

Gesneriaceae and Scrophulariaceae: Robert Brown and now

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Abstract

Weber, Anton (Institute of Botany, University of Vienna, Rennweg 14, A-1030 Vienna, Austria) 2004. *Gesneriaceae and Scrophulariaceae: Robert Brown and now*. *Telopea* 10(2): 543–571. Though Robert Brown seems to have seen only one or two species of Gesneriaceae in the field, he understood the family admirably well and had an everlasting influence on it. Apart from contributing to Wallich's 'Plantae Asiaticae Rariores', he prepared a most significant treatment of the family for the 'Plantae Javanicae Rariores' (Bennett & Brown 1838–1852). This treatment appeared as a preprint, entitled 'On Cyrtandreae', in 1839. It was based on Thomas Horsfield's collections from Java and Sumatra, but included also collections from elsewhere. From the two new genera established, only one (*Monophyllaea*) survived, the other (*Loxocarpus*) has been recently reduced to sectional level (*Henckelia* sect. *Loxocarpus*, Weber & Burt 1998b). The species listed or described as new are briefly surveyed. Brown conceived the family Gesneriaceae in its modern circumscription and presented convincing arguments for the union of the paleotropical Didymocarpaceae D. Don (1822) = Cyrtandraceae Jack (1823) with the neotropical Gesneriaceae. The justification for the union and the monophyly of the family has been confirmed by recent molecular systematic studies. Today, the family includes over 140 genera and over 3500 species. Previous and current classifications are compared, and the four major groups are briefly reviewed using informal names: Coronantheroid, Gesnerioid, Epithematoid and Didymocarpeoid Gesneriaceae.

Regarding Scrophulariaceae, Brown's most significant contribution is the treatment of the family in his 'Prodromus florae Novae Hollandiae ...' (1810). This was based on material collected by Brown himself on Flinders' expedition to Australia 1801–1805. Five of the six new genera established there are still in use. There is still much debate on the circumscription of Scrophulariaceae. Partly it is conceived in a very wide sense, including the parasitic Orobanchaceae, and encompassing over 300 genera and 5800 species, yet, based on molecular data, partly it is split into some eight independent families.

Gesneriaceae

Robert Brown dealt with Gesneriaceae on two occasions. Firstly, he contributed to Wallich's 'Plantae Asiaticae Rariores' in that he permitted Wallich to publish some observations and manuscript notes. Secondly, Brown wrote up the Gesneriaceae for the 'Plantae Javanicae Rariores'. This treatment was published as a separate issue, entitled 'On Cyrtandreae', in 1839. The most significant aspect of this treatment is that Brown formally united the Old World Cyrtandraceae with the New World Gesneriaceae and thus gave the family its present shape. The details are given below.

The early history of Gesneriaceae

Gesneriaceae was one of the last major families to take on its present form. It was first recognised by Jussieu (1806, quoting Richard), but was formally established much later, by De Candolle (1816)¹. This group comprised only neotropical plants, namely *Gesneria* and allies. In the eighteen twenties, two new Old World families, Didymocarpaceae (Don 1822, 'Didymocarpeae') and Cyrtandraceae (Jack 1823, 'Cyrtandreae') were established in order to accommodate plants from Asia and the

Pacific. Don (1822, 1825) worked essentially with the plants collected by Nathaniel Wallich and collaborators in Nepal. The family name was based on the genus *Didymocarpus* Wall., which name (and a description) had appeared in a note published by F. Hamilton in 1819. D. Don described the first seven species in 1825. This account comprised two additional genera: *Lysionotus* D. Don (1 sp.) and *Trichosporum* D. Don (the earlier name for *Aeschynanthus* Jack, see below, 2 spp.).² William Jack (1823) collected in Penang and Sumatra. When establishing the 'Cyrtandreae' as 'a new natural order of plants' (1823), he recognised four genera: *Cyrtandra* J. & G. Forst. (11 spp.), *Didymocarpus* Wall. (7 spp.; now distributed over four genera: *Didissandra* C. B. Clarke, *Didymocarpus* Wall. s. str., *Chirita* [Buch.-Ham. ex] D. Don, and *Henckelia* Spreng.; Weber & Burt 1998a,b), *Loxonia* Jack (2 spp.), and *Aeschynanthus* Jack (antedated by *Trichosporum* D. Don, but widely adopted and conserved later; 2 spp.).

According to Burt (1998a), Don's paper setting up Didymocarpaceae was read to the Wernerian Society in Edinburgh on 26 January 1822 and was published in July 1822; Jack's paper was read at the Linnean Society of London on 7 May 1822, but not published till May 1823. It is clear, therefore, that Don's name Didymocarpaceae has priority over Jack's Cyrtandraceae, yet it was Jack's name that was adopted by those who kept the Old World plants distinct from the American Gesneriaceae, most notably by De Candolle (1845).

In 1829 Martius compared the New World Gesneriaceae with the Old World Cyrtandraceae (incl. Didymocarpaceae). He was apparently the first to notice the close affinity of the two families, but concluded that they could be kept distinct.

Brown recognised clearly that the differences between these two groups did not warrant familial separation. The union of the two families was announced in the manuscript notes he permitted Wallich to publish under the new genus *Aikinia* in the 'Plantae Asiaticae Rariores' (1832, see below)³.

¹ Until recently, the formal establishment of Gesneriaceae was attributed to Dumortier (1822), but De Candolle's short reference "Gesnerieae. Rich. et Juss., Ann. Mus. 5, p. 428. Propriétés inconnues." is enough to validate the name and has priority (Greuter & al. 2000, App. IIB).

² Don (1922) mentioned in the introduction also the genus *Chirita*, giving enough description to validate the name. However, Don referred the genus to Scrophulariaceae instead of Didymocarpaceae/Gesneriaceae, where it actually belongs.

³ The conclusion that the two families must be united was reached at about the same time also by David Don (Burt 1965). In a hidden place, namely in the notes following the description of *Leucocarpus alatus* D. Don (in Sweet, Brit. Fl. Gard. ser 2, 2: t. 124, 1831) he stated: 'I had, formerly, [...] proposed to separate *Didymocarpus*, and certain other genera akin to it, into a distinct family [Didymocarpaceae]; but a more accurate examination has fully convinced me that they must be united to the Gesneriaceae, which again are hardly distinguishable by any tangible character from the *Scrophularinae*'. As neither Brown nor Don referred to each other, it is not clear whether the conclusion was reached independently or who was influenced by whom. As Don confesses in the same paper that the 'inverted embryo' assumed to be characteristic of Didymocarpaceae was based on a misobservation (as pointed out by Brown), it may be assumed that Don's 'more accurate examination' was induced by Brown.

The formal union of Gesneriaceae and Didymocarpaceae/Cyrtandraceae was published several years later by David Don's brother, George Don (1838), without giving reasons or making mention of R. Brown. This publication antedates Brown's formal union of the two families in the 'Cyrtandreae' (1839).

Brown's contributions to Wallich's 'Plantae Asiaticae Rariores' (1832)

An essential point of Brown's Gesneriad contribution to this important work is the establishment of two genera: *Aikinia* and *Antonia*. Neither name, however, is in use.

Aikinia [R.Br. ex] Wall., Pl. Asiat. Rar. 3: 65, t. 288 (1832)

As was pointed out by Brown himself later (1839, 1840: 104), this is a synonym of Blume's *Epithema* (Blume 1826). Blume had placed *Epithema* in the family Primulaceae on grounds of the *Anagallis*-like fruits (capsules with circumscissile dehiscence) and, therefore, was overlooked by Brown.

Two species were addressed in Wallich: *A. brunonis* and *A. horsfieldii* [now *Epithema horsfieldii* (R.Br.) DC.]. The former was the principal taxon, the latter only appended. Therefore, *Aikinia* was lectotypified with *A. brunonis* (Morton & Denham 1972). Another genus *Aikinia* was published in the same issue (Wall., Pl. Asiat. Rar. 3: 46, t. 273, 1832) as a synonym (this was regarded as invalid by Morton and Denham (1972), but is valid and in fact was a rejection of Wallich; for details see Feuillet (1993)). Wallich had intended to publish a grass genus as *Aikinia*, and had a plate already engraved as *Aikinia elegans* Wall., but found at the last minute that the genus had been previously described by Kunth as *Ratzeburgia*.

When referring to *Aikinia*, Brown was already aware that the Old World Cyrtandraceae and the New World Gesneriaceae did not warrant separation at family level. The reasons for uniting the two families were promised in the 'forthcoming' volume of 'Plantae Javanicae Rariores', which actually came forth six years later, after many complaints by Horsfield at the delays.

Antonia [R. Br. ex] Wall., Pl. Asiat. Rar. 3: 65. 1832, nom. nud., non Pohl (1828–1829) ('1831').

Although sometimes cited as validly published, this is a nomen nudum only. It is stated to be an intended change of name for *Loxotis* R. Br., but *Loxotis* was published only later, by Bentham in 1835. The type was intended to be *Wulfenia obliqua* Wall. (Brown 1839: 104) (Morton & Denham 1972). *Antonia* is a synonym of *Rhynchoglossum* Blume. See also below under *Loxotis*.

Brown's treatment of Gesneriaceae in the preprint 'On Cyrtandreae' and in the 'Plantae Javanicae Rariores' (collectively referred to here as 'Cyrtandreae')

Details of the history of the admirable 'Plantae Javanicae Rariores' have been reported by Mabberley (1985: 303 ff.; 1986). Here a brief summary, with emphasis on Gesneriaceae, is given. When Brown was librarian for Joseph Banks, he prepared lists of the plant species collected by the American surgeon and naturalist Thomas Horsfield in Java and Sumatra and received in 1814 and 1815. Horsfield proposed that a selection should be made and published under the above title. Brown began preparing the descriptions in 1821. He got John and Charles Curtis to make drawings in the style of the Bauer brothers. One drawing, that of the Gesneriad '*Loxotis obliqua*' (*Rhynchoglossum obliquum*) was from Ferdinand Bauer himself, and we know that the cost for the engraving of this single plate was £3 10s 0d (Mabberley 1986: 309). Horsfield wrote a prospectus, indicating that the first part was to appear in 1831 and the rest to follow in nine-monthly intervals. However, there was much delay, caused by Brown's manifold interests in other subjects. Horsfield suggested that J.J. Bennett, Brown's assistant at the British Museum, should make the book ready for publication. In 1835 Brown made over a number of specimens, drawings and engravings to Bennett. However, by May 1838, the text accompanying plates 24 (Bauer's *Loxotis*

obliqua) and 25 (the second Gesneriad illustrated, *Loxonia acuminata* R.Br. = *L. hirsuta* Jack, prepared by the Curtis brothers) was still not with the printer. Finally, between July 4th and 7th the first part appeared, consisting of pages 1–104 and plates 1–24, the last being *Loxotis*. In March 1839 the final part of plate 25 (*Loxonia*) had still not reached Horsfield who, not unreasonably, lost his control and complained bitterly that 18 years had elapsed since Brown had started work in 1821. The second part was published in May 1840, consisting of pages 105–196 and plates 25–40, the first one illustrating *Loxonia*.

In the year before (late 1839), a special 'preprint' appeared, consisting of plates 24 (*Loxotis*) and 25 (*Loxonia*) and pages 102–122. This preprint was entitled 'On Cyrtandreae' and covered Brown's remarkable essay on Gesneriaceae. It was subsequently translated into French [(*Ann. Sci. nat. (Bot.)* 13: 149–180 (1840)] and German [*Flora* 25: 193–206, 209–219 (1842)]. A large and more general part of the essay, which is in fact an extensive footnote (pp. 107–112), appeared as a separate paper under the title 'On the relative position of the divisions of stigma and parietal placentae in the compound ovary of plants' in *Ann. Mag. Nat. Hist.* 11: 35–42 (1843) and in a German translation in *Bot. Zeitg.* 1: col. 193–201 (1843).

In the 'Cyrtandreae', the part on Gesneriaceae starts with the texts accompanying plates 24 (*Loxotis obliqua*) and 25 (*Loxonia acuminata*). In direct connexion, Brown refers to Jack's new family Cyrtandraceae, 'to which *Loxonia* and *Loxotis* belong', to Don's new 'Didymocarpeae', and to Blume's Bignoniaceae. 'It is somewhat remarkable that none of these writers should have adverted the affinity of this new family [Cyrtandraceae] to Besleriaceae of Richard and De Jussieu, now generally named Gesneriaceae' (see, however, footnote 3). He mentions that Martius (1829) 'considers Cyrtandraceae as sufficiently distinct' and starts to discuss the possible affinities of the groups. An important distinguishing feature between the Cyrtandraceae and the Gesneriaceae is seen in the position of the stigma lobes in relation to the position of the placentae. This feature is discussed in a very broad context in the ample footnote already addressed and later published separately.

Brown reaches the conclusion that 'in a natural classification Cyrtandreae must stand next to Beslerieae', one of the two tribes then recognised in Gesneriaceae. In consequence, Brown includes Cyrtandreae as a third tribe in that family. His classification thus reads:

Gesneriaceae: (1) Gesnerieae ('Calyx cum ovario plus minus connatus. Pericarpium capsulare. Semina albumine copioso'), (2) Beslerieae ('Calyx liber. Pericarpium baccatum v. capsulare. Semina albuminosa'), (3) Cyrtandreae ('Calyx liber. Pericarpium capsulare v. baccatum. Semina exalbuminosa v. albumine parco'). The latter tribe is characterised in great detail.

In contrast to the general part, the following taxonomic section is in Latin. This is introduced by a survey ('Cyrtandrearum synopsis genera'), in which the genera are enumerated, with indication of their distinctive characters. Two groups are distinguished, one with capsular fruits, the other with berry fruits. In the final part the genera are listed again, giving more morphological details of the respective species, with references and/or brief descriptions.

It is important to note that the taxonomic part is a complete survey of the 'Cyrtandreae' known in Brown's times. The treatment is not only based on Horsfield's collections from Java and Sumatra, but includes many others as well, e.g. Thompson's and Hilsenberg's collections from Madagascar. It covers a huge geographical area from South Africa over Madagascar, India, South China and the Himalayas, the Malay archipelago, to the Pacific.

Brown's revision is almost exclusively based on herbarium material. As far as is known, he encountered only two species of Gesneriaceae in the field: '*Loxotis obliqua*' = *Rhynchoglossum obliquum* (see below), and *Epithema brunonis*, both collected at Coepang in Timor.

The genera and species treated in the 'Cyrtandreae'

The following list presents the taxa referred to in Brown's treatise. The order of the genera and the species is given as by Brown (but in nomenclaturally updated form), as the sequence clearly reflects Brown's ideas on the affinities. Species synonyms cited by Brown are not given. In the 'synopsis' Brown made a subdivision between the genera with 'pericarpium capsulare' (*Aeschynanthus* to *Rhabdothamnus*) and with 'pericarpium baccatum' (*Fieldia* to *Whitia*).

Aeschynanthus Jack: *A. volubilis* Jack, *A. radicans* Jack, *A. parvifolius* R.Br., *A. fulgens* Wall., *A. parasiticus* (Roxb.) Wall., *A. ramosissimus* [Wall. ex] DC., *A. griffithii* R.Br., *A. horsfieldii* R.Br., *A. bracteatus* [Wall. ex] DC., *A. acuminatus* [Wall. ex] DC., *A. wallichii* R.Br., *A. longicaulis* [Wall. ex] R.Br.

Tromsdorffia Blume [now *Agalmyla* Blume and *Chirita* Buch.-Ham., see Hilliard & Burt, 2002]: *T. ? elongata* Blume [now *Agalmyla elongata* (Blume) B.L.Burt].

Agalmyla Blume: *A. staminea* Blume [now *A. parasitica* (Lam.) O.Kuntze].

Lysionotus D.Don: *L. serratus* D.Don.

Chirita [Buch. Ham. ex] D.Don: *C. urticifolia* [Buch. Ham. ex] D.Don., *C. flava* [Wall. ex] R.Br., nom. superfl. (= *Chirita pumila* D.Don), *C. acuminata* [Wall. ex] R.Br. [= *C. oblongifolia* (Roxb.) Sinclair], *C. dimidiata* [Wall. ex] R.Br. [included in *C. anachoreta* Hance by Wood 1974, which is however a later name; but the species is probably distinct, B.L. Burt, pers. comm.], *C. bifolia* D.Don, *C. macrophylla* Wall., *C. horsfieldii* R.Br. [included in *C. asperifolia* (Blume) B.L.Burt by Wood 1974, but distinct, Hilliard, 2003], *C. scaberrima* R.Br. [included in *C. asperifolia* (Blume) B.L.Burt by Wood 1974, but to be included in *C. horsfieldii* R.Br., Hilliard, 2004], *C. caerulea* R.Br., *C. hamosa* R.Br.

Didymocarpus Wall.: *D. aromaticus* Wall., nom. illeg. [*D. primulifolius* D.Don, see below], *D. villosus* D.Don, *D. oblongus* [Wall. ex] D.Don, *D. punduanus* R.Br., *D. acuminatus* R.Br., *D. pedicellatus* R.Br., *D. macrophyllus* [Wall. ex] D.Don, *D. subalternans* [Wall. ex] R.Br., nom. illegit. [now *D. aromaticus* [Wall. ex] D.Don], *D. obtusus* [Wall. ex] R.Br., nom. illegit. [now *D. cinereus* D.Don], *D. crinitus* Jack [now *Henckelia crinita* (Jack) Spreng.], *D. serratus* R.Br. [now *Henckelia serrata* (Jack) A.Weber & B.L.Burt], *D. racemosus* Jack [now *Henckelia racemosa* [Jack] A.Weber & B.L.Burt], *D. corniculatus* Jack [now *Henckelia corniculata* (Jack) A.Weber & B.L.Burt], *D. cordatus* [Wall. ex] DC., *D. corchorifolius* [Wall. ex] DC., *D. reptans* Jack [now *Henckelia reptans* (Jack) Spreng.], *D. missionis* [Wall. ex] R.Br. [now *Henckelia missionis* ([Wall. ex] R.Br.) A.Weber & B.L.Burt], *D. zeylanicus* R.Br. [now *Henckelia zeylanica* (R.Br.) A.Weber & B.L.Burt], *D. rottlerianus* Wall., nom. illeg. [now *Henckelia incana* (Vahl) Spreng.], *D. frutescens* Jack [now *Didissandra frutescens* (Jack) C.B.Clarke], *D. elongatus* Jack [now *Didissandra elongata* (Jack) C.B.Clarke], *D. lanuginosus* [Wall. ex] R.Br. [now *Corallodiscus lanuginosus* ([Wall. ex] R.Br.) B.L.Burt].

Streptocarpus Lindl.: *S. rexii* Lindl., *S. hilsenbergii* ['helsingbergii'] R.Br., *S. bojeri* R.Br. [now *S. thompsonii* R.Br. var. *bojeri* (R.Br.) C.B.Clarke], *S. thompsonii* R.Br., *S. paniculatus* R.Br. [now reduced to *S. thompsonii* R.Br.].

Boea Commers.: *B. commersonii* R.Br. [now included in *B. magellanica* Lam.], *B. hygrometrica* R.Br., *B. wallichii* R.Br., *B. multiflora* [Wall. ex] R.Br. [now *Paraboea multiflora* ([Wall. ex] R.Br.) B.L.Burt].

Loxocarpus R.Br. [now *Henckelia* sect. *Loxocarpus* (R.Br.) A.Weber & B.L.Burtt]: *L. incanus* R.Br. [now *Henckelia browniana* A.Weber].

Epithema Blume: *Aikinia* R.Br. in Wall. is cited as a synonym.

Stauranthera Benth.: *Stauranthera grandiflora* Benth., *Stauranthera ecalcarata* R.Br. [now included in *S. caerulea* (Blume) Merr.].

Loxonia Jack: *L. acuminata* R.Br. [now included in *L. hirsuta* Jack], illustrated in tab. 25 (p. 104).

Glossanthus [Klein ex] Benth. [now *Rhynchoglossum* Blume]: *G. malabaricus* Klein [now *Rhynchoglossum obliquum* Blume], *G. notonianus* (Wall.) R.Br. [*Rhynchoglossum notonianum* (Wall.) B.L.Burtt], *G. zeylanicus* R.Br. [now *Rhynchoglossum gardneri* Theob. & Grupe], *G. mexicanus* R.Br., nom. illegit. [now *Rhynchoglossum azureum* (Schltdl.) B.L.Burtt].

Loxotis Benth. [now *Rhynchoglossum* Blume]: *L. obliqua* (Wall.) Benth. [now *Rhynchoglossum obliquum* Blume], illustrated in tab. 24 (p. 102).

Monophyllaea R.Br.: *M. horsfieldii* R.Br.

Platystemma Wall.: no species is quoted, but the only species known then (and at present) is *P. violoides* Wall.

Rhabdothamnus Cunn.: *R. solandri* Cunn.

Fieldia Cunn.: *F. australis* Cunn.

Rhynchotechum Blume: *Corysanthera* Wall. is cited as a generic synonym, no species are recorded.

Centronia Blume [this is a synonym of *Aeginetia* L., a genus of Orobanchaceae or Scrophulariaceae in the wide sense of Takhtajan 1987 and Fischer 2004, in press]: *C. mirabilis* Blume [now *Aeginetia mirabilis* Levira].

Cyrtandra J. & G. Forster: The manuscript name *Getonia* Banks & Soland. is quoted, but no species are given.

Whitia Blume [now included in *Cyrtandra* J. & G. Forster]: no species are quoted.

The new genera

In the 'Cyrtandreae' Brown described two new genera, *Monophyllaea* and *Loxocarpus*. Only the first is still in use at generic level, and this is the only Brown genus that has survived until now.

Monophyllaea R.Br.: This is a most interesting and peculiar genus. As the name indicates, the plant bears only a single, large leaf. Brown did not know the nature of the leaf. The fact that the single leaf of 'unifoliate' Gesneriads represents an enormously enlarged cotyledon ('macrocotyledon') was discovered much later by Caspary (1858) and Crocker (1860) in *Streptocarpus*, and confirmed for *Monophyllaea* by Ridley (1906).

Monophyllaea was described by Brown on the basis of a single species and specimen, collected by Horsfield in Sumatra (preserved at BM). Brown named it in honour of the collector *M. horsfieldii*. The species was for the next 20 years the only one known in the genus, until in 1860 a second species, *M. hirtella* Miq., also from Sumatra, was added. In 1883, Clarke raised the species number to six. In 1979, Burtt published a 'preliminary' revision of the genus, adding many new species, and demonstrating a surprising morphological diversity, and a remarkable range and pattern of distribution.

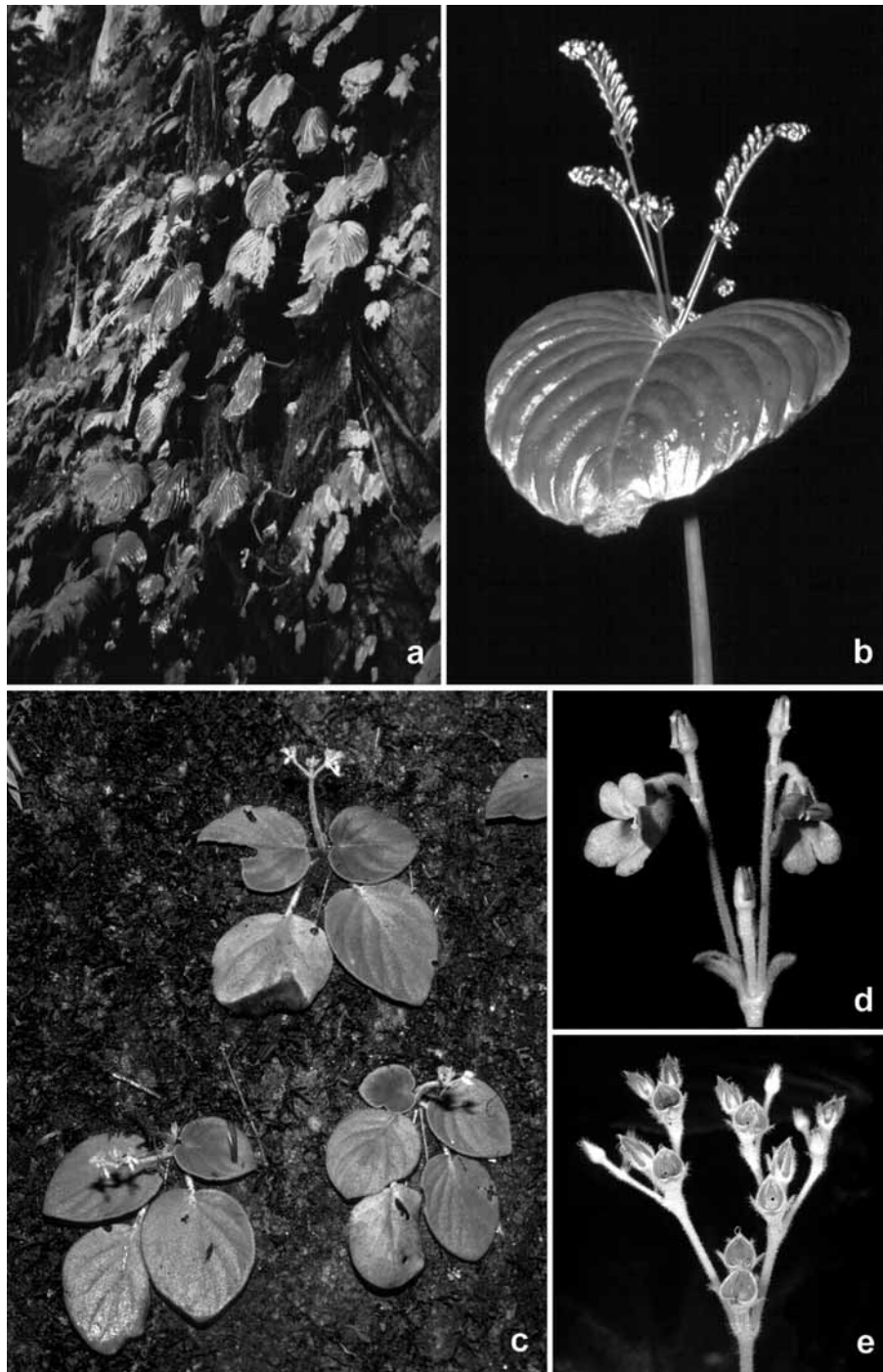


Fig. 1a,b *Monophyllaea horsfieldii* R.Br., **a**, plants in their natural habitat (limestone cliffs in rainforest), Peninsular Malaysia, Selangor, Bkt. Takun; **b**, cultivated plant; **c–e** *Henckelia browniana* A.Weber (= *Loxocarpus incanus* R.Br.); **c**, plants in their natural habitat (mossy slopes near streams), Penins. Malaysia, Penang, Penang Hill (Bkt. Penara) (type locality); **d**, flowers; **e**, capsules (seeds mostly washed out by rain); *ibid.*; all photos by the author.

So far, c. 35 species are known, ranging from the northern part of the Malay Peninsula throughout Malesia to New Guinea. The greatest species number is found in Borneo, while New Guinea has only one species. The species are typically rain-forest plants, growing on rocks and slopes in an everwet climate. Brown's *M. horsfieldii* was later found also on the Malay Peninsula, where it is fairly common on moist limestone rock faces in shady forest (Fig. 1a,b). *M. glabra* Ridl., the northernmost species, is remarkable in its annual habit and the ability to live in a seasonal climate, surviving the dry period only by seeds.

Burt (1978) showed that the unifoliate habit is not a constitutive feature of the genus: there are some species (*M. caulescens* B.L.Burt, Sumatra, *M. ramosa* B.L.Burt, Ceram, and, according to pers. observ. also *M. elongata* B.L.Burt, Malay Peninsula) that produce several leaves similar to the macrocotyledon and exhibit a phyllomorphic structure.

Certainly the most curious species is the Bornean *M. singularis* (Balf. & Smith) B.L.Burt, in which the inflorescences (reduced to few-flowered glomerules) are produced along the stalk. As was shown by Weber (1987, 1990) and Imaichi et al. (2001) the inflorescence primordia result from re-embryonalisation of cells on the stalk surface. As in *Streptocarpus* the inflorescence-bearing part corresponds to a mesocotyl (see below).

The morphological analyses of Weber (1975, 1976a) showed that the unifoliate growth pattern of *Monophyllaea* is derived from an anisophyllous-caulescent pattern as is represented in the small South Chinese-Taiwanese genus *Whytockia*. Specific floral characters (Weber 1976a) as well as molecular data (Mayer et al. 2003) show, that *Whytockia* is indeed the closest relative. From this relationship it can be concluded that the origin of *Monophyllaea* was on the Asiatic continent (and not, as suggested by Burt 1978 on account of geographical considerations, in eastern Malesia). This is in agreement with Burt's recent view (1998b) of a general E→W expansion of Gesneriaceae (see below).

***Loxocarpus* R.Br.:** This genus is based on a species collected by Wallich in Penang Island (Malay Peninsula) and referred to as *Loxonia* ? *alata* in his 'Numerical List'. Brown described it as *Loxocarpus incanus*. Benth (1876) and Clarke (1883) included *Loxocarpus* as a section in *Didymocarpus*. Ridley (1896) followed them at first, but from 1905 onwards he referred to it as a separate genus. Also Burt (1958, 1962) adopted the generic rank.

Recently, *Didymocarpus* and its allied genera were re-investigated at a broad scale (Weber & Burt 1998b), with the result that *Didymocarpus* had to be split into three genera: *Didymocarpus* Wall., *Henckelia* Spreng., and *Hovanella* A.Weber & B.L.Burt. *Didymocarpus* is an essentially Sino-Himalayan genus, *Henckelia* an essentially Malesian genus, and *Hovanella* is confined to Madagascar. The large genus *Henckelia* can be subdivided into five sections, and Brown's *Loxocarpus* is one of them [*Henckelia* sect. *Loxocarpus* (R.Br.) A.Weber & B.L.Burt]. This section includes about 15 species, most representing small rosette plants with white-silvery indumentum and blue flowers. The fruits are usually short capsules, held horizontally and opening only on the upper side. In most species the fruit base is distinctly 'humped'. One species from Sumatra, *H. caulescens* (B.L. Burt) A.Weber & B.L.Burt, deviates from the rosette habit by producing long internodes between the alternate leaves. With the inclusion of Brown's *Loxocarpus incanus* into *Henckelia*, a nomen novum had to be established. The name is now *Henckelia browniana* A.Weber. This is a charming little herb, growing on shady banks of streams in the northern part of the Malay Peninsula. It has blue flowers and short, bowl-shaped fruits which function as rain-splash capsules (Fig. 1c-d).

The new species

From the new species described by Brown some are still in use in the original form (e.g., all four species of *Aeschynanthus*, some species of *Didymocarpus*, *Boea*, *Streptocarpus* etc.), some have been transferred to other genera (see below), and a few have been sunk into synonymy.

Some species of *Didymocarpus* deserve special mention, as Brown's (re-)naming caused confusion. Wallich, then director of the Botanical Garden of Calcutta, sent his material (uniformly attributed to 'Wallich, Nepal', but originating from various collectors) to A.B. Lambert in London, whose librarian was David Don. Don prepared the 'Prodromus florum Nepalensis' which was published in 1825, that is before Wallich came to England (1828) and started to prepare his 'Numerical list' (1829). Don usually adopted any manuscript name that Wallich had suggested, and thus Don's published names are in fact Wallich's names. However, probably due to unmounted material and the lack of clear notes, Don attributed a wrong name to a few plants. Brown knew this and reverted in his 'Cyrtandreae' (1839) to Wallich's original names. However, Don's names were published earlier (1825) and have priority. Thus, Don's *D. aromaticus* is not identical with Wallich's and Brown's *aromaticus*, but nonetheless must be retained in Don's sense, while the latter must be referred to as *D. primulifolius* D. Don. Similarly, Wallich's and Brown's *D. obtusus* and *D. subalternans* must be qualified as illegitimate names and referred to Don's *D. cinereus* and *D. aromaticus*, respectively.

Transfers of Brown's new species to other genera

(1) One species of *Boea* was transferred to the newly segregated *Paraboea* (Burt 1984). The genus *Paraboea* was established by Ridley (1905) for the accommodation of *Boea*-like plants with straight (not twisted) fruits. Burt (1984), however, based his definition of *Paraboea* essentially on the interwoven arachnoid tomentum of branched hairs, irrespective of the fruit type. Brown's *Boea multiflora* (with twisted fruits) has the typical indumentum of *Paraboea* and was, therefore, transferred to that genus.

(2) Several species of *Didymocarpus* were transferred to the later-established genera *Didissandra* C.B. Clarke (Clarke 1883), *Corallodiscus* Batalin (see Burt 1947) and the recently re-established genus *Henckelia* Spreng. (see above under *Loxocarpus*). The essentially Sino-Himalayan *Didymocarpus* s.str. is morphologically characterised by seasonal flowering shoots, cartilaginous bracts and sepals with smooth-polished surface, usually long-tubed, claret-coloured flowers and orthocarpic fruits dehiscing into two valves. Eleven species of Brown's list belong to that genus. From these, three bear Brown's name today: *D. punduanus*, *D. acuminatus*, and *D. pedicellatus*. Some names are illegitimate for the reasons given above. *Henckelia* is an essentially Malesian genus extending (with the type section *Henckelia* which includes Brown's *D. missionis* and *D. zeylanicus*) into South India and Sri Lanka. The plants show a continuous growth, have bracts and sepals of the usual texture (usually hairy), flowers very variable in shape and colour, and plagiocarpic fruits opening only along the upper suture. *Didymocarpus crinitus* is now placed in *Henckelia* sect. *Heteroboea*, *D. serratus* and *D. reptans* in sect. *Didymanthus*, and *D. corniculatus* in sect. *Glossadenia*, a section newly established by Weber & Burt (1998b).

(3) All species of *Glossanthus* are now placed in *Rhynchoglossum* (Burt 1962). The generic name *Glossanthus* was established by Klein in Wallich's Numerical list. It was a nomen nudum, but it was later validated by Bentham (1835) and used by G. Don (1838), Brown (1839) and Endlicher (1839). It is, however, antedated by *Klugia* Schltdl. (1833), and that name was used for a long time to accommodate the species similar to *Rhynchoglossum* Blume, but having large flowers with four stamens instead of small

flowers with two stamens. In fact, under *G. mexicanus*, Brown cites *Klugia azurea* as a synonym. In 1962 Burttt united *Klugia* and *Rhynchoglossum* under the latter name, in that he demonstrated in a new species from Borneo (*R. medusothrix* B.L.Burttt) a transitional flower form: a large corolla, and four fertile, but markedly didynamous stamens with the shorter pair having much smaller anthers. The species listed under *Glossanthus* as well as Brown's *Loxotis obliqua* of plate 24 are now all in *Rhynchoglossum*.

As is apparent from the text accompanying the illustration of *Loxotis obliqua*, Brown was well aware of the close relationship of *Loxotis* and *Glossanthus* (p. 104: '... it may be doubted whether *Loxotis* and *Glossanthus* ought to be generically distinguished merely or chiefly on account of the difference in number of their antheriferous stamina, especially as they entirely agree in habit...') and Brown was also aware that his '*Glossanthus mexicanus*' was '...the only plant belonging to Cyrtandreae hitherto observed in any part of America'. The situation is the same at present. Though additional species have been described from the Americas [*R. grandiflorum* (Fritsch) B.L.Burttt, *R. violaceum* (Fritsch) B.L.Burttt] they are believed to be conspecific with Brown's '*Glossanthus mexicanus*' = *Rhynchoglossum azureum* by Wiehler (1983) and thus this species figures as the only representative of Old World Gesneriaceae in the New World. An explanation for the enigmatic distribution is still needed. While Li (1996) suggested that the link between America and Asia was across Africa, the molecular data of Mayer et al. (2003) indicate that *R. azureum* is very close to the South Indian *R. notonianum*, and *R. azureum* is perhaps a rather recent introduction into the Americas.

The two Gesneriads illustrated in the 'Cyrtandreae'

Brown's treatment of Gesneriaceae contains only two illustrations. These page-sized plates are not only of high scientific accuracy and excellent artistic quality, but depict morphologically very interesting plants. Therefore, a detailed reference is made here.

'*Loxotis obliqua* Wall. Benth.' (= *Rhynchoglossum obliquum* Blume). This is the plant of plate 24, prepared by Ferdinand Bauer (Fig. 2). This colour plate shows very accurately the habit and the flower details of the plant. Brown observed it 'in the Island of Timor near Coepang, chiefly in shady places, but sometimes in more exposed situations, in April 1803'. He reports that Horsfield had later collected the plant in many parts of Java and 'if I am correct in referring *Rhynchoglossum obliquum* to our plant, it was observed also by Dr. Blume in mountainous situations of the same island'. This phrase shows that Brown was aware of the possible conspecificity with Blume's *Rhynchoglossum obliquum* (the specific epithet '*obliqua*' seems to have been chosen independently on account of the conspicuous strongly asymmetrical leaves). Further on, Brown refers to other collections, expressing his view that this was a widespread and variable species. In addition, Brown also explains the adoption of the name *Loxotis* in contrast to *Antonia*, and the priority problems involved. 'This difficulty would be easily removed were it absolutely certain that *Rhynchoglossum* of Dr. Blume was identical with *Loxotis*; but from some of the characters ascribed to it I am not entirely satisfied that such is the case'. Today we are satisfied: *Loxotis* is without a doubt identical with *Rhynchoglossum*.

The morphology of *Rhynchoglossum* was studied in the recent past by the author (Weber 1978a,b). The peculiar shape and arrangement of the leaves can be derived from anisophylly of the *Goldfussia*-[*Strobilanthes*]-type (Goebel 1928, Troll 1937) which is found in many Gesneriaceae, and which is characteristic of most 'Epithematoid Gesneriaceae', to which *Rhynchoglossum* belongs. In *Rhynchoglossum*, anisophylly has proceeded to its extreme in that the small leaves are usually completely reduced and only the strongly asymmetrical plus-leaves remain, being placed in two near-distichous ranks. The opposite leaf arrangement, found in the bulk of Gesneriaceae,



Fig. 2. Reproduction of plate 24 from Robert Brown, *Cyrtandreae* (1839), '*Loxotis obliqua* (Wall.) Benth.' = *Rhynchoglossum obliquum* Blume



Fig. 3. Reproduction of plate 25 from Robert Brown, *Cyrtandreae* (1839), '*Loxonia acuminata* R.Br.'
= *Loxonia hirsuta* Jack

thus has changed to an alternate-(near-) distichous phyllotaxis (alterniphyllly, Weber et al. 1992). Of unique structure are the inflorescences. They have been often regarded as 'pseudo-racemose' equivalents of the cymes of other Gesneriaceae, but represent true racemes, though strongly modified. As in the following genus, *Loxonia*, they are terminal, but the cymes are reduced to single flowers. From the original four ranks of bracts only two are fertile and produce axillary flowers, while the others (sterile minus-bracts) are partly reduced and confined to the dorsal side of the inflorescence axis). Thus there are only two flower-rows present, often (especially in the annual, small-flowered species such as *R. obliquum*) with highly increased flower number.

Formally, *Rhynchoglossum* can be well associated with and derived from the morphological organization of the following *Loxonia*, but molecular data show, that the relationship is not very close: the genus is sister to all other Epithematoid Gesneriaceae (Mayer et al. 2003).

'*Loxonia acuminata* R.Br.' (= *L. hirsuta* Jack). This plant is depicted in plate 25, prepared by the Curtis brothers (Fig. 3). It was collected by Horsfield in Sumatra, when he accompanied Sir Stamford Raffles from Padang to the Menangkaboo (Minangkabau) country. Brown was well aware that the plant could be conspecific with Jack's *L. hirsuta* (p. 106): 'I have considered the plant here figured as distinct from *Loxonia hirsuta* of Jack, which, however, it appears from his description to resemble in so many points that it may actually belong to the same species, differing only somewhat in the form of the leaves and in being less pubescent.' Brown was also deterred by the fact that Jack described the phyllotaxis of *Loxonia* as alternate, and therefore he related the plant 'ad eandem sectionem cum *Loxoti*, sed affinitate arctius junctum cum *Stauranthera*' (p. 105). However, Jack simply had overlooked the (often caducous) small leaves in the plants described by him. The conspecificity of *L. acuminata* and *L. hirsuta* was confirmed in the revision of Weber (1977a), who added a third species to the two species described by Jack, *L. burttiana*, occurring in the eastern part of Borneo.

Brown's illustration shows very precisely the flowering shoot portion of a plant and separately some flower and fruit details. The flower colour is given as blue, but this is obviously a fiction, perhaps induced by the general similarity of the plant with *Loxotis/Rhynchoglossum*. No collection of any species records blue flowers. The small flowers of *Loxonia hirsuta* are greenish-white, eventually with a red dot on either side of the mouth, the upper lip is translucent greenish.

Loxonia has also strongly asymmetrical and seemingly alternate leaves, but on closer inspection one can see that the leaves are actually placed in pairs, and that one of a pair is reduced to a tiny, heart-shaped, stipule-like structure. The branched inflorescences seem to arise from the axils of the tiny leaves. Jack (1823), Brown (p. 105: 'racemi subcymosi, recurvi, saepe bifidi, ex alis [sic; this should probably read „axillis"] foliorum stipuliformium'), Clarke (1823), Fritsch (1893) and Troll (1964) have definitely stated that it is so. This, however, would be in strong contrast with the also strongly anisophyllous Chinese genus *Whytockia* in which the inflorescences (pair-flowered cymes) emerge clearly from the axils of the large leaves (Weber 1976a). The study of Weber (1977b) resulted in the following findings: the flowering region of *Loxonia* is a sympodium composed of shoot units, each comprising an anisophyllous leaf pair and a terminal (!) inflorescence. The inflorescence is complex in structure. There is a flexuous main axis, bearing two or three tiny bract pairs. Though the bracts of a pair are of equal size and shape, only one is capable of producing an axillary inflorescence. The latter is either a pair-flowered cyme (cincinnus) (*L. discolor*, *L. burttiana*) or a conventional cincinnus with the front-flowers in the pairs reduced (*L. hirsuta*).

R. Brown's modern concept of Gesneriaceae: the union of Old and New World Gesneriaceae

Brown knew about Jack's Cyrtandraceae and Don's Didymocarpaceae and their identity. He also knew that Martius (1829) was the first to discuss the affinity with the New World family Gesneriaceae. Martius had reached the conclusion that Cyrtandraceae should be kept distinct, essentially on account of (1) the absence of albumen (endosperm) and (2) the 'inverted embryo' (quoted on the authority of Don). Brown added another 'very remarkable' difference: the position of the stigma lobes. In the New World Gesneriaceae the stigma lobes 'are placed left and right in relation to the parts of the flower, and consequently opposite to the lateral parietal placentae, while in Cyrtandraceae the lips of the stigma ... are anterior and posterior, and therefore alternate with the lateral placentae'. Brown knew well about the special situation in *Chirita*, in which the bilobed stigma resembles the stigma of American Gesneriaceae: in this genus the upper lobe is reduced and the lower lobe is bilobed.

Nonetheless, Brown did not think that these characters would warrant strict separation. He knew that the presence/absence of albumen is not 'absolutely constant, there being cases in Cyrtandraceae where the remains of albumen are visible in the ripe seed; and in several Gesneriaceae it exists so sparingly as to become a character of very little value'. Secondly, Brown made clear that the 'embryo inversus' was based on a misobservation (see also footnote 3). Thirdly, he stated that the differences in stigma lobe position 'is certainly not without exception'.

After all, Brown reached the conclusion that Cyrtandraceae and Gesneriaceae should be united and that Cyrtandreae should represent a tribe within the latter family and 'stand next to Beslerieae'. The third tribe recognised in the expanded family was Gesnerieae (with inferior ovary).

It is important to note that Brown did not mix American and Afro-Asian genera in the same tribe. Unfortunately, this was done later by Bentham (1876) and Fritsch (1893–94) (see below).

Adoption of Brown's union

Apparently the first to adopt Brown's union was Endlicher in his 'Genera plantarum' (1839).

In the 'Prodromus', Auguste P. de Candolle's still followed Martius (1829) and kept Gesneriaceae (published in vol. VII, 1839) and Cyrtandraceae (vol. IX, 1845) distinct. His account on Cyrtandraceae must have been written before publication of Brown's 'Cyrtandreae' in late 1839 for it was made available to Meisner who published in 1840. De Candolle's death in 1841 delayed publication of the Cyrtandraceae until 1845, when vol. IX of the 'Prodromus' was edited by Alphonse de Candolle.

Bentham (1876) was the first to publish an overall account of Gesneriaceae in Brown's sense. He attached primary importance to the position of the ovary: superior or inferior. Genera with inferior ovaries, known only from the New World, formed Bentham's tribe Gesnerieae; but all genera with superior ovaries were classified in tribe Cyrtandreae which thus comprised New World and Old World genera. Fritsch (1893–1894) followed Bentham in this, but his classification was much more detailed. Fritsch raised Bentham's two tribes to subfamilies, and his subtribes to tribes, with the addition of further subtribes. Thus, in contrast to Brown, both these major systems have neotropical and palaeotropical genera mixed together, giving some very improbable groupings.

Gesneriaceae now: taxa number and distribution

Since Brown's times, Gesneriaceae has grown to a considerable size. At present, between 140 and 150 genera are distinguished (depending on the concept of some genera, a full consensus has not been reached yet, Weber 2004). Species number is around 3500. Distribution is mainly in the tropics and subtropics both of the Old and the New World, with transgressions both to the north (Europe: Pyrenees, Balkan Peninsula; Asia: Himalayas, China incl. N China) and to the south (SE Australia, New Zealand, S Chile).

Characters distinguishing Gesneriaceae from Scrophulariaceae and linking the New and Old World Gesneriaceae

In fact, it is not very easy to give a morphological definition of Gesneriaceae. Above all, the family is very similar to Scrophulariaceae and there is general agreement that the two families (if Scrophulariaceae are regarded as a single family at all, see below) are most closely allied. The main characters used for separation of the families are largely those binding the New and Old World Gesneriaceae together.

Ovary structure: The classical feature distinguishing Gesneriaceae from Scrophulariaceae is the 'unilocular' ovary. Unilocular means that the fused carpel flanks that protrude into the ovary are not fused at the tips and do not form a complete septum. However, in the lower part of the ovary, there is usually a portion with a complete septum ('synascidiate zone') and it is only the expanded upper part of the ovary ('symplicate zone') that exhibits a unilocular structure. Secondly, there are some Gesneriaceae in which the completely septate part makes up the whole ovary (e.g., *Whytockia*, *Monophyllaea*, *Asteranthera*) and in which the placentation is axile as in Scrophulariaceae (Weber 1971, Wilson 1974a,b). However, none of these genera is particularly closely allied or transitional to Scrophulariaceae.

Pair-flowered cymes: Another significant feature, recognised only recently (Weber 1973), is the branching pattern of the axillary inflorescences. These represent cymes (compound dichasia, double cincinni or cincinni), but each flower is accompanied by an additional, subsidiary flower ('front-flower'). For this unusual type of cyme the term 'pair-flowered cyme' has been established (Weber 1973, 1995). Pair-flowered cymes are characteristic both of New and Old World Gesneriaceae.

Unfortunately, there are some cases in which difficulties may arise: (a) there exist some genera in Scrophulariaceae which exhibit pair-flowered cymes as well (see Weber 1973): *Penstemon*, *Russelia*, *Tetranema*, *Calceolaria*, *Jovellana*, *Stemotria*), (b) there are a few members of Gesneriaceae, in which the 'front-flowers' within the pair-flowered cymes are subject to partial or complete reduction (*Chrysothemis*, *Loxonia hirsuta*, *Stauranthera caerulea*, see Weber 1977b, 1978c); (c) in both families the reduction of the cymes to single flower occurs (very common in Scrophulariaceae, rather rare in Gesneriaceae, e.g. *Koellikeria*, *Diastema*, for the unilateral racemes of *Rhynchoglossum* see above). In these cases a discrimination on grounds of the inflorescence structure is impossible.

Classification of Gesneriaceae

The infrafamilial classification of Gesneriaceae still poses problems. Traditionally, two subfamilies have been distinguished, the Gesnerioideae and Cyrtandroideae. Bentham (1876) and Fritsch (1893–94) used the ovary position as the primary criterion for their separation, with the consequence that neotropical and paleotropical representatives occurred side by side in some groups. In 1954, B.L. Burtt commenced an important series entitled 'Studies in the Gesneriaceae of the Old World'. In 1963 the firm

statement was made that the title was not to be read as a merely geographical restriction: it was (with the exception of Coronanthereae, see below) a taxonomic group: Gesneriaceae subfam. Cyrtandroideae. Thus Burttt reverted principally to the strict geographical separation of Brown. The justification for making a clear break between the New and Old World Gesneriaceae lies in the structure of the seedlings. It has long been known (Caspary 1858, Crocker 1860) that after germination the seedlings of *Streptocarpus* show remarkable growth of one cotyledon while the other remains small and eventually withers. A large-scale study of gesneriaceous seedlings was made by Fritsch (1904), and this showed that anisocotily was widespread in Cyrtandroideae. Further records were made by Hill (1938) and Burttt and Woods (1958). Lack of evidence of isocotily in Cyrtandroideae and the absence of any report of anisocotily in the New World, suggested that anisocotily provides the best diagnostic character, although in Cyrtandroideae anisocotily is sometimes only weakly expressed and the larger cotyledon is not long-lived.

Burttt (1963) divided subfam. Cyrtandroideae into five tribes (Cyrtandreae, Trichosporeae, Didymocarpeae, Klugieae and Loxonieae) and later (Burttt & Wiehler 1995), into four by the amalgamation of the two latter tribes.

When comparing this classification with R. Brown's list, it becomes apparent that Brown had a very good feeling about the relationships. Though he divided his 'Cyrtandreae' explicitly only in capsule- and berry-fruited taxa, the sequence of the genera is in good accordance with Burttt's classification: *Aeschynanthus*, *Tromsdorffia* (= *Agalmiyla*), *Agalmiyla*, and *Lysionotus* represent tribe Trichosporeae; *Chirita*, *Didymocarpus*, *Streptocarpus*, *Boea*, *Loxocarpus* (= *Henckelia*) represent tribe Didymocarpeae; *Epithema*, *Stauranthera*, *Loxonia*, *Glossanthus* (= *Rhynchoglossum*, formerly *Klugia*), *Loxotis* (= *Rhynchoglossum*), and *Monophyllaea* represent tribe Epithemateae; *Rhynchothecum*, *Cyrtandra* and *Whitia* (= *Cyrtandra*) represent tribe Cyrtandreae. Out of place is *Platystemma*, a curious tiny herb from the Himalayas. *Rhabdothamnus* and *Fieldia*, now placed in Coronanthereae, are separated by the different fruit type.

As envisaged from morphological characters (Burttt 1977) and now clearly confirmed by molecular data (Mayer et al. 2003), the Klugieae incl. Loxonieae (now called Epithemateae, Burttt 1997) form a very distinct group, sister to the remaining Cyrtandroideae. Informally, the two groups can be referred to as Epithematoid and Didymocarpoid Gesneriaceae.

The small group of Coronanthereae (with *Fieldia* and *Rhabdothamnus* already known to Brown) has, though representing principally a paleotropical group (restricted to E Australia, New Caledonia and some other islands of the SW Pacific), isocotylous seedlings. Burttt (1963) referred it to subfam. Gesnerioideae, together with a closely related new tribe, Mitrarieae, consisting of three monotypic genera from temperate South America. The whole alliance was raised to subfamily rank by Wiehler (1983), distinguished from all other Gesneriaceae by the nectary adnate to the ovary wall (subfam. Coronantheroideae). This group is referred to here as Coronantheroid Gesneriaceae.

The fourth informal group, the Gesnerioid Gesneriaceae, encloses the neotropical Gesneriaceae (Gesnerioideae sensu Wiehler 1983). In the following section the four groups are addressed in some more detail, stressing some salient features.

Coronantheroid Gesneriaceae: This small group, comprising 5–6 genera with c. 17 species, was rather neglected for a long time, but has recently received considerable attention in the discussion of the question of the origins of the Gesneriaceae. One hypothesis proposed is that the family is of Chinese (Cathaysian) origin (H.W. Wang 1989). This may appear plausible at first sight because of the many (31) gesneriaceous

genera endemic there and the up to three times higher number of genera in mainland Asia as compared to Malesia. However, this opinion does not take into account that (a) the generic concepts of many Chinese genera are very narrow, (b) that the centre of evolutionary diversification is uncritically equated with the centre of origin, and (c) that it is based solely on the consideration of Asiatic Gesneriaceae and ignores other parts of the family such as the neotropical Gesneriaceae. When considering these other parts it is almost inevitable to link the present distribution with continental drift and plate tectonics.

Recently, Burt (1998b) proposed an interesting 'highly speculative' hypothesis. The essential points are: (1) Gesneriaceae are a family of Gondwanaland origin. (2) The small group of Coronantheroid Gesneriaceae is a relict group that has, by the Australasian members, survived on the Australian plate. (3) This group invaded the Americas via the Antarctic and southern South America and gave rise to the Gesnerioid Gesneriaceae. While the Coronantheroid Gesneriaceae became nearly extinct (the three Chilean genera being the last survivors), the Gesnerioid Gesneriaceae evolved explosively in the American tropics. (4) The Australasian part of Coronantheroid Gesneriaceae gave rise to the present paleotropical Gesneriaceae. These moved northwards on the Indian plate and split very early in the Epithematoid and Didymocarpoid Gesneriaceae. Before the split, one must assume that the mutation(s) resulting in anisocotly occurred. (5) The presently small group of Epithematoid Gesneriaceae is a relict group that was once much larger and had a much wider distribution in Asia and Africa. *E. tenue* can be considered as the last remnant of Epithematoid Gesneriaceae on the African continent. *Rhynchoglossum* reached America (where it is now represented by *R. azureum*) across Africa, from where it now has completely disappeared. (6) On the way north, a part of Didymocarpoid Gesneriaceae spread to Madagascar and colonised mainland Africa from there. (7) The Indian plate carried the Didymocarpoid Gesneriaceae finally to the Asiatic continent. Here a division took place between the plants of northern India and the south, probably as the result of desiccation. The northern group became established in the Sino-Himalayan area and spread from here, under active evolutionary diversification, east- and south eastwards to China and adjacent areas, as well as westwards to Europe. The southern group spread from south India and Sri Lanka into Sundaland and moved eastwards. Though species reached New Guinea and (*Cyrtandra*) even the Hawaiian islands, time was apparently too short that endemic genera evolved east of Wallace's line.

In this scenario the Coronantheroid Gesneriaceae appear as a relict of the stock from which Gesneriaceae have evolved, giving rise both to the neotropical and the Afro-Eurasian-Pacific Gesneriaceae. Though Burt's hypothesis appears plausible from the recent distribution patterns of the family, one must not overlook the problems of timing with geological history. It is hard to believe that the family Gesneriaceae originated before or in the early stages of Gondwanaland breakup, 100 or 80 million years ago. Molecular data (Smith et al. 1997, Mayer et al. 2003) are also not in clear agreement with this hypothesis. Though the genera involved form a distinct clade, the clade is not sister to neo- plus paleotropical Gesneriaceae (thus the establishment of a third subfamily is not clearly supported). It occurs either in a sister position to the Gesnerioid Gesneriaceae or (rather basally) nested within this group (Smith et al. 1997, Mayer et al. 2003). No link to the paleotropical Gesneriaceae is apparent in any part of this group, but this is perhaps not too surprising, seeing how little of the Coronantheroid Gesneriaceae has survived. At any rate, this small alliance is of great phylogenetical interest and more studies are needed to get a clearer picture.

Gesnerioid Gesneriaceae: This group is very large, comparable in genus and species number to the Didymocarpoideae Gesneriaceae. Its classification seems to approach some consensus. The five tribes recognised by Wiehler (Gloxinieae, Gesnerieae, Episcieae, Beslerieae, and Napeanthaeae) are supported by recent molecular data, and a sixth tribe (Sinningieae, its three genera previously placed in Gloxinieae) was suggested by Smith et al. (1997) and confirmed by Zimmer et al. (2002) and Perret et al. (2003).

There are some notable differences to the paleotropical Gesneriaceae in the biochemical and karyological patterns.

Anthocyanidins such as the widespread pelargonidin and cyanidin, characteristic of red flowers of Old World Gesneriaceae, are not found in the Gesnerioid Gesneriaceae. Here 3-desoxy-anthocyanins are found instead: apigeninidin, luteolinidin and columbinidin (Harborne 1966, 1967, Lowry 1972).

The chromosome numbers of the Gesnerioid Gesneriaceae are largely consistent within genera, and, if dysploidy is taken into account, even within tribes: in tribe Gloxinieae most genera have $x = n = 13$ (a few $n = 12$, 11 or 10), the number $n = 9$ is constant almost throughout Episcieae, $n = 9$ (two genera have $n = 8$), in Sinningieae $n = 13$, in Gesnerieae $n = 14$ (see Wiehler 1983, Burt & Wiehler 1995). Based on a combination of molecular and karyological data two base numbers are assumed by Zimmer et al. (2002): $n = 16$ (Beslerieae and Napeanthaeae) and $n = 13$. The latter number has been retained in Gloxinieae (with rare reductions to 12, 11 or 10) and Sinningieae, but has been increased to $n = 14$ (Gesnerieae) and reduced to $n = 9$ in Episcieae (with further reduction to $n = 8$). With very few exceptions, polyploidy is unknown in the Gesnerioid Gesneriaceae.

In contrast, in the paleotropical Gesneriaceae the karyological situation is confusingly diverse and no clear patterns can be recognised at present. The larger genera exhibit often two, three or more base numbers. Polyploidy is not uncommon.

There are also striking ecological differences: (1) A large proportion of Gesnerioid Gesneriaceae, especially of tribe Episcieae, is epiphytic (in the paleotropical Gesneriaceae epiphytes are mainly represented in two genera: *Aeschynanthus* and *Lysionotus*). (2) Ornithophily plays a very important role (essentially ornithophilous genera of paleotropical Gesneriaceae are only *Aeschynanthus* and *Agalmiyla*, otherwise bird-pollination is found only exceptionally). (3) Seed dispersal by birds is frequent. Soft and fleshy berry fruits are represented throughout Episcieae and in many Beslerieae. In contrast, indehiscent fruits are found only in very few paleotropical Gesneriaceae, soft fleshy berries only in *Rhynchoetichum* and the Pacific species of *Cyrtandra*.

Epithematoid Gesneriaceae: This small group of paleotropical Gesneriaceae (7 genera, c. 80 species) is notable in several respects. Though the core distribution is in S and SE Asia, there are two remarkable disjunctions: one species of *Epithema* (*E. tenue*) occurs in West Africa, and one species of *Rhynchoglossum* (*R. azureum*) in Central America. In the first case, molecular data indeed indicate an isolated position of *E. tenue* and thus suggest that the disjunction is old. In contrast, *R. azureum* is very close to the South Indian species of *Rhynchoglossum* and its occurrence in the neotropics probably due to a rather recent introduction (see above).

The whole group is characterised by a complex and complicated morphology, usually associated with anisophylly. The peculiar morphology of Brown's *Monophyllaea*, '*Loxotis obliqua*' = *Rhynchoglossum obliquum*, and '*Loxonis acuminata*' = *L. hirsuta* has been already addressed above. Also the South Chinese genus *Whytockia* was mentioned, which, despite its caulescent-anisophyllous habit and thus very different appearance, is close to *Monophyllaea* in shoot architecture and apparently represents a

relic of the stock from which *Monophyllaea* evolved. Molecular data confirm the close relationship of the two genera (Mayer et al. 2003). *Stauranthera*, described by Bentham (1835), has an architecture similar to *Loxonia*, that is a floral region composed of shoot units with a single strongly anisophyllous leaf pair and a terminal inflorescence in the form of an alternicladic thyse (Weber 1977b). Though the flowers of the two genera are very different, the molecular data confirm their close relationship. Recently, Wang (1981) described a new genus, *Gyrogynae*, which is apparently very close to *Stauranthera*, but has isophyllous leaves and thus suggests an ancestral position. Most peculiar is also the morphology of the genus *Epithema* (Weber 1976b, 1988). Above the strongly unequal, soon decaying cotyledons a large solitary leaf is formed, resembling the single cotyledonary leaf of *Monophyllaea*. This is followed by one or two $\pm$ isophyllous leaf pairs. The inflorescences terminating the main axis and the axillary branches consist of a large cucullate bract embracing a single, much contracted pair-flowered cyme. The last genus, *Rhynchoglossum*, with alterniphyllous leaves and the inflorescences reduced to unilateral racemes, was dealt with above in the context of Brown's illustrations in the 'Cyrtandreae'. The molecular data suggest that this genus is sister to all other Epithematoid Gesneriaceae.

Didymocarpoid Gesneriaceae: With regard to classification and relationships of the genera, this large group is the least understood group of Gesneriaceae. It comprises the tribes Didymocarpeae, Trichosporeae and Cyrtandreae in the classification of Burt (1963) and Burt and Wiehler (1995). This is a large assemblage of genera from Europe (Pyrenees, Balkan Peninsula), tropical and subtropical Africa, E, S and SE Asia and the Malay Archipelago, the more humid parts of Australia, and the Pacific. The available molecular data (Smith 1997, Mayer et al. 2003, Pfosser et al., unpubl. data) reveal that the current classification cannot be upheld. The tribe Cyrtandreae (2–3 genera with indehiscent fruits) is surely artificial, and the same seems to apply to Trichosporeae (5–6 genera with appendaged seeds). Unpublished data indicate that a small number of Asiatic genera (including *Corallodiscus*) is basal to the European Gesneriaceae, the compact group of African Gesneriaceae and the large rest of Asiatic Gesneriaceae, the relationships of which are still little understood (one of the better demarcated groups is that with twisted fruits). The large genus *Chirita* proves highly polyphyletic, with species turning up in four or five clades.

Not surprisingly, the morphology of the large group of Didymocarpoid Gesneriaceae is extremely diverse. The range of growth patterns is from annual herbs and perennials to shrubs and small trees, from rosette plants to large caulescent plants, and from creepers to climbers and epiphytes. The morphologically most remarkable genus is *Streptocarpus*. Brown knew already Lindley's *S. rexii*, a 'rosulate' representative of the genus. This and its allies have been noted and studied since their introduction into cultivation in the early 19th century (Caspary 1858, Crocker 1860). Significant modern studies include Hilliard and Burt (1971), Noel and van Staden (1975), Jong (1970, 1973, 1978) and Jong and Burt (1975).

In subg. *Streptocarpus*, to which *S. rexii* belongs, a wide array of unusual morphologies is found. The most conspicuous is that in which only a single foliar organ is present in the form of a giant and ever-growing macrocotyledon. In these plants a mesocotyl is developed (internode between the macro- and the microcotyledon), but the hypocotyl and the mesocotyl remain short and develop into a stout 'stalk'. The macrocotyledon and the 'stalk' form an integrated structure which has been termed 'phyllomorph' by Jong (1970). Growth is by a trinity of meristems: (1) the 'basal meristem' which is situated at the lamina base and which is responsible for the continuous growth of the foliar structure, (2) the 'petiolode meristem' which is an intercalary meristem located in the upper part of the stalk ('petiolode'), and (3) the 'groove meristem' situated at the junction of the petiolode and the lamina. The most remarkable structure is the

'petiolode'. It forms a continuous transition between the axial mesocotyl and the lamina base and represents functionally a petiole. Jong, therefore, regards it as a mixture of leaf-like and stem-like properties.

These 'unifoliate' species of *Streptocarpus*, consisting of the 'cotyledonary phyllomorph' only, are monocarpic, perishing after producing inflorescences, flowers and fruits. Maturity is reached in most species after two or several years growing. In the species living in a marked seasonal climate, a unique mode of survival of the unfavourable dry period has developed: the lamina sheds a large distal part (60% in *S. molweniensis*) through abscission. On the return of favourable conditions growth is resumed from the remaining basal region of the lamina. By this type of unique perennation the basal meristem is safeguarded against a depletion of nutrient and water reserves.

The phyllomorphic organisation is not only characteristic of the unifoliate species, but also of the 'plurifoliate' and 'rosulate' species. Their plant body can be understood as a succession of phyllomorphs. In the plurifoliate species (e.g., *S. polyanthus*) two or few phyllomorphs are produced, each repeating the structure of the cotyledonary phyllomorph. Perhaps the most remarkable plurifoliate species is *S. fanniniiae*, in which the curious complexity and morphological unorthodoxy has been studied in detail by Jong (1970) and Jong et Burt (1975). The plant produces long petiolodes, so that a long-creeping, climbing and trailing habit is reached. From the petiolodes vegetative buds and new branches are produced. By its open and diffuse habit of growth the species helped to lay the foundation of the phyllomorph concept.

'Rosulate' species such as *S. rexii*, *S. gardenii* etc. bear a close resemblance to familiar rosette plants. However, the rosette is not made up of simple leaves, but of phyllomorphs with a distinct petiolode at the lamina base. Within the rosulate species at least two distinct patterns can be recognised: the centric and the excentric pattern. In the first the phyllomorphs are arranged in a spiral phyllotactic sequence on a condensed vertical axis. In the latter the phyllomorphs are arranged in two ranks on the upper surface of a horizontal rhizomatous axis. Here the axis is composed of an aggregation of petiolode bases. These are often pigmented, supplied with stomata and bear roots. The resemblance to a conventional rhizome is largely superficial. Both in the centric and excentric pattern the phyllomorphs produce vegetative buds on the petiolodes and from these buds lateral rosettes or branch 'rhizomes' develop. Roots arise regularly from the base of the petiolodes, so that each phyllomorph is provided with its own root system. Each individual phyllomorph of the rosette is monocarpic and perishes after flowering and fruiting.

All these properties show that the 'rosettes' of rosulate *Streptocarpus* are far from being ordinary rosettes, but consist of subsequent, highly integrated, repetitive units with morphological and developmental features not found in other plants.

The various growth forms found in *Streptocarpus* seem to have either evolved several times independently, including reversals and intermediate architectures, or are the result of horizontal gene transfer (Möller & Cronk 2001).

Concluding remarks

With his treatise on Gesneriaceae in the 'Cyrtandreae' and 'Plantae Javanicae rariores', Robert Brown laid an important foundation for the knowledge of one of the most fascinating families of Angiosperms. Apart from describing a number of new taxa, Brown provided strong arguments for the amalgamation of the paleotropical Cyrtandraceae/Didymocarpaceae with the neotropical Gesneriaceae, a conclusion which was reached (independently or induced by Brown?) also by D. and G. Don

(1831 and 1838, respectively). Molecular data confirm that the paleo- and neotropical Gesneriaceae indeed belong together and that Gesneriaceae, unlike Scrophulariaceae, represent a monophyletic family. Each of the four groups recognised here informally, exhibits interesting and uncommon features as to morphology, phytogeography, ecology and/or evolutionary history.

Scrophulariaceae

To the author's knowledge, Robert Brown's did not discuss or essentially contribute to the circumscription and systematics of Scrophulariaceae. Therefore, this aspect can be kept very brief, and only a comparison is given what Scrophulariaceae have been in Brown's time and what they are now. Brown's importance is to be seen in the establishment of a number of new genera and numerous new species, especially from Australia.

The Scrophulariaceae in Brown's 'Prodromus'

Robert Brown's most significant contribution to the knowledge of Scrophulariaceae is the treatment of the family in his 'Prodromus florae Novae Hollandiae et Insulae Van Diemen' (1810). This significant early flora of Australia and Tasmania was the result of Robert Brown's personal (and his companions') collections and observations in this then very remote part of the world. Brown went as a naturalist on one of the expeditions of Mathew Flinders to Australia in 1801 (with the ship 'Investigator') and returned to England in 1805. In the subsequent years Brown worked hard on the collected material. In the 'Prodromus', Latin descriptions of 464 genera and ca. 1000 species were provided. 187 genera were described as new, the majority (146) still standing today (Mabberley 1985: 164).

The treatment of Scrophulariaceae, under the name 'Scrophularinae' and including 'Personatarum genera L., Scrophulariae Juss., and Pedicularum genera Juss.', covers 10 pages (433–443) and includes the following genera and species (the names are given here in alphabetical order and in nomenclaturally updated form). Current names are given where easily possible, but no guarantee upon completeness can be given.

Adenosma R.Br.: *A. caerulea* R.Br.

Buchnera L.: *B. asperata* R.Br. [now considered conspecific with *B. linearis* R.Br.], *B. curviflora* R.Br. [now *Striga curviflora* (R.Br.) Benth.], *B. gracilis* R.Br., *B. linearis* R.Br., *B. parviflora* R.Br. [now *Striga parviflora* (R.Br.) Benth.], *B. ramosissima* R.Br., *B. tenella* R.Br., *B. tetragona* R.Br., *B. urticifolia* R.Br.

Centranthera R.Br.: *C. hispida* R.Br.

Euphrasia L.: *E. alpina* R.Br., *E. arguta* R.Br., *E. collina* R.Br., *E. paludosa* R.Br. [now *E. collina* R.Br. subsp. *paludosa* (R.Br.) W.R. Barker], *E. scabra* R.Br., *E. speciosa* R.Br. [now *E. collina* R.Br. subsp. *speciosa* (R.Br.) W.R. Barker], *E. striata* R.Br., *E. tetragona* R.Br. [now *E. collina* R.Br. subsp. *tetragona* (R.Br.) W.R. Barker].

Gratiola L.: *G. latifolia* R.Br. [now *G. peruviana* L.], *G. pedunculata* R.Br., *G. pubescens* R.Br.

Herpestis Gaert.: *H. floribunda* R.Br. [now *Bacopa floribunda* (R.Br.) Wettst.].

Limnophila R.Br.: *L. gratioloides* R.Br., nom. illegit. [= *Limnophila indica* (L.) Druce, based on *Hottonia indica* L.].

Limosella L.: *L. australis* R.Br.

Lindernia L.: *L. alsinoides* R.Br., *L. scapigera* R.Br., *L. subulata* R.Br.

Mazus Lour.: *M. pumilio* R.Br.

Microcarpaea R.Br.: *M. muscosa* R.Br., nom. illegit. [now *Microcarpaea minima* (Koen. ex Retz.) Merr.

Mimulus L.: *M. gracilis* R.Br., *M. repens* R.Br.

Morgania R.Br.: *M. glabra* R.Br., *M. pubescens* R.Br.

Ourisia Commers.: *Ou. integrifolia* R.Br.

Scoparia L.: *S. dulcis* L.

Torenia L.: *T. flaccida* R.Br. [now *Lindernia crustacea* (L.) F.Muell.], *T. hexandra* R.Br. [now *Lindernia crustacea* (L.) F.Muell.], *T. scabra* R.Br. [now *Lindernia crustacea* (L.) F.Muell.].

Uvedalia R.Br. [now included in *Mimulus* L.]: *U. linearis* R.Br. [now *Mimulus uvedaliae* Benth.].

Veronica L.: *V. arguta* R.Br., *V. calycina* R.Br., *V. distans* R.Br., *V. formosa* R.Br., *V. gracilis* R.Br., *V. labiata* R.Br., nom. illegit. [now *Derwentia derwentiana* (Andrews) B.G.Briggs & Ehrend.], *V. perfoliata* R.Br. [now *Derwentia perfoliata* (R.Br.) B.G.Briggs & Ehrend.], *V. plebeia* R.Br.

The new genera

As is apparent from the list, Brown described six new genera. With the exception of *Uvedalia* all genera still stand today. From these, only *Morgania* is a 'truly' Australian genus, while the others proved to have a wide distribution, with Brown's species occurring rather at the periphery. In the following the genera are briefly surveyed.

Adenosma, described by Brown from a single species from Australia (*A. caerulea* R.Br., the type species), is now a genus of some 15 species, with the distribution ranging from China over Indomalesia to Australia.

Centranthera: also described from a single Australian species (*C. hispida*, the type), includes now 5–6 species with similar distribution as *Adenosma*.

Limnophila: This is a conserved name, antedated by *Ambulia* Lam. (1789). *Limnophila* is a well-known genus, in which at present c. 35 species are distinguished, occurring mainly in tropical Africa and Asia.

Microcarpaea: a monospecific genus distributed in tropical Asia and Australia.

Morgania: this is the only genus with exclusive distribution in Australia. Four species have been described so far. The best known is perhaps *M. glabra* with charming blue flowers (Fig. 4).

Uvedalia: this has been reduced to *Mimulus* by Bentham (1846).

The new species

Nearly all species listed and described by Brown were new to science - not surprising, of course, as Australia was largely terra incognita at his time.

The few exceptions include: *Scoparia dulcis*, already known to Linnaeus (1753),

'*Microcarpaea muscosa*', already described by Koenig (in Retz 1789) as *Paederota minima*, 'Limnophila gratioloides', already known to Linnaeus as *Hottonia indica*, and the illegitimate '*Veronica labiata*', for which Brown quoted *Veronica derwentia* as a synonym (see below).

Transfers and reductions

Two of Brown's species of *Buchnera* have been transferred to *Striga* (Bentham 1835). The only species of *Uvedalia* is now in *Mimulus*, as *M. uvedaliae* Benth. Some of Brown's species of *Euphrasia* have been ranked as subspecies of *E. collina* (Barker 1982). Brown's species of *Lindernia* and *Torenia* have been transferred to *Vandellia* by Bentham (1846), but this is now regarded a subgenus of *Lindernia*. *Veronica perfoliata* and the illegitimate *V. labiata* (*V. derwentia* Andrews) have been transferred to *Parahebe* (Briggs & Ehrendorfer 1968) and recently to *Derwentia* (Briggs & Ehrendorfer 1992). Recent molecular studies (Albach & Chase 2001), however, point to a union of *Hebe*, *Parahebe* and *Derwentia* with the genus *Veronica*.

Extinct or threatened species

One of the scrophulariaceous species described by Brown is recorded as extinct on the list of Australia's endangered species: *Euphrasia arguta*



Fig. 4. *Morgania glabra* R.Br., ANBG photo no. a4397, phot. M. Fagg, reproduced with permission of Australian National Botanic Gardens.

(<http://www.nationalparks.nsw.gov.au/npws.nsf/Content/Euphrasia+arguta+presumed+extinct+species+listing>).

Euphrasia scabra R.Br. is recorded as endangered

(<http://www.nationalparks.nsw.gov.au/npws.nsf/Content/Euphrasia+scabra+a+herb++endangered+species+listing>) and the same holds true for *E. collina* R.Br. subsp.

muelleri (Wettst.) Barker

(http://www.nationalparks.nsw.gov.au/PDFs/lost_flora_approved.pdf). Others may be threatened or vulnerable as well, but no information is available at present.

The Scrophulariaceae in Salt's 'Voyage to Abyssinia' (1814)

In 1809 and 1810, Henry Salt conducted his well known 'Voyage to Abyssinia'. This was primarily for commercial reasons, but Salt had also an eye on the political conditions, customs, folklore, languages, etc. His freight included a number of plants which were collected for Joseph Banks. Banks, however, had died when Salt returned to England and the plant collection was passed to R. Brown. Brown identified the plants and published them in a part of Appendix 4 of Salt's 'Voyage' under the heading 'List of new and rare plants, collected in Abyssinia...'. The list was re-printed in *Flora* 4(1), 1821. Of the 146 species, all but 15 were new (Mabberley 1985: 193). Unfortunately, the new names are almost exclusively nomina nuda; some species were validly published by others elsewhere. With respect to Scrophulariaceae, the following species names were validated or synonymised later by Bentham (1846):

Buchnera orobanchoides R.Br., nom. nud. = *Striga orobanchoides* R.Br. ex Benth. = *Striga gesnerioides* (Willd.) Vatke

L. gracilis R.Br., nom. nud. = *L. gracilis* R.Br. ex Benth., *L. hastata* R.Br., nom. nud. = *L. hastata* R.Br. ex Benth., *L. propinqua* R.Br., nom. nud. [already considered conspecific with *L. gracilis* by Bentham 1846].

Meisarrhenia tomentosa R.Br., nom. nud. = *Anticharis arabica* Endl., Bentham 1846

New species of *Pedicularis* from the north polar regions

Later, around 1820, Brown was also engaged with collections brought back by William Perry, John Franklin and others from the polar regions. Two new species of *Pedicularis* were named by him: *P. arctica* R.Br. [now *P. langsдорffii* [Fisch. ex] Stev. var. *arctica* (R.Br.) L.I.Ivanina] and *P. nelsonii* R.Br.

Scrophulariaceae in Brown's time and now

When Brown's 'Prodromus' appeared 1810, Scrophulariaceae was already a considerably large family. Until 1800 around 70 genera had been established, more than 30 genera (mixed with representatives of various other families) were already listed in Linné's 'Species plantarum' (1753). This is in great contrast to Gesneriaceae, but not surprising, as Scrophulariaceae is an essentially temperate family with many genera and species occurring in Europe. In 1846 and 1876, Bentham published his classical treatments on the family, which then were followed by that of Wettstein for Engler and Prantl's 'Natürliche Pflanzenfamilien' (1891). At that time c. 180 genera were known and the species number amounted to about 2600. Many authors followed Bentham's and Wettstein's circumscription and subdivision of the family into three subfamilies: Pseudosolaneae, Anthirrhinoideae and Rhinanthoideae.

Many more genera and species have since been added and the family Scrophulariaceae has grown to a considerable size. Conventional estimates give a number of c. 3000 species, but the actual number is certainly much higher (see below).

Like most large families, the history of the classification of Scrophulariaceae comprises many treatments differing in circumscription of the family (see Olmstead and Reeves (1995)) and the dispute has not come to an end yet. It is impossible to refer in detail to the many attempts to classify this family, the morphological heterogeneity of which is well known.

The molecular data of Olmstead and Reeves (1995), Olmstead et al. (2001), Beardsley and Olmstead (2002), yielded clear evidence that Scrophulariaceae and some other families of the Lamiales are not tenable in the traditional sense and have to be split into several independent families. They suggest the following classification:

- (1) Scrophulariaceae s.str. (part or all of the traditional tribes Aptosimeae, Hemimerideae, Leucophylleae, Manuleae, Selagineae, and Verbasceae = Scrophularieae, plus the traditional families Buddlejaceae and Myoporaceae)
- (2) Plantaginaceae (= Veronicaceae, the name used by Olmstead et al. 2001, but being not in agreement with the rules of ICBN) (all or part of the scrophulariaceous tribes Angelonieae, Antirrhineae, Cheloneae, Digitaleae, Gratiroleae, and Veroniceae plus the conventional families Callitrichaceae, Globulariaceae, Hippuridaceae, and Plantaginaceae).
- (3) Orobanchaceae (tribes Buchnereae, Rhinanthaeae, plus the conventional Orobanchaceae plus *Lindenbergia*, see also Young et al. 1999).
- (4) Calceolariaceae (tribe Calceolarieae). This family, newly established by Olmstead et al. 2001) comprises the three genera *Calceolaria*, *Jovellana* and *Stemotria* (= *Porodittia*). Olmstead's and some other molecular studies indicate that *Calceolaria*/Calceolariaceae occupy a rather basal position within the order Lamiales, only preceeded by Plocospermataceae, Oleaceae and Tetrachondraceae.
- (5) Stilbaceae (expanded by the inclusion of *Halleria*).
- (6) Phrymaceae (with *Phryma* – formerly placed in Verbenaceae, *Glossostigma*, *Peplidium*, *Mimulus* – apparently not monophyletic and indicating that at least six other genera have been derived from within this taxon, *Mazus*, *Lancea*, *Hemichaena*, *Berendtiella* and *Leucocarpus*), see Beardsley and Olmstead (2002).

The most recent treatment of overall Scrophulariaceae is that of E. Fischer for Kubitzki's 'Families and genera of vascular plants' (2004, in press). Formally, Fischer (2004) maintains Scrophulariaceae as a single family, even in a very wide sense with the inclusion of the parasitic Orobanchaceae (following Takhtajan 1997). The number of genera and species is given with 306 and 5850, respectively. Even if Orobanchaceae are excluded, the species number goes far beyond 5000 species.

Informally, however, Fischer divides the Scrophulariaceae into 8 'families', with

- (7) Schlegeliaceae (with *Schlegelia*, *Gibsoniothamnus*, *Synapsis*, *Exarata*) and
- (8) Paulowniaceae (with *Paulownia* and the possibly congeneric *Shiuyinghua*) additional to those listed above.

Brown's new genera fall into three families: *Adenosma*, *Limnophila* and *Morgania*: Plantaginaceae (Veronicaceae); *Centranthera*: Orobanchaceae; *Uvedalia* (*Mimulus*) and (?) *Microcarpaea*: Phrymaceae.

Concluding remarks

With the advent of molecular methods Scrophulariaceae have become a rather bewildering assemblage of plant groups. In contrast to Gesneriaceae, which clearly

represent a monophyletic group, traditional Scrophulariaceae obviously must be abandoned and replaced by a series of some 8 families of their own. The morphology of the families and the relationships of the genera within the families are still incompletely understood. Without a doubt, Scrophulariaceae s.l., to which R. Brown has contributed a number of interesting new genera and species, especially from Australia, provide a wide and promising field of future research, both in molecular and morphological respects.

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