

**Remodelling of Didymocarpus and associated genera  
(Gesneriaceae).**

**Beitr. Biol. Pflanzen 70: 293-363.**

**REFNO: 2949**

**KEYWORDS:**

**Africa, Asia, Borneo, Burma, China, Chromosome Numbers, Codonoboea, Didymocarpus, Fruit, Gyrocheilos, Henckelia, Himalayas, Hovanella, India, Indonesia, Loxocarpus, Madagascar, Malaysia, Morphology, New Guinea, Platyadenia, Seed Morphology, Sulawesi, Sumatra, Thailand**

## Remodelling of *Didymocarpus* and associated genera (Gesneriaceae)

By A. WEBER\* & B. L. BURTT\*\*

\* Institute of Botany, University of Vienna, Austria  
\*\* Royal Botanic Garden Edinburgh, Scotland, U. K.

(With 7 figures)

**Key words:** Gesneriaceae, *Codonoboea*, *Didymocarpus*, *Gyrocheilos*, *Henckelia*, *Hovanella*, *Loxocarpus*, *Platyadenia*. – Taxonomy, morphology. – Borneo, Burma, China, Himalayas, India, Indonesia, New Guinea, Madagascar, Malaya, Malesia, Myanmar, Sulawesi, Sumatra, Thailand.

### Abstract

A survey of *Didymocarpus* Wall. (Gesneriaceae-Cyrtandroideae) in its current, unwarrantably wide usage is made and results in its division into three, apparently not very closely related genera: (1) *Didymocarpus* Wall. s. str. (including *Gyrocheilos* W. T. Wang), (2) *Henckelia* Spreng. (1817: previously nomen rejiciendum in favour of *Didymocarpus*) and (3) *Hovanella* A. Weber & B. L. Burtt (previously *Didymocarpus* sect. *Hova* C. B. Clarke). *Didymocarpus* is now an essentially Sino-Himalayan genus of about 80 species, extending southwards through Myanmar (Burma), Vietnam and Thailand to the Malay Peninsula where there are about eight species (one, *D. cordatus*, being also recorded here from Sumatra); its salient features are its fruits ('orthocarpic', dehiscent loculicidally along both sutures, usually narrowed at base and often distinctly stipitate) and the habit (perennials with annual or monocarpic flowering stems). *Henckelia*, of which the type is a S. Indian plant, becomes a large genus that includes not only all the species of S. India and Sri Lanka (*Didymocarpus* sect. *Orthoboea* Benth.), but also the bulk of the Malesian species hitherto referred to *Didymocarpus*, as well as the genera *Loxocarpus* R. Br., *Codonoboea* Ridl. and *Platyadenia* B. L. Burtt.; its salient features lie in the fruits ('plagiocarpic': making an angle with the pedicel and held more or less horizontally, dehiscent only along the dorsal suture, not narrowed at base) and its habit (perennial, often woody stems or rosettes with continuous growth). *Hovanella*, with two species in Madagascar, somewhat resembles *Henckelia* in the plagiocarpic-follicular fruits, but has distinctive seed-coat-characters (as seen under SEM) that confirm its alliance with other African genera.

The new classification is shown to be supported by the available cytological data and is consistent with the general pattern of the phytogeography of Old

World Gesneriaceae. Some evolutionary trends in this group are briefly discussed. The better-established sections of 'Malesian *Didymocarpus*' are transferred to *Henckelia* (other names available for future transfer if required are listed) and one new section *Glossadenia* A. Weber & B. L. Burtt is diagnosed.

The necessary new specific combinations into *Henckelia* and *Hovanella* are incorporated in a list of names (alphabetical by specific epithet), which includes all those placed under *Didymocarpus* for Malesia, with their correct assignments.

### Zusammenfassung

Ein Merkmalsüberblick über die unhaltbar weit gefaßte Gattung *Didymocarpus* Wall. (Gesneriaceae-Cyrtandroideae) zeigt, daß sie drei offenkundig miteinander nicht näher verwandte Artenkomplexe umfaßt. Diese werden den folgenden Gattungen zugeordnet: (1) *Didymocarpus* Wall. s.str. (inkl. *Gyrocheilos* W. T. Wang), (2) *Henckelia* Spreng. (1817; bisher nom. rejic. für *Didymocarpus*), und (3) *Hovanella* A. Weber & B. L. Burtt, gen. nov. (= *Didymocarpus* sect. *Hova* C. B. Clarke). *Didymocarpus* s.str. erweist sich als eine Sino-Himalayische Verwandtschaftsgruppe (ca. 100 Arten), die nach Süden ausgreift und mit etwa acht Arten die Malaiische Halbinsel erreicht (eine davon, *D. cordatus*, wird hier auch für Sumatra nachgewiesen). Als kennzeichnende Merkmale können die "orthokarpen" (d.h. in gerader Fortsetzung des Fruchtsstiels stehenden), meist basal verschmälerten oder deutlich stipitaten Früchte, die sich entlang der Mittelrippe beider Karpelle öffnen, sowie die Wuchsform (perennierend mit annuellen bzw. monokarpischen Blühtrieben) genannt werden. *Henckelia* umfaßt neben den wenigen Arten aus Südinien und Sri Lanka (= *Didymocarpus* sect. *Orthoboea* C. B. Clarke), zu denen auch die Typusart gehört, die Hauptmasse der Malesischen Arten, die bisher in der Gattung *Didymocarpus* untergebracht waren. Weiters müssen auch die Gattungen *Loxocarpus* R. Br., *Codonoboea* Ridl. und *Platyadenia* B. L. Burtt eingegliedert werden. Hier sind die Früchte "plagiokarp", d.h. sie bilden mit dem Fruchtsiel einen stumpfen bis rechten Winkel, werden annähernd horizontal gehalten und öffnen sich nur an der Mittelrippe des oberen Karpells. Weiters zeichnen sich die Pflanzen durch kontinuierliches Wachstum der (oft Holzigen) verlängerten oder gestauchten Sprossachse aus. *Hovanella* (zwei Arten in Madagaskar) zeigt im Fruchtbau zwar Anklänge an *Henckelia*, doch belegen die Samenmerkmale klar die unmittelbare Verwandtschaft mit afrikanischen Gattungen wie *Saintpaulia*, *Schizoboea* und *Streptocarpus*.

Die neue Klassifikation wird durch die verfügbaren karyologischen Daten gestützt und steht im Einklang mit dem allgemeinen Verbreitungsmuster der altweltlichen Gesneriaceen. Einige evolutionäre Trends der Gruppen werden diskutiert. Die gut abgesicherten Sektionen der Malesischen (früheren) *Didymocarpus*-Arten werden zu *Henckelia* transferiert (weitere verfügbare Namen für allfällige zukünftige Transfers werden angeführt), und eine neue Sektion, *Glossadenia* A. Weber & B. L. Burtt, wird aufgestellt.

Die erforderlichen Neukombinationen werden in einer (nach Artnamen alphabetisch geordneten) Liste durchgeführt, welche alle Malesischen Vertreter des vorliegenden Verwandtschaftskreises enthält.

### Introduction

The genus *Didymocarpus* Wall. in its broadest sense is widespread in eastern Asia, from the Himalayas and southern China to Malesia; a few species reach Sulawesi and at least one is found in western New Guinea. Its taxonomic problems have, in part, been due to the fact that almost from the time of its establishment it has included N. Indian, S. Indian and Malasian species held together by little more than the unilocular ovary with deeply intrusive parietal placentae and the long slender capsular fruit. As more species became known subsidiary groups became recognizable and were given sectional or independent rank. Four genera, apart from those discussed in detail here, are now generally accepted as distinct from *Didymocarpus*; they are (with some recent references): *Chirita* D. Don (WOOD 1974, WANG 1990), *Didissandra* C. B. Clarke (a highly artificial genus of tetrandrous species recently reclassified by WEBER & BURTT 1998a), *Paraboea* (C. B. Clarke) Ridl. (BURTT 1984, XU & BURTT 1991) and *Schizoboea* (K. Fritsch) B. L. Burtt (BURTT 1974, WEBER 1980). These genera now cover about 250 species, and are not further considered here.

*Didymocarpus*, so reduced, still holds an extremely wide range of plants linked by the possession of two fertile stamens and a more or less capitate stigma. At present there is no general consensus whether some groups such as *Loxocarpus* R. Br. and *Codonoboea* Ridl. should stand as sections of *Didymocarpus* or as independent genera, while the continued inclusion of others, such as sect. *Orthoboea* Benth. (= the genus *Henckelia* Spreng.), sect. *Heteroboea* Benth. and sect. *Didymanthus* C. B. Clarke, is in default of critical study, not a result of it. Therefore, a survey was made covering *Didymocarpus* and its allied genera (*Codonoboea*, *Loxocarpus* and *Platyadenia*) in their whole area of distribution. In this paper the results of the study are presented, they lead to the recognition of three genera: *Didymocarpus* s.str., *Henckelia* and *Hovanella*, which are apparently not very closely related.

### Taxonomic history

*Didymocarpus* has had a very complex taxonomic history. The short summary that follows deals solely with aspects of it that are relevant to the present study. A more detailed account is presented by BURTT (1998).

The genus was formally established in a letter that WALLICH sent to Francis HAMILTON, who passed it on for publication under the heading "Notice of the Progress of Botanical Science in Bengal" (HAMILTON 1819). In this letter *Didymocarpus* was briefly diagnosed as a new genus of Bignoniaceae to accommodate some species from Nepal.

It must be uncertain whether WALLICH was aware that his letter was being published (he would, it seems, have considered his name validly established once he had written up the specimens in his herbarium). Be that as it may, the letter was published in October 1819 and in December of that year he was working with W. JACK in Calcutta on specimens JACK had collected on Penang, among them three species that they decided should be added to WALLICH's Nepalese genus *Didymocarpus*. This increased the range of variation in that genus (especially by adding a species that had four fertile stamens – the rest of the genus had only two); WALLICH accordingly supplied JACK with a description of *Didymocarpus* that covered the Penang plants and it was published by JACK in the following year (JACK 1820) with a note of acknowledgment to WALLICH and the statement that the genus was hitherto unpublished, showing that JACK, at least, was unaware of the publication of WALLICH's letter to HAMILTON.

WALLICH's and JACK's plants were not the first representatives of this group to be studied. The Danish missionary ROTTLEH had sent a plant from southern India to VAHL in Copenhagen, and VAHL (1804) published this under the name *Rottlera* (VAHL's spelling of ROTTLEH's name with an *umlaut* is to be regarded as an orthographic error, see note in formal citation, p. 333). A genus of the same name had, however, previously been proposed by WILLDENOW in 1797, and SPRENGEL renamed VAHL's genus as *Henckelia* (SPRENGEL 1817) two years before *Didymocarpus* Wall. was published. Later SPRENGEL (1827) transferred to *Henckelia* all the specific names that had been established by JACK (1820) and DON (1825) under *Didymocarpus*. Whether WALLICH (1829) was aware of SPRENGEL's work is not known, but he reversed the process and included the type species of *Henckelia* in *Didymocarpus*, giving it an illegitimate new epithet, *D. rottlerianus*, but citing only *Rottlera incana* Vahl as the basionym. Much of the succeeding work on this group was carried out in Britain, and R. BROWN (1839), WIGHT (1848), BENTHAM (1876) and C. B. CLARKE (1883) all followed WALLICH's lead, as did DE CANDOLLE (1845). BAILLON (1888) and FRITSCH (1894) reverted to the illegitimate *Rottlera* Vahl (for some reason preferring that to its replacement *Henckelia* Spreng.), but the position was finally stabilized by conservation of *Didymocarpus*, with *Henckelia* as *nomen rejiciendum*. In this paper it will be shown that these two generic names are not synonymous: they represent distinct genera.

### Characters

The particular morphological characters on which the classification is based will be discussed under the appropriate groups: they need no general introduction. There are, however, three items that require some preliminary comment: (a) the patterns of vegetative growth (habit), (b) the way in which the poise of the fruit (and thus its efficient dehiscence) is controlled, and (c) the micro-characters of the seed-coat as shown by the Scanning Electron Microscope.

**Habit.** Though there are several distinct patterns of vegetative growth in the group under study, two principal types can be recognized: (1) production of short-lived (annual or monocarpic) shoots from a basal (underground) rootstock or condensed rhizome, (2) presence of (mostly unbranched, sometimes woody) shoots with continuous growth.

The first type is largely, but not exclusively, associated with a seasonal climate and characteristic of the Sino-Himalayan species of *Didymocarpus* (*Didymocarpus* s.str.). After fruiting, the fully herbaceous stems die down at the beginning of the unfavourable season, while new leafy shoots are developed from the base of the plant and rise just above the soil surface, and will elongate as flowering shoots when favourable conditions return (Fig. 1, 2). This pattern, whose superficial appearance may be much modified by variations in internodal development (phyllotaxis is essentially opposite/decussate, sometimes with a single leaf on a lower node, but never alternate throughout) is uncommon in Gesneriaceae (its rareness emphasising that the family is primarily one of non-seasonal climate). The same habit persists in the Malay Peninsula, which is not surprising in the northern, monsoon-influenced mountains; for example, *D. citrinus* on Gunung Jerai in Kedah always has dead fruiting shoots from the last year alongside the flowering ones (Fig. 3a). However, this pattern is still found in the species that grow in the everwet (montane) rain forest (observed in *D. cordatus*, *D. corchorifolius*, *D. antirrhinoides*; Fig. 3b,c). In these species the rhythm seems to differ in that the new shoots do not form leaves that pass into a resting phase. Nonetheless, the plants of a population show a somewhat rhythmical (not necessarily annual-seasonal) flowering/fruiting period.

The second type, characterized by continuous growth, includes several, partly intergrading patterns. Leaves may be opposite/decussate or alternate, a point of taxonomic significance.

One pattern is the dwarf rosette plant with numerous long-lived leaves, persistent vegetative apex and axillary inflorescences. It is typically a Sino-Himalayan/European-temperate growth form, well known in the genera *Ramonda*, *Haberlea*, *Corallo-discus* etc. In the group under

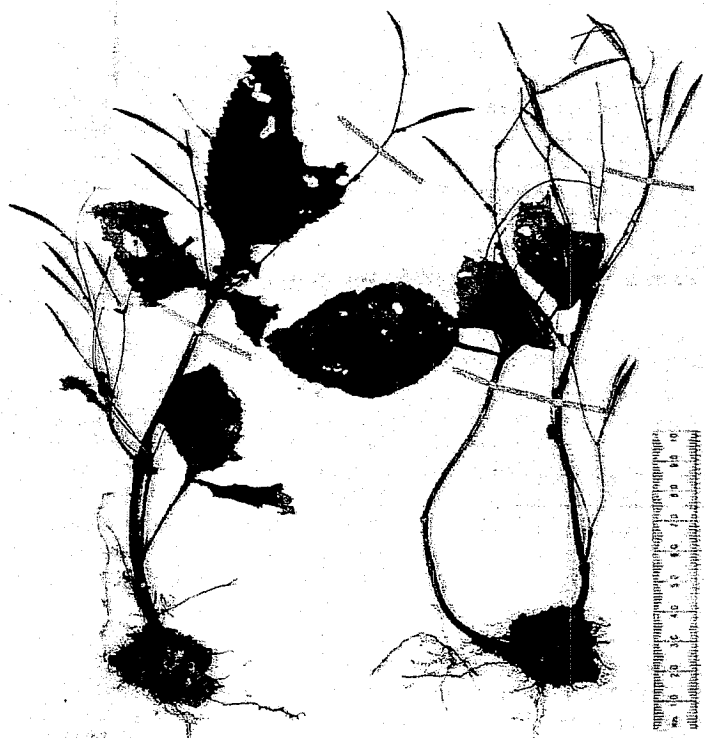


Fig. 1. *Didymocarpus kerrii* (MAXWELL 89-1433, E); note leafy shoots (with young fruits) and dead, leafless shoots (with old, open fruits) arising from an underground rootstock.

consideration it is found (with the exception of *D. repens*) in the whole of *Didymocarpus* sect. *Orthoboea* from S. India and Sri Lanka. It is a pattern completely at variance with that of true *Didymocarpus*, just described. In the rainforests rosette plants are uncommon (RICHARDS 1952): in this group they are present in *Loxocarpus* and in a number of species of 'Malesian *Didymocarpus*' (particularly in those placed in sect. *Boeopsis*), but the rosettes have only few leaves and closely related species may have creeping stems. No tropical genus or group of species is characterized by a well-formed many-leaved rosette. Some species that



Fig. 2. *Didymocarpus* sp. ined. (KINGDON-WARD 19018, E), lower part of plant; note new resting shoot with two leaf pairs) arising from the rootstock; note also upright fruits opening on both sides.

at first sight look like dwarf rosettes prove on closer examination to have quite a long trailing woody stem below the apical tuft of leaves (e.g., *Didymocarpus bakoensis*): this forms a link to the next pattern, which may be called the 'caulescent rosette'.

Caulescent rosettes are a rather characteristic growth form on the floor of the rainforest. An unbranched, erect woody stem bears a terminal tuft

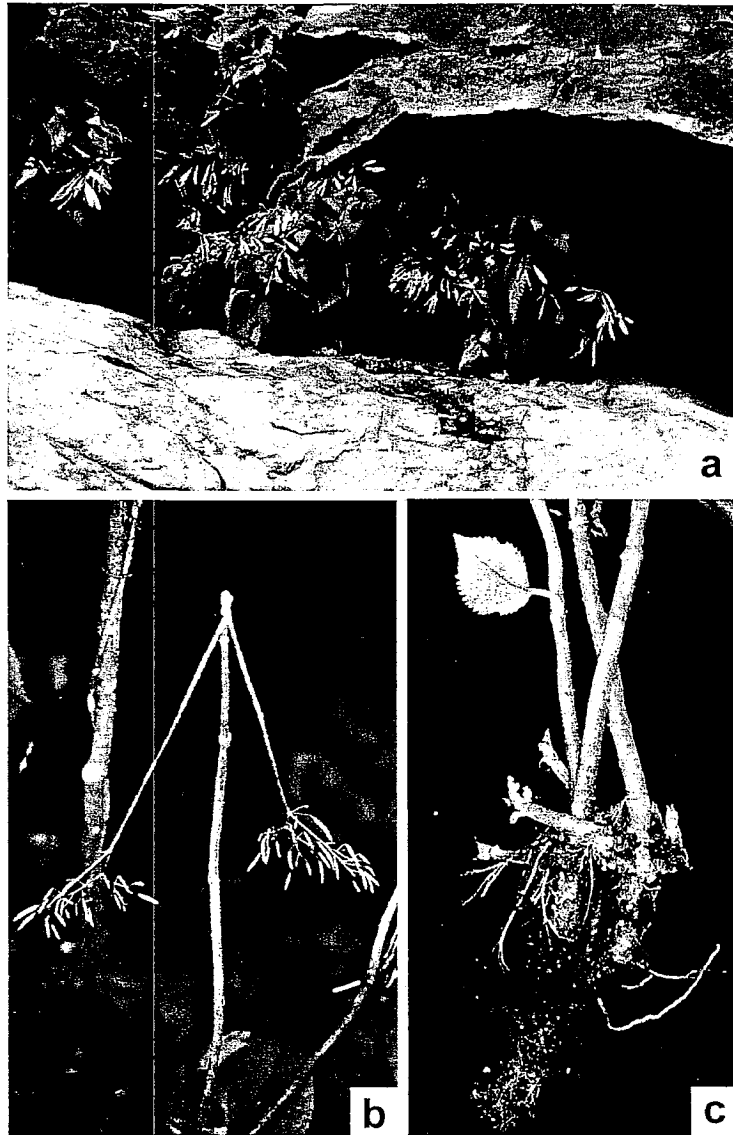


Fig. 3. a *Didymocarpus citrinus*, fresh leafy shoots and last-year shoots with old fruits (Kedah., Gunung Jerai); b *D. cordatus*, dying shoot with old fruits; c *D. cordatus*, rootstock with innovation shoots (Perak, Maxwell's Hill). Phot. AW.

of leaves with axillary inflorescences. This habit is characteristic of most species of sect. *Heteroboea*, in other alliances the leaves are separated by distinct internodes so that a normal erect flowering stem with a loose apical leaf tuft is developed. The terminal bud remains in the vegetative condition. A few species (cliff-dwellers or rheophytes such as *Didymocarpus salicinus*) form branched shrublets with tufts of leaves at the ends of woody branches. Some forms of the Bornean *Didymocarpus gracilipes* may have as many as twenty leaf-tufts on a single plant.

Finally there is the herb with well-developed internodes. This pattern is characteristic of *Didymocarpus* sect. *Didymanthus*. The erect or ascending stems are often woody towards the base. Side branches may develop from the lower part of the stem. Within a population flowering and fruiting is  $\pm$  all the year round. When the stems are prostrate they remain more herbaceous and root at the nodes while the older parts decay.

**Fruit.** Common terminology to describe fruits is not always in accord with strict morphology, but may have advantages in brevity. We use the following terms: suture, for any of the four possible lines of dehiscence of the bicarpellary ovary: for the lateral (septicidal) sutures, which are the true sutural union of the carpels, and for the dorsal and ventral sutures (the lines of loculicidal dehiscence) which are really splits along the carpellary midribs. A follicle, strictly speaking, consists of a single carpel, but a bicarpellary ovary dehiscing along the dorsal suture looks so like a follicle that it is commonly described as follicular (e.g., *Didymocarpus follicularis* C. B. Clarke). We use that term here.

In 'Sino-Himalayan *Didymocarpus*' (see below) the fruit (or at least the base of its stipe if it has one) is placed in a straight line with the pedicel: it is 'orthocarpic'. It opens along the median line of both carpels and is thus a straight (or slightly curved), loculicidally dehiscent, bivalved capsule (Fig. 1, 4). The position is erect or suberect, but may be also pendulous, either because the branches of the inflorescence, or the pedicels, curve over, or because a thin cylindrical stipe is developed at the base of the ovary: it is then the stipe that curves.

In the other groups of *Didymocarpus*, as well as in *Codonoboea*, *Loxocarpus* and *Platyadenia*, the fruit has its primary line of dehiscence along the dorsal suture (though old fruits may split into two valves before they fall). It makes a distinct angle (between 90 and 135°) with the pedicel (for the various modes of fruit attachment see below) and is held roughly horizontally (Fig. 5, 6). We therefore refer to that fruit type as 'plagiocarpic'. Some major variation in the poise of the fruits is found in 'S. Indian *Didymocarpus*', where a correlation with fruit length seems

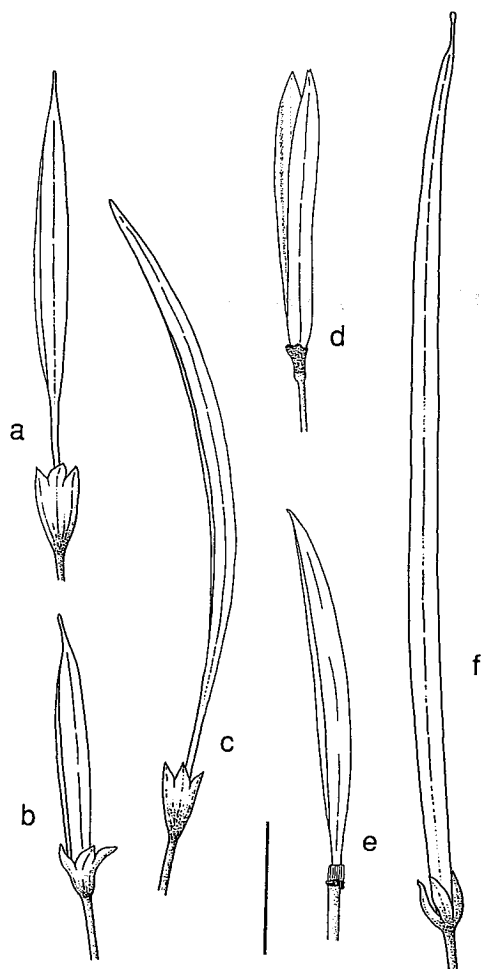


Fig. 4. Fruits of *Didymocarpus* s.str., a *D. acuminatus* (HOOKER & THOMSON s.n., W); b *D. oblongus* (HOOKER & THOMSON s.n., W); c *D. punduanus* (GRIFFITH 3840, W); d *D. macrophyllus* (WALLICH 784, W); e *D. citrinus* (WEBER 840801-1/4, WU); f *D. sulphureus* (WEBER 790819-1/1, WU). Bar: 1 cm.

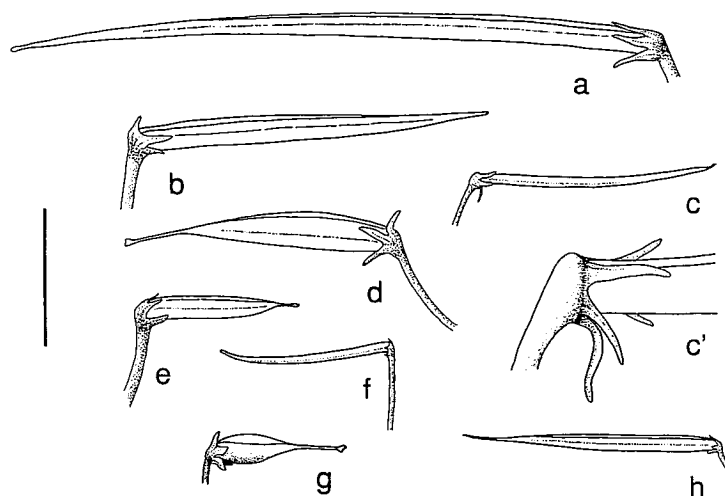


Fig. 5. Fruits of 'Malesian *Didymocarpus*', *Platyadenia* and *Codonoboea* (all becoming *Henckelia*); a *D. hispidus* (WEBER 860819-1/2, WU); b *D. beccarii* (CHAI S. 34802, L); c *D. floribundus* (WEBER 870609-1/10, WU), c' fruit base enlarged; d *D. puncticulatus* (WEBER & ANTHONYSAMY 870530-1/1, WU); e *D.* sp. (sect. *Glossadenia*) (BUWALDA 6611, L); f *D.* aff. *heterophyllus* (SHAH & SHUKOR MS 2238, SING); g *Platyadenia descendens* (WEBER 790913-1/5, WU); h *Codonoboea nivea* (WEBER & ANTHONYSAMY 860825-2/1, WU). Bar: 1 cm.

to exist: long fruits (e.g., *D. meeboldii*) are placed more or less horizontally, while short fruits (e.g., *D. tomentosus*) are held at a steep, ascending angle.

It is important to note that ortho-/plagiocarpic is not strictly correlated with the actual poise of the fruit and its dehiscence. In *Ridleyandra*, the fruits are held horizontally and open dorsally just as in 'Malesian *Didymocarpus*'. Nonetheless, they are  $\pm$  orthocarpic. The horizontal poise is mainly due to bending of the peduncle because of the fruit weight (see WEBER & BURTT 1998a).

The dehiscence and the posture of the fruits are functionally important. The seeds of the orthocarpic *Didymocarpus*-fruits, whether these are erect or pendulous, may be shaken out by wind, rain or passing animals. There is no specialized dispersal mechanism or agent.

In contrast, the fruit held horizontally or at an angle represents a special type of rain-splash capsule and the seeds are primarily dispersed by

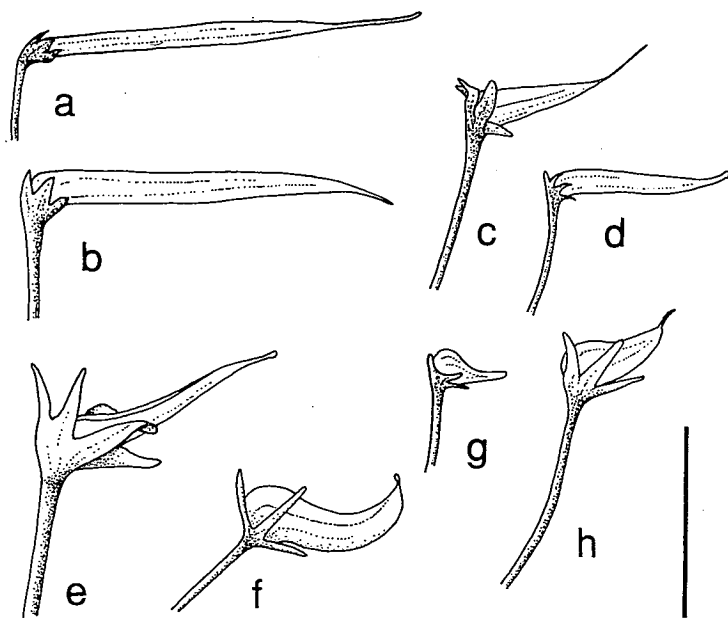


Fig. 6. Fruits of *Loxocarpus* (becoming *Henckelia*); a *L.* sp. (G. Mulu, Borneo; BURTT & WOODS B. 2087, E); b *L.* sp. (Borneo, NOTEBOOM & CHAI 1711, E); c *L. holttumii* (WEBER 840723-2/1, WU); d *L. caulescens* (MEIDER 6893, L); e *L. semitorvus* (WEBER 840716-2/1, WU); f *L. caeruleus* (WEBER 860816-1/7, WU); g *L.* cf. *longipetiolatus* (BURTT & WOODS B. 2681, E); h *L. incanus* (WEBER 840803-1/2, WU). Bar: 1 cm.

rain. This is why (a) species with horizontal-follicular fruits seem to be restricted to an everwet climate and (b) many taxa of humid-tropical distributions have independently developed this fruit type: apart from the alliance under discussion, it is also found in *Ridleyandra*, species of *Paraboea* (*P. capitata* and allies), *Beccarinda*, *Platyadenia* and others in SE. Asia; in W. Africa this fruit type is represented in *Trachystigma*, and in the neotropics in species of *Diastema*, *Monopyle*, *Gloxinia* and *Kohleria* (WIEHLER 1983).

For species with long narrow capsules without any further elaboration (e.g., most species of sections *Heteroboea*, *Didymanthus*, and *Glossadenia*), the line of dehiscence is a narrow channel and rain may merely wash the seeds out, so that they will scarcely fall free of the parent

plant. This is probably not a very efficient dispersal mechanism and apparently has been improved by evolution towards a more definite splash-bowl. The essence of this change is that at least part of the fruit has a wider opening from which heavy rain drops can actually splash the seeds out; some of them then have a good chance of landing clear of the parent plant. It is also possible that the bowl formed actually fills with water in which seeds float loose and are thus better prepared for splash-dispersal. This is almost certainly what happens in *Epithema* (tribe *Epithemateae*), in which the campanulate calyx acts as the splash-bowl and the little round fruit packed with seeds on long funicles sits in the centre: the seeds are easily detached from the funicles. R. BROWN (1839), when establishing the genus *Loxocarpus*, already pointed out that the seeds had long funicles.

Among groups that show some species with a swelling of the fruit, which leads to an enlargement of the dehiscence channel, are *Beccarinda*, *Paraboea* (e.g., *P. burttii*), *Platyadenia* (Fig. 5g), *Didymocarpus* sect. *Boeopsis* (those with a boat-shaped capsule, Fig. 5d), sect. *Orthoboea*, sect. *Hova*, and *Loxocarpus* (Fig. 6). The patterns in these groups are not identical, but seem to tend towards the same end.

The posture of the fruit and its degree of opening is intimately associated with postfloral growth processes at the base of the flower. Growth on the dorsal side of the pedicel/receptacle junction leads to the surface of the receptacle becoming oblique. This, combined with the angle at which the pedicel is held brings the fruit into a horizontal position. If the pedicel is nearly erect more growth at this junction is needed to bring this about. The surface of the receptacle can then be nearly vertical. The basal part of the ovary may also take part in this post-floral growth, and again development on the upper side of the ovary, resulting in a basal hump, helps to bring about the horizontal position. In some species the pedicel/receptacle junction is entirely inactive and the receptacle surface remains horizontal with respect to the pedicel, the poise of the fruit being entirely controlled by differential growth at the base of the ovary. Differential distribution of growth at the junction pedicel/receptacle and/or ovary base may lead to different patterns of fruit development (but yield a similar functional result):

(a) One-sided growth of the pedicel/receptacle junction (attachment of ovary) leads to what can be called an 'oblique receptacle' (this is the common pattern of 'Malesian *Didymocarpus*', but is also found in *Codonoboea* and in *Loxocarpus holttumii*).

(b) One-sided growth of pedicel/receptacle junction associated with dilation of the carpels in the middle, resulting in a boat-shaped capsule (*Didymocarpus* sect. *Boeopsis*, *Platyadenia*).



(c) One-sided growth both of receptacle and ovary base (*Paraboea burtii*, similar also in *Loxocarpus verbeniflos* and allies).

(d) One-sided growth of carpel bases only, resulting in distinct basal humps, leading in its extreme form to a 'corniculate' capsule (*Loxocarpus caeruleus*).

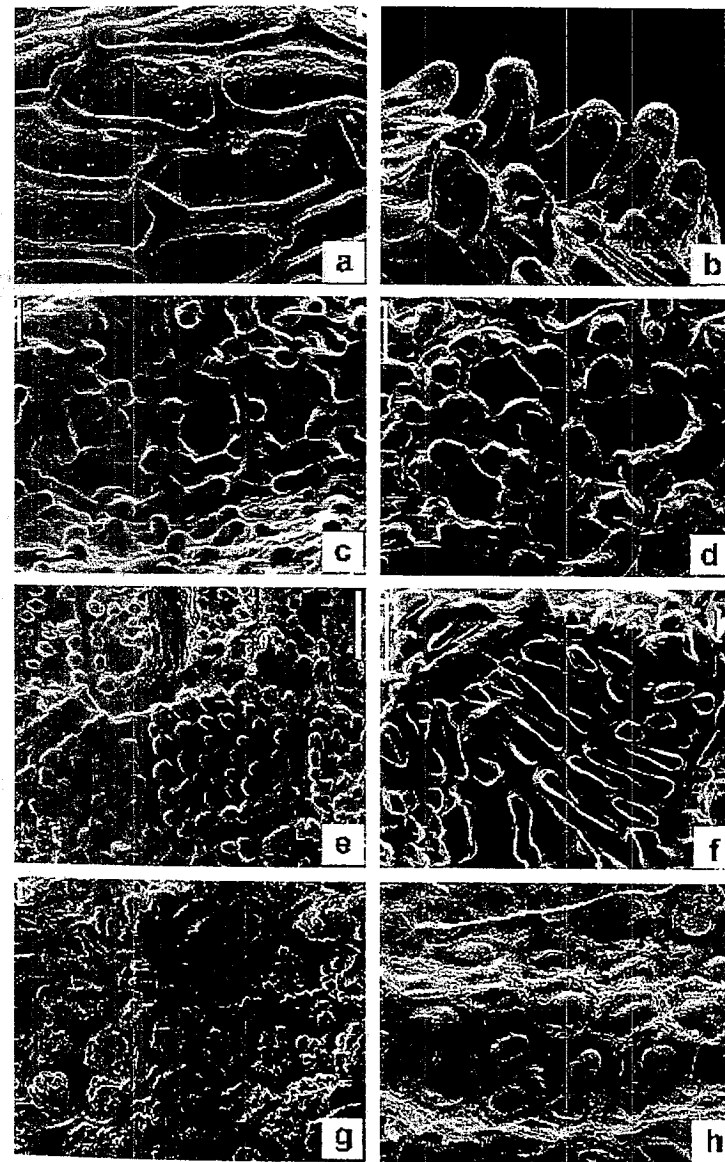
(e) One-sided growth of ovary base associated with dilation of the bases of very short carpels, yielding a wide bowl (*Loxocarpus incanus*).

In conclusion, several patterns for bringing the fruit into an appropriate position for rain-splash dispersal can be observed. None is exclusively represented in a single group and, therefore, none can be considered a distinctive generic feature.

**Seeds.** The seeds match in size, general shape and structure the usual type found in the family. Testa sculpture is very variable and has proved a good character for indicating affinities in former investigations (e.g., *Didymocarpus* sect. *Elati*, *Didissandra*, *Ridleyandra*, WEBER & BURTT 1983, 1998a) as well as in the present work. In fact, the seed structure of Madagascan *Didymocarpus* links the species at once to the African taxa. In other cases seed characters can be used for delimiting alliances of lower rank.

The seed surface must be seen also in its functional connexion to dispersal. In Sino-Himalayan *Didymocarpus*, with orthocarpic fruits and unspecialized seed dispersal, the seed surface is mostly reticulate-smooth (e.g., *D. aromaticus*, *D. kerrii*, *D. mollis*, *D. yunnanensis*), while in the Malesian species (with the few orthocarpic species of *Didymocarpus* s. str. and otherwise plagiocarpic species) the surface is usually distinctly sculptured with processes and appendages of different form and size. A selection of testa patterns is shown in Fig. 7.

Fig. 7. Seed surfaces of various species of *Didymocarpus* (a, b *Didymocarpus* s. str., c - g 'South Indian' and 'Malesian *Didymocarpus*', becoming *Henckelia*, h 'Madagascan *Didymocarpus*', becoming *Hovanella*). a *D. kerrii* (MAXWELL 89/1338, L); b *D. antirrhinoides* (WEBER 840801-1/4, WU); c *D. tomentosus* (VOGEL 40, WU); d *D. puncticulatus* (WEBER 870530-1/1, WU); e *D. reptans* var. *monticolus* (WEBER 840806-1/3, WU); f *D. parviflorus* (WEBER 860729-3/1, WU); g *D. atrosanguineus* (WEBER 870514-4/3, WU); h *D. madagascariensis* (VOGEL, FISCHER & al. M. 388, WU). SEM-micrographs taken by I. MÜHLBAUER. Bar: 10 µm.



'Sino-Himalayan *Didymocarpus*': *Didymocarpus* s. str.

## Content:

- (A) *Didymocarpus* sect. *Didymocarpus* (= sect. *Eudidymocarpus* Benth.), including the genus *Gyrocheilos* W. T. Wang, and *D. mollis* C. B. Clarke and *D. paucinervis* C. B. Clarke, originally placed in the Malesian sect. *Didymanthus* C. B. Clarke, but better accommodated here. Distribution of genus, but only reaching N. Malaya with three species (*D. purpureus*, *D. violaceus*, *D. citrinus*) and excluding Sumatra.
- (B) *Didymocarpus* sect. *Elati* Ridl. [see WEBER & BURTT (1983, 1985)]. S. Thailand and Malay Peninsula.
- (C) Species of uncertain position:
- (1) *Didymocarpus aureoglandulosus* C. B. Clarke, from E. India (Mizoram), Burma (Pegu) and N. Thailand (see HILLIARD & BURTT 1995).
  - (2) *Didymocarpus cordatus* A. DC., an anomalous species from Malay Peninsula and Sumatra.
  - (3) *Didymocarpus platycalyx* C. B. Clarke, from the Moulmein distr. of Myanmar (Burma).
  - (4) *Didymocarpus elatior* Prain, from the Kachin Hills of Myanmar (Burma).
  - (5) *D. barbinervis* C. B. Clarke, from Moulmein distr. Myanmar (Burma).
  - (6) *D. rufipes* C. B. Clarke, from Mt. Mooleyit (Mülayit Taung), Moulmein distr. of Myanmar (Burma).

**Distribution.** The geographical range of *Didymocarpus* s. str. is from NW. India eastwards through Nepal, Sikkim and Bhutan to NE. India and south to Mizoram (Lushai Hills), Myanmar (Burma) and S China (S & SE Xizang, Yunnan, W. & SW. Sichuan, E. & S. Guangxi, W. Guangdong), Vietnam, Thailand, Malay Peninsula (a few species, chiefly in the north, but two species reaching Johore) and Sumatra (one species, also in Malay Peninsula).

**Exclusions.** Apart from the plants dealt with under the headings S Indian, Malesian and Madagascan *Didymocarpus*, *Didymocarpus* s. str. is deemed to exclude:

- (a) *D. venosus* Barnett (Thailand). This is an erect annual herb with spaced decussate leaves and the axillary inflorescence an erect pair-flowered monochasium. The calyx is persistent and reflexed in fruit; the fruit is c. 20 x 3 mm excluding the 4 mm stipe and dehisces loculicidally; the seed-coat is highly distinctive, the cell surface being densely and evenly studded with globose knobs. *D. venosus* will be re-classified for Flora of Thailand (BURTT, in prep.).
- (b) *D. hancei* Hemsl. (China) and *D. bonii* Pellegr. (Vietnam & E. Thailand): these two species will be transferred to *Calcareaoboa* H. W. Li (BURTT, in prep.).
- (c) *D. demissus* Hance (China), which appears to be a species of *Chirita* sect. *Gibbosaccus*.
- (d) The species [excl. *D. hancei*, see (b), and *D. demissus*, see (c)] included in sect. *Heteroboaea* auct. non Benth. (WANG 1990: 441) They are of rosulate habit, with thick rootstock and in general have a more north-easterly distribution in China than *Didymocarpus* s. str. These species are *D. mollifolius* W. T. Wang (n.v.), *D. niveolanosus* W. T. Wang (n.v.) which may possibly prove akin to *Calcareaoboa*, and six species, *D. heucherifolius* Hand.-Mazz., *D. sinoprimuminus* W. T. Wang (n.v.), *D. yuenlingensis* W. T. Wang (n.v.), *D. cortusifolius* (Hance) W. T. Wang, *D. reniformis* W. T. Wang (n.v.) and *D. salviiflorus* Chun (n.v.), that form a distinct group with more or less orbicular, petiolate leaves, often cordate at the base and coarsely toothed, with subpalmate venation. *D. heucherifolius* and *D. cortusifolius* were treated as species of *Chirita* by WOOD (1974), but they are equally out of place in that genus. The material available to us is insufficient for a critical study.
- (e) *D. lacunosus* Hook.f., referred to sect. *Eudidymocarpus* by RIDLEY (1923), but since transferred to *Chirita* (BURTT 1965, WOOD 1974).
- (f) *D. inaequalis* Ridl. was wrongly referred to sect. *Eudidymocarpus* by RIDLEY (1923). It is a 'Malesian *Didymocarpus*' and in this study is referred to *Henckelia* sect. *Glossadenia* (see p. 335).

The three groups (A-C) mentioned under the heading Content above, will be discussed separately. The first is by far the largest and demands more detail, the others will be compared with it.

(A) *Didymocarpus* sect. *Didymocarpus*

**Habit:** the plants are perennial, producing herbaceous annual stems that die after fruiting. The stems for the next season develop while the fruits are ripening and it seems that the number of leaves to be produced

next season may in some species be determined at that time. The new stem lives through the unfavourable season in a completely dwarfed condition with its leaves already formed, but very small: because they are hairy the hairs at this stage are very close together and form a dense silvery protective layer for the young leaf: if the species is one of those producing pigmented glands (see below) the underside of the leaf may be very densely covered with these. In due season, when conditions favourable for growth return, the stem elongates; but this elongation may follow a number of different patterns. Elongation sometimes takes place only below the lowest node, so that the leaves (now expanding) are carried up in a cluster at the top of a bare stem and, because of the lack of internodal growth, they appear as a loose rosette. Sometimes the internode above the lowest pair of leaves elongates, and then these leaves are often small and ill-developed. Curiously, however, in other species there is only a single unpaired leaf at the first node and then this may be very much larger than any others. Occasionally there is a pseudowhorl of leaves at the top of a bare stem, and then a further extension of stem followed by another pseudowhorl of leaves (smaller than the first): axillary inflorescences arise from both whorls. More rarely all the internodes are developed (as in *D. ovatus* Barnett and *D. megaphyllus* Barnett, both from S. Thailand), thus approaching the condition found in sect. *Elati* (see below). Leaves are normally opposite, except where only one leaf develops at a node, and often those of a pair are unequal in size. These patterns of growth deserve careful study, they cannot be satisfactorily understood merely by looking at herbarium specimens.

**Indumentum:** there are three elements to be considered, normal eglandular hairs, glandular hairs and pigmented glands. The normal leaf-indumentum consists of uniseriate pointed hairs. If hairs are present in the inflorescence, they are usually tipped by an oblong gland: presence or absence of these hairs may be a useful specific character.

Pigmented glands are found especially on the underside of the leaf, but may occur elsewhere as well; they are red, brownish red or orange-red. Their presence or absence is constant within a species. These glands were already known to WALLICH (see HAMILTON 1819) for he had received specimens from Mr. GARDNER, British Resident at Katmandu with the information (in WALLICH's words) that "the plants abound in a resinous fragrant exudation and among the natives are called by the generic name Kumkuma, yielding a drug of this name. Their primordial leaves [those that are formed at fruiting time but will not expand fully till the next growing season, as described above] dried form the drug Rani Govindhi. These drugs are in high esteem and are used as a sacerdotal offering by the Brahmans, and also as a perfume by the Hindu ladies". In fact the

specimen in WALLICH's herbarium with primordial leaves, and bearing GARDNER's ticket with the information on their use, is a plant that D. DON described as *Didymocarpus plicatus*, subsequently reduced to *D. macrophyllus* D. Don by C. B. CLARKE.

The structure of these glands varies within the genus and may be of taxonomic importance. For instance in *Didymocarpus hookeri* C. B. Clarke there is a single spherical head-cell; in *D. antirrhinoides* A. Weber and *D. sulphureus* Ridl. (of sect. *Elati*) the head is unicellular but is bluntly conoid or rod-shaped; *D. citrinus* Ridl. has a 2-celled head with a constriction between the cells; *D. insulsus* Craib has a 4-celled cruciform head, while in *D. aureoglandulosus* the head is suborbicular-lobulate with several cells (SEMs of all these are shown in WEBER & BURTT 1983, Figs. 1 & 2, the last under the synonym *D. rodgeri* var. *siamensis*).

A variety of different chalcones and flavanones have been isolated from these leaves with pigmented glands; for example, from *Didymocarpus pedicellatus* R. Br. (RATHORE, GARG & GUPTA 1981), from *D. aurantiacus* C. B. Clarke (ADITYACHAUDHURY & al. 1976) and '*D. corchorifolius* DC.' (WOLLENWEBER, REHSE & DIETZ 1981; the plant studied later became *D. antirrhinoides* A. Weber).

**Inflorescences:** These are pedunculate, axillary, solitary, pair-flowered cymes usually arising only from the axils of the 1 - 2 uppermost pairs of leaves (and therefore only 1 - 4 per stem) but occasionally also from lower leaves (e.g., in *D. megaphyllus* Barnett). Most often they have more or less regular dichasial branching, at least in the lower part, but sometimes it becomes monochasial immediately above the first dichotomy. The bracts within the cyme (bracteoles) are usually conspicuous, often broad and rounded at the tip. Like the sepals they are often wine-red in colour and of a smooth polished cartilaginous texture.

**Calyx:** often wine-red in colour and of a smooth polished firm texture; sometimes more or less white (e.g. *D. albicalyx*, but colour not a specific character). Calyx may be tubular with lobes reaching less than half-way, or it may be lobed to the base. In a number of species the three upper segments are partially united while the lower two are free to the base, and other irregularities of union may occur.

**Corolla:** mostly tubular with oblique limb, often wine-red, and sometimes with lighter lines or streaks, or with white tube and red lobes. Two striking variants are known: in *D. bicolor* Craib the lower lip is green, in *D. wengeri* C. E. C. Fischer it is bright yellow; in both the rest of the corolla is red.

Stamens: anthers cohering face to face, sometimes bearded, the thecae are always divaricate. In some species the anthers are turned to one side of the corolla tube, the style and stigma to the other (the flowers are enanthostylous), flowers with stigma to left or right are found on the same plant. This form of enanthostyly is also found in *Henckelia*, *Streptocarpus* and probably elsewhere in the family. In *Saintpaulia* only the position of the style changes, from one side to the other: the anthers are always central.

Disc: this is in the form of a cylindrical cup and is usually persistent on the fruit.

Ovary and fruit are usually glabrous, more rarely lightly pubescent; they may be sessile or stipitate. The fruit opens loculicidally along both sutures, and is straight or sometimes slightly curved; it may be held at an ascending angle or it may be pendulous and is normally brown when ripe.

Seeds are of two distinct-types: in most species examined the seed coat is smooth, the cell walls are thickened but contiguous ones are not fused together; the two walls remain discrete (e.g., *D. yunnanensis*, *D. kerrii*; Fig. 7a). In species occurring in southern Thailand (*D. ovatus*, *D. megaphyllus*) the testa cells produce lobe-like tubercles from the centre of the cell surface. This is also found in *D. purpureus* and *D. citrinus* from N. Malaya and these plants are transitional to sect. *Blati*.

Chromosome number: the species analyzed so far display a fair amount of variation (see KERN & al. 1987: Tab. 3) but the sample available for study has been too small to permit the base number to be established. It may be noted that *D. citrinus* has  $n = 11$ , the number characteristic of sect. *Blati*.

The synonymy *Gyrochelis* W. T. Wang is now added to *Didymocarpus* for the first time. The genus was proposed for a small group of Chinese species, said to differ from *Didymocarpus* in having the upper lip of the corolla entire (not bilobed), corolla-tube broad and nearly as long as the limb (not relatively slender and frequently longer than the limb), and stigma exerted beyond the mouth of the corolla. An undescribed species from Vietnam agrees with *Gyrochelis* in all these features except that the upper lip of the corolla is shallowly notched, which is the important character used to separate these two genera (WANG 1990: 130, 1992: 13).

However, it is not the failure of this single character that prompts the reduction of *Gyrochelis*. It is its manifold resemblances to *Didymocarpus*. None of the suggested differential characters intringe the definition of *Didymocarpus* given in the preceding survey. Indeed *Gyrochelis* quite clearly represents a small group of species within *Didymocarpus*: a

group that is less discordant than *D. aureoglandulosus* or *D. cordatus*, two species discussed below. It is here placed within sect. *Didymocarpus* but its revival, at subsectional level perhaps, is a possibility when the genus is fully revised.

C. B. CLARKE (1883) placed *Didymocarpus mollis* and *D. paucinerervis* in sect. *Didymanthus*, but they were both described as having bivalved capsules and there is no reason to exclude them from sect. *Didymocarpus*. CLARKE's definition of sect. *Didymanthus* was far from precise; it is lecto-typified below by the Sumatran *D. serratus*, which permits its continued use, in the only sense that has become current, for most of the species referred to it by RIDLEY (1923).

#### (B) *Didymocarpus* sect. *Blati* Ridl.

The section was established by RIDLEY (1905), but has been emended by WEBER & BURTT (1983, 1985) and limited to four species: *D. corchorifolius*, *D. antirrhinoides*, *D. sulphureus* and *D. robustus*. The first two and last two form closely related species-pairs. The features that distinguish this group are: stems tall (1.5 - 2.5 m), axes somewhat lignified; leaves in numerous unequal pairs separated by well-developed internodes. Pigmented glands with a single elongate head-cell. Corolla infundibuliform and yellow or personate (antirrhinoid) and white. Stamens with swollen or lobed connective at head of filament. Stigma bilobed. Seeds tuberculate. Chromosome number  $x = 11$ .

WEBER & BURTT (1983, 1985) took a narrow view of sect. *Blati* restricting it to the four tall species characterized by pigmented glands having a single celled head, tuberculate seeds, and a chromosome number based on  $x = 11$ . *D. citrinus* was excluded: it has a lower, more compact stature and pigment-glands with a 2-celled head. However, it shares yellow flowers with *D. sulphureus* and *D. robustus* and has tuberculate seeds and  $n = 11$  chromosomes like the rest of the section. If the section is maintained *D. citrinus* should probably be included. *D. purpureus* on Langkawi has the characteristic wine-red corolla of sect. *Didymocarpus*, and has  $n = 16$  chromosomes but its tuberculate seeds are like those of sect. *Blati*. Two other species from S. Thailand, *D. ovatus* and *D. megaphyllus*, have tuberculate seeds and also approach sect. *Blati* in their leafy stems with well-developed internodes. A much more extended survey of *Didymocarpus* in Thailand is necessary before a final decision can be reached on maintaining the section.

## (C) Species of uncertain position

Nos. 1 and 2 below are apparently correctly placed in *Didymocarpus*, but are of uncertain affinity within the genus.

(1) *D. aureoglandulosus* (incl. *D. rodgeri* and its var. *siamensis*)

This rather anomalous species has recently been fully discussed (HILLIARD & BURTT 1995). It is closely allied to sect. *Didymocarpus* and the young leaves are very densely beset with pigmented glands, which are distinctive in having a multicelled head. It differs, however, from sect. *Didymocarpus* in a number of floral characters. Bracts and calyx-segments are thin in texture, green and narrowly lanceolate; the calyx-segments may fall individually after flowering. The corolla is infundibuliform, widening smoothly from the base to mouth; it is cream-coloured with red lines and dots in the throat and on the lobes. Most remarkable are the lateral staminodes, which are falcate and 4 mm long. The fruit, however, is typical of *Didymocarpus* sens. strict.

(2) *D. cordatus*

This comprises several closely related varieties (or perhaps independent species) and was placed by CLARKE (1883) in sect. *Didymanthus* and by RIDLEY (1905) in *Paraboea* sect. *Campanulatae*. In fact, the white, widely open corolla displaying the large pair of anthers, is quite unlike a *Didymocarpus* s.str. However the orthocarpic bivalved fruit places this species clearly within that genus. Furthermore the seeds have a tuberculate testa similar to that of *Didymocarpus* sect. *Elati* and some other species of sect. *Didymocarpus* from S. Thailand. There are no pigmented glands, but leaves, sepals and even the fruit itself have peculiar flat, usually purple blisters. The range of *D. cordatus* has recently been extended to NW. Sumatra (DE WILDE & DE WILDE-DUYFIES 18298: upper Mamas River Valley, 15 km W of Kutacane, c. 3°25' N, 97°40' E, 1250 m, L).

(3) *D. elatior*

PRAIN (1901) described this as 'a small undershrub'; unfortunately the specimens at Kew show no basal parts, nor does the illustration. The shoots are twiggy and thus possibly not annual. The bivalved fruit is against the plant being referred to *Henckelia*, as is its location in the Kachin Hills.

(4) *D. platycalyx*

PARISH made a sketch of this species, which he had collected near Moulmein. It shows a flower with a dark blue-purple tube and a slightly oblique pure white limb. The elongate ovary is shortly stipitate and passes into a very short style (CLARKE 1883: 82 wrote 'stylus vix ullus'). The calyx is a broad cup (6 x 8 mm), subentire or somewhat undulate. Fruit is as yet unknown and until it is found the position of the species must be uncertain.

(5) *D. barbinervius*, (6) *D. rufipes*

These two species are known only from the type specimens, which are in both cases incomplete and do not allow critical investigation.

'South Indian and Malesian *Didymocarpus*': *Henckelia* Spreng., emend.

## Content:

(A) 'South Indian *Didymocarpus*'.

This corresponds to *Didymocarpus* sect. *Orthoboea* Benth. (= *Henckelia* Spreng. s.str.)

(B) 'Malesian *Didymocarpus*'.

That is all Malesian sections of *Didymocarpus* in the former sense, except the Malayan representatives of sect. *Didymocarpus* and sect. *Elati* (see genus *Didymocarpus* above).

(C) *Codonoboea* Ridl., recently included in *Didymocarpus* by KIEW (1990).(D) *Loxocarpus* R. Br. [= *Didymocarpus* sect. *Loxocarpus* (R. Br.) Benth.](E) *Platyadenia* B. L. Burt

Distribution: South (Peninsular) India and Sri Lanka, S. Thailand, Malay Peninsula, Sumatra, Borneo, Philippines (Palawan), Sulawesi and western New Guinea.

## Exclusions:

(a) *Didymocarpus frutescens* Jack

*D. elongatus* Jack

*D. triflorus* (C. B. Clarke) B. L. Burt

*D. violascens* Ridl.

All these belong to *Didissandra* (see WEBER & BURTT 1998b)

(b) All species placed under *Didymocarpus* in BACKER & BAKHUIZEN'S Flora of Java (1965) belong to the genus *Chiritia*.

(A) 'South Indian *Didymocarpus*'

This group includes about 15 species restricted to S. India and Sri Lanka; they are currently attributed to *Didymocarpus* sect. *Orthoboea* Benth., which includes the genus *Henckelia* Spreng., at present listed as nomen rejciendum against the conserved *Didymocarpus* but available for use if considered distinct from it.

Morphologically, the group is marked by the following characters:

**Habit:** acaulescent (rhizomatous) rosette plants or (*D. repens*) creeping with elongated internodes.

**Phyllotaxy:** alternate (spiral).

**Leaf shape** rather varied, ranging from lyrate over rhomboid and ovate to suborbicular-cordate, margin sinuate-crenate to entire, lamina often rugose, base attenuate, decurrent or cordate, petiole winged or terete.

**Indumentum** mostly of dense, woolly or silky hairs, or just pubescent; pigmented glands absent.

**Inflorescence:** pair-flowered cymes with few to many flowers, with long peduncle, unilateral cymes (cincinni) seem to be present in *D. missionis* (see BEDDOME 1868 - 1874; t. 176, as *D. membranaceus*); pedicels of flower pairs (?always) of unequal length (that of the front-flower being  $\frac{1}{3}$  -  $\frac{1}{2}$  as long; observations refer to *D. humboldtianus*, *D. ovalifolius*, *D. zeylanicus*, *D. innominatus* and *D. tomentosus*).

**Calyx:** 5-lobed almost to the base, either persistent or caducous at fruiting the caducous condition being commoner in the longer and more slender fruits.

**Corolla shape** fairly uniform: rather small, short- and broad-tubed, with a tendency to be ventricose (strongly ventricose and constricted at the throat in *D. floccosus*); *D. missionis* has, however, flowers with a 2 cm long tube, recalling in shape and size the flowers of some 'Malesian *Didymocarpus*'; colour is usually chalky blue, lavender, pink or pale blue-violet, sometimes with yellow in the mouth or throat; *D. zeylanicus* differs slightly in having prominent darker veins.

**Disc** absent.

**Fruits** are often rather short and stout, but variation is considerable (2 - 4 mm x 1.5 mm to 30 x 3 or 35 x 1 mm). Fairly long (but never stipitate) fruits are found in *D. meeboldii*, *D. humboldtianus* and *D. missionis*. The fruit opens only dorsally; the angle between the pedicel and the fruit is variable (even in a single plant), usually it is c. 135° or more, and

rarely approaches 90°. In some of the specimens with rather long, slender fruits the fruiting receptacle is slightly oblique (for further discussion of this character see p. 301 ff. above).

Photographs of *D. tomentosus* (taken by Prof. S. VOGEL in the Nilghiri Hills) show the fruits usually pointing obliquely upwards, and not held horizontally. A similar situation is shown in the illustrations of *D. lyratus* and *D. humboldtianus* (WIGHT 1848, t. 1350; THEOBALD & GRUPE 1973, 1981, Fig. 2). The obliquely suberect position of the fruit suggests that the seeds are washed out from the tip to the base (see also *Loxocarpus*), though they may also be slung out if the inflorescence is brushed by a passing animal.

**Seeds:** all species examined (*D. humboldtianus*, *D. innominatus*, *D. lyratus*, *D. macrostachyus*, *D. tomentosus*) exhibit a distinct ornamentation of the testa with knob-, erythrocyte-like or short-tubular upthrustings along the contiguous walls, occasionally placed additionally in the central area (Fig. 7c).

**Chromosome number:** the few counts available (see KIEHN & al. 1998) indicate some variation ( $n = 16, 27, \pm 45$ ).

The characters given above show that the plants of S India and Sri Lanka have very little in common with the Sino-Himalayan *Didymocarpus*. They can easily be separated from that group, not only on habit and by the fruits opening only along the dorsal suture (these are the two simplest key characters), but by a number of features that nearly always hold good. Bracts and calyces never have the thick smooth texture that is found in most of the true *Didymocarpus*; the calyx is never tubular, as it is in many species of *Didymocarpus*; corolla always light-coloured (never wine-red nor bright yellow); disc absent; fruits not turning chestnut brown when ripe; seeds with distinctive seed-coat. Geographically there is no overlap between the southern plants and true *Didymocarpus*.

The revival of *Henckelia* Spreng. as a separate genus is fully justified. Its affinities lie with the Malesian plants currently placed in *Didymocarpus* sens. lat. or *Loxocarpus*, a fact already remarked by both BENTHAM (1876) and C. B. CLARKE (1883).

(B) 'Malesian *Didymocarpus*'

This group comprises most of the species enumerated for the Malay Peninsula by RIDLEY (1923) under *Didymocarpus* and the allied species in S. Thailand, Sumatra, Borneo, Philippines (Palawan only), Sulawesi

<sup>1</sup> CLARKE 1883 (p. 101): "Capsula linearis...erecta vel obliqua, rarius angulum fere rectum cum pedicello efficiens."

and western New Guinea. RIDLEY arranged the peninsular species in 5 sections (of rather unequal value) and one further section is diagnosed in the new classification (*Henckelia* sect. *Glossadenia*, p. 335). Most of the species from outside the Peninsula have never been assigned to sections; some fit perfectly well into the existing pattern, others though fitting well enough force an extension of sectional characters (e.g. *D. gracilipes* and *D. murutorum* can be placed in sect. *Heteroboaea* but have small obliquely campanulate flowers, unlike the large trumpet-shaped ones of most other species); a few species do not happily fit anywhere. *D. violoides* and *D. alternifolius*, two Bornean species, are each transitional to *Loxocarpus* in certain respects and are discussed there (p. 323).

**Habit:** the plants are perennial, the shoots are herbaceous or slightly to strongly woody; growth is  $\pm$  continuous, with the stem creeping, ascending or erect.

**Phyllotaxis:** basically opposite, the leaves of a pair usually somewhat unequal; but alternate-spiral in sect. *Heteroboaea* and sect. *Glossadenia*.

**Leaf form:** variable from narrow lanceolate to suborbicular; margin entire, dentate or serrate, sometimes cut almost to midrib. Petiole sometimes in sect. *Heteroboaea* with lacinate wing and basal auricles.

**Indumentum:** variable, of eglandular and glandular hairs, sometimes very dense but not woolly; sunken glands sometimes present; pigmented glands absent.

**Inflorescence:** pair-flowered cymes with few to many flowers  $\pm$  densely crowded in sect. *Glossadenia*, or reduced to solitary flowers (sect. *Heteroboaea*, particular species of other alliances); bracteoles present or (especially in case of solitary flowers) absent. Peduncles often several in one leaf axil and sometimes serially arranged on the petiole.

**Calyx:** Sepals usually free to base, rarely slightly connate.

**Corolla form:** continuous spectrum from tubular-infundibuliform (e.g., *D. platypus*) through campanulate (e.g., *D. geitleri*) to extremely short-tubed and flat-faced (e.g., *D. puncticulatus*). Parallel series from tubular-infundibuliform are found in several groups: in sect. *Glossadenia* (*D. inaequalis* to *D. beccarii*), in sect. *Heteroboaea* (*D. crinitus* and *D. platypus* to *D. gracilipes* and *D. murutorum*). Sect. *Boeopsis* shows campanulate to short-tubed corolla with flat spreading limb; tubular flowers are at present excluded by definition, but should probably be added to the section as *D. bakoensis* (Sarawak) has a tube 13 mm long, but in all other respects seems very close to *D. battamensis* (tube 3 mm) and *D. puncticulatus*.

**Stamens:** filaments long or short corresponding to length of corolla tube; anthers coherent; connectives often thickened with tooth-like appendage.

**Disc:** cup-shaped, rim sometimes lobed (e.g., *D. ascendens*), dorsal portion sometimes shorter and narrower (e.g., *D. albomarginatus*), in sect. *Boeopsis* sometimes completely reduced, in sect. *Glossadenia* developed as a ventral gland with entire or trifid tip.

**Fruit:** plagiocarpic, terete, usually long, sometimes rather short (species of sect. *Boeopsis*; 12 - 25 mm long), opening dorsally; usually cylindrical, but some species with short fruits narrowly ellipsoid.

**Seeds:** testa cells with slightly to distinctly thickened contiguous walls, sculpture extremely variable, so that no generalization can be made.

**Chromosome number:** The base number is  $x = 9$ . Most species are diploid with  $2n = 18$ . There are also some tetraploids based on that number (*D. hispidus* and allies).

As the list of characters shows, 'Malesian *Didymocarpus*' is morphologically extremely diverse. The key characters that separate it from *Didymocarpus* s.str. are the habit (growth continuous, not seasonal with monocarpic shoots) and the plagiocarpic fruit opening along the median line of the dorsal carpel. That, however, does not distinguish it from the S India/Sri Lanka plants that we have seen must be separated under the name *Henckelia*. In the longer-fruited species of that genus, where the capsule may be nearly plagiocarpic, the receptacle is slightly oblique: such fruits cannot be distinguished from some of those found among Malesian *Didymocarpus*. There are, in fact, no good reasons for separating this group from *Henckelia*, and it must be included therein.

### (C) *Codonoboaea*

The genus *Codonoboaea* was established by RIDLEY (1923) for three species: *C. leucocodon*, *C. ericiflora* and *C. lilacina*. The first species was originally described by RIDLEY (1915) as *Paraboaea leucocodon*, the two latter were first placed in *Didymocarpus*.

RIDLEY's association of these three species in a new genus is difficult to understand. Perhaps his right eye was impressed by the epipetiole position of the flowers in *C. ericiflora* and *C. lilacina*, while his left eye noted particularly the unusual tooth-like corolla-lobes of *C. ericiflora* and *C. leucocodon*. It was the latter character that he used in his generic key. Unfortunately, he did not indicate a type species for the genus and, sub-

sequently, two different lectotypes have been chosen. IVANINA (1967) designated *C. leucocodon* as the type of the genus; KIEW (1990) reduced the genus to sectional rank under *Didymocarpus* and chose *C. lilacina* as its type, relying for her definition of the section chiefly on the epipetiole inflorescence.

IVANINA's choice of type clearly has priority and this species meets the generic criterion of tooth-like corolla-lobes. Also it is reasonable to suppose that RIDLEY's name *Codonoboea* was a deliberate echo of his specific epithet *leucocodon*. *C. leucocodon* must therefore be retained as lectotype of the genus, and, necessarily, it overrides KIEW's choice of *C. lilacina* as lectotype of the sectional name. The affinity of *C. leucocodon* in *Didymocarpus* is, as KIEW points out, unresolved, but it certainly must be transferred, with other Malesian *Didymocarpus*, to the genus *Henckelia*. The sectional name may, meantime, be left in abeyance.

The species which formed *Didymocarpus* sect. *Codonoboea* sensu KIEW were only four in number: *D. lilacinus*, *D. niveus*, *D. corneri* and *D. ericiflorus*. *D. ericiflorus*, one of the original species of *Codonoboea*, stands apart because of its opposite leaves with entire margins. Its position is uncertain.

The species *D. niveus*, *D. lilacinus*, and *D. corneri* are certainly closely related and form a compact group. They bear the flowers in a short series on the petiole. The series is extended in subsequent flowering periods; in each period several flowers are produced in serial succession. The leaves are alternate, coarsely hairy and tend to be fimbriate at base. Although the epipetiole displacement of the flower is more marked, the habit of the plants matches with that of *D. crinitus* and its allies.

Many gesneriads have the facility to form serial axillary buds, each successive bud arising between the previous one and the subtending leaf. Most often the buds are inflorescences and the production of a series of such buds is sometimes associated with the reduction of each individual inflorescence to a single pair of flowers, or even to a single flower. There is also a tendency for the meristem producing such serial inflorescences to be closely associated with the meristem producing growth in the basal region of the petiole, so that new inflorescence buds are produced on the 'petiole' (see WEBER 1975).

The condition has long been known. An early description reads: 'peduncles two to five in each axil, one-flowered, round, two inches long, uniting at the base into a short thick unilateral rachis, densely pilose and adhering beneath to the petiole' and in notes after the description we find the phrase 'the crested disposition of the flowers'. The author was William JACK, writing of *Didymocarpus crinitus* which he discovered

on Penang in 1819 (JACK 1820, 1823); indeed the epithet *crinitus* was obviously given in the sense of 'crested', not of 'having long hairs'. *Didymocarpus crinitus* is the lectotype (BURTT 1954) of sect. *Heteroboea*, the species of which display a considerable range of corolla size and form when the whole distributional range is considered. The three species *D. lilacinus*, *D. niveus* and *D. corneri* can certainly be accommodated here; there is a related species, as yet undescribed, in Sarawak.

#### (D) *Loxocarpus*

The genus *Loxocarpus* was established by R. BROWN in 1839. BENTHAM (1876) and C. B. CLARKE (1883) included it as a section in *Didymocarpus*. In 1896 RIDLEY still included the species in *Didymocarpus*, but from 1905 onwards he referred to it as a separate genus, as it seemed "...sufficiently distinct in its short tubed and short stamened flowers and horn-like capsule" (RIDLEY 1905: 4). BURTT (1954: 201) referred to *Loxocarpus* first again as a section of *Didymocarpus* ("without prejudice to its eventual status"), but later (1958, 1962) adopted the generic rank, influenced by the knowledge that *Loxocarpus* might well become the correct name for nearly all the Malesian plants then placed in *Didymocarpus*.

Characteristic features:

Habit: Often rosette plants, less frequently caulescent and erect (*L. caulescens*, *L. meijeri*) and sometimes creeping (*L. repens*).

Phyllotaxis: usually alternate, very rarely opposite.

Leaf form: usually petiolate, lamina ranging from band-like-filiform over lanceolate and ovate to suborbicular.

Indumentum: sometimes densely silvery silky-hairy, sometimes pilose or pubescent.

Inflorescence: pedunculate pair-flowered cyme, with several to few, occasionally solitary, flowers; bracteoles present.

Calyx: Sepals free to base or nearly so.

Corolla: usually with rather short and broad tube, or with very short tube and limb spreading at right angles, more or less rotate or distinctly bilabiate.

Androecium: filaments and anthers included in the tubular-flowered species, otherwise exposed, with a yellow knee on the filament more conspicuous than the paler anther.

Disc: absent.

Ovary and fruit: rather short, conical; fruit plagiocarpic, short, opening dorsally, with several modes of attachment of the fruit valves to



the receptacle or pedicel (see below), in most cases valves with a distinct 'hump' at the base, the fruit sometimes looking 'corniculate'.

The reader knowing *Loxocarpus* only on the Malay Peninsula will certainly be surprised (and probably annoyed) to find that the genus is here included in *Henckelia*. On the Peninsula it is easy to recognize a *Loxocarpus* in the field or in the herbarium (even in the vegetative state) and to distinguish it from a 'Malesian *Didymocarpus*'. Here *Loxocarpus* are all rosette plants with silky-haired leaves (silvery-white when dry) in alternate arrangement. Their flowers fall roughly into two groups: one has a rather short and broad tubular corolla with the stamens included (e.g., *L. incanus*), the other a very short corolla tube with a flat spreading limb anthers exposed at the mouth of the corolla and the filaments having a yellow-coloured knee (*L. caeruleus*; pollen deceptive flowers, see WEBER & KREW 1983, VOGEL 1993). In both groups the fruit is short, thick-conical and opens by a dorsal split. The 'horn-like' appearance is due to the fact that the fruit valves usually have a wide dorsally rounded base. The fruit, therefore, is often referred to as 'humped' and it is convenient to retain this term.

*Loxocarpus* is not restricted to the Malay Peninsula, it is also found in Sumatra and in Borneo, both areas adding to the range of variation in the genus. Whereas the Peninsular species are all rosette plants with silvery indumentum, on Sumatra two erect caulescent species are found: *L. caulescens* with the characteristic silvery indumentum and *L. meijeri* which has a sparser covering of harsher and more spreading hairs. The number of species in Borneo is at present uncertain, but it will probably reach at least 20 when undetermined specimens already in herbaria are described. Some are rosette plants (with or without silvery foliage), others have a creeping habit. In general it seems as though the rosette plants are found chiefly on rocks, cliffs or steep banks, the creeping forms are found on the floor of submontane moss-forests.

The essential feature of *Loxocarpus* lies in the fruit. A typical species (e.g., *L. incanus*) has fruits with the following properties: (a) capsule short, widely opening at the base (giving rise to basal 'humps') and recurving to an oblique or horizontal position, so that a short boat-shaped or nearly cup-shaped splash-capsule is formed, (b) receptacle horizontal, somewhat swollen. In contrast, typical 'Malesian *Didymocarpus*' has a long, cylindrical capsule, attached to an oblique receptacle, and opening with a narrow channel (see above).

However, on closer inspection, quite a variety of slightly different fruit constructions can be observed, and the clear distinction becomes blurred:

- (a) Receptacle oblique to vertical, capsule long (c. 30 mm), without basal hump (this is the typical fruit of 'Malesian *Didymocarpus*'): *Didymocarpus violoides* (see below).
- (b) Receptacle oblique to erect, capsule 6 - 8 mm long, with slight basal hump: *Loxocarpus conicapsularis* (Kalimantan, Karimata: peduncle 3 - 7 flowered), *L. aff. conicapsularis* (Sarawak, Gunung Mulu N.P.: peduncle 1-flowered).
- (c) Receptacle slightly oblique, capsule slender c. 15 mm long, with very slight basal hump: *Didymocarpus alternifolius*.
- (d) Receptacle oblique/vertical, capsule short, without basal hump: *L. holttumii*.
- (e) Receptacle horizontal, capsule rather short, with  $\pm$  prominent basal hump: *L. caeruleus*.
- (f) Receptacle horizontal, capsule very short (c. 8 mm),  $\pm$  corresponding to the prominent basal hump: *L. incanus* and allies.

It is the Bornean *Didymocarpus violoides* - *Loxocarpus conicapsularis* alliance (with some new species still to be described) that provides evidence that *Loxocarpus* may have evolved from or within 'Malesian *Didymocarpus*'.

The two species *Didymocarpus violoides* and *Loxocarpus aff. conicapsularis* are obviously very closely related, but have been accommodated in different genera. They approach one another in flower morphology to a remarkable degree: both have blue, almost rotate, flowers with exposed stamens: the filaments have a knee of yellow colour. The fruits range from 6 - 30 mm and are humped in the species with shorter fruits, *L. conicapsularis*, without a hump in *D. violoides*.

There is another group of species that shows the transition from a long cylindrical fruit to a short broad-based one. This group is held together by vegetative and other characters, the most obvious being the indumentum, a dense covering of matted silky hairs on both petiole and stem. The sequence starts with *Didymocarpus alternifolius* (fruit 15 - 18 mm long, 1 mm diam., scarcely or very slightly humped on the upper side at the base), includes *Loxocarpus rufescens* and one or two undescribed species (one with fruit conical 5 mm long and 2 mm diam. at the base). All these species are from SW. Kalimantan and S. Sarawak and the group is represented by *Loxocarpus holttumii* (fruit conical, 6 mm x 1.5 mm at base) in Johore. Available flowering material of *D. alternifolius* is not good enough to permit a detailed account of floral changes, but in this sequence the organization runs no further than a pollen flower; there is no development of a yellow patch acting as a dummy anther.

These two bridges between 'Malesian *Didymocarpus*' and *Loxocarpus* are both centred in Borneo, one in the north west, the other in the south west. RIDLEY's recognition of *Loxocarpus* as a genus can now be seen as a Peninsula-generated approach. Although he was so intensely interested in the Gesneriaceae of the Malay Peninsula, he seems to have paid scarcely any attention to them on his trips to Borneo.

Remembering the considerable spectrum of fruit constructions, generic separation based on the fruit differences is no longer tenable. It is therefore best to amalgamate *Loxocarpus* with 'Malesian *Didymocarpus*' and include both in *Henckelia*. There is, indeed, a somewhat parallel series in *Henckelia* sect. *Henckelia*, from the long cylindrical fruits of *H. meeboldii* (35 mm long) to the shorter conical (but never humped) fruits of, e.g., *H. incana*.

#### (E) *Platyadenia*

The genus *Platyadenia* was established by BURTT (1971) for a single, most curious species from Borneo (Sarawak, Bako National Park): *P. descendens*. The plants are found on sandstone rocks in dark shady forest, with the stems growing downwards (cf. epithet!). The arrangement of the rather thick hairy, oblong-subfalcate leaves was described as alternate, the flower as *Didymocarpus*-like, the fruit as *Loxocarpus*-like, and the disc, a ventral apically trifid scale, was recorded as a unique feature.

The species was recollected by A.W. in 1979. The field observations, together with our studies in *Didymocarpus*, change the morphological picture and taxonomical assessment to some extent. Firstly, the phyllotaxis is not alternate, but opposite. The impression of an alternate arrangement is caused by the strong anisophylly, by which one of the two leaves of a pair is reduced to a small, stipule-like appendage. The corolla is rather short, funnellform, with wide open mouth. The fruit is, though short (c. 6 mm) and boat-like, not typically *loxocarpoid*, as it lacks basal humps. The mode of opening corresponds to some species of 'Malesian *Didymocarpus*' (*D. puncticulatus*-alliance). The special type of disc has been found in the meantime in a number of 'Malesian *Didymocarpus*' species, now to be placed in *Henckelia* sect. *Glossadenia*.

In conclusion, there is good evidence that *Platyadenia* is nothing but a somewhat aberrant species of 'Malesian *Didymocarpus*'. If the relationship with sect. *Glossadenia* proves close indeed, *Platyadenia* could serve to explain the alternate phyllotaxis of sect. *Glossadenia* perhaps via anisophylly (complete reduction of the smaller leaf at each node and change to a spiral phyllotaxy). Sect. *Glossadenia* would thus contrast with sect.

*Heteroboaea*, where, as observations in seedlings of *Didymocarpus platypus* show, the alternate phyllotaxis is apparently achieved by disintegration of leaf pairs ('Wirtelauflösung', as often found in Scrophulariaceae; cf. HACCUS 1939, 1950). Like 'Malesian *Didymocarpus*', *Codonoboaea* and *Loxocarpus* (treated above), *Platyadenia* must be absorbed into *Henckelia*.

#### 'Madagascan *Didymocarpus*': *Hovanella* A. Weber & B. L. Burt

Content: *Didymocarpus* sect. *Hova* C. B. Clarke

Distribution: Madagascar.

CLARKE (1883) established *Didymocarpus* sect. *Hova* for a single species from Madagascar, described by himself: *D. madagascariensis*. Two more species from there, *D. pusillus* (1887) and *D. vestitus* (1885) were then described by BAKER. When revising the Gesneriaceae of Madagascar and the Comores, HUMBERT & al. (1971) reduced *D. pusillus* to synonymy with *D. madagascariensis* (erroneously called *D. madagascariensis*) and added another species as 'D. sp.'. This is an ill-known and problematic plant. It certainly does not belong to *Didymocarpus* sect. *Hova* and will not be further considered here.

Thus, as things stand, 'Madagascan *Didymocarpus*' includes only two species with certainty: *D. madagascariensis* C. B. Clarke and *D. vestitus* Baker.

CLARKE's characterization of sect. *Hova* reads: "tenuiter suffruticulosa, ramulis elongatis. - Folia parva, distantia, opposita. - Calyx, corolla, stamina, capsula, fere ut in sect. *Loxocarpus*." It was obviously the dorsally dehiscent fruit with a basal hump that induced CLARKE to relate sect. *Hova* to sect. *Loxocarpus* and to include it in *Didymocarpus*.

'Madagascan *Didymocarpus*' is characterized by the following features:

Shoots: herbaceous, weak, erect, with decumbent, rooting base.

Phyllotaxis: decussate, leaf pairs distant.

Indumentum: mostly of several-celled, eglandular hairs, some of those in the inflorescence gland-tipped.

Inflorescence: a few-flowered cyme.

Sepals: somewhat unequal, the two lower ones longer; persistent in fruit.

Corolla: small, rather short-tubed, distinctly ventricose in *D. vestitus*.

Disc: reduced to a low, inconspicuous ring; not recognizable in the fruit.

Fruit: plagiocarpic, differing considerably in the two species: in *D. madagascariensis* the fruit is laterally flattened, straight or slightly curved (with the distal part directed downwards), and there is a distinct invagination along the upper suture ("cannelure médiane"). The ripe fruit exhibits a kind of compressed hump at the base. The hump is in no way comparable to that of *Loxocarpus*, but represents a basal, dorsally enlarged and raised fruit portion that does not open (in other words, the splitting on the upper side of the fruit is not along its whole length, but stops at a defined point distinctly above the base). Dehiscence is along the median line of the upper carpel, with the infolded valve portions covering the inner sides of the (in cross-section) v-shaped fruit. In *D. vestitus* the fruits have a simpler structure: they are terete and open along their whole length.

In both species the fruit is attached to a slightly swollen (cup-shaped) receptacle. Slightly unequal growth and curving of the upper part of pedicel are apparently responsible for the fruit making an angle (c. 90° in *D. madagascariensis*) with the pedicel.

Seeds: The seeds of *D. madagascariensis* have already been examined by SEM by BEAUFORT-MURPHY (1983). Her observations have been confirmed in the present investigation, which also includes *D. vestitus*. In both species the testa cells produce a single, prominent dome-shaped upthrusting in the centre (Fig. 7h).

Chromosome number:  $2n = 28$  (*D. madagascariensis*, KIEHN & al. 1998).

Most of the characters quoted are of wide occurrence in Gesneriaceae and of little taxonomic value. Only the fruits and seeds merit discussion.

The specialized fruit type of *D. madagascariensis* is unique and found neither in the other *Didymocarpus* groups nor in other genera. The simple fruit type of *D. vestitus* might, however, raise the question, if this species perhaps represents a remote link to 'Malesian *Didymocarpus*'. In view of the limited taxonomic value of the plagiocarpic fruit, support must be sought from other characters. Such support has not been found, on the contrary, the structure of the seed coat points in another geographical direction.

The testa type found in both species of 'Madagascan *Didymocarpus*' is well known from African genera such as *Saintpaulia*, *Schizoboea*, *Linnaeopsis*, *Streptocarpus* (subg. *Streptocarpella*) and is referred to as 'verrucate' or 'verruculose' in the literature (see HILLIARD & BURTT 1971,

BEAUFORT-MURPHY 1983). This shows that 'Madagascan *Didymocarpus*' is closely linked with the African genera and not with 'Malesian (or other) *Didymocarpus*' and confirms BEAUFORT-MURPHY's statement (1983: 359): 'The seeds of *Didymocarpus madagascariensis* are also similar to those of *Schizoboea*, but unlike the other examined species of *Didymocarpus*'.

BURTT (1971) has expressed his view that the African-Madagascan genera (*Acanthonema*, *Colpogyne*, *Linnaeopsis*, *Nodonema*, *Saintpaulia*, *Schizoboea*, *Streptocarpus*, *Trachystigma*) represent a distinct group that has long been independent from the Asian taxa.

There is little doubt that 'Madagascan *Didymocarpus*' belongs to the African alliance, but it certainly cannot be included in one of the existing genera. It is, therefore, given the rank of a distinct genus. For this C. B. CLARKE's sectional name *Hova* is not convenient as it would be liable to confusion with *Hovea* R. Br. (Leguminosae). We therefore propose *Hovanella*, which preserves the link to the Hova, one of the peoples of Madagascar.

#### Chromosome numbers

The data available are still too scanty for wide generalizations, but recent chromosome counts (KIEHN & al. 1998) cover a large number of species from the Malay Peninsula. From these and from the available literature data it is apparent that *Didymocarpus* s. str. (with numerous base numbers) has a different cytological pattern from *Henckelia*. Within *Henckelia*, as accepted above, there is a remarkable consistency of  $x = 9$  in Malesia, most species being diploids but a few tetraploids being found in sect. *Didymanthus*. In the S. India and Sri Lanka plants discordant numbers ( $n = 16, 27, \pm 45$ ) have been recorded but could well be simple dysploids and polyploids on  $x = 9$  and they do not provide a strong argument for separating the two geographical groups. On the other hand, the constancy of  $n = 9$  (which runs across sects. *Didymanthus*, *Heteroboea*, *Glossadenia* and *Loxocarpus*) reinforces the intergrading morphologies in binding these groups together.

Thus, current knowledge of cytology provides modest confirmation of the classification proposed here. In contrast, *Hovanella*, as represented by *Didymocarpus madagascariensis*, has  $2n = 28$ . A haploid number of  $n = 14$  has not otherwise been recorded in this affinity, but as  $n = 15$  and  $n = 16$  are common in Gesneriaceae on the African mainland, the record of  $n = 14$  for *D. madagascariensis* does not provide a strong denial of its affinity with the African genera.

## Phytogeography

An analysis of the distribution of the genera of subfamily Cyrtandroideae (BURTT unpubl.) indicates that there are three main phytogeographical groups. One comprises the African genera. The other two groups are largely Asiatic: one has its centre in S. China, but embraces the whole of the Sino-Himalayan and Burmese element and also the three relict genera in Europe (*Ramonda*, *Jancaea* and *Haberlea*); the third is a more tropical group centred on the Malay Peninsula, Sumatra and Borneo (known collectively as Sundaland). The first, the Sino-Himalayan group for short, shows some penetration southwards into Sundaland: the Sundaland group shows some penetration northwards through Thailand, and it is Sundaland genera that supply the whole of the gesneriad flora to the east: there is no endemic genus of Cyrtandroideae east of Borneo.

The foregoing taxonomic study of *Didymocarpus* in its current sense, has shown that it must be divided into three. *Didymocarpus* in the strict sense is clearly a Sino-Himalayan genus, though it has a few species in the Malay Peninsula and one of them (*D. cordatus*) reaches Sumatra. That *Didymocarpus* has a northern centre is emphasized by its habit of producing annual flowering stems, which are adapted to a strongly seasonal climate. The Malayan species still retained in *Didymocarpus* grow in a more tropical area that can, in part at least, be labelled 'everwet', but they also have this pattern of growth. Species of sect. *Elati* admittedly look different at first sight because of the much taller stems, the habit being rather a scrambling one up through other vegetation, but these stems are, as in typical *Didymocarpus*, monocarpic. This is strong evidence that their origin has been from the north. Such a pattern is not found in any of the other groups hitherto assigned to 'Malesian *Didymocarpus*' and herein recognized as belonging to *Henckelia*.

*Henckelia* belongs to the Sundaland group. That it is also found in southern India and Sri Lanka does not militate against this, for the links between the floras of these areas and those of Malesia are well attested. Examples of this relationship are *Pleiospermium* (Engl.) Swingle (Rutaceae), one species in Sri Lanka, one in Java, one in Sumatra and two in Borneo; *Osmelia* Thwaites, one in Sri Lanka, three in Malaya; *Acrotrema* Jack (Dilleniaceae), about nine species in Sri Lanka, one in Malaya, two genera of *Viscaceae* (*Notothizos* Oliv., *Ginalba* Korth.) and one of *Loranthaceae*, *Tolypanthus* (Blume) Blume each with one species in Sri Lanka and the rest in Malesia. Apart from small genera like these, the relationship can be traced in such large families as *Dipterocarpaceae*.

The Malesian distribution of *Henckelia* is firmly centred on Sundaland. The approximate number of species is about 90 in Peninsular

Malaysia, 12 in Sumatra and 50 in Borneo; very few of these species are found in more than one of these areas, and only *H. crinita*, in its broadest sense, and perhaps *H. platypus* is found in all three. Southern Thailand has a typically marginal representation of *Henckelia*; there are approximately twelve species (only four of them endemic) but representing four different sections. There is only one species in the Philippines and this is *H. woodii* on the island of Palawan, which is well known for its Bornean affinities. East of Borneo only two species are known from Sulawesi, and further east still the only specimen that has come to light so far was collected by EXMA (nr. 4750) in the Wissel Lakes area of western New Guinea. Records of '*Didymocarpus*' from eastern New Guinea and Australia refer to species of *Boea*, those in the Flora of Java (BACKER & BAKHUIZEN 1965) are species of *Chirita*.

A rough numerical summary of the species of *Henckelia*, with some allowance for those known but not yet described, is:

S India	12
Sri Lanka	3
Thailand	12
Sumatra	12
Malay Peninsula	c. 100
Borneo	50
Philippines	1
Sulawesi	2
New Guinea	1
<hr/>	
Total (allowing for overlaps)	c. 180

The genus *Hovanella* consists of only two species, both confined to Madagascar. Their affinity (see above p. 325) has been determined as lying with the African group of genera.

In general, therefore, the distributions of the three genera recognized in this study accord well with the more general survey of generic distributions in Cyrtandroideae.

With regard to the various groups that have here been included under *Henckelia*, it can be said that sect. *Heteroboea*, *Loxocarpus*, *Glossadenia*, *Didymanthus* all occur in the Peninsula, Sumatra and Borneo. The internal classification of *Henckelia* requires a lot more work and the circumscription of other sections is not yet clear: it can only be said that there is at present no firm evidence of morphological groups that show differential distributions within Sundaland except at a low taxonomic level.

### Conclusions and Discussion

The view that *Didymocarpus*, in the sense in which the name has been used in recent years, was highly heterogeneous, has been confirmed. The two Madagascan species, not unexpectedly, seem to have their affinity with other African genera and yet do not fit precisely with any; the new genus *Hovanelia* has therefore been established.

The Asiatic species divide into two main blocks: *Didymocarpus* s.str. and *Henckelia*. Their differential distributions have been discussed in the preceding section.

*Didymocarpus* remains a genus of about 80 species; its internal classification and detailed morphological range (especially in floral form) needs further study; only then can the best treatment of the few anomalous species be satisfactorily decided. *Didymocarpus* s.str. is not further considered here.

The remainder of the erstwhile *Didymocarpus*, the more tropical component, has become the revived genus *Henckelia*. It has necessarily been studied in rather more detail in order to decide whether other genera that have sometimes been independently recognized, should be maintained. Technical reasons for the eventual decision to recognize only *Henckelia* have been given under the relevant names above. It would, however, be a mistake not to try to summarize some of the information that has come to light.

*Henckelia* appears to be a genus that is still undergoing active evolution. This is evidenced by the way some of its component sections consist of a series linked by small changes but with marked differences between the terminal species. These, of course, are much more difficult to handle taxonomically than groups of species that can be precisely defined by small but constant characters.

Recent evolutionary pressure in *Henckelia* seems to have been occasioned chiefly by the need for effective pollinators. The primary floral condition is probably represented by flowers with a well-developed corolla tube and a clearly functional (cup-shaped or cylindrical) disc (nectar-flowers). Evidence suggests that change has been in the direction of attracting pollinators with shorter tongues (progressive shortening of the corolla tube), the next stage leading to flowers that offer only pollen as a reward (reduction of the disc). The final achievement is a pollen-deceit flower in which two- or three-dimensional anther/pollen dummies are presented. These may be yellow blotches in the corolla mouth (e.g., *H. puncticulata*, WEBER 1989), a long exserted, bright yellow style (*H. geitleri*, WEBER 1989) or a yellow swelling or knee on the filaments (*H.*

*caerulea*, WEBER & KIEW 1983, VOGEL 1993, see above under *Loxocarpus*). While the dummies look deceptively like pollen, the true pollen-bearing parts, the anthers, are much less conspicuous, and in the latter case, are placed out of reach of the insect's forelegs.

To trace such sequences in detail, a better internal classification of the genus is required than is at present available. Current weaknesses are due in large part to sections being based entirely on material from the Malay Peninsula: they have never been redefined to embrace Bornean and Sumatran species. For example *Didymocarpus* sect. *Boeopsis* is defined as having a short corolla-tube, either broad and open with small lobes (as in *Didymocarpus pumilus* = *Henckelia nana*), or with a very short tube and broad flat spreading limb (as in *H. puncticulata*, see above). There is a long-tubed representative of this group in Sarawak, *H. bakoensis* (tube 13 mm long): in vegetative characters it is very similar to *H. puncticulata*. The limits of the section need to be redefined if it is to be maintained: for that reason it is not, at present, transferred to *Henckelia*.

In the newly established sect. *Glossadenia* (see below p. 335, a full account will be published shortly), there is a range of corolla length from 50 mm in *H. inaequalis* from Langkawi and S. Thailand to 13 mm in the Bornean *H. beccarii*, the corresponding range for fruit length is from 30 mm to 20 mm. This section differs from sect. *Boeopsis* in being throughout a nectar-producing group, the well developed unilateral nectary is placed below the ovary and is an important diagnostic feature of the section.

That there has been selective pressure driving a trend towards flowers adapted to short-tongued pollinators is at present no more than supposition. Field-work is needed even though it could only give evidence on whether such conditions exist now. It would have to be based on communities, not on species of *Henckelia* alone, and would need to investigate at least two possibilities. The first is that there may be numerous long-tongued pollinators in the community but that they visit preferentially quite different flowers. The second is that the potential pollinator population shows a significant bias towards short-tongued insects. A third possibility is that short-tubed flowers simply require less investment of resources by the plant. These ideas are mentioned simply to emphasize the complexity of the problem; it is not simply a question of finding a few colonies of *Henckelia* and settling down to observe pollination, necessary though that is.

The ultimate result of successful pollination is that there are seeds to be dispersed. The basic type of capsule in *Henckelia* is slender, cylindric-

cal, opening only by a dorsal split. Although no detailed field studies have been made, it was observed (by A. W.) that open fruits of *H. quinquevulnera* filled with seeds were completely washed out by a shower of rain: furthermore, as mentioned above (p. 305), swelling of part of the fruit-wall permits a wider opening which may act as a more efficient splash cup. Such wider openings are not found in the long cylindrical fruits of sect. *Heteroboaea* or sect. *Didymanthus*. They are associated with short-tubed flowers. But it seems that shortening of the ovary and fruit is a trend that lags behind that of the flower. Thus some flowers have already reached the pollen-flower level while still producing a long cylindrical fruit (e.g., *H. violoides* with corolla tube 3 mm, but fruit 30 mm). In the functionally similar flowers of *H. puncticulata* (*Didymocarpus* sect. *Boeopsis*) the fruit is only 15 mm long and narrowly ellipsoid in shape (which permits a wider opening), while that of *H. caerulea* (sect. *Loxocarpus*) has a well developed swollen hump at the base and is only 8 mm long.

A corollary of these sequential changes in flowers and fruits has been that some vegetative characters have been less labile and are of great taxonomic value. However, 'less labile' is a purely relative term, for vegetative change within a group may also be very obvious. For instance, the old segregate *Loxocarpus* was once diagnosed as a group of rosette plants found on rocks and cliffs, but is now known to include small erect herbs as well as others with creeping habit found in the moss or submontane forest. Nevertheless, vegetative characters are of considerable importance; for example in *Henckelia*, sect. *Didymanthus* has opposite and decussate leaves whereas the sections *Henckelia*, *Heteroboaea*, *Glossadenia* and *Loxocarpus* have alternate leaves, sometimes in tight rosettes (which make observations of phyllotaxy very difficult; but some rosette plants also produce runners with a few scattered leaves showing their phyllotaxy quite clearly).

A full account of Malesian *Henckelia* requires much more field-work, especially in Borneo where there are undoubtedly several, perhaps many, undescribed species: some are already known, and will be described shortly, but the herbarium material of others is, as yet, inadequate for description. The range of morphological variation known in Borneo will certainly be increased.

#### Acknowledgments

The first author acknowledges support by the Austrian "Fonds zur Förderung der wissenschaftlichen Forschung" (project numbers P 8166-B, P 6969-B, P 7984-BIO). Thanks are specially due to Dr. RUTH KIEW (UPM, now SING) for hospitality

and collaboration and to Mr. ANTHONYSAMY for field assistance. For technical help the authors are indebted to Mag. SUSANNE SONTAG, Mrs. MONIKA PASCHINGER, Dr. RALF BUCHNER, Dr. ROLAND EBERWEIN, Dr. PETER LASSNIG, Mr. JOHANNES SELINGER, and Dr. ERNST VITEK. Thanks also go to the directors of the herbaria A, AA, BM, CGE, E, K, KEP, KUN, L, P, SAR, SING, UPM, W, and WU for the loan of material and/or facilities for consultation.

#### Appendix I. Generic nomenclature

- Didymocarpus* Wall., Edinburgh Philosoph. J. 1: 378 (1819), nom. cons.  
Typ. cons.: *D. primulifolius* D. Don, Prodr. Fl. Nep. 123 (1825).  
= *Gyrocheilos* W. T. Wang, Bull. Bot. Res. 1 (3): 28 (1981) & Fl. Reipubl. Pop. Sin. 69: 451 (1990). Type: *G. chorisepalus* W. T. Wang.  
*Henckelia* Spreng., Anleit. 2: 405 (1817), Syst. Veg. 1: 38 (1824) & 4 (2); cur. post. 13 (1827).  
Type: *Henckelia incana* (Vahl) Spreng., Syst. Veg. 1: 38 (1824).  
= *Roettlera* Vahl, Enum. 1: 88 (1804) [*Roettlera*], nom. illegit. non Willd. (1797) nec Roxb. (1802).  
VAHL wrote *Röttlera*, which under ICBN becomes *Roettlera*, and referred to the collector as RÖTTLER; however, no other indication has been found that RÖTTLER spelt his name with an *umlaut*, and it has therefore been discarded as an orthographic error.  
= *Loxocarpus* R. Br., Cyrtandreae 120 (1839). Type: *L. incanus* R. Br. ≡ *Henckelia browniana* A. Weber  
= *Codonoboea* Ridl., Fl. Malay Penins. 2: 533 (1923). Lectotype: *C. leucocodon* Ridl.  
= *Platyadenia* B. L. Burt, Notes Roy. Bot. Gard. Edinburgh 31: 51 (1971). Type: *P. descendens* B. L. Burt  
*Hovanella* A. Weber & B. L. Burt, stat. & nom. nov.  
≡ *Didymocarpus* sect. *Hova* C. B. Clarke in A. & C. DC., Monogr. phan. 5 (1): 108 (1883).  
Type: *Hovanella madagascariensis* (C. B. Clarke) A. Weber & B. L. Burt

## Appendix II. Sectional names in *Henckelia*

Although the infrageneric classification of *Henckelia* requires careful study, the genus is so large (approximately 180 species) that it seems advisable to transfer the better established sections that have existed under *Didymocarpus*. This does not mean that every species can be placed in a section, but these sections, with their types as listed below, provide the focal points around which the final classification will have to be devised. Other available sectional names, for which the transfers to *Henckelia* are not made here, are listed with notes at the end. In both lists the order is chronological. Synonyms under the illegitimate generic name *Rottlera* Vahl are omitted.

1. *Henckelia* sect. *Henckelia* (autonym established here).

≡ *Didymocarpus* sect. *Orthoboea* Benth., in Benth. & Hook. f., Gen. Pl. 2: 1022 (1876).

Type: *Henckelia incana* (Vahl) Spreng.

2. *Henckelia* sect. *Heteroboea* (Benth.) A. Weber & B. L. Burt, comb. nov.

≡ *Didymocarpus* sect. *Heteroboea* Benth., in Benth. & Hook. f., Gen. Pl. 2: 1022 (1876).

Lectotype (BURTT 1954, sub *Didymocarpo*): *H. crinita* (Jack) Spreng.

3. *Henckelia* sect. *Loxocarpus* (R. Br.) A. Weber & B. L. Burt, comb. nov.

≡ *Loxocarpus* R. Br., Cyrtandreae 120 1839; *Didymocarpus* Wall. sect. *Loxocarpus* (R. Br.) Benth., in Benth. & Hook. f., Gen. Pl. 2: 1022 (1876).

Type: *Henckelia browniana* A. Weber ≡ *Loxocarpus incanus* R. Br., non *Henckelia incana* (Vahl) Spreng.

4. *Henckelia* sect. *Didymanthus* (C. B. Clarke) A. Weber & B. L. Burt, comb. nov.

≡ *Didymocarpus* Wall. sect. *Didymanthus* C. B. Clarke, in A. & C. DC. Monogr. phan. 5(1): 82 (1883).

Lectotype (chosen here): *H. serrata* (R. Br.) A. Weber & B. L. Burt

BURTT (1954) discussed the lectotypification of this section in which CLARKE originally included nine species of rather varying affinity. At that time no final decision was taken, but the choice was narrowed down to *D. serratus* R. Br., *D. rufipes* C. B. Clarke and *D. barbinervius* C. B. Clarke. The last two are known only from rather incomplete type specimens and their position in the genus is uncertain. *D. serratus* is the only original species whose choice as lectotype would enable the sectional

name to be retained for most of the species assigned to it by RIDLEY (1923), none of which were known to CLARKE.

5. *Henckelia* sect. *Glossadenia* A. Weber & B. L. Burt, sect. nov.

Inter sectiones adhuc descriptas foliis alternis et nectario unilaterali (cum apice trilobo vel integro) distincta. Praeterea floribus plerumque in inflorescentiis densis pedicellis sub fructu saepe incrassatis recognoscenda.

Type: *H. flavobrunnea* (Ridl.) A. Weber.

A revision of this section is in preparation. In addition to *H. flavobrunnea* it will include *H. beccarii*, *H. corniculata*, *H. falcata*, *H. inaequalis*, *H. koerperi*, *H. pyroliflora* and a number of species not yet described.

### Other available sectional names

These names, with the exception of *Didymocarpus* sect. *Kompsoboea*, all refer to groups that can be subsumed under sect. *Didymanthus* in the broadest sense.

1. *Didymocarpus* sect. *Kompsoboea* C. B. Clarke, in A. & C. DC., 5(1): 87, tab. 10 (1883).

Type: *D. kompsoboea* C. B. Clarke

*D. kompsoboea* belongs, in our view, to sect. *Heteroboea* of which the sectional name therefore becomes a synonym. The species is a rare one from central Borneo, known with certainty only from the type specimen. If it is rediscovered and found to have distinctive characters now overlooked the sectional name remains available for reinstatement.

2. *Didymocarpus* Wall. sect. *Salicini* Ridl., J. Linn. Soc. Bot. 32: 514 (1896).

Type: *D. salicinus* Ridl.

KIEW (1992) has suggested that this section be reduced to a narrow alliance of the type species, *D. densifolius* Ridl., *D. salicinoides* Kiew and *D. tiumanicus* (Ridl.) B. L. Burt. Such a group may be better ranked at a lower level than section. The section needs to be re-assessed before transfer to *Henckelia*.

3. *Didymocarpus* Wall. sect. *Reptantes* Ridl., J. Straits Branch Roy. As. Soc. 44: 29 (1905).

Type: *D. reptans* Jack

This group is probably not separable from sect. *Didymanthus* at sectional level.

4. *Paraboea* sect. *Campanulatae* Ridl., J. Straits Branch Roy. As. Soc. 44: 63 (1905).

Type: *Paraboea campanulata* Ridl.; this is possibly an abnormal plant of *Didymocarpus hirtus* (sect. *Didymanthus*) with short corolla.

As proposed the sectional name was illegitimate since it contained *P. salicinus*, the type of the earlier *Didymocarpus* sect. *Salicini* (see above).

5. *Didymocarpus* Wall. sect. *Boeopsis* Ridl., J. Straits Branch Roy. As. Soc. 49: 22 (1907).

Lectotype (KIEW 1992): *D. heterophyllus* Ridl.

Like sect. *Salicini*, this needs re-assessment before transfer to *Henckelia*.

6. *Didymocarpus* sect. *Pectinati* Ridl., Fl. Malay. Penins. 2: 508 (1923).

Type: *Didymocarpus pectinatus* Oliv.

7. *Didymocarpus* sect. *Codonoboea* (Ridl.) Kiew, Gard. Bull. Singapore 44: 41 (1992).

Lectotype (chosen for genus – IVANINA 1967): *C. leucocodon* Ridl.

R. KIEW chose *D. lilacinus* Ridl. as lectotype and formed her sect. *Codonoboea* round it, excluding *C. leucocodon* from the section. This has to be treated as a mistake and both generic and sectional names are tied to *C. leucocodon*, which is a rather isolated species in the genus. Sect. *Codonoboea* sensu KIEW (1992) can be included in a slightly enlarged concept of sect. *Heteroboea*.

8. *Didymocarpus* sect. *Venusti* Kiew, Malay. Nat. J. 48: 203 (1995) [*Venustus*].

Type: *D. venustus* Ridl.

Other species referred here by KIEW (1995) are *D. calcareus* Ridl., *D. castaneifolius* Ridl., *D. dawnii* Kiew and *D. tahanicus* B. L. Burt. *D. vulcanicus* Ridl. from Sumatra also belongs here, as does *D. vandaalenii* Steenis if distinct – the latter name has been much used in herbaria but is only in print as a *nomen nudum*. Sect. *Venusti* undoubtedly represents a group of allied species, but may be ranked too high at sectional level. This can only be decided when the whole genus is surveyed.

### Appendix III. List of specific names and new combinations

This is a list of names relevant to the revival of *Henckelia* and the establishment of *Hovanella* as an independent genus.

The names are arranged in a single alphabetical order of specific epithets, whether published under *Didymocarpus*, *Henckelia*, *Loxocarpus*, *Codonoboea* or *Platyadenia*. New combinations, or new names are supplied as appropriate.

All epithets that have been published under the last four of these genera are included in the list, but names correctly referred to *Didymocarpus* s.str. in the Sino-Himalayan-Vietnam-Thailand area have not been included nor have those from the same area that are referable to *Chirita* or other genera. For Thailand all species listed by BARNETT (1962) are true *Didymocarpus* except *D. crinitus*, *flavus*, *hispidus*, *platypus*, *pumilus* (a misidentification, the plant is identical or closely allied to *D. ascendens*), *reptans* and *venosus* – these all appear in the list.

Many epithets were transferred to *Rottlera* Vahl by O. KUNTZE (1891) and K. FRITSCH (1894). That generic name was illegitimate and none of these synonyms is cited.

Epithets below the rank of species have only been cited or transferred to *Henckelia* in a very few instances: most of them need more critical study and are not in constant use.

To accommodate our individual local specializations, transfers of Malay Peninsula names are attributed to A.W. alone, those for Borneo and nearby islands to B. L. B. The responsibility for the remainder is shared.

It is important to note that this list in no way represents a critical revision. The new combinations follow largely the traditional and current handling of the species. Current species concepts are generally rather narrow in the Malay Peninsula, which is the best collected area under consideration. This results in an exceedingly high number of more than one hundred species for this comparatively small area. The authors feel that many of these, though probably worthy of taxonomic recognition, do not merit specific rank. However, in many cases, the morphology, the variability and the distribution of the plants is still incompletely known and the time is not ripe for a thorough revision. Probably this aim can be reached only step-wise. KIEW (1987, 1992, 1995) has made some initial steps in this direction in keying out and/or revising some alliances (referring to them as sections of *Didymocarpus*, though a lower rank may be more appropriate). The present list, covering the whole distribution area of *Henckelia*, may serve as a basic inventory and starting point



for future work. Accordingly, only a few substantial changes (reductions) have been made. Comments are given under the respective species.

Typography of names, synonymy signs

- a) Italics, bold face: Current name  
 b) Italics, not bold: name validly published, but present position of species in another genus  
 c) Roman letters: illegitimate name  
 ≡ homotypic synonym  
 = heterotypic synonym (inclusion); the reference to the authority followed is given in parentheses

Notes on references

1. R. BROWN's memoir on Cyrtandreae (1839) was largely a preprint from J. J. BENNETT 'Plantae Javanicae Rariores' part 2 (1840). So far as *Didymocarpus* is concerned, the pagination is the same as in the book, which is therefore not cited separately (for details see MABBERLEY 1986).
2. RIDLEY's paper 'The Gesneriaceae of the Malay Peninsula' was published in J. Straits Branch Roy. Asiat. Soc. 44 (1905). Unfortunately the number printed at the foot of each right hand page is 43, and this has often been quoted. It is, however, an error. Pagination is continuous to the next paper, which is properly marked 44 and this number is correctly cited in Index Kewensis and in RIDLEY's own Flora of the Malay Peninsula.

*Henckelia alata* (Roxb.) A. Dietr., Sp. pl., ed. 6, 1: 573 (1831)  
 ≡ *Gratiola alata* Roxb., Fl. Ind. 1: 134 (1820)  
 ≡ *Torenia ? alata* (Roxb.) Benth., in. DC., Prodr. 10: 411 (1846)

*Loxocarpus alatus* DC. = *Henckelia browniana* (see there)

*Henckelia alba* (Ridl.) A. Weber, comb. nov.

≡ *Didymocarpus albus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 41 (1905)

*Didymocarpus albinus* Ridl. = *Henckelia hispida* (see there)

*Didymocarpus albinellus* Ridl. = *Henckelia hispida* (see there)

*Henckelia albomarginata* (Hemsl.) A. Weber, comb. nov.

≡ *Didymocarpus albomarginatus* Hemsl., J. Bot. 25: 204 (1887)

*Henckelia alternans* (Ridl.) A. Weber, comb. nov.

≡ *Didymocarpus alternans* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 41 (1905)

*Henckelia alternifolia* (C. B. Clarke) B. L. Burtt, comb. nov.

≡ *Didymocarpus alternifolius* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 106 (1883)

≡ *Paraboea alternifolia* (C. B. Clarke) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 46 (1962)

*Henckelia amoena* (C. B. Clarke) B. L. Burtt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996)

≡ *Didymocarpus amoenus* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 87 (1883)

*Henckelia angustifolia* (C. B. Clarke) B. L. Burtt, comb. nov.

≡ *Didymocarpus angustifolius* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 89 (1883)

*Loxocarpus angustifolius* Ridl. = *Henckelia stenophylla* (see there)

*Henckelia anthonyi* (Kiew) A. Weber, comb. nov.

≡ *Didymocarpus anthonyi* Kiew, Gard. Bull. Singapore 44: 24 (1992)

*Didymocarpus antirrhinoides* A. Weber, Blumea 28: 303 (1983)

*Didymocarpus areolatus* Stapf, Trans. Linn. Soc., ser. 2, Bot. 4: 213 (1894)

≡ *Cyrtandra areolata* (Stapf) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 30: 26 (1970)

*Henckelia argentea* (B. L. Burtt) B. L. Burtt, comb. nov.

≡ *Loxocarpus argenteus* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 47 (1971)

*Didymocarpus aristatus* (Blanco) F.-Vill., in Blanco, Fl. Filip., ed. 3, Noviss. App. 150 (1883)

≡ *Kyrtandra aristata* Blanco, Fl. Filip. 18 (1837)

= ? *Dopatrium junceum* (Roxb.) Buch.-Ham. (cf. Merrill 1918: 346)

*Henckelia aromatica* (D. Don) Spreng., Syst. veg. 4(2): 13 (1827)

≡ *Didymocarpus aromaticus* D. Don, Prodr. fl. nepal. 123 (1825)

*Henckelia ascendens* (Ridl.) A. Weber, comb. nov.

≡ *Didymocarpus ascendens* Ridl., J. Linn. Soc. 22: 512 (1896)

*Didymocarpus asperifolius* (Blume) Bakh. f., Blumea 6: 394 (1950)

≡ *Chirita asperifolia* (Blume) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 41 (1962)

- Henckelia atrosanguinea* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus atrosanguineus* Ridl., Trans. Linn. Soc., ser. 2, Bot. 3: 328 (1893)
- Didymocarpus azureus* B. L. Burtt = *Henckelia densifolia* (see there)
- Henckelia bakoensis* (B. L. Burtt) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus bakoensis* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 36: 152 (1978)
- Henckelia bakoensis* (B. L. Burtt) B. L. Burtt var. *tenuior* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus leptocalyx* C. B. Clarke var. *tenuior* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 91 (1883)
- Didymocarpus bancanus* Scheff., Natuurk. Tijdschr. Nederl. Ind. 7. ser. 2: 418 (1873), reimp. Obs. Bot. part 3: 96 (1873) – presumably *Henckelia* sp.: not seen by C. B. CLARKE or ourselves.
- Henckelia barbata* (Jack) Spreng., Syst. veg. 4 (2): 13 (1827)  
 ≡ *Didymocarpus barbatus* Jack, Trans. Linn. Soc. 14: 38 (1823)  
 = *Chirita asperifolia* (Blume) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 21 (1962)
- Didymocarpus barbinervius* C. B. Clarke in A. & C. DC., Monogr. phan. 5(1): 85 (1883) & Hook. f., Fl. Brit. Ind. 4: 350 (1884) – Position uncertain.
- Henckelia battamensis* (Ridl.) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus battamensis* Ridl., J. Straits Branch Roy. Asiat. Soc. 49: 22 (1908)
- Henckelia beccarii* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus beccarii* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 89 (1883)
- Henckelia bifolia* (D. Don) A. Dietr., Sp. pl., ed. 6, 1: 574 (1831)  
 ≡ *Chirita bifolia* D. Don, Prodr. fl. nepal. 90 (1825)
- Didymocarpus* ? *blancoi* Hassk., Flora 47: 155 (1864)  
 = *Lindernia antipoda* (L.) Alston, in Trimen, Fl. Ceylon 6: suppl. 214 (1931) (cf. MERRILL 1918: 349)
- Henckelia bombycina* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus bombycinus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 48 (1905)
- Henckelia breviflora* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didissandra breviflora* Ridl., Kew Bull. 1926: 474 (1926)  
 ≡ *Didymocarpus breviflorus* (Ridl.) A. Weber & Kiew, Gard. Bull. Singapore 41: 7 (1988)

- Didymocarpus brownii* Koord., Meded. 's Lands Plantent. 19: 551, 628 (1898); Suppl. Fl. N. O. Celebes: t. 121 (1922), ['*brownei*']  
 ≡ *Dichrotrichum brownii* (Koord.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 41 (1962)
- KOORDERS gave no information about the man to whom he dedicated this species; however, the next new species, on the same page, is *Didissandra clarkei*, which leaves little room for doubt that he was honouring Robert BROWN and C. B. CLARKE, two outstanding workers on Gesneriaceae. The epithet may therefore be corrected to *brownii*.
- Henckelia browniana* A. Weber, nom. nov.  
 ≡ *Loxocarpus incanus* R. Br., Cyrtandreae 120 (1839), non *Henckelia incana* (Vahl) Spreng.  
 ≡ *Loxocarpus alatus* DC., Prodr. 9: 277 (1845), nom. illegit.  
 ≡ *Didymocarpus incanus* (R. Br.) C. B. Clarke
- Henckelia bullata* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus bullatus* C. B. Clarke in A. & C. DC., Monogr. phan. 5 (1): 92 (1883)
- Henckelia caelestis* (Ridl.) A. Weber, comb. nov.  
 ≡ *Codonoboea caelestis* Ridl., Kew Bull. 1929: 259 (1929)  
 ≡ *Didymocarpus caelestis* (Ridl.) Kiew, Blumea 35: 174 (1990)
- Didymocarpus caeruleus* (R. Br.) Koord., Exkurs.-Fl. Java 3: 189 (1912)  
 ≡ *Chirita caerulea* R. Br., Cyrtandreae 117 (1839)
- Henckelia caerulea* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus caeruleus* Ridl., J. Linn. Soc. 32, 513 (1896)  
 ≡ *Loxocarpus caeruleus* (Ridl.) Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 62 (1905)
- Paraboea caerulea* Ridl. = *Henckelia densifolia* (see there)
- Henckelia calcarea* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus calcareus* Ridl., Kew Bull. 1929: 258 (1929)
- Paraboea campanulata* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 65 (1905)  
 ≡ *Didymocarpus campanulatus* (Ridl.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971)
- This is probably no more than an abnormal specimen of *Henckelia hirta* with a very short corolla.
- Henckelia castaneifolia* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus castaneifolius* Ridl., J. Straits Branch Roy. Asiat. Soc. 86: 302 (1922) ['*castanaefolius*'].

- Henckelia caulescens* (B. L. Burtt) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Loxocarpus caulescens* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 44 (1962)
- Henckelia cinerea* (D. Don) Spreng., Syst. veg. 4 (2): 14 (1827)  
 ≡ *Didymocarpus cinereus* D. Don, Prodr. fl. nepal. 122 (1825)
- Didymocarpus citrinus* Bidl., J. Linn. Soc. Bot. 32: 508 (1806)
- Henckelia codonion* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus codonion* Kiew, Gard. Bull. Singapore 42: 49 (1989)
- Henckelia conicapsularis* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus conicapsularis* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 100 (1883)  
 ≡ *Loxocarpus conicapsularis* (C. B. Clarke) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 45 (1962), quoad typus tantum.
- Didymocarpus consobrinus* Kraenzl., Mitt. Inst. Bot. Hamburg 7: 86 (1927)  
 = *Ridleyandra* sp. aff. *R. rufa* (C. B. Clarke) B. L. Burtt
- Henckelia coodei* B. L. Burtt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 437 (1996)
- Didymocarpus corchorifolius* A. DC., Prodr. 9: 265 (1845)
- Didymocarpus cordatus* A. DC., Prodr. 9: 265 (1845)  
 ≡ *Paraboea cordata* (A. DC.) Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 64 (1905)  
 = *Didymocarpus schlechterianus* Kraenzl., Notizbl. Bot. Gart. Berlin: 4: 293 (1907) – (RIDLEY 1923)
- Henckelia corneri* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus corneri* Kiew, Blumea 35: 172 (1990)
- Henckelia corniculata* (Jack) Spreng., Syst. veg., ed. 16, 4 (2): 13 (1827)  
 ≡ *Didymocarpus corniculatus* Jack, Malayan Misc. I (2): 4 (1820)
- Henckelia craspedodroma* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus craspedodromus* Kiew, Malayan Nat. J. 41: 213 (1987)
- Henckelia crenata* (Baker) B. L. Burtt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996)  
 ≡ *Didymocarpus crenatus* Baker, Kew. Bull. 1896: 25 (1896)  
 = *Didymocarpus multinervius* Merr., J. Malayan Branch Roy. Asiat. Soc. 1: 32 (1923) – (BURTT 1971)

- Henckelia crinita* (Jack) Spreng., Syst. veg., ed. 16, 4 (2): 13 (1827)  
 ≡ *Didymocarpus crinitus* Jack, Malayan Misc. I, 2: 1 (1820)  
 = *Cyrtandra verrucosissima* Kraenzl., Philipp. J. Sci. 8: 174 (1913), e descr. (BURTT 1978)
- Henckelia crocea* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus croceus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 44 (1905)
- Henckelia curtisii* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus crinitus* var. *curtisii* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 49 (1905)  
 ≡ *Didymocarpus curtisii* (Ridl.) Ridl., Fl. Malay Penins. 2: 520 (1923)
- Didymocarpus cyaneus* Ridl., J. Bot. 38: 68 (1900)  
 ≡ *Chirita cyanea* (Ridl.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 26: 267 (1965)
- Henckelia davisonii* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus davisonii* Kiew, Malayan Nat. J. 43: 242 (1990)
- Henckelia dawnii* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus dawnii* Kiew, Malayan Nat. J. 48: 201 (1995)
- Henckelia densifolia* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus densifolius* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 51 (1905)  
 ≡ *Paraboea densifolia* (Ridl.) M. R. Hend., Gard. Bull. Straits Settlements 5: 79 (1930)  
 = *Paraboea caerulea* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 66 (1905), non *Didymocarpus caeruleus* Ridl.  
 = *Didymocarpus azureus* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971) (KIEW 1987)
- Henckelia dentata* (Ridl.) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus dentatus* Ridl., J. Linn. Soc. 32: 515 (1896)
- Henckelia descendens* (B. L. Burtt) B. L. Burtt, comb. nov.  
 ≡ *Platydenia descendens* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 51 (1971)
- Didymocarpus detergibilis* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 107 (1883)  
 ≡ *Paraboea detergibilis* (C. B. Clarke) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 46 (1962)
- Henckelia diffusa* B. L. Burtt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 437 (1996)

- Henckelia doryphylla* (B. L. Burtt) A. Weber, comb. nov.  
 ≡ *Didymocarpus doryphyllus* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 23: 99 (1960)  
 ≡ *Didymocarpus lanceolatus* Ridl., J. Fed. Malay States Mus. 4: 50 (1909), non C. B. Clarke (1883)
- Henckelia elegans* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus elegans* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 88 (1883)
- Henckelia elongata* (Jack) Spreng., Syst. veg. 4 (2): 13 (1827)  
 ≡ *Didymocarpus elongatus* Jack, Trans. Linn. Soc. 14: 37 (1823)  
 ≡ *Didissandra elongata* (Jack) C. B. Clarke, in A. & C. DC., Monogr. phan. 5(1): 67 (1883) – (WEBER & BURTT 1998b)
- Henckelia ericiflora* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus ericiflorus* Ridl., J. Fed. Malay States Mus. 6: 166 (1915) [*ericaeflorus*].  
 ≡ *Codonoboea ericiflora* (Ridl.) Ridl., Fl. Malay Penins. 2: 533 (1923)
- Henckelia ericii* A. Weber, nom. nov.  
 ≡ *Loxocarpus holttumii* M. R. Hend., Gard. Bull. Straits Settlements, ser. 3, 4: 412 (1929), non *Henckelia holttumii* (M. R. Hend.) A. Weber (v. infra) based on *Paraboea holttumii* M. R. Hend. (1927)
- Henckelia falcata* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus falcatus* Kiew, Malayan Nat. J. 41: 218 (1987)
- Henckelia fasciata* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus fasciatus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 50 (1905) [*fasciatus*].
- Didymocarpus filicifolius* Ridl. = *Henckelia salicina* (see there)
- Henckelia fischeri* (Gamble) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus fischeri* Gamble, Kew Bull. 1923: 117 (1923)
- Henckelia flava* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus flavus* Ridl., J. Linn. Soc. 32: 507 (1896)
- Henckelia flavescens* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus flavescens* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 35 (1905)
- Henckelia flavobrunnea* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus flavobrunneus* Ridl., Trans. Linn. Soc., ser. 2, Bot. 3: 329 (1893)
- Henckelia floccosa* (Thwaites) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus floccosus* Thwaites, Enum. pl. Zeyl. 207 (1860)

- Henckelia floribunda* (M. R. Hend.) A. Weber, comb. nov.  
 ≡ *Paraboea floribunda* M. R. Hend., Gard. Bull. Singapore 7: 117 (1933)  
 ≡ *Didymocarpus floribundus* (M. R. Hend.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971)
- Henckelia follicularis* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus follicularis* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 98 (1883)  
 = [*Didymocarpus fascicularis* Clarke], in A. & C. DC., Monogr. phan. 5 (1): 295 (Index) (1883), error for *follicularis*.
- Didissandra frutescens* (Jack) C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 64 (1883) – (WEBER & BURTT 1998b)  
 ≡ *Didymocarpus frutescens* Jack, Malayan Misc. 1 (2): 5 (1920)  
 ≡ *Henckelia frutescens* (Jack) Spreng., Syst. veg. 4 (2): 13 (1827)
- Henckelia gambleana* (C. E. C. Fischer) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus gambleanus* C. E. C. Fischer, Kew Bull. 1938: 36 (1938)  
 ≡ *Didymocarpus rottlerianus* var. *lanuginosus* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 102 (1883)  
 ≡ *Didymocarpus tomentosus* var. *lanuginosus* (C. B. Clarke) C. B. Clarke, in Hook. f., Fl. Brit. India 4: 353 (1884)  
 ≡ *Didymocarpus lanuginosus* [Wight ex] Gamble, Fl. Pres. Madras, 989 (1924), non *D. lanuginosus* Wall. ex R. Br. (1839); non *D. lanuginosus* Wall. ex DC. (1845); non *D. lanuginosus* Wall. sensu Maxim. (1874)
- Henckelia gardneri* B. L. Burtt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 437 (1996)
- Henckelia geitleri* (A. Weber) A. Weber, comb. nov.  
 ≡ *Didymocarpus geitleri* A. Weber, Pl. Syst. Evol. 165: 95 (1989)
- Henckelia glabrata* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus glabratus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 38 (1905)
- Henckelia gracilipes* (C. B. Clarke) B. L. Burtt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996)  
 ≡ *Didymocarpus gracilipes* C. B. Clarke in A. & C. DC., Monogr. phan. 5 (1): 97 (1883)
- Henckelia grandiflora* (Retz.) A. Dietr., Sp. pl., ed. 6, 1: 573 (1831)  
 = *Lindernia antipoda* (L.) Alston, in Trimen, Fl. Ceylon 6: suppl. 214 (1931)
- Didymocarpus grandiflorus* Ridl. ≡ *Henckelia ridleyana* (see there)
- Didymocarpus grandifolius* Ridl. ≡ *Henckelia tahanica* (see there)

*Henckelia grandifolia* A. Dietr., Sp. pl., ed. 6, 1: 574 (1831)  
 ≡ *Didymocarpus grandifolius* (A. Dietr.) F. G. Dietr., Vollst. Lexik. Gaertn., Neue Nachtr. 2, 3: 387 (1834)  
 ≡ *Chirita macrophylla* Wall., Pl. Asiat. rar. 1: 56, t. 72 (1830), non *Henckelia macrophylla* (D. Don) Spreng.

*Henckelia heterophylla* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus heterophyllus* Ridl., Trans. Linn. Soc., ser. 2, Bot. 3: 329 (1893)

*Henckelia hirsuta* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus hirsutus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 48 (1905)

*Henckelia hirta* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus hirtus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 36 (1905)  
 = *Chirita uniflora* Ridl., J. Straits Branch Roy. Asiat. Soc. 61: 34 (1912)

*Henckelia hispida* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus hispidus* Ridl., J. Linn. Soc. 32: 507 (1896) [in error *D. hispidulus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 35 (1905)].  
 = *Didymocarpus albinus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 41 (1905), syn. nov.  
 = *Didymocarpus albinellus* Ridl., J. Fed. Malay States Mus. 4: 51 (1909), syn. nov.

These are probably not worth taxonomic recognition, at any rate not at specific level.

= *Staurogyne macrantha* C. B. Clarke, J. Asiat. Soc. Bengal 74: 642 (1908) - (BURTT 1978)

*Didymocarpus hispidulus* Ridl. ≡ *Henckelia hispida* (see there)

*Henckelia holttumii* (M. R. Hend.) A. Weber, comb. nov.  
 ≡ *Paraboea holttumii* M. R. Hend. Gard. Bull. Singapore 4: 54 (1927)  
 ≡ *Didymocarpus holttumii* (M. R. Hend.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971)

*Loxocarpus holttumii* M. R. Hend. ≡ *Henckelia ericii* (see there)

*Didymocarpus horsfieldii* (R. Br.) Koord., Exkurs.-Fl. Java 3: 190 (1912); Fl. Tjibodas, pt. 4: 116 (1918)  
 ≡ *Chirita horsfieldii* R. Br., Cyrtandreae 117 (1839)

*Henckelia humboldtiana* (Gardner) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus humboldtianus* Gardner, Calcutta J. Nat. Hist. 6: 477 (1846)  
 = *Didymocarpus primulifolius* Gardner, Calcutta J. Nat. Hist. 6: 478 (1846), nom. illegit., non *D. primulifolius* Don.

*Henckelia humilis* (Miq.) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Chirita humilis* Miq., Fl. Ind. Bat. 2: 729 (1858).  
 ≡ *Didymocarpus humilis* (Miq.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 43 (1962).

*Henckelia inaequalis* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus inaequalis* Ridl., J. Linn. Soc. 32: 506 (1896).

*Henckelia incana* (Vahl) Spreng., Syst. veg. 1: 38 (1824).  
 ≡ *Rottlera incana* Vahl, Enum. pl. 1: 88 (1804).  
 ≡ *Didymocarpus rottlerianus* Wall., Numer. List no. 778 (1829), nom. illegit.  
 = *Didymocarpus tomentosus* Wight, Icon. pl. Ind. orient. 4(2): 10, t. 1349 (1848).

*Loxocarpus incanus* R. Br. ≡  
*Didymocarpus incanus* (R. Br.) C. B. Clarke. ≡ *Henckelia browniana* (see there).

*Henckelia innominata* (B. L. Burtt) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus innominatus* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 21: 201 (1954).

*Didymocarpus johannis-winkleri* Kraenzl. = *Henckelia rufescens* (see there).

*Henckelia johorica* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didissandra johorica* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 22 (1905).

Recent collections by A. W. have shown that this species has only two fertile stamens and plagiocarpic fruits opening dorsally.

*Didymocarpus kinnearii* F. Muell., Victorian Naturalist 3: 159 (1887) & Bot. Centralbl. 30: 278 (1887).  
 ≡ *Boea kinnearii* (F. Muell.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 41: 418 (1984).

*Henckelia koerperi* (B. L. Burtt) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus koerperi* B. L. Burtt, Edinburgh J. Bot. 47: 236 (1990).

*Henckelia kompsoboea* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus kompsoboea* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 92, tab. 10 (1883).

*Didymocarpus labiatus* Ridl., Kew Bull. 1926: 76 (1926)  
 Generic position uncertain; possibly a diandrous species of *Didissandra*, but fruit not yet known.

- Didymocarpus lacunosus* Hook.f., Bot. Mag. t. 7236 (1892)  
 ≡ *Chirita lacunosa* (Hook.f.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 26: 267 (1965)
- Henckelia lanceolata* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus lanceolatus* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 89 (1883)
- Didymocarpus lanceolatus* Ridl. (1909), nom. illegit. ≡ *Henckelia doryphylla* (see there)
- Henckelia lancifolia* (M. R. Hend.) A. Weber, comb. nov.  
 ≡ *Didymocarpus lancifolius* M. R. Hend., Gard. Bull. Straits Settlement. 4: 52 (1927)
- Didymocarpus lanuginosus* [Wight ex] Gamble ≡ *Henckelia gambleana* (see there)
- Didymocarpus lawesii* F. Muell., S. Sci. Rec. 2: 229 (1882)  
 = *Boea lawesii* H. O. Forbes, J. Bot. 25: 348 (1887)
- Didymocarpus laxus* Ridl., J. Linn. Soc., Bot. 32: 510 (1896)  
 ≡ *Paraboea laxa* (Ridl.) Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 70 (1905), basionym not quoted, but the two names are homotypic
- Henckelia leiophylla* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus leiophyllus* Kiew, Gard. Bull. Singapore 44: 28 (1992)
- Henckelia leptocalyx* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus leptocalyx* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 91 (1883)
- D. leptocalyx* var. *tenuior* C. B. Clarke ≡ *Henckelia bakoensis* var. *tenuior* (see there)
- Henckelia leucantha* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus leucanthus* Kiew, Gard. Bull. Singapore 44: 31 (1992)
- Henckelia leucocodon* (Ridl.) A. Weber, comb. nov.  
 ≡ *Paraboea leucocodon* Ridl., J. Fed. Malay States Mus. 6: 167 (1915)  
 ≡ *Codonoboea leucocodon* (Ridl.) Ridl., Fl. Malay. Pen. 2: 533 (1923)  
 ≡ *Didymocarpus leucocodon* (Ridl.) Kiew, Gard. Bull. Singapore 42: 53 (1939)
- Henckelia lilacina* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus lilacinus* Ridl., Trans. Linn. Soc., ser. 2, Bot. 3: 330 (1893); Kiew, Gard. Bull. Singapore 42: 54 (1939)  
 ≡ *Codonoboea lilacina* (Ridl.) Ridl., Fl. Malay Penins. 2: 534 (1923)
- Didymocarpus lithophilus* Kiew = *Henckelia rugosa* (see there)

- Henckelia longipes* (C. B. Clarke) A. Weber, comb. nov.  
 ≡ *Didymocarpus longipes* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 86 (1883)
- Didymocarpus longipetiolatus* Gardner = *Henckelia zeylanica* (see there)
- Henckelia longipetiolata* (B. L. Burtt) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus longipetiolatus* Merr., Sarawak Mus. J. 3: 549 (1928), nom. illegit., non Gardner (1846)  
 ≡ *Loxocarpus longipetiolatus* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 22: 309 (1958)
- Henckelia lyrata* (Wight) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus lyratus* Wight, Icon. pl. Ind. orient. 42: 10, tab. 1350 (1848)
- Henckelia macrophylla* (D. Don) Spreng., Syst. veg. 4 (2): 14 (1827)  
 ≡ *Didymocarpus macrophyllus* D. Don, Prodr. fl. nepal. 122 (1825)
- Henckelia macrostachya* (E. Barnes) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus macrostachyus* E. Barnes, Kew Bull. 1938: 37 (1938)
- Hovanella madagascariensis* (C. B. Clarke) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus madagascariensis* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 108 (1883)  
 = *Didymocarpus pusillus* Baker, J. Linn. Soc. Bot. 22: 508 (1887)
- Didymocarpus 'madagascariensis'* C. B. Clarke: Humbert & al., Flore de Madagascar, 180e fam. 143 (1971), sphalm.  
 ≡ *Hovanella madagascariensis* (see there)
- Henckelia malayana* (Hook.f.) A. Weber, comb. nov.  
 ≡ *Didymocarpus malayanus* Hook.f., Gard. Chron. 20: 123 (1896) & Bot. Mag., t. 7526 (1897)  
 = *Didymocarpus winkleri* Ridl., J. Straits Branch Roy. Asiat. Soc. 50: 123 (1908), syn. nov.
- Henckelia marginata* (C. B. Clarke) A. Weber, comb. nov.  
 ≡ *Didymocarpus marginatus* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 96 (1883)  
 = *Didymocarpus ophirensis* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 43 (1905) - (RIDLEY 1923)
- Henckelia meeboldii* (W. W. Smith & Ramaswami) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus meeboldii* W. W. Smith & Ramaswami, Rec. Bot. Surv. India 6: 43 (1913)

- Henckelia meijeri* (B. L. Burt) A. Weber & B. L. Burt, comb. nov.  
 ≡ *Loxocarpus meijeri* B. L. Burt, Notes Roy. Bot. Gard. Edinburgh 24: 45 (1962)
- Didymocarpus membranaceus* Bedd. = *Henckelia missionis* (see there)
- Didymocarpus minahassae* (Teysm. & Binn.) H.O. Forbes, J. Linn. Soc., Bot. 19: 298 (1882)  
 ≡ *Paraboea minahassae* (Teysm. & Binn.) B. L. Burt, Kew Bull. 1948: 56 (1948)
- Henckelia miniata* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus miniatus* Kiew, Novon 5: 40 (1995)
- Henckelia minima* (Ridl.) A. Weber, comb. nov.  
 ≡ *Loxocarpus minimus* Ridl., J. Straits Branch Roy. Asiat. Soc. 86: 302 (1922)
- Didymocarpus minutus* Kraenzl., Mitt. Inst. Bot. Hamburg 7: 88 (1927)  
 ≡ *Paraboea minuta* (Kraenzl.) B. L. Burt, Notes Roy. Bot. Gard. Edinburgh 41: 433 (1984)
- Henckelia missionis* (R. Br.) A. Weber & B. L. Burt, comb. nov.  
 ≡ *Didymocarpus missionis* [Wall. ex] R. Br., Cyrtandreae 119 (1839)  
 = *Didymocarpus membranaceus* Bedd., Icon. pl. Ind. orient. 1: 39, t. 176 (1868 - 1874)
- Henckelia modesta* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus modestus* Ridl., J. Fed. Malay States Mus. 6: 53 (1915)
- Didymocarpus modestus* Ridl. (1920) - non. Ridl. (1915)  
 ≡ *Didymocarpus reptans* var. *modestus* Ridl. (1923)
- Didymocarpus multinervius* Merr. = *Henckelia crenata* (see there)
- Henckelia murutorum* (B. L. Burt) B. L. Burt, comb. nov.  
 ≡ *Didymocarpus murutorum* B. L. Burt, Notes Roy. Bot. Gard. Edinburgh 36: 153 (1978)
- Henckelia myricifolia* (Ridl.) B. L. Burt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996)  
 ≡ *Didymocarpus myricifolius* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 53 (1905)
- Henckelia nana* A. Weber, nom. nov.  
 ≡ *Didymocarpus pumilus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 56 (1905), non *Henckelia pumila* (D. Don) A. Dietr.
- Henckelia nervosa* (C. B. Clarke) B. L. Burt, comb. nov.  
 ≡ *Didymocarpus nervosus* C. B. Clarke, Monogr. phan. 5 (1): 95 (1883)

- Henckelia nitida* (Kiew & A. Weber) A. Weber, comb. nov.  
 ≡ *Didymocarpus nitidus* Kiew & A. Weber, Gard. Bull. Singapore 41: 4 (1988)
- Henckelia nivea* (Kiew) A. Weber, comb. nov.  
 ≡ *Codonoboea nivea* Kiew, Malayan Nat. J. 41: 210 (1987)  
 ≡ *Didymocarpus niveus* (Kiew) Kiew, Blumea 35: 174 (1990)
- Henckelia oblonga* (D. Don) Spreng., Syst. veg. 4 (2): 13 (1827)  
 ≡ *Didymocarpus oblongus* D. Don, Prodr. Fl. Nep. 123 (1825)
- Didymocarpus ophirensis* Ridl. = *Henckelia marginata* (see there)
- Henckelia oppositifolia* (Retz.) A. Dietr., Sp. pl., ed. 6, 1: 573 (1831)  
 ≡ *Lindernia oppositifolia* (Retz.) Mukerjee, J. Ind. Bot. Soc. 24: 134 (1945)
- Henckelia ovalifolia* (Wight) A. Weber & B. L. Burt, comb. nov.  
 ≡ *Didymocarpus ovalifolius* Wight, Icon. pl. Ind. orient. 42: 10, t. 1351 (1848)
- Henckelia pagonensis* B. L. Burt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 437 (1996)
- Didymocarpus pallidus* Kraenzl., Philipp. J. Sci. 8 (1913), Bot. 167.  
 ≡ *Cyrtandra copelandii* Merr., Enum. Philipp. Fl. Pl. 3: 458 (1923), nom. illegit., non Elmer (1915), nec *Cyrtandra pallida* Elmer (1908)  
 If this proves to be a good species it will require a new epithet in *Cyrtandra*.
- Henckelia papillosa* (M. R. Hend.) A. Weber, comb. nov.  
 ≡ *Loxocarpus papillosus* M. R. Hend., Gard. Bull. Straits Settlements 4: 53 (March 1927)
- Didymocarpus papillosus* Kraenzl., Mitt. Inst. Bot. Hamburg 7: 86 (15 July 1927)  
 ≡ *Ridleyandra rufa* (C. B. Clarke) A. Weber & B. L. Burt - (WEBER & BURTT, 1998c)
- Didymocarpus paraboea* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 106 (1883)  
 ≡ *Paraboea clarkei* B. L. Burt, Kew Bull. 1948: 56 (1948)
- Didymocarpus paraboeoides* Kraenzl., Mitt. Inst. Bot. Hamburg 7: 90 (1927)  
 ≡ *Paraboea paraboeoides* (Kraenzl.) B. L. Burt, Notes Roy. Bot. Gard. Edinburgh 41: 401 (1984)

- Henckelia parviflora* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus parviflorus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 33 (1905)
- Henckelia pectinata* (Oliv.) A. Weber, comb. nov.  
 ≡ *Didymocarpus pectinatus* [C. B. Clarke ex] Oliv., in Hook., Icon. pl. 23: t. 2246 (1892)
- Didymocarpus perakensis* Kraenzl., Notizbl. Bot. Gart. Berlin 4: 294 (1907), doubtful species.
- Didymocarpus perditus* Ridl. = *Henckelia puncticulata* (see there)
- Henckelia petiolaris* (C. B. Clarke) B. L. Burttt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996)  
 ≡ *Didymocarpus petiolaris* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 100 (1883)  
 ≡ *Loxocarpus petiolaris* (C. B. Clarke) B. L. Burttt, Notes Roy. Bot. Gard. Edinburgh 22: 309 (1958)
- Henckelia platypus* (C. B. Clarke) A. Weber, comb. nov.  
 ≡ *Didymocarpus platypus* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 94 (1883)
- Henckelia pleuropogon* (B. L. Burttt) B. L. Burttt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996)  
 ≡ *Didymocarpus pleuropogon* B. L. Burttt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971)
- Henckelia plicata* (D. Don) Spreng., Syst. veg. 4 (2): 14 (1827)  
 ≡ *Didymocarpus plicatus* D. Don, Prodr. fl. nepal. 122 (1825)  
 = *Didymocarpus macrophyllus* D. Don, Prodr. fl. nepal. 122 (1825)
- Henckelia polyanthoides* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus polyanthoides* Kiew, Gard. Bull. Singapore 42: 56 (1989)
- Henckelia primulifolia* (D. Don) Spreng., Syst. veg. 4 (2): 14 (1827)  
 ≡ *Didymocarpus primulifolius* D. Don, Prodr. fl. nepal. 123 (1825)
- Didymocarpus primulifolius* Gardner = *Henckelia humboldtiana* (see there)
- Henckelia primulina* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus primulinus* Ridl., J. Fed. Malay States Mus. 10: 250 (1922)

- Didymocarpus primuloides* Kraenzl., Mitt. Inst. Bot. Hamburg 7: 90 (1927), nom. illegit., non (Miq.) Maxim.  
 = *Paraboea* sp. aff. *P. schefferi* (Forbes) B. L. Burttt.
- Henckelia procumbens* B. L. Burttt, nom. nov.  
 ≡ *Loxocarpus repens* B. L. Burttt, Bot. J. Linn. Soc. 85: 24 (1982) – non *Henckelia repens* (Bedd.) A. Weber & B. L. Burttt (v. infra)
- Didymocarpus* ? *productus* C. B. Clarke = *Henckelia reptans* var. *monticola* (see there)
- Didymocarpus pubiflorus* (Ridl.) B. L. Burttt = *Henckelia venusta* (see there)
- Henckelia pulchella* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus pulchellus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 44 (1905)
- Henckelia pumila* (D. Don) A. Dietr., Sp. pl., ed 6, 1: 574 (1831)  
 ≡ *Chirita pumila* D. Don, Prodr. fl. nepal. 90 (1825)
- Didymocarpus pumilus* Ridl. ≡ *Henckelia nana* (see there)
- Henckelia punctata* (C. B. Clarke) B. L. Burttt, comb. nov.  
 ≡ *Didymocarpus punctatus* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 90 (1883)
- Henckelia puncticulata* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus puncticulatus* Ridl., J. Linn. Soc. 32: 510 (1896)  
 = *Didymocarpus perditus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 54 (1905) – (KIEW 1987)
- Didymocarpus purpureus* Ridl., J. Linn. Soc. Bot. 32: 508 (1896)
- Didymocarpus pusillus* Baker = *Hovanella madagascariensis* (see there)
- Henckelia pyroliflora* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus pyroliflorus* Ridl., Trans. Linn. Soc., ser. 2, Bot. 3: 330 (1893)  
 ≡ *Paraboea pyroliflora* (Ridl.) Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 67 (1905)
- Henckelia quinquevulnera* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus quinquevulnerus* Ridl., Trans. Linn. Soc., ser. 2, Bot. 3: 328 (1893)
- Henckelia racemosa* (Jack) Spreng., Syst. veg., ed. 16, 4 (2): 13 (1827)  
 ≡ *Didymocarpus racemosus* Jack, Trans. Linn. Soc. 14: 34 (1823)
- Henckelia ramosa* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus ramosus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 34 (1905)



- Didymocarpus regularis* Ridl., J. Linn. Soc. Bot. 32: 515 (1896)  
 ≡ *Paraboea regularis* (Ridl.) Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 68 (1905)
- Loxocarpus repens* B. L. Burt ≡ *Henckelia procumbens* (see there)
- Henckelia repens* (Bedd.) A. Weber & B. L. Burt, comb. nov.  
 ≡ *Didymocarpus repens* Bedd., Icon. pl. Ind. orient. 1: 24, t. 120 (1868 - 1874)
- Henckelia reptans* (Jack) Spreng., Syst. veg., ed. 16, 4 (2): 14 (1827)  
 ≡ *Didymocarpus reptans* Jack, Malayan Misc. 1, 5: 3 (1820)  
 = *Didymocarpus modestus* Ridl., J. Straits Branch Roy. Asiat. Soc. 82: 186 (1920), non *D. modestus* Ridl. (1915)
- var. *monticola* (Ridl.) A. Weber, comb. nov.,  
 ≡ *Didymocarpus reptans* Jack var. *monticola* Ridl., J. Linn. Soc. 32: 511 (1896)  
 = *Didymocarpus productus*, C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 96 (1883) - (RIDLEY 1905, RIDLEY in KING & GAMBLE 1909 with doubt)
- Henckelia reticulosa* (C. B. Clarke) A. Weber, comb. nov.  
 ≡ *Didymocarpus reticulosus* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 90 (1883)
- Henckelia ridleyana* A. Weber, nom. nov.  
 ≡ *Didymocarpus grandiflorus* Ridl., J. Fed. Malay States Mus. 6: 167 (1915), non *Henckelia grandiflora* (Retz.) A. Dietr. (1831)  
 ≡ *Didymocarpus ridleyanus* B. L. Burt, Notes Roy. Bot. Gard. Edinburgh 23: 99 (1960), nom. illegit.
- Henckelia robinsonii* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus robinsonii* Ridl., J. Linn. Soc., Bot. 38: 318 (1908)
- Didymocarpus robustus* Ridl., J. Fed. Malay States Mus. 6: 52 (1916)
- Didymocarpus rottlerianus* Wall. ≡ *Henckelia incana* (see there)
- Didymocarpus rottlerianus* var. *wightii* C. B. Clarke ≡ *Henckelia wightii* (see there)
- Didymocarpus rottlerianus* var. *tomentosus* (Wight) C. B. Clarke = *Henckelia incana* (see there)
- Didymocarpus rottlerianus* var. *lanuginosus* C. B. Clarke ≡ *Henckelia gambleana* (see there)

- Henckelia roxburghiana* A. Dietr., Sp. pl., ed. 6, 1: 572 (1831)  
 ≡ *Gratiola reptans* Roxb., Fl. Ind. 1: 140 (1832), non *Henckelia reptans* (Jack) Spreng.  
 = *Lindernia ruellioides* (Colsm.) Pennell, Brittonia 2: 182 (1936)
- Henckelia rubiginosa* (Ridl.) A. Weber, comb. nov.  
 ≡ *Paraboea rubiginosa* Ridl., J. Linn. Soc. 38: 319 (1908)  
 ≡ *Didymocarpus rubiginosus* (Ridl.) B. L. Burt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971)
- Henckelia rufescens* (C. B. Clarke) B. L. Burt, comb. nov.  
 ≡ *Didymocarpus rufescens* C. B. Clarke, in A. & C. DC. Monogr. phan. 5 (1): 99 (1883)  
 ≡ *Loxocarpus rufescens* (C. B. Clarke) B. L. Burt, Notes Roy. Bot. Gard. Edinburgh 22: 309 (1958)  
 = *Didymocarpus johannis-winkleri* Kraenzl., Mitt. Inst. Bot. Hamburg 7: 89 (1927)
- Didymocarpus rufipes* C. B. Clarke, in A. & C. DC., Monogr. phan. 5(1): 84 (1883) & Fl. Brit. Ind. 4: 351 (1884)  
 Position uncertain.
- Henckelia rugosa* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus rugosus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 45 (1905)  
 = *Didymocarpus lithophilus* Kiew [in Gard. Bull. Singapore 42: 54 (1989), nomen], Gard. Bull. Singapore 44: 38 (1992). So far there is no convincing evidence that this is distinct from *D. rugosus*.
- Henckelia salicina* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus salicinus* Ridl., Trans. Linn. Soc. ser 2, Bot., 3: 329 (1893)  
 ≡ *Paraboea salicina* (Ridl.) Ridl., Fl. Malay Penins. 2: 530 (1923)  
 = *Didymocarpus filicifolius* Ridl., J. Fed. Malay States Mus. 6: 116 (1916) - (KIEW 1989)  
 ≡ *Paraboea filicifolia* (Ridl.) Ridl., Fl. Malay Penins. 2: 530 (1923)
- Henckelia salicinoides* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus salicinoides* Kiew, Gard. Bull. Singapore 44: 35 (1992)  
 ≡ *Paraboea salicina* (Ridl.) Ridl. var. *major* Ridl., Fl. Malay Penins. 5: 325 (1925)
- Henckelia scabrinervia* (C. B. Clarke) B. L. Burt, comb. nov.  
 ≡ *Didymocarpus scabrinervius* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 41 (1883)

- Didymocarpus schefferi* H. O. Forbes, J. Linn. Soc. Bot. 19: 298 (1892)  
 ≡ *Paraboea schefferi* (H. O. Forbes) B. L. Burtt, Kew Bull. 1948: 56 (1948)
- Didymocarpus schlechterianus* Kraenzl. = *Didymocarpus cordatus* (see there)
- Henckelia scortechinii* (Ridl.) A. Weber, comb. nov.  
 ≡ *Paraboea scortechinii* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 65 (1905)  
 ≡ *Didymocarpus scortechinii* (Ridl.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971)
- Henckelia semitorta* (C. B. Clarke) A. Weber, comb. nov.  
 ≡ *Didymocarpus semitortus* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 99 (1883)  
 ≡ *Loxocarpus semitortus* (C. B. Clarke) Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 61 (1905)
- Henckelia sericea* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus sericeus* Ridl., J. Linn. Soc. 32: 513 (1896)  
 ≡ *Loxocarpus sericeus* (Ridl.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 49 (1971)
- Henckelia serrata* (R. Br.) A. Weber & B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus serratus* R. Br., Cyrtandreae 119 (1839)
- Didymocarpus serratus* Ridl. ≡ *Henckelia serratifolia* (see there)
- Henckelia serratifolia* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus serratifolius* Ridl., J. Asiat. Soc. Bengal 74: 761 (1909)  
 ≡ *Didymocarpus serratus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 52 (1905), non R. Br. (1839)
- Henckelia simplex* (Kraenzl.) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus simplex* Kraenzl., Mitt. Inst. Allg. Bot. Hamburg 7: 88 (1927)
- Henckelia soldanella* (Ridl.) A. Weber, comb. nov.  
 ≡ *Didymocarpus soldanella* Ridl., J. Straits Branch Roy. Asiat. Soc. 61: 33 (1912)
- Henckelia stapfii* (Kraenzl.) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus stapfii* Kraenzl., Mitt. Inst. Allg. Bot. Hamburg 7: 89 (1927)  
 ≡ *Loxocarpus stapfii* (Kraenzl.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 24: 46 (1962)

- Henckelia stenophylla* A. Weber, nom. nov.  
 ≡ *Loxocarpus angustifolius* Ridl., J. Linn. Soc. Bot. 38: 319 (1908), non *Henckelia angustifolia* (C. B. Clarke) B. L. Burtt.
- Henckelia stolonifera* (Kiew) A. Weber, comb. nov.  
 ≡ *Didymocarpus stoloniferus* Kiew, Gard. Bull. Singapore 44: 36 (1992)
- Didymocarpus sulphureus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 32 (1905)
- Henckelia taeniophylla* B. L. Burtt, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996)
- Henckelia tahanica* (B. L. Burtt) A. Weber, comb. nov.  
 ≡ *Didymocarpus tahanicus* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 46 (1971)  
 ≡ *Didymocarpus grandifolius* Ridl., J. Linn. Soc. Bot. 38: 318 (1908), nom. illeg., non (A. Dietr.) F. Dietr. (1834), nec *Henckelia grandifolia* A. Dietr.  
 ≡ *Paraboea grandifolia* Ridl., Fl. Malay Penins. 2: 531 (1923)
- Henckelia teres* (C. B. Clarke) B. L. Burtt, comb. nov.  
 ≡ *Didymocarpus teres* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 88 (1883)
- Didymocarpus ternatus* Miq., Fl. Ind. Bat., suppl. 564 (1861)  
 ≡ *Didissandra ternata* (Miq.) A. Weber & B. L. Burtt - (WEBER & BURTT 1998b)
- Henckelia tiumanica* (Ridl.) A. Weber, comb. nov.  
 ≡ *Paraboea tiumanica* [Burkill ex] Ridl., Fl. Malay Penins. 2: 530 (1923)  
 ≡ *Didymocarpus tiumanicus* (Ridl.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971)
- Didymocarpus tomentosus* Wight = *Henckelia incana* (see there)
- Didymocarpus tomentosus* var. *lanuginosus* C. B. Clarke = *Henckelia gambleana* (see there)
- Didymocarpus triflorus* (C. B. Clarke) B. L. Burtt  
 ≡ *Didissandra triflora* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 69 (1883) - (WEBER & BURTT 1998b)
- Henckelia tunkui* (Kiew) A. Weber, comb. nov.  
 ≡ *Loxocarpus tunkui* Kiew, Malayan Nat. J. 41: 221 (1987)
- Chirita uniflora* Ridl. = *Henckelia hirta* (see there)
- Didymocarpus urticifolius* Ridl. ≡ *Henckelia urticoides* (see there)
- Henckelia urticifolia* (D. Don) A. Dietr., Sp. pl., ed. 6, 1: 573 (1831)  
 ≡ *Chirita urticifolia* D. Don, Prodr. fl. nepal. 90 (1825)

***Henckelia urticoides* A. Weber, nom. nov.**

≡ *Didymocarpus urticifolius* Ridl., Fl. Malay Penins. 2: 511 (1923), nom. illegit., non (D. Don) Wonsich, nec *Henckelia urticifolia* (D. Don) A. Dietr.

*Didymocarpus vandaalenii* [Valeton] van Steenis, Tijdschr. K. Nederl. Aardrijksk. Genootsch. 55 (Expl. Gajo-Land., algem. result. Losir-Exped. 1937): 771 (1938) – nomen nudum. Possibly the same as *H. vulcanica*: to be clarified before the name is validated.

*Didymocarpus venosus* Barnett, Nat. Hist. Bull. Siam Soc. 20: 13 (March 1961) & Kew Bull. 16: 251 (Oct. 1961). Genus uncertain (see p. 309 above).

***Henckelia venusta* (Ridl.) A. Weber, comb. nov.**

≡ *Didymocarpus venustus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 51 (1905)

= *Paraboea pubiflora* Ridl., J. Fed. Malay States Mus. 4: 51 (1909) – (KIEW 1995).

≡ *Didymocarpus pubiflorus* (Ridl.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 31: 44 (1971)

***Henckelia verbeniflos* (C. B. Clarke) B. L. Burtt, comb. nov.**

≡ *Didymocarpus verbeniflos* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 99 (1883) [*verbenaeiflos*']

≡ *Loxocarpus verbeniflos* (C. B. Clarke) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 22: 309 (1958)

***Hovanella vestita* (Baker) A. Weber & B. L. Burtt, comb. nov.**

≡ *Didymocarpus vestitus* Baker, J. Linn. Soc. Bot. 21: 427 (1885)

*Henckelia villosa* (D. Don) Spreng., Syst. veg., ed. 6, 4 (2): 13 (1827)

≡ *Didymocarpus villosus* D. Don, Prodr. fl. nepal. 123 (1825)

*Didymocarpus violaceus* Ridl., J. Linn. Soc. Bot. 32: 509 (1896)

*Didymocarpus violascens* Ridl., Kew Bull. 1925: 87 (1925)

≡ *Didissandra elongata* (Jack) C. B. Clarke – (BURTT 1971)

***Henckelia violoides* (C. B. Clarke) B. L. Burtt**, in Kirkup, D. W. & al.: Checklist of the flowering plants and gymnosperms of Brunei Darussalam: 438 (1996)

≡ *Didymocarpus violoides* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 97 (1883)

***Henckelia virginea* (B. L. Burtt) B. L. Burtt, comb. nov.**

≡ *Didymocarpus virgineus* B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 36: 154 (1978)

***Henckelia viscida* (Ridl.) A. Weber, comb. nov.**

≡ *Didymocarpus viscidus* Ridl., J. Straits Branch Roy. Asiat. Soc. 44: 36 (1905)

***Henckelia vulcanica* (Ridl.) A. Weber & B. L. Burtt, comb. nov.**

≡ *Didymocarpus vulcanicus* Ridl., J. Malayan Branch Roy. Asiat. Soc. 1: 80 (1923)

*Didymocarpus vulpinus* Kraenzl., Mitt. Inst. Bot. Hamburg 7: 87 (1927)

≡ *Cyrtandra vulpina* (Kraenzl.) B. L. Burtt, Notes Roy. Bot. Gard. Edinburgh 36: 178 (1978)

*Henckelia wallichiana* A. Dietr., Sp. pl., ed. 6, 1: 574 (1831)

≡ *Chirita grandiflora* Wall., Pl. Asiat. Rar. 1: 43, t. 50 (1830)

= *Chirita urticifolia* D. Don, Prodr. fl. nepal. 90 (1825)

***Henckelia wightii* (C. B. Clarke) A. Weber & B. L. Burtt, comb. nov.**

≡ *Didymocarpus rotlerianus* var. *wightii* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 101 (1883)

≡ *Didymocarpus wightii* (C. B. Clarke) Gamble, Fl. Madras: 989 (1924)

*Didymocarpus winkleri* Ridl. = *Henckelia malayana* (see there)

***Henckelia woodii* (Merr.) A. Weber & B. L. Burtt, comb. nov.**

≡ *Didymocarpus woodii* Merr., Philipp. J. Sci. 26: 489 (1925)

***Henckelia yongii* (Kiew) A. Weber, comb. nov.**

≡ *Didymocarpus yongii* Kiew, Gard. Bull. Singapore 42: 62 (1989)

***Henckelia zeylanica* (R. Br.) A. Weber & B. L. Burtt, comb. nov.**

≡ *Didymocarpus zeylanicus* R. Br., Cyrtandreae 119 (1839)

= *Didymocarpus longipetiolatus* Gardner, Calcutta J. Nat. Hist. 6: 475 (1846)

*Didymocarpus zollingeri* (C. B. Clarke) Koord., Exkurs.-Fl. Java 3: 190 (1912)

≡ *Chirita zollingeri* C. B. Clarke, in A. & C. DC., Monogr. phan. 5 (1): 127 (1883)

= *Chirita caerulea* R. Br., Cyrtandreae 114 (1839), non *Didymocarpus caeruleus* Ridl. (1896)

## References

- ADITYACHAUDHURY, N., A. K. DAS, A. CHOUDHURY, P. L. DASKANUNGO: Aurantiacin, a new chalcone from *Didymocarpus aurantiaca*. - *Phytochemistry* 15: 229 - 230 (1976).
- BACKER, C. A. & R. C. BAKHUIZEN VAN DEN BRINK: Flora of Java, 2. - Groningen (1965).
- BAILLON, H. E.: Histoire des Plantes 10 (1). (Monographie des Bignoniacees et Gesneriacees). - Paris (1888).
- BAKER, J. G.: Further contributions to the Flora of Madagascar - second and final part. - *J. Linn. Soc. Bot.* 21: 407 - 455 (1885).
- Further contributions to the Flora of Madagascar. - *J. Linn. Soc. Bot.* 22: 441 - 537 (1887).
- BARNETT, E. C.: Gesneriaceae. In: *Florae Siamensis Enumeratio* 3 (3): 211 - 219. - Bangkok: Siam Society (1962).
- BEAUFORT-MURPHY, H. T.: The seed-surface morphology of the Gesneriaceae, utilizing the scanning electric microscope and a new system for diagnosing seed morphology. - *Selbyana* 6: 220 - 422 (1983).
- BEDDOME, R. H.: *Icones plantarum Indiae orientalis*. - Madras, London (1868 - 74).
- BENTHAM, G.: Gesneriaceae. In BENTHAM, G., HOOKER, J. D., *Genera plantarum* 2(2): 990 - 1025. - London (1876).
- BROWN, R.: On *Cyrtandrea*. [Part reprint from J. J. BENNETT, *Plantae Javanicae Rariores*, part 1, mostly preprint from part 2: 105 - 122. See MABBERLEY 1986]. - London (1839).
- BURT, B. L.: Studies in the Gesneriaceae of the Old World II: Types and lectotypes of certain genera, subgenera and sections. - *Notes Roy. Bot. Gard. Edinburgh* 21: 193 - 208 (1954).
- Id. XIII. Miscellaneous transfers and reductions. - *Notes Roy. Bot. Gard. Edinburgh* 22: 305 - 314 (1958).
- Id. XXIV. Tentative keys to tribes and genera. - *Notes Roy. Bot. Gard. Edinburgh* 24: 205 - 220 (1962).
- The transfer of *Cyrtandromoea* from Gesneriaceae to Scrophulariaceae, with notes on the classification of that family. - *Bull. Bot. Surv. India* 7: 73 - 88 (1965).
- Studies in the Gesneriaceae of the Old World XXXIV: A miscellany from South Eastern Asia. - *Notes Roy. Bot. Gard. Edinburgh* 31: 35 - 52 (1971).
- Id. XXXVII. *Schizoboea*, the erstwhile African *Didymocarpus*. - *Notes Roy. Bot. Gard. Edinburgh* 33: 265 - 267 (1974).
- Id. XLIII. Notes on Malesian *Didymocarpus*. - *Notes Roy. Bot. Gard. Edinburgh* 36: 151 - 155 (1978).
- Id. XLIV. New and little known species of *Cyrtandra*, chiefly from Sarawak. - *Notes Roy. Bot. Gard. Edinburgh* 36: 157 - 179 (1978).
- Id. XLVII. Revised generic concepts for *Boea* and its allies. - *Notes Roy. Bot. Gard. Edinburgh* 41: 401 - 452 (1984).

- Taxonomic history of *Didymocarpus* and *Henckelia* (Gesneriaceae). - *Beitr. Biol. Pflanzen* 70: 365 - 375 (1998).
- CLARKE, C. B.: *Commelynaceae et Cyrtandraceae Bengalenses*. - Calcutta (1874).
- *Cyrtandreae*, A. & C. DE CANDOLLE (eds.). - *Monographiae Phanerogamarum* 5 (1). - Paris (1883).
- DE CANDOLLE, A.: Gesneriaceae, in *Prodromus regni vegetabilis*. IX. - Paris (1845).
- DON, D.: *Prodromus florae nepalensis*. - London (1825).
- FRITSCH, K.: Gesneriaceae. In ENGLER, A., PRANTL, K., *Die natürlichen Pflanzenfamilien* 4/3B: 133 - 144 (1893 - 1894).
- HACCIUS, B.: Untersuchungen über die Bedeutung der Distichie für das Verständnis der zerstreuten Blattstellung bei den Dikotylen. - *Bot. Archiv* 40: 58 - 150 (1939).
- Weitere Untersuchungen zum Verständnis der zerstreuten Blattstellung bei den Dikotylen. - *Sitzber. Heidelberg. Akad. Wiss., math.-naturwiss. Kl., Heidelberg* 6: 1 - 51 & 289 - 337 (1950).
- HAMILTON: Notice on the progress of botanical science in Bengal, being the substance of a letter from N. Wallich. - *Edinburgh Philosoph. J.* 1: 376 - 381 (1819).
- HILLIARD, O. M., B. L. BURT: Old World Gesneriaceae, IV: Notes on *Didymocarpus* and *Lysionotus*. - *Edinburgh J. Bot.* 52: 215 - 224 (1995).
- HUMBERT, H., B. L. BURT, M. KERAUDREN-AYMONIN: 180e famille, Gesneriacees. In LEROY, J. F. (ed.), *Flore de Madagascar et des Comores*. - Paris (1971).
- IVANINA, L.: Gesneriaceae: the carpological review. [In Russian]. - Leningrad (1967).
- JACK, W.: Descriptions of Malayan plants 2. *Malayan Miscellanies* 1 (5). Bencoolen (1820). [Reimp. in *Bot. Miscellany* (ed. HOOKER) 2: 60 (1830)].
- On *Cyrtandraceae*, a new Natural Order of plants. - *Trans. Linn. Soc.* 14 (1): 23 - 44 (1823).
- KIEHN, M., E. HELLMAYR, A. WEBER: Chromosome numbers of Malayan and other paleotropical Gesneriaceae. I. Tribe *Didymocarpeae*. - *Beitr. Biol. Pflanzen* 70: 407 - 444 (1998).
- KIEW, R.: The herbaceous flora of Ulu Endau, Johore-Pahang, Malaysia, including taxonomic notes and descriptions of new species. - *Malayan Nat. J.* 41: 201 - 234 (1987).
- *Didymocarpus* (Gesneriaceae) on Gunung Tahan, Malaysia. - *Gard. Bull. Singapore* 42: 47 - 64 (1989).
- Reassessment of the generic status of *Codonoboea* (Gesneriaceae) and its species. - *Blumea* 35: 167 - 176 (1990).
- Five new species of *Didymocarpus* (Gesneriaceae) from Peninsular Malaysia. - *Gard. Bull. Singapore* 44: 23 - 42 (1992).
- A new species and section of *Didymocarpus* (Gesneriaceae) from Belum and Temengor, Hulu Perak, Peninsular Malaysia. - *Malayan Nat. J.* 48: 201 - 207 (1995).

- KUNTZE, O.: Revisio generum plantarum, vol. 2. - Paris (1891).
- MABBERLEY, D.: Jupiter Botanicus: ROBERT BROWN of the British Museum. - Braunschweig (1986).
- MERRILL, E. D.: Species Blancoanae. A critical revision of the Philippine species of plants described by Blanco and by Llanos. - Bur. Sci. Publ. 12: 1 - 423 (1918).
- PRAIN, D.: A second century of new and rare Indian plants. - Ann. Roy. Bot. Gard. Calcutta 9: 1 - 80 (1901).
- RATHORE, J. S., S. K. GARG & S. R. GUPTA: A chalcone and flavonones from *Didymocarpus pedicellatus*. - Phytochemistry 20: 1455 - 1756 (1981).
- RICHARDS, P. W.: The tropical rain forest. An ecological study. - Cambridge (1952).
- RIDLEY, H. N.: Cyrtandraceae malayenses. - J. Linn. Soc. Bot. 32: 497 - 528 (1896).
- The Gesneraceae of the Malay Peninsula. - J. Straits Branch Roy. Asiat. Soc. 44: 1 - 92 (1905).
- The botany of Gunung Tahan, Pahang. - J. Fed. Malay States Mus. 6: 127 - 202 (1915).
- The Flora of the Malay Peninsula, vol. 2. - London (1923).
- ROXBURGH, W.: Plantae Coromandelianae 2: 36, t. 168. - London (1802).
- SPRENGEL, K.: Anleitung zur Kenntnis der Gewächse, ed. 2, 2. - Halle (1817).
- Systema vegetabilium, 4 (2), Curae posteriores. - Gottingae (1827).
- THEOBALD, W. & D. A. GRUPE: Gesneriaceae. In: ABEYWICKRAMA, B. A., (ed.): A revised handbook of the Flora of Ceylon 1/1 (1973); reimpr. in ibid. DASSANAYAKE, M. D. (ed.) 3: 79 - 107 (1981).
- VAHL, M.: Enumeratio plantarum 1. - Hauniae (1804).
- VOGEL, S.: Betrug bei Pflanzen: Die Täuschblumen. - Abhandl. Akad. Wiss. u. Lit. Mainz, math.-naturw. Kl., H. I: 1 - 48 (1993).
- WALLICH, N.: Numerical List (1829). - London (1828 - 1849).
- WANG, W. T.: Gesneriaceae. In: Flora Reipublicae Popularis Sinicae 69: 131 - 581 (1990). - Beijing.
- WANG, W. T., K. Y. PAN, Z. Y. LI: Keys to the Gesneriaceae of China. - Edinburgh J. Bot. 49: 5 - 74 (1992).
- WEBER, A.: The cristate inflorescence of *Chirita* sect. *Microchirita* (Gesneriaceae). - Notes Roy. Bot. Gard. Edinburgh 34: 221 - 230 (1975).
- Die Gattungsmerkmale von *Schizoboea* (Gesneriaceae). - Pl. Syst. Evol. 134: 183 - 192 (1980).
- *Didymocarpus geitleri*, a remarkable new species of Gesneriaceae with deceptive pollen flowers. - Pl. Syst. Evol. 165: 95 - 100 (1989).
- & BURTT, B. L.: *Didymocarpus corchorifolius* and its allies (Gesneriaceae). - Blumea 28: 291 - 309 (1983).
- Supplementary notes on '*Didymocarpus corchorifolius* and its allies (Gesneriaceae)'. - Blumea 31: 155 - 159 (1985).
- *Didissandra*: redefinition and partition of an artificial genus of Gesneriaceae. - Beitr. Biol. Pflanzen 70: 153 - 177 (1998a).

- Revision of the genus *Didissandra* (Gesneriaceae). - Beitr. Biol. Pflanzen 70: 191 - 223 (1998b).
- Revision of the genus *Ridleyandra* (Gesneriaceae). - Beitr. Biol. Pflanzen 70: 225 - 273 (1998c).
- KIEW, R.: Gesneriads of Peninsular Malaysia. - Nature Malaysiana 8: 24 - 31 (1983).
- WIEHLER, H.: A synopsis of Neotropical Gesneriaceae. - Selbyana 6: 1 - 219 (1983).
- WIGHT, R.: Icones plantarum Indiae orientalis, 4. - Madras (1848).
- WOLLENWEBER, E., C. REHSE, V. H. DIETZ: The occurrence of aurantiacin and flavokawin B on *Pityrogramma triangularis* var. *pallida* and *Didymocarpus* species. - Phytochemistry 20: 1167 - 1168 (1981).
- WOOD, D.: A revision of *Chirita* (Gesneriaceae). - Notes Roy. Bot. Gard. Edinburgh 33: 123 - 205 (1974).

## Addresses of the authors:

A. WEBER

Institute of Botany, University of Vienna  
Rennweg 14  
A-1030 Vienna  
Austria

B. L. BURTT

Royal Botanic Garden  
Edinburgh EH3 5LR  
Scotland, U. K.