<td>dianthoides</td>
<td>158</td>
</tr>
<tr>
<td>fasciculata</td>
<td>150</td>
</tr>
<tr>
<td>gasparrinii</td>
<td>154</td>
</tr>
<tr>
<td>Gypsophila—contd.</td>
<td></td>
</tr>
<tr>
<td>glomerata</td>
<td>171</td>
</tr>
<tr>
<td>graminea</td>
<td>155</td>
</tr>
<tr>
<td>haynaldiana</td>
<td>134</td>
</tr>
<tr>
<td>illyrica</td>
<td>133</td>
</tr>
<tr>
<td>multicaulis</td>
<td>151</td>
</tr>
<tr>
<td>ochroleuca</td>
<td>138</td>
</tr>
<tr>
<td>pachygyona</td>
<td>142</td>
</tr>
<tr>
<td>rigida</td>
<td>154</td>
</tr>
<tr>
<td>saxifraga</td>
<td>151</td>
</tr>
<tr>
<td>var. glomerata</td>
<td>154</td>
</tr>
<tr>
<td>strieta</td>
<td>145</td>
</tr>
<tr>
<td>thessala</td>
<td>156</td>
</tr>
<tr>
<td>velutina</td>
<td>166</td>
</tr>
<tr>
<td>Hedyotis herbacea</td>
<td>103</td>
</tr>
<tr>
<td>Herposiphonia paniculata</td>
<td>179, 180, 228</td>
</tr>
<tr>
<td>Heywood, V. H.</td>
<td>119–172</td>
</tr>
<tr>
<td>Hildenbrandia</td>
<td>179</td>
</tr>
<tr>
<td>Hippia integrifolia</td>
<td>103</td>
</tr>
<tr>
<td>Hymenocallis littoralis</td>
<td>115</td>
</tr>
<tr>
<td>Hypolytrum grande</td>
<td>117</td>
</tr>
<tr>
<td>Imperatia</td>
<td>129</td>
</tr>
<tr>
<td>piformis</td>
<td>151</td>
</tr>
<tr>
<td>Ipomoea alba</td>
<td>105</td>
</tr>
<tr>
<td>digitata</td>
<td>106</td>
</tr>
<tr>
<td>involucrata</td>
<td>105</td>
</tr>
<tr>
<td>mauritiana</td>
<td>106</td>
</tr>
<tr>
<td>nil</td>
<td>106</td>
</tr>
<tr>
<td>Iridaea augustina</td>
<td>222</td>
</tr>
<tr>
<td>boryana</td>
<td>219</td>
</tr>
<tr>
<td>ciliata</td>
<td>222</td>
</tr>
<tr>
<td>cordata</td>
<td>218</td>
</tr>
<tr>
<td>var. ciolata</td>
<td>222</td>
</tr>
<tr>
<td>crispatula</td>
<td>222</td>
</tr>
<tr>
<td>heterococca</td>
<td>218</td>
</tr>
<tr>
<td>laminarioides</td>
<td>222</td>
</tr>
<tr>
<td>micans var. ciolata</td>
<td>179, 180, 218</td>
</tr>
<tr>
<td>undulososa</td>
<td>178, 179, 180</td>
</tr>
<tr>
<td>Iridophycus boryanum</td>
<td>219</td>
</tr>
<tr>
<td>ciliatum</td>
<td>223</td>
</tr>
<tr>
<td>crispatum</td>
<td>223</td>
</tr>
<tr>
<td>laminarioides</td>
<td>218</td>
</tr>
<tr>
<td>undulosum</td>
<td>223</td>
</tr>
<tr>
<td>Ixora cocinea</td>
<td>102</td>
</tr>
<tr>
<td>Jatropha multifida</td>
<td>112</td>
</tr>
<tr>
<td>Justicia umbellata</td>
<td>108</td>
</tr>
<tr>
<td>Kalanchoe crenata</td>
<td>99</td>
</tr>
<tr>
<td>Kohlraviscia</td>
<td>129, 160</td>
</tr>
<tr>
<td>diminuta</td>
<td>161</td>
</tr>
<tr>
<td>glucinae</td>
<td>169</td>
</tr>
<tr>
<td>nanteutii</td>
<td>164</td>
</tr>
<tr>
<td>obcordata</td>
<td>169</td>
</tr>
<tr>
<td>proliferar</td>
<td>161</td>
</tr>
<tr>
<td>saxifraga</td>
<td>151</td>
</tr>
<tr>
<td>sibthorpiii</td>
<td>158</td>
</tr>
<tr>
<td>velutina</td>
<td>166</td>
</tr>
</tbody>
</table>
INDEX

Labiatae .................................................. 108
Lactuopylis angolensis .............................. 104
annobonensis ........................................ 104
mannii .................................................. 104
thomensis .............................................. 105
Lagenaria breviflora ................................. 101
sicerraria .............................................. 101
Laureaceae ............................................... 110
Leguminosae .......................................... 98
Leonotis nepetifolia .................................. 108
Lessoniaceae ............................................ 205
Lewis, J. .................................................. 104–105
Lauraceae ................................................ 110
Lagenaria siceraria ................................... 101

Liatris angolensis ...................................... 104
annobonensis .......................................... 104
inannii ..................................................... 104
thomensis .............................................. 105
Lippia breviflora ...................................... 108
siceraria ................................................. 108
Lauraceae ............................................... 110
Leguminosae .......................................... 98
Leonotis nepetifolia .................................. 108
Lessoniaceae ............................................ 205
Lewis, J. .................................................. 104–105
Lauraceae ............................................... 110
Lagenaria siceraria ................................... 101

Laticarpus angolensis ................................ 104
annobonensis .......................................... 104
inannii ..................................................... 104
thomensis .............................................. 105
var. thomensis ......................................... 105

Lilium angolensis ....................................... 104

Lithothamnion muelleri forma neglectum ...... 217
neglectum ................................................. 178, 179, 180, 186
Loganiaceae ............................................. 104
Lola tortuosa ........................................... 189
Lophosiphonia scopulorum ......................... 179, 231
Lophurella sp. .......................................... 179, 229
Loranthaceae ............................................ 110
Luffa aegyptiaca ....................................... 101
Lycaetae novae-zelandiae .......................... 187
Lycopersicon esculentum ........................... 106
Lyngbya roseum ......................................... 114
Macrocystis pyriforma ............................... 178, 205
Malgaceae ................................................. 98
Mangifera indica ....................................... 98
Marine algae of Gough Island ...................... 173–232
Maytenus annobonensis ............................. 97
Megacantha melanorhachis .......................... 115
Melampodium ruderal ................................ 103
Melasma indicum var. monticola .................. 107
Melastomataceae ....................................... 100
Meliaeeae ................................................. 97
Melobesia ................................................ 178
Melothria capillacea .................................. 101
cordifolia ................................................. 101
gilletii ..................................................... 101
minutiflora .............................................. 102
Microcladia alternata ................................ 179, 227
Micronesia hungarica ................................ 85
Mikania cordata ......................................... 103
sandens ................................................... 103
Sp .......................................................... 103
Moringaceae ............................................. 113
Mucuna sloanci ......................................... 98
uren ....................................................... 98
Nasturtium sinapis ..................................... 96
Navicula aquaeductae ................................ 87
bacilliformis ............................................. 89
caucasica ............................................... 89
scutella ................................................... 72
fimbriata ............................................... 89
fusiformis ................................................. 89

Navicula—contd. ........................................ 87
granum .................................................... 87
karstenii .................................................. 55
laevissima ................................................. 89
laevissima ................................................. 87
mutata ..................................................... 87

Nicotiana tabacum ...................................... 107
Nitophyllum sp. ......................................... 179
Nuxia angolensis ....................................... 104
var. annobonensis ..................................... 104
congesta .................................................. 104

Ochnea cf. gigiana ...................................... 97
membranacea ............................................ 97
Ochnaceae ................................................. 97
Ocimum basilicum ....................................... 108
Odontium baldickii .................................... 81
Oldenlandia herbaeac ................................ 103
Oplismenus hirtellus ................................... 117
Ophiocystis .............................................. 114
Oscillatoria nigroviridis ............................ 179, 182
Oscillatoriaceae ........................................ 182

Palmella conferta ....................................... 181
Pancreum littorale ...................................... 115
Panicum brevifolium ................................... 117
Paspalum commersonii ............................... 117
conjugatum ............................................... 117
Pennisetum polystachion ......................... 118
Peperomia annobonensis ............................ 110
hygrophila ................................................. 110
Peponia vogelii ......................................... 100
Peponiun braealatum ................................. 100
togelii ..................................................... 100
Persea americana ...................................... 110
Petrohagia, A revision of the genus ............. 119–172
Petrohagia ................................................. 129
sect. Diantha ........................................... 159
sect. Kohlrauschia .................................... 160
sect. Petrohagia ......................................... 148
sect. Pseudogyypsophila ............................ 145
sect. Pseudotunica ..................................... 132
subsect. Cretica ......................................... 142
subsect. Lyricract ....................................... 133
subsect. Saxifragae .................................... 148
subsect. Thessalae ..................................... 156
alpina ....................................................... 145
subsp. olympica ........................................ 146
arabica ..................................................... 143
armerioides .............................................. 139
var. laxa .................................................. 139
<table>
<thead>
<tr>
<th>Species</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ralfsia</td>
<td>179</td>
</tr>
<tr>
<td>Rama novae-zelandiae</td>
<td>187</td>
</tr>
<tr>
<td>Ramatella</td>
<td>38</td>
</tr>
<tr>
<td>argentea</td>
<td>39</td>
</tr>
<tr>
<td>crispialata</td>
<td>44</td>
</tr>
<tr>
<td>var. obtusa</td>
<td>45</td>
</tr>
<tr>
<td>latifolia</td>
<td>43</td>
</tr>
<tr>
<td>maguirei</td>
<td>41</td>
</tr>
<tr>
<td>obtusa</td>
<td>45</td>
</tr>
<tr>
<td>virens</td>
<td>42</td>
</tr>
<tr>
<td>Renvirea maritima</td>
<td>117</td>
</tr>
<tr>
<td>pedunculata</td>
<td>117</td>
</tr>
<tr>
<td>Rhaphoneis baldjickii</td>
<td>81</td>
</tr>
<tr>
<td>fluminensis</td>
<td>82</td>
</tr>
<tr>
<td>lorenziana</td>
<td>82</td>
</tr>
<tr>
<td>scutellum</td>
<td>82</td>
</tr>
<tr>
<td>Rhizoclonium africanum</td>
<td>187</td>
</tr>
<tr>
<td>ambiguum</td>
<td>179, 180, 187</td>
</tr>
<tr>
<td>hookeri</td>
<td>187</td>
</tr>
<tr>
<td>riparium</td>
<td>179, 189</td>
</tr>
<tr>
<td>subsp.? validum</td>
<td>189</td>
</tr>
<tr>
<td>var. validum</td>
<td>189</td>
</tr>
<tr>
<td>tortuosum</td>
<td>189</td>
</tr>
<tr>
<td>Rhizophoraceae</td>
<td>100</td>
</tr>
<tr>
<td>Rhodoglossum revolutum</td>
<td>179, 180, 225</td>
</tr>
<tr>
<td>Rhodomelaceae</td>
<td>179, 227</td>
</tr>
<tr>
<td>Rhodophyta</td>
<td>208</td>
</tr>
<tr>
<td>Rhynchosia glomerata</td>
<td>99</td>
</tr>
<tr>
<td>Ricinus communis</td>
<td>113</td>
</tr>
<tr>
<td>Rivulariaceae</td>
<td>182</td>
</tr>
<tr>
<td>Rorippa indica</td>
<td>96</td>
</tr>
<tr>
<td>sinapis</td>
<td>96</td>
</tr>
<tr>
<td>Ross, R.</td>
<td>47-92</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>102</td>
</tr>
<tr>
<td>Rutaceae</td>
<td>97</td>
</tr>
<tr>
<td>Sanseveria metallica</td>
<td>116</td>
</tr>
<tr>
<td>Sapontaria cretica</td>
<td>142</td>
</tr>
<tr>
<td>illyrica</td>
<td>133</td>
</tr>
<tr>
<td>Schizachyrium brevifolium</td>
<td>118</td>
</tr>
<tr>
<td>Schizostauron</td>
<td>66</td>
</tr>
<tr>
<td>andicola</td>
<td>84</td>
</tr>
<tr>
<td>brasiliense</td>
<td>60</td>
</tr>
<tr>
<td>crucicula</td>
<td>54, 59</td>
</tr>
<tr>
<td>fimbriatum</td>
<td>72</td>
</tr>
<tr>
<td>karstenii</td>
<td>55</td>
</tr>
<tr>
<td>ludigianum</td>
<td>69</td>
</tr>
<tr>
<td>ovatum</td>
<td>69</td>
</tr>
<tr>
<td>reichardtianum</td>
<td>70</td>
</tr>
<tr>
<td>rhombiculum</td>
<td>91</td>
</tr>
<tr>
<td>traticum</td>
<td>87</td>
</tr>
<tr>
<td>verbanium</td>
<td>87</td>
</tr>
<tr>
<td>Scrophulariaceae</td>
<td>107</td>
</tr>
<tr>
<td>Scytosiphon lomentaria</td>
<td>179, 180, 205</td>
</tr>
<tr>
<td>Sellaphora pupula</td>
<td>87</td>
</tr>
<tr>
<td>Sida rhombifolia</td>
<td>97</td>
</tr>
<tr>
<td>Silene angustifolia</td>
<td>136</td>
</tr>
<tr>
<td>Stizymbriini indicum</td>
<td>96</td>
</tr>
<tr>
<td>Sledge, W. A.</td>
<td>233-277</td>
</tr>
<tr>
<td>Solanaceae</td>
<td>106</td>
</tr>
<tr>
<td>Index</td>
<td>Page</td>
</tr>
<tr>
<td>-------</td>
<td>------</td>
</tr>
<tr>
<td>Solanum dasyphyllum</td>
<td>106</td>
</tr>
<tr>
<td><em>duplosinuatum</em></td>
<td>106</td>
</tr>
<tr>
<td><em>nigrum</em></td>
<td>106</td>
</tr>
<tr>
<td><em>nodiforum</em></td>
<td>106</td>
</tr>
<tr>
<td><em>Solenia bulbosa</em></td>
<td>184</td>
</tr>
<tr>
<td><em>Sphacelaria furcigera</em></td>
<td>178, 202</td>
</tr>
<tr>
<td><em>Sphacelariaceae</em></td>
<td>202</td>
</tr>
<tr>
<td><em>Stace, C. A.</em></td>
<td>1-46</td>
</tr>
<tr>
<td><em>Stanfieldiella imperforata</em></td>
<td>114</td>
</tr>
<tr>
<td><em>Stauroneis undicola</em></td>
<td>84</td>
</tr>
<tr>
<td><em>cornuta</em></td>
<td>72</td>
</tr>
<tr>
<td><em>crucicula</em></td>
<td>59</td>
</tr>
<tr>
<td><em>grunowii</em></td>
<td>60</td>
</tr>
<tr>
<td><em>karstenii</em></td>
<td>55</td>
</tr>
<tr>
<td><em>lindigiana</em></td>
<td>69</td>
</tr>
<tr>
<td><em>merrimacensis</em></td>
<td>60</td>
</tr>
<tr>
<td><em>ovata</em></td>
<td>69</td>
</tr>
<tr>
<td><em>reichardtiana</em></td>
<td>70</td>
</tr>
<tr>
<td><em>rectangularis</em></td>
<td>87</td>
</tr>
<tr>
<td><em>sagitta</em></td>
<td>92</td>
</tr>
<tr>
<td><em>smithii</em></td>
<td>92</td>
</tr>
<tr>
<td><em>stefanssonii</em></td>
<td>92</td>
</tr>
<tr>
<td><em>taxtiana</em></td>
<td>87</td>
</tr>
<tr>
<td><em>verbania</em></td>
<td>87</td>
</tr>
<tr>
<td><em>witirockii</em></td>
<td>89</td>
</tr>
<tr>
<td><em>Stearn, W. T.</em></td>
<td>106-107, 110-111</td>
</tr>
<tr>
<td><em>Summerhayes, V. S.</em></td>
<td>114-115</td>
</tr>
<tr>
<td><em>Syndrella nodiflora</em></td>
<td>103</td>
</tr>
<tr>
<td><em>Talinum triangulare</em></td>
<td>97</td>
</tr>
<tr>
<td><em>Tarachia falcata</em></td>
<td>261</td>
</tr>
<tr>
<td><em>furcata</em></td>
<td>267</td>
</tr>
<tr>
<td><em>var. platyphylla</em></td>
<td>262</td>
</tr>
<tr>
<td><em>nitida</em></td>
<td>265</td>
</tr>
<tr>
<td><em>Telanthera maritima</em></td>
<td>109</td>
</tr>
<tr>
<td><em>Terminalia catappa</em></td>
<td>100</td>
</tr>
<tr>
<td><em>hilariana</em></td>
<td>12</td>
</tr>
<tr>
<td><em>macrophylla</em></td>
<td>32</td>
</tr>
<tr>
<td><em>obovata</em></td>
<td>12</td>
</tr>
<tr>
<td><em>oxycarpa</em></td>
<td>24</td>
</tr>
<tr>
<td><em>punctata</em></td>
<td>17</td>
</tr>
<tr>
<td><em>suaveolens</em></td>
<td>21</td>
</tr>
<tr>
<td><em>tomentosa</em></td>
<td>19</td>
</tr>
<tr>
<td><em>vasivae</em></td>
<td>21</td>
</tr>
<tr>
<td><em>Tetracera alnifolia</em></td>
<td>96</td>
</tr>
<tr>
<td><em>Thamnopteris nidus</em></td>
<td>242</td>
</tr>
<tr>
<td><em>Thecacoris annobonae</em></td>
<td>111</td>
</tr>
<tr>
<td><em>Trichomanes adiantoides</em></td>
<td>261</td>
</tr>
<tr>
<td><em>aethiopicum</em></td>
<td>267</td>
</tr>
<tr>
<td><em>Tristemma oreothamnos</em></td>
<td>100</td>
</tr>
<tr>
<td><em>Tunica</em></td>
<td>129</td>
</tr>
<tr>
<td><em>sect. Dianthella</em></td>
<td>159</td>
</tr>
<tr>
<td><em>sect. Eutunica</em></td>
<td>148</td>
</tr>
<tr>
<td><em>sect. Fiederia</em></td>
<td>129</td>
</tr>
<tr>
<td><em>sect. Gyspophiloides</em></td>
<td>132, 148</td>
</tr>
<tr>
<td><em>sect. Kohrauschia</em></td>
<td>160</td>
</tr>
<tr>
<td><em>sect. Leptopleura</em></td>
<td>145</td>
</tr>
<tr>
<td><em>sect. Pachypepla</em></td>
<td>132</td>
</tr>
<tr>
<td><em>sect. Pleurotunica</em></td>
<td>132</td>
</tr>
<tr>
<td><em>sect. Pseudodianthus</em></td>
<td>148</td>
</tr>
<tr>
<td><em>Tunica—contd.</em></td>
<td></td>
</tr>
<tr>
<td><em>sect. Pseudogypsophila</em></td>
<td>145</td>
</tr>
<tr>
<td><em>sect. Pseudosaponaria</em></td>
<td>132</td>
</tr>
<tr>
<td><em>sect. Tunicastrum</em></td>
<td>148</td>
</tr>
<tr>
<td><em>subgen. Imperialis</em></td>
<td>129</td>
</tr>
<tr>
<td><em>subgen. Leptopleura</em></td>
<td>145</td>
</tr>
<tr>
<td><em>subgen. Pachypepla</em></td>
<td>132</td>
</tr>
<tr>
<td><em>alpina</em></td>
<td>145</td>
</tr>
<tr>
<td><em>angustifolia</em></td>
<td>134, 136</td>
</tr>
<tr>
<td><em>arabica</em></td>
<td>143</td>
</tr>
<tr>
<td><em>arenicola</em></td>
<td>151</td>
</tr>
<tr>
<td><em>argentii</em></td>
<td>139</td>
</tr>
<tr>
<td><em>armerioidea</em></td>
<td>139</td>
</tr>
<tr>
<td><em>var. laxa</em></td>
<td>139</td>
</tr>
<tr>
<td><em>bicolor</em></td>
<td>151</td>
</tr>
<tr>
<td><em>brachypetala</em></td>
<td>142</td>
</tr>
<tr>
<td><em>ciliata</em></td>
<td>151</td>
</tr>
<tr>
<td><em>compressa</em></td>
<td>134, 136</td>
</tr>
<tr>
<td><em>cretica</em></td>
<td>147</td>
</tr>
<tr>
<td><em>cypria</em></td>
<td>147</td>
</tr>
<tr>
<td><em>davaana</em></td>
<td>136</td>
</tr>
<tr>
<td><em>dianthoides</em></td>
<td>158</td>
</tr>
<tr>
<td><em>erecta</em></td>
<td>151</td>
</tr>
<tr>
<td><em>fasciculata</em></td>
<td>150</td>
</tr>
<tr>
<td><em>filiformis</em></td>
<td>147</td>
</tr>
<tr>
<td><em>gasparrinii</em></td>
<td>154</td>
</tr>
<tr>
<td><em>glumacea</em></td>
<td>169</td>
</tr>
<tr>
<td><em>var. obcordata</em></td>
<td>169</td>
</tr>
<tr>
<td><em>gracilis</em></td>
<td>158</td>
</tr>
<tr>
<td><em>graminea</em></td>
<td>155</td>
</tr>
<tr>
<td><em>haynaida</em></td>
<td>134</td>
</tr>
<tr>
<td><em>hispidula</em></td>
<td>145</td>
</tr>
<tr>
<td><em>illyrica</em></td>
<td>133, 134</td>
</tr>
<tr>
<td><em>subsp. angustifolia</em></td>
<td>136</td>
</tr>
<tr>
<td><em>subsp. haynaida</em></td>
<td>134</td>
</tr>
<tr>
<td><em>var. haynaida</em></td>
<td>134</td>
</tr>
<tr>
<td><em>var. taygetea</em></td>
<td>137</td>
</tr>
<tr>
<td><em>kennedyae</em></td>
<td>147</td>
</tr>
<tr>
<td><em>lycica</em></td>
<td>142</td>
</tr>
<tr>
<td><em>macra</em></td>
<td>158</td>
</tr>
<tr>
<td><em>nanteuilii</em></td>
<td>104</td>
</tr>
<tr>
<td><em>ochroleuca</em></td>
<td>134, 138</td>
</tr>
<tr>
<td><em>var. phthiota</em></td>
<td>149</td>
</tr>
<tr>
<td><em>olympica</em></td>
<td>147</td>
</tr>
<tr>
<td><em>orphanidesiana</em></td>
<td>156</td>
</tr>
<tr>
<td><em>pachygyona</em></td>
<td>142</td>
</tr>
<tr>
<td><em>var. hirittuba</em></td>
<td>143</td>
</tr>
<tr>
<td><em>pamphyllica</em></td>
<td>159</td>
</tr>
<tr>
<td><em>peronii</em></td>
<td>159</td>
</tr>
<tr>
<td><em>phthiota</em></td>
<td>149</td>
</tr>
<tr>
<td><em>prolifera</em></td>
<td>161</td>
</tr>
<tr>
<td><em>subsp. nanteuilii</em></td>
<td>164</td>
</tr>
<tr>
<td><em>var. nanteuilii</em></td>
<td>164</td>
</tr>
<tr>
<td><em>rhaphaea</em></td>
<td>156</td>
</tr>
<tr>
<td><em>rhodopea</em></td>
<td>134</td>
</tr>
<tr>
<td><em>rigida</em></td>
<td>154</td>
</tr>
<tr>
<td><em>saxifraga</em></td>
<td>151</td>
</tr>
<tr>
<td><em>var. gasparrinii</em></td>
<td>154</td>
</tr>
<tr>
<td><em>scoparia</em></td>
<td>136</td>
</tr>
<tr>
<td><em>sibthorpii</em></td>
<td>139</td>
</tr>
</tbody>
</table>
INDEX

Tunica—contd.
  stricta .................. 145
  syriaca .................. 170
  taygetea .................. 137, 141
  thessala .................. 156
    var. cyrenaica .............. 158
  velutina .................. 166
  xerophila .................. 151
Turraea glomeruliflora .............. 97

Ulva intestinalis var. nana .............. 183
  lactuca .................. 178, 179, 186
  sinuosa .................. 203
ULVACEAE .................. 183

Uncaria africana .............. 102
Urera cameroonensis .............. 114
URTICACEAE .................. 114

Verbenaceae .............. 108
Vigna alba .............. 99
unguiculata .............. 99
Viscum engleri .............. 110

Xanthosoma sagittifolium .............. 116

Zehneria gilletii .............. 101
  scabra .............. 102
  serobiculata .............. 102
PRINTED IN GREAT BRITAIN
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