Tecophilaeaceae

M.G. Simpson and P.J. Rudall

Tecophilaeaceae Leyb., Bonplandia 10: 370 (1862), nom. cons.
Cyanastraceae Engler (1900).

Erect, perennial, terrestrial *herbs*. Roots fibrous. Subterranean stem a globose to ellipsoid corm, 1–4 cm in diameter, in some genera with a membranous to fibrous tunic consisting of persistent sheathing leaves or fibrovascular bundles. *Leaves* basal to subbasal, or cauline in *Walleria*, spiral; base sheathing or non-sheathing, blades narrowly linear to lanceolate-ovate, or more or less petiolate in *Cyanastrum* and *Kabuyea*; entire, glabrous, flat, or marginally undulate; venation parallel with a major central vein. *Flowers* terminal and either solitary (or in small groups) and a panicle or (in *Walleria*) solitary in the axils of cauline leaves. Bracts and bracteoles (prophylls) often present on pedicel. Flowers 1–3 cm long, pedicellate, bisexual, trimerous. Perianth variable in color, zygomorphic or actinomorphic, homochlamydeous, basally syntepalous; perianth lobes 6, imbricate in 2 whorls, the outer median tepal positioned anteriorly; minute corona appendages present between adjacent stamens in some taxa. Androecium arising at mouth of perianth tube, opposite the tepals and either actinomorphic or zygomorphic, composed of either 6 fertile stamens or combinations of fertile stamens and staminodes; fertile stamens similar in size and shape or dimorphic, oriented equally in a circle or oriented in anterior and posterior groups. Fertile anthers 2-locular, poricidally dehiscent (or almost so). Gynoecium syncarpous; ovary semiinferior to almost superior; carpels and locules 3; placentation axile; ovules 2 to numerous per carpel. *Fruit* a loculicidal capsule. Seeds ranging from yellow to brown to black, and of varied size and shape.

Eight genera, ca. 23 species, Chile, southern and tropical Africa, Madagascar, and California.

Vegetative Morphology. All genera of Tecophilaeaceae have a subterranean, oblate to globose corm, 1–4 (generally 2) cm in diameter. In five genera (*Conanthera*, *Cyanella*, *Odontostomum*, *Tecophilaea*, and *Zephyra*) the corm is enveloped by a tunica, which consists of membranous to fibrous scale leaves or leaf bases or the reticulate fibrovascular remains of these scale leaves (Fig. 123). The tunic often continues above the corm, in some cases forming an apical tuft. Corms of *Walleria*, *Cyanastrum*, and *Kabuyea* lack a corm tunic (Fig. 122).

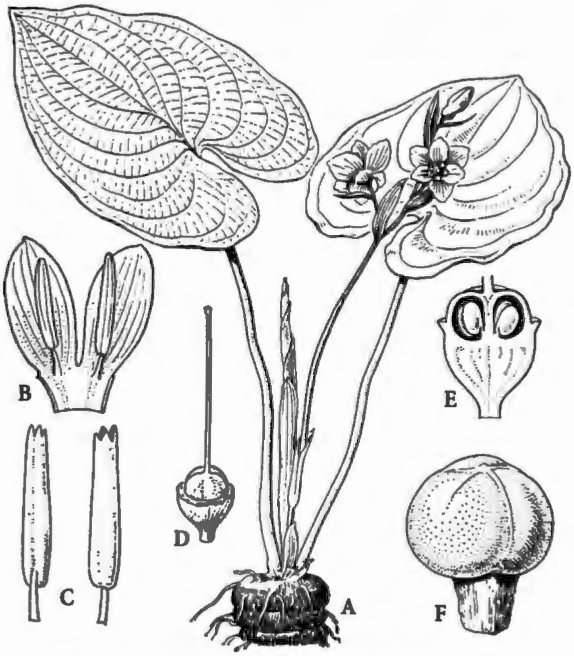

Fig. 122A–F. Tecophilaeaceae. *Cyanastrum cordifolium*. A Flowering plant. B Tepals with stamens. C Stamens. D Pistil. E Ovary, longitudinal section. F Capsule. (Takhtajan 1982)

Leaves are bifacial and spirally arranged. Leaf venation is parallel, with 1 major central vein. Photosynthetic leaves of some genera are basal to subbasal with a tubular sheath surrounding the base of the aerial stem axis. One or 2 sheathing non-photosynthetic leaves are sometimes present at the base of the photosynthetic leaves. Leaf blades are glabrous, entire, flat or marginally undulate and are very narrowly linear, lanceolate, or lanceolate-ovate in shape, or more or less petiolate in *Cyanastrum* and *Kabuyea*. *Walleria* differs in having cauline photosynthetic leaves (basal leaves being absent) which are equally inserted along the aerial stem. Leaves of *Walleria* are sessile, lanceolate, entire, glabrous, and scabrous on the abaxial midrib.

Tillich (1995) described seedling structure in *Cyanastrum cordifolium*, *Cyanella*, and *Walleria*. In *Cyanella* and *Walleria* there is a haustorial hyperphyll, a short tubular sheath and a coleoptile, which becomes very long in *Cyanella*. In *Cyanastrum cordifolium* the hypocotyl and pri-

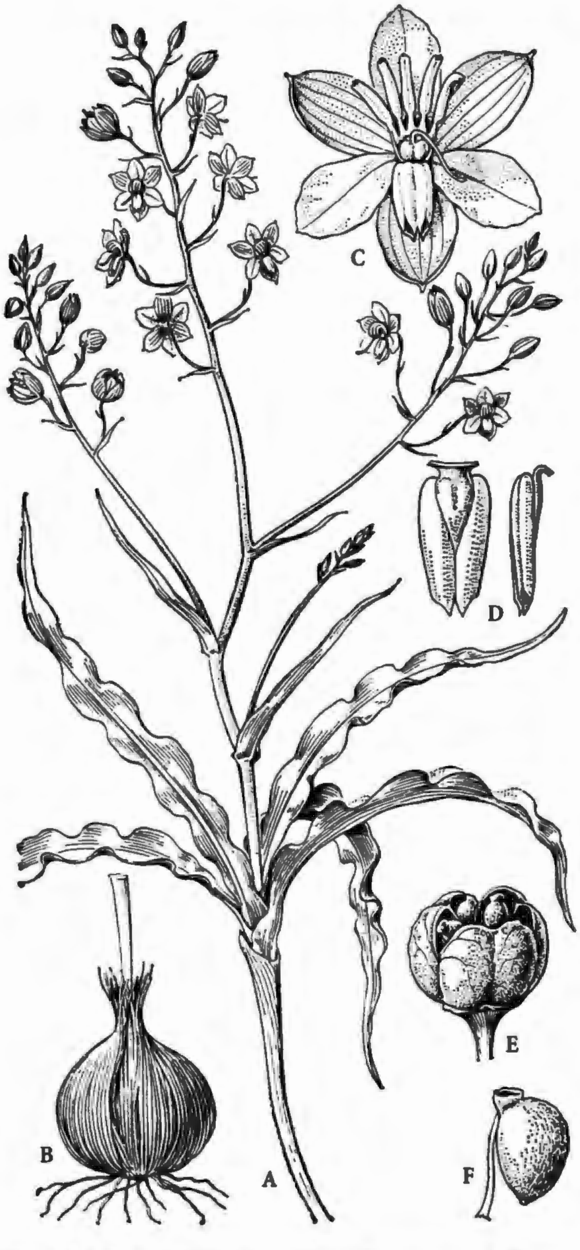

Fig. 123A–F. Tecophilaeaceae. *Cyanella capensis*. **A** Flowering shoot. **B** Tunicated corm. **C** Flower (the upper 5 stamens sterile. **D** Stamens in ventral and lateral view. **E** Dehiscing capsule. **F** Seed. (Takhtajan 1982)

mary root are missing (as in some other endospermless monocotyledons). In *Cyanastrum cordifolium* and *Walleria* the first few leaves are cataphylls.

VEGETATIVE ANATOMY. (Data from Schulze 1893; Cheadle 1969; Arroyo 1986; M.G. Simpson, unpubl.; P. Rudall, unpubl.) Vessels are absent from above-ground organs. Stomata are anomocytic (subsidiary cells absent), or occasionally indistinctly paracytic in cases where epidermal cells are irregularly shaped (e.g., in *Cyanastrum*). Trichomes are absent, except in *Cyanella* spp., which have tapering unicellular or short multiseriate trichomes, and *Walleria*, which has scabrate trichomes along the abaxial midrib and pedicel. Leaf mesophyll cells are relatively undifferentiated. Vascular bundles are in a single row, with sclerenchyma lacking or present in small amounts at larger bundles. Raphide crystals are present in the mesophyll of most species, but absent from *Cyanastrum* and *Kabuyea*. Secretory canals are present in the leaf mesophyll of *Cyanastrum* and *Kabuyea*, but not recorded in other genera. Occasional indigo blue anthocyanin cells are also present in *Cyanastrum* and *Kabuyea*.

INFLORESCENCE STRUCTURE. In *Conanthera*, *Cyanella*, *Odontostomum*, and *Zephyra* the inflorescence is a panicle, either irregularly branched or consisting of a raceme of racemes (*Cyanella* rarely being 1-flowered). *Tecophilaea* has either a solitary flower or an irregular aggregate of 2–3 flowers. *Walleria* has solitary flowers in the axils of the cauline photosynthetic leaves. In *Cyanastrum* and *Kabuyea* the inflorescence is a simple raceme or the flowers are rarely paired (Brummitt et al. submitted).

FLOWER MORPHOLOGY. Flowers are long-pedicellate with a single lanceolate to ovate bract subtending the pedicel and, in several taxa, a similar bracteole (prophyll) inserted opposite to the bract, approximately $^3/_4$ the length of the pedicel. Flowers are 1–3 cm in size, bisexual, and ascending to divergent in orientation. Perianth color is blue, purple, pink, white, or yellowish. The perianth is membranous, glabrous, actinomorphic or zygomorphic, syntepalous with a short to elongate, basal perianth tube and 6 perianth lobes, imbricate in 2 whorls (the outer median lobe anteriorly positioned). Outer and inner perianth lobes are glabrous, entire (to undulate), and variable in shape. Outer lobes have a distinctive mucronate to aristate (often involute-tubular) apical extension whereas the inner perianth lobes have an obtuse to rounded (rarely mucronulate) apex. Perianth lobes 3–7-veined (always from 3 major veins). Minute corona appendages are present between adjacent stamens in *Odontostomum* and *Zephyra*. The androecium is inserted at the mouth of the perianth tube, and consists of either: (1) 6 fertile stamens, (2)4 fertile stamens+2 staminodes (*Zephyra*), or (3) 3 fertile stamens + 3 staminodes

(*Tecophilaea*). In *Cyanella* the fertile stamens are dimorphic, either with (1) 3 small posterior + 3 large anterior stamens, or (2) 5 small posterior + 1 large anterior stamens (Fig. 123c), sometimes basally connate. Filaments of fertile stamens are terete, short to elongate. Fertile anthers are basifixed to subbasifixed, narrowly lanceolate, oblanceolate, or ovoid (with a basal caudate appendage in *Tecophilaea* and *Zephyra*, pubescent in *Zephyra*). Anthers are characteristically long and poricidally dehiscent by means of a small adaxial, apical pore (Fig. 122–124) or introrse slit. Thecae are parallel (or rarely adaxially swollen), and the connective has black spots in *Cyanella alba* and *C. lutea*. The gynoecium is syncarpous; the ovary is semiinferior (ranging from $\frac{1}{4}$ to $\frac{2}{3}$ inferior, or almost superior in *Walleria*), ellipsoid, ovoid, or obovoid, often 3-lobed, glabrous. There are 3 carpels and locules, the 3 carpels oriented opposite the outer perianth lobes, with the median carpel positioned anteriorly. In *Walleria* (Sterling 1974) and *Cyanastrum* and *Kabuyea* (P. Rudall, unpubl.) the style is sunken, i.e., lateral on each carpel. Placentation is axile, the placentae nonprotuberant, generally linear. The style is terminal, terete, straight, or curved with a rudimentary, minutely papillate stigma.

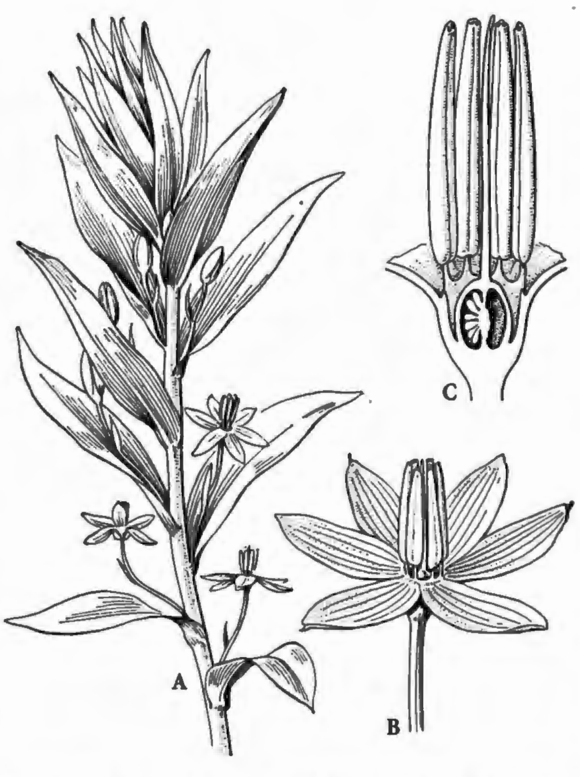

Fig. 124A–C. Tecophilaeaceae. *Walleria mackenzii*. A Flowering shoot. B Flower. C Same, longitudinal section. (Takhtajan 1982)

Floral Anatomy. *Zephyra* is poorly known. *Walleria* was described by Sterling (1974). Other data are from M.G. Simpson (unpubl.) and P. Rudall (unpubl.). Septal nectaries are present throughout the ovary in *Conanthera*, *Odontostomum*, *Cyanastrum*, and *Kabuyea*, but absent or present as very short septal slits at the top of the ovary in *Cyanella*, *Tecophilaea*, and *Walleria*. Secretory canals are present scattered in the tepal mesophyll of *Cyanastrum*. Obturators are normally present. Ovules are bitegmic and campylotropous or anatropous and numerous, or 2 per carpel (in *Cyanastrum*, *Kabuyea* and *Odontostomum*). In mature ovules of many Tecophilaeaceae, the chalazal end of the nucellus is substantial, for example in *Cyanella* and *Tecophilaea* (where this region later persists as a postament: Rudall 1997), *Conanthera*, *Cyanastrum*, (P. Rudall, unpubl.) *Odontostomum* (Cave 1952) and *Walleria* (Sterling 1974). This substantial nucellus region is not the region which later becomes chalazosperm in *Cyanastrum*, which lies outside the raphal bundle, in the chalaza (see below).

Embryology. Data are largely from Cave (1952), De Vos (1950), Fries (1919), Nietsch (1941) Rudall (1997) and P. Rudall (unpubl.). Some genera, especially *Zephyra*, are poorly known. In all taxa examined, microsporogenesis is simultaneous (Rudall et al. 1997). The pollen grain generative cell is distal in position. The tapetum is secretory. Ovules are crassinucellate (the archesporial cell forms a parietal cell). Megasporogenesis is monosporic and embryo sac formation is of the Polygonum type. De Vos (1950) and Rudall (1997) reported a chalazal haustorium in *Cyanella*. Endosperm formation is variable, reported as Nuclear in *Cyanella* (De Vos 1950) and probably Helobial in *Odontostomum* (Cave 1952).

Pollen Morphology. (Data are from Erdtman 1952; Radulescu 1973; Schulze 1983; Simpson 1983, 1985; Zavada and Scott 1993). Tecophilaeaceae have sulcate, heteropolar, generally foveolate pollen grains (rugulose in *Zephyra*) with a tectate-columellate exine architecture, with a relatively thick, homogeneous foot-layer. Most genera (except *Cyanastrum* and *Kabuyea*) have an operculate aperture. The operculum consists of a band of tectate-columellate exine positioned median and parallel to the aperture. A characteristic electrondense endexinous layer occurs inner to the ektexine both in the operculum and along the periphery of the aperture. *Walleria* differs in that the operculum consists of a band of granular ektexine atop the endexinous basal layer; otherwise the operculum of *Walleria* is ultrastructurally identical to that of other Tecophilaeaceae.

KARYOLOGY. (Data from Cave 1970; La Cour 1956; Nietsch 1941; Ornduff 1979; Satô 1942; Sen 1975). The basic chromosome number is mainly $x = 12$ or 11 ($x = 10$ in *Odontostomum*). Most species are diploid, with $2n = 24$, for example in *Cyanastrum cordifolium* (Nietsch 1941) (although $2n = 22$ was recorded by Sato 1941 for *Cyanastrum cordifolium*), *Cyanella alba*, *C. orchidiformis*, *Tecophiliaea cyanocrocus* and *Walleria*. *Cyanella* is the most variable genus, with $2n = 24$, 28, or 48 in *C. hyacinthoides*, $2n = 16$, 24, or 48 in *C. lutea*, indicating both aneuploidy and tetraploidy (Ornduff 1979).

POLLINATION. The poricidal anthers and flower structure of Tecophilaeaceae indicate buzz pollination, at least in the taxa with small, dry pollen (e.g., *Cyanella*) (Endress 1996). Only *Cyanella* has been studied with regard to pollination and reproductive biology (Dulberger and Ornduff 1978, 1980). No nectar is produced in observed species of *Cyanella*. Flowers are slightly scented. Insect guides are present in some species; in *C. alba* and *C. lutea* black spots occur on the connectives of the 5 posterior stamens; in *C. orchidiformis* tepals are light purple with dark purple bases. *Cyanella* spp. are heterantherous, having either 5 or 3 smaller posterior stamens and either 1 or 3 large anterior stamen(s). Pollen escapes only when the anthers are pulled down and released, the resultant snapping action producing a cloud of pollen. A springlike mechanism in the posterior stamen(s) may be enhanced by versatile anthers (in *C. lutea* and *C. orchidiformis*) and by the occurrence in the posterior anther(s) of an abaxial fleshy "cushion" (in *C. hyacinthoides* and *C. lutea*). Under natural conditions, pollen is thought to be discharged by rapid vibration from a heavy-bodied bee, as into other poricidally dehiscent flowers. The posterior stamens may function primarily in insect feeding and the anterior stamen(s) in pollination, although no significant differences in pollen size, morphology, or viability occur (Dulberger and Ornduff 1980; M.G. Simpson, pers. observ.).

Stylar enantiomorphy occurs in both *Cyanella alba* and *C. lutea* by the deflection of the style in a direction opposite to that of the anterior stamen. In these species pollen would tend to be deposited to one side of an insect's body in a location that would promote pollen flow only to a flower with a different stylar orientation. Thus, stylar enantiomorphy might tend to promote pollen transfer between different enantiomorphic flower types (Dulberger and Ornduff 1980). In *C. alba*, in which left-handed and right-handed flowers occur mostly on different individuals, stylar enantiomorphy would enhance outcrossing. However, moderate to strong self-incompatibility is reported in all investigated species of *Cyanella*.

FRUIT AND SEED. The fruit of Tecophilaeaceae is a globose, ovoid, or obovoid, generally 3-lobed loculicidal capsule (perhaps berry-like in *Walleria*). Laterally branched dorsal veins are often prominently visible in the fruit wall.

Seed structure is highly variable in the family (Huber 1969; Brummitt et al. submitted; P. Rudall, unpubl.). Seeds are ellipsoid, ovoid, or roughly spherical in *Kabuyea*. Seeds of *Conanthera*, *Cyanella*, *Odontostomum*, *Tecophilaea*, and *Zephyra* are small, whereas those of *Walleria*, *Kabuyea* and *Cyanastrum* are relatively large (up to 9 mm long in *Cyanastrum*). Seed colour ranges from phytomelan-black in *Cyanella* (Huber 1969) to brown in *Conanthera*, yellow to mid brown in *Kabuyea* and *Cyanastrum*, and dark brown in *Walleria*. In *Kabuyea* and *Cyanastrum* the testa is deeply pitted, either over the entire surface (*Kabuyea*) or at the chalazal end (*Cyanastrum*). In *Kabuyea* the pits contain rows of tiny microprickles. *Cyanastrum* seeds have an obvious swollen region at the chalazal end, which is lacking from the other taxa. In cross-section this region consists of loosely packed thin-walled cells in long strands, derived from the chalazal region outside the vascular bundle (i.e., not from the nucellus). Fries (1919) considered this tissue (which he called a chalazosperm, pointing out that it is not a perisperm) most likely to be a storage tissue, because mature seeds of *Cyanastrum* lack endosperm. However, he conceded that it has similarities with the elaiosomes found in seeds of other asparagoid taxa, and it could well have a role in seed dispersal. The role of this tissue is still unresolved. It is apparently lacking from most other Tecophilaeaceae, such as *Cyanella* (De Vos 1950), although Cave (1952) noted a similar, probably homologous, starch-rich chalazal tissue with loose strands of cells in the seed of *Odontostomum*. In *Tecophilaea* seeds there is no massive "chalazosperm", but the chalazal tissue proliferates and becomes loosely packed (Rudall 1997).

The presence of "chalazosperm" in *Cyanastrum*, which is a highly unusual tissue (if the storage function is confirmed), has been the main reason that many authors since Engler (1901) have separate family status accorded to *Cyanastrum* (see below), although Engler mistakenly called it perisperm.

Seeds are bitegmic, with the outer integument thick and multilayered. The epidermis of the outer integument is composed of thick-walled palisade cells. Endosperm is lacking in the mature seed of *Cyanastrum*, although present in the related genus *Kabuyea* and all other Tecophilaeaceae. The embryo is short to elongate, micropylar in position, and slightly swollen at the micropylar end.

PHYTOCHEMISTRY. Little is known about the chemistry of Tecophilaeaceae (see Gibbs 1974, and references therein). Saponins have been reported as absent in *Tecophilaea* and both absent and present in *Conanthera* spp. Leucoanthocyanins are absent from the leaves of *Cyanella orchidiformis*. Chelidonic acid is present in *Conanthera*. Slob (1973) reported small amounts of the potential allergens, tuliposides A and B, in *Tecophilaea cyanocrocus*.

RELATIONSHIPS WITHIN THE FAMILY. Tecophilaeaceae (including *Cyanastrum*, *Kabuyea*, and *Walleria*) are a well-defined family, characterized by the presence of a corm, mucronate to apically tubular outer perianth tepals, poricidal anthers (with minute apical introrse slits) and a semi-inferior ovary. All genera except *Cyanastrum* and *Kabuyea* have distinctive operculate pollen grains. The absence of operculate pollen grains in *Cyanastrum* and *Kabuyea*, and the presence of "chalazosperm" in *Cyanastrum* have been regarded as evidence against their inclusion in Tecophilaeaceae. However, the lack of "chalazosperm" in *Kabuyea* (Brummitt et al. submitted), which is clearly the sister genus to *Cyanastrum*, weakens this argument. Furthermore, *Odontostomum* probably shares the "chalazosperm" tissue (Cave 1952), and also resembles both *Cyanastrum* and *Kabuyea* in other respects, such as ovary and ovule structure. *Walleria* also resembles *Cyanastrum* and *Kabuyea* in some respects; for example, the corm is not tunicated and the style is sunken. Dahlgren and Van Wyk (1988) discussed the systematic relationships of *Walleria*, which was previously considered close to Uvulariaceae, and has sometimes been placed in its own family. Analysis of molecular data from *rbc*L (Chase et al. 1995) indicates that both *Cyanastrum* and *Walleria* are embedded in Tecophilaeaceae. Hutchinson (1934) also placed them in Tecophilaeaceae, and considered *Cyanastrum* close to *Cyanella*. Further morphological analysis is required to clarify these relationships. The Chilean genera *Tecophilaea* and *Zephyra* are probably sister taxa, by the common occurrence of staminodes. *Odontostomum* (California), *Cyanella* (South Africa), *Tecophilaea* and *Zephyra* are similar in the segregation of the androecium into a posterior and anterior group of stamens, *Odontostomum* and *Cyanella* having 1 anterior and 5 posterior stamens.

AFFINITIES. Analysis of data from *rbc*L (Chase et al. 1995), supported by the presence of simultaneous microsporogenesis (Rudall et al. 1997), indicated a placement for Tecophilaeaceae amongst the "lower" Asparagales, close to Iridaceae, Doryanthaceae, and the astelioid/orchid clade (including Lanariaceae). The presence of phytomelan in the seed coat of some taxa also indicates an asparagoid affinity. Serological analysis of seed proteins supports a relationship between Tecophilaeaceae and Iridaceae (Shneyer 1983).

Tecophilaeaceae were previously considered closely related to Haemodoraceae. However, there is now much evidence (including pollen structure: Simpson 1983) against this, since Haemodoraceae belong in the commelinoid clade, characterized by the presence of cell-wall ferulates (Harris and Hartley 1980; Rudall and Caddick 1994).

DISTRIBUTION AND HABITATS. Apart from *Odontostomum*, which is endemic to north-central California, USA, Teophilaeaceae occur either in Chile (*Conanthera*, *Tecophilaea*, and *Zephyra*) or Africa. *Cyanella* is restricted to South Africa; *Cyanastrum* and *Kabuyea* occur in tropical Africa, and *Walleria* is more widespread, with distributions in southern and tropical Africa and Madagascar.

Habitats vary only slightly. *Conanthera* grows in open hills and grasslands. *Tecophilaea* is found in rocky grasslands or river borders, and *Zephyra* in loose rocky soil of talus slopes. *Odontostomum* is reported in clay soil of grassy fields or forest openings. *Cyanella* is located in sandy or rocky soil of riverine slopes or grasslands. *Walleria* grows in generally sandy soil of open hill slopes or dense woodlands, and *Cyanastrum* and *Kabuyea* in woodland or stream banks.

ECONOMIC IMPORTANCE. *Conanthera* spp., *Cyanella* spp. and *Tecophilaea cyanocrocus* are utilized as ornamentals.

KEY TO THE GENERA

1. Corm lacking a tunic 2
- Corm with a membranous or fibrous tunic 4
2. Leaves cauline, ovary almost superior, seeds brown, warty 7. ***Walleria***
- Leaves basal to subbasal, ovary semiinferior, seeds yellow, pitted 3
3. Leaves usually solitary, distinctly petiolate, perianth blue, seeds with chalazosperm 2. ***Cyanastrum***
- Leaves 4 per corm, indistinctly petiolate, perianth white, seeds lacking chalazosperm 4. ***Kabuyea***
4. Fertile stamens 6, staminodes absent 5
- Fertile stamens 3 or 4, staminodes present 7
5. Stamens dimorphic, of 2 different sizes and shapes 3. ***Cyanella***
- Stamens all of similar size and shape 6
6. Stamens apically connivent, equal in a single ring; anthers narrowly lanceoloid 1. ***Conanthera***
- Stamens distinct, positioned 5 posterior and 1 anterior; anthers obloid 5. ***Odontostomum***
7. Fertile stamens 3, staminodes (posterior) 3 6. ***Tecophilaea***
- Fertile stamens 4, staminodes (latero-posterior) 2 8. ***Zephyra***

1. *Conanthera* Ruíz & Pav.

Conanthera Ruíz & Pav., Fl. Per. 3: 68, t. 301 (1802).

Herbs with tunicated corm; leaves basal, narrowly linear, glabrous, twisted and curled at anthesis; inflorescence an elongate panicle (raceme of racemes); bracts subtending only pedicels; flowers ca. 1.5 cm long; tepals blue to purple (sometimes blotched with black and white), zygomorphic; stamens 6; pollen operculate; ovary semiinferior; ovules numerous; seeds ellipsoid, laterally flattened. Five spp., Chile, open hills and grasslands.

2. *Cyanastrum* Oliv. Fig. 122

Cyanastrum Oliv., Hook. Icon. Pl. 10: t. 1965 (1891).

Herbs with nontunicated corm, bearing leaf and inflorescence separately, each surrounded by different cataphylls; leaves usually solitary, basal, petiolate, with ± cordate base; inflorescence a raceme; bracts and bracteoles sometimes absent; tepals blue; stamens 6, equal; pollen nonoperculate; ovary semiinferior, with sunken style; ovules 2 per carpel; seeds large, ovoid, yellow to brown, deeply pitted, with "chalazosperm". Three spp., tropical Africa.

3. *Cyanella* Royen ex L. Fig. 123

Cyanella Royen ex L., Gen. ed. 5: 149, et add. post index. (1754).

Herbs with tunicated corm; leaves basal, sheathing (outer leaf sheath large and enclosing other leaf bases in some spp.), lanceolate to acicular; inflorescence a panicle or flowers solitary; bracts subtending pedicels and bracteole inserted ca. 2/3 along length of pedicel; flowers ca. 2.5 cm wide; tepals white, yellowish, or violet (with dark purple bases in *C. orchidiformis*) zygomorphic (or slightly asymmetric by virtue of stylar enantiomorphy); stamens 6, dimorphic, either with 5 small posteriorly positioned stamens and 1 large anterior stamen or with 3 small posterior and 3 large anterior stamens; filaments stout, abrubtly incurved in posterior stamens; connectives of the 5 posterior stamens with black spots in *C. alba* and *C. lutea*; pollen operculate; ovary semiinferior; ovules numerous; seeds dark brown, ovoid, laterally flattened. Seven spp., S Africa.

4. *Kabuyea* Brummitt

Kabuyea Brummitt, Kew Bull. (in press) (*Cyanastrum hostifolium* Engl.)

Herbs with nontunicated corm, bearing leaf and inflorescence together, both surrounded by the same cataphyll; leaves basal, indistinctly petiolate; inflorescence a raceme; bracts sometimes absent; tepals white; stamens 6, equal; anthers dehiscing by a short clavate introrse slit near apex; pollen nonoperculate; ovary semiinferior, with sunken style; ovules 2 per carpel; seeds large, ± spherical, yellow, deeply pitted, lacking "chalazosperm". Only one sp., *K. hostifolia* (Engl.) Brummitt, tropical Africa.

5. *Odontostomum* Torr.

Odontostomum Torr., Pacif. Rail. Rep. 4: 150 (1856).

Herbs with tunicated corm; leaves basal, sheathing, very narrowly lanceolate; inflorescence a panicle (a raceme of 1–3 racemes); bracts very narrowly triangular; flowers ca. 1 cm long; tepals creamy white, slightly zygomorphic, with a relatively long (ca. 5 mm) ascending tube, minute coronal appendages arising at mouth of perianth tube between adjacent tepals; stamens 6, identical in size and shape, with 5 stamens positioned posteriorly in a semicircle and 1 stamen positioned anteriorly; pollen operculate; ovary mostly (ca. ⅔) superior, slightly 3-lobed apically; ovules 2 per carpel; seeds brown, obovoid. Only one sp., California.

6. *Tecophilaea* Bertero ex Colla

Tecophilaea Bertero ex Colla, Mem. Acc. Torin. 39: 19, t. 55 (1836).

Herbs with tunicated corm; leaves two, basal, the outer a nonphotosynthetic tubular sheath, the inner photosynthetic leaf narrowly lanceolate; inflorescence with 1 or occasionally 2–3 flowers, racemose; peduncles of solitary flowers or inflorescences with a subtending bract and a subapical bracteole; flowers ca. 1.5 to 3 cm long; tepals purple, slightly zygomorphic, with constricted basal perianth tube; fertile stamens 3, anteriorly positioned, anthers with a basal caudate appendage arising from the 2 fused adaxial sporangia of adjacent thecae; staminodes 3, posteriorly positioned, with a minute terminal, adaxial cleft; pollen operculate; ovary semiinferior; ovules numerous; seeds ellipsoid. Two spp., Chile.

7. *Walleria* J. Kirk Fig. 124

Walleria J. Kirk, Trans. Linn. Soc. 24: 497. t. 52 (1864).

Herbs with nontunicated lobate corm (with a fibrous root arising from each lobe); aerial stem erect, scabrid (from inconspicuous hooks present on longitudinal ridges), foliose; cauline leaves progressively larger apically, spiral, flat, sessile (rarely ca. amplexicaul), linear to broadly lanceolate-ovate; flowers solitary in leaf axils; pedicels long, slender, scabrid; dorsal bracteole arising from pedicel near flower (at least in *W. nutans*); flowers ca. 2 cm long; perianth actinomorphic; tepals white or pink to light blue; stamens 6, equal, anthers yellow/blue or yellow/blue/yellow from base to apex; ovary almost superior (perianth tube fused to extreme base of ovary), with sunken style; pollen indistinctly operculate; ovules numerous; seeds dark brown, obloid, deeply lobed, each lobe bearing a tuft of minute hairs. Three spp., tropical and S Africa, Madagascar

doubtful, according to
John Manning
National Bot. Inst., CT

8. *Zephyra* D. Don

Zephyra D. Don, Edinb. N. Phil. J.: 236 (Oct. 1832).

Herbs with tunicated corm; leaves generally 2, basal, sheathing very narrowly lanceolate; inflorescence a narrow panicle (raceme of racemes) with bracts; flowers ca. 1.5 cm long; tepals white with blue on adaxial surfaces; perianth actinomorphic, with a short, basal perianth tube; fertile stamens 4, with short filaments, anthers with a basal pubescent, caudate appendage; staminodes 2, positioned opposite outer latero-posterior tepals, cylindrical, contorted, with a minute apical slit; pollen operculate; ovary ca. $^{3}/_{4}$ superior; seeds ellipsoid, laterally flattened. Only one sp., *Z. elegans* D. Don, Chile.

Selected Bibliography

Arroyo, S. 1986. Leaf anatomy in the Tecophilaeaceae. Bot. J. Linn. Soc. 93: 323–328.

Brummitt, R.K., Rudall, P.J., Banks, H., Johnson, M.A.T., Chase, M.W. Taxonomy of the former Cyanastraceae. Kew Bull. (submitted).

Carter, Susan [rensim Walker]
Kew Bulletin 16: 185-195
(1962)

Cave, M.S. 1952. Sporogenesis and gametogenesis in *Odontostomum hartwegii*. Phytomorphology 2: 210–214.

Cave, M.S. 1970. Chromosomes of the Californian Liliaceae. Univ. Calif. Publ. Bot. 57: 1–48.

Chase et al. 1995. See general references.

Cheadle, V.I. 1969. Vessels in Amaryllidaceae and Tecophilaeaceae. Phytomorphology 19: 8–16.

Dahlgren, R., Van Wyk, A.E. 1988. Structures and relationships of families endemic to or centered in southern Africa. Mon. Syst. Bot. Mo. Bot. Gard. 25: 1–94.

De Vos, M.P. 1950. Die Ontwikkeling van die Saadknop en Saad by *Cyanella capensis*: 'n Gefal von Polyembryonie. S. Afr. J. Sci. 46: 220–226.

Dulberger, R., Ornduff, R. 1978. The breeding system in dimorphic *Cyanella alba* and *C. lutea* (Tecophilaeaceae). Bot. Soc. 27: 31–32.

Dulberger, R., Ornduff, R. 1980. Floral morphology and reproductive biology of four species of *Cyanella* (Tecophilaeaceae). New Phytol. 86: 45–56.

Endress, P.K. 1996. Diversity and evolutionary trends in angiosperm anthers. In: D'Arcy, W.G., Keating, R.C. (eds.) The anther. Cambridge: Cambridge University Press, pp. 92–110.

Engler, A. 1901. Beiträge zur Flora von Afrika XX: Berichte über die botanischen Ergebnisse der Nyassa-See- und Kinga-Gebirgs-Exped., Gyanastraceae. Bot. Jahrb. 28: 357.

Erdtman, G. 1952. See general references.

Fries, T.C.E. 1919. Der Samenbau bei *Cyanastrum*. Sven. Bot. Tidskr. 13: 295–304.

Gibbs, R.D. 1974. Chemotaxonomy of flowering plants. London: McGill-Queen's University Press.

Harris, P.J., Hartley, R.D. 1980. See general references.

Huber, H. 1969. See general references.

Hutchinson, J. 1934. The families of flowering plants. II. Monocotyledons. Oxford: Clarendon Press.

LaCour, L.F. 1956. In: Darlington, C.D., Wylie, A.P. (eds.) Chromosome atlas of flowering plants. London: Macmillan.

Nietsch, H. 1941. Zur systematischen Stellung von *Cyanastrum*. Oesterr. Bot. Z. 90: 31–52.

Ornduff, R. 1979. Chromosome numbers in *Cyanella* (Tecophilaeaceae). Ann. Mo. Bot. Gard. 66: 581–583.

Radulescu, D. 1973. La morphologie du pollen chez quelques Haemodoraceae. Lucr. Gradinii Bot. Bucur. 1972–73: 123–132.

Rudall, P. 1997. The nucellus and chalaza in monocotyledons: structure and systematics. Bot. Rev. 63: 140–181.

Rudall, P., Caddick, L.R. 1994. Investigation of the presence of phenolic compounds in monocot cell walls, using UV fluorescence microscopy. Ann. Bot. 75: 483–491.

Rudall, P. et al. 1997. See general references.
Satô, D. 1942. Karyotype alteration and phylogeny of Liliaceae and allied families. Jpn. J. Bot. 12: 57–161.
Schulze, R. 1893. Beiträge zur vergleichenden Anatomie Liliaceen, Haemodoraceen, Hypoxidaceen und Veloziaceen. Bot. Jahrb. Syst. 17: 295–394.
Schulze, W. 1983. Beiträge zur Taxonomie der Liliifloren. XI. Tecophilaeaceae und Cyanastraceae. Wiss. Z. Friedrich-Schiller Univ. Math.-Naturwiss. Reihe 32: 957–964.
Sen, S. 1975. Cytotaxonomy of Liliales. Feddes Repert. 86: 255–305.
Shneyer, V.S. 1983. The relationships between the Iridaceae and Liliaceae s.l. as revealed by the serological analysis of seed proteins. Bot. Zh. (Moskau) 68: 49–54 (in Russian).
Simpson, M.G. 1983. Pollen ultrastructure of the Haemodoraceae and its taxonomic significance. Grana 22: 79–103.
Simpson, M.G. 1985. Pollen ultrastructure of the Tecophilaeaceae. Grana 24: 77–92.
Slob, A. 1973. Tulip allergens in Alstroemeria and some other Liliiflorae. Phytochemistry 12: 811–815.
Sterling, C. 1974. Comparative morphology of the carpel in the Liliaceae: *Baeometra*, *Burchardia* and *Walleria*. Bot. J. Linn. Soc. 68: 115–125.
Takhtajan, A.L. 1982. See general references.
Tillich, H.-J. 1995. Früchte, Samen und Keimpflanzen bei den Cyanastraceae Engler 1900 und einigen vermuteten Verwandten. Feddes Repert. 106: 483–493.
Zavada, M.S., Scott, G. 1993. Pollen morphology of *Cyanella* species (Tecophilaeaceae). Grana 32: 189–192.

Themidaceae

K. RAHN

Themidaceae Salisb., Gen. Pl.: 85 (1866).
Alliaceae subfam. Brodiaeoideae Traub (1972).

Acaulescent or short-stemmed perennial *geophytes* without alliaceous odour; stem swollen, forming a starch-storing corm; shoot growth monopodial; each shoot forming a new corm every year on top of and from apex of the corm of the previous year; green leaves and scapes appearing from the upper part of the young corm; the dried leaf bases of previous year enveloping the young corm and forming a membranous, reticulate, or fibrous tunic. *Leaves* spirally arranged, linear, flat, angular, terete, or fistular, often fleshy, forming closed sheaths below; veins parallel. Scape usually solitary, from a leaf axil near the top of the new corm. *Inflorescence* an umbel, rarely reduced to a single flower. Pedicels often articulated at base and/or at apex, and subtended by an individual small bract (2 when the flower solitary). *Flowers* hermaphroditic, actinomorphic. Tepals 3 + 3, usually ± united below. Three or 6 stamens fertile, the missing ones often transformed into staminodes. Filaments inserted on the tepals, free from each other or united, often with lateral, dorsal, or apical appendices. A corona, scales or appendices often present between tepals and stamens. Anthers versatile except in *Brodiaea* and *Dichelostemma*, ± basifixed, introrse, opening with longitudinal slits. Ovary superior, sometimes on a gynophore, tricarpellate, trilocular. Style solitary, erect, at apex of ovary. Stigma capitate or trilobate with a Dry or sometimes Wet (*Bloomeria*) surface. Two or several ovules in each locule. Ovules anatropous. *Fruit* a loculicidal capsule with few to numerous seeds. Seeds 2–several in each loculus, angular or semiovoid (triangular in transection). Testa usually with a thick crust of phytomelan. Endosperm with fatty oils and aleuron, but no starch. Embryo short and straight.

Comprising 12 genera and about 60 species in western N America, a single species reaching Guatemala.

VEGETATIVE MORPHOLOGY. The leafy part of the stem is short in all species, and transformed to a