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Four new genera of woody *Apiaceae* of Madagascar

Ben-Erik Van Wyk, Patricia M. Tilney & Pieter J. D. Winter¹

Summary

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Eight Malagasi species of *Apiaceae* were previously misplaced in the African genus *Heteromorpha* but have been recently excluded from it. They, with the E. African species of *Pseudocarum*, have remarkably unspecialised fruits and do not fit within Drude's classification system for the family, as they combine vittae characteristic of the *Saniculoideae* and *Apioideae*. They have oil ducts in the fruit ribs (intrajugal vittae) in addition to the normal ones between the ribs (vallecular vittae). The species (except one) have dentate-serrate leaf segments, and some also have dentate involucre bracts, reminiscent of the *Saniculoideae*. These characteristics are interpreted as symplesiomorphies, and the group of species as a whole is undoubtedly paraphyletic. A new generic classification is proposed, and a key to the genera and species is provided. Four genera, *Andriana*, *Cannaboides*, *Pseudocannaboides*, and *Tana*, are described as new, to accommodate seven species and one additional variety: *A. coursii*, *A. marojejensis*, *A. tsaratananensis*, *C. andohahelensis*, *C. andohahelensis* var. *denudata*, *C. betsileensis*, *Pseudocannaboides andringitrensis*, and *T. bojeriana*. *Pseudocarum laxiflorum* and *P. laxiflorum* var. *alticola* are additional new combinations.

Introduction

In our revision of the African genus *Heteromorpha* Cham. & Schldl. (Winter & Van Wyk, 1996) we excluded the eight Madagascar endemics that had been previously assigned to it. These species, together with the E. African genus *Pseudocarum*, show an interesting combination of unspecialised morphological features which, we believe, will eventually prove to be of importance in resolving relationships amongst the woody African umbel genera and indeed also between the subfamilies *Apioideae* and *Saniculoideae*. The characteristics in question include the woody or suffruticent habit, the remarkably unspecialised fruit, the dentate-serrate leaflet margins and (in some species) the dentate involucre bracts. All these features are reminiscent of the *Saniculoideae*, whereas in other respects these species belong to the *Apioideae*, thus establishing a link between the two subfamilies.

The woody habit was probably the main reason why Humbert (1955, 1956) broadened the circumscription of *Heteromorpha* to accommodate the Madagascar species related to *Pseudocarum*. As we have shown in previous papers (Winter & al., 1993; Winter & Van Wyk, 1994) the similarity between genuine *Heteromorpha* and the Madagascar species of the *Pseudocarum* group does not extend much beyond the woody habit, and the two groups are unlikely to be even closely related. Genuine *Heteromorpha* species of Africa have unusual heteromorphic ovaries and fruits (Winter & al., 1993), not present in any other woody umbel species. Other important differences are the virtual absence of oil ducts in the ribs and the entire margins of the leaflets; or they concern some leaf anatomical characters (e.g. stomata, see Winter & Van Wyk, 1994). The diversity of habit in African *Heteromorpha* (trees, shrubs, climbers, and suffrutices) has nevertheless an interesting parallel

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in the *Pseudocarum* group. Amongst them are woody shrubs or shrublets (*H. coursii*, *H. tsaratananensis*, *H. marojejyensis*), suffrutescent climbers (*H. laxiflora*, *P. eminii*), suffrutices (*H. andohalelensis*, *H. betsileensis*, *H. bojeriana*), and an herbaceous perennial (*H. andringitrensis*).

Another parallel between *Heteromorpha* and the *Pseudocarum* group is the exceptionally variable leaf morphology, the variation being even more extreme in the latter group, ranging from tripinnately divided (*H. andringitrensis*) to bipinnately divided (*H. andohalelensis*, *H. betsileensis*), palmate (*H. tsaratananensis*), palmately divided (*H. bojeriana*), trifoliolately divided (*H. coursii*), ternate (*H. laxiflora*, *P. eminii*), and unifoliolate (*H. marojejyensis*, some forms of *H. laxiflora*). This degree of diversity of leaf type between species (with much less infraspecific variation when compared to genuine *Heteromorpha*) is unlikely to be found in a single natural genus. A noteworthy feature of all but one species of the *Pseudocarum* group are the dentate or serrate leaflet margins (resulting in a close similarity with the leaflets of *Cannabis*, see below). Dentate leaf margins are characteristic for the *Saniculoideae* but rather unusual in the *Apioideae*. Some discontinuities in leaf epidermal characters have been reported (Winter & Van Wyk, 1994), notably the high density of stomata in the three woody species, *H. coursii*, *H. marojejyensis*, and *H. tsaratananensis*, and the presence of anisocytic stomata in *H. betsileensis*.

The most significant morphological evidence to support the exclusion of the Madagascar species from *Heteromorpha* was found in the fruit (Winter & al., 1993). The arguments are not repeated here, except to point out that the fruit structure of all species of the *Pseudocarum* group is surprisingly similar – perhaps a reason why Humbert (1955, 1956) considered the Madagascar species to be congeneric. Fig. 1 shows transverse sections of the fruits of the eight Madagascar species. The fruits are quite unspecialised, not only in the context of the *Apioideae* but indeed of the family as a whole. The plesiomorphic states are unobtrusive and easily overlooked: the presence of intrajugal vittae (oil ducts within the ribs); the perfect isodiametry of the mericarps, devoid of any dorsal or lateral flattening; and the absence of wings. The presence of both intrajugal and vallecular vittae is of particular importance. In the classification system of Drude (1898), this combination of states was not provided for in the key to the subfamilies. Based on the criterion of fruit vittae alone, the *Pseudocarum* group thus provides a phylogenetic link between the *Saniculoideae* and the *Apioideae*. What makes that link even more convincing is the co-occurrence of serrate leaf margins, dentate involucre bracts, and a woody habit. This combination of features is exactly what we would expect in an ancestral lineage leading to the woody African genera. Recent phylogenetic studies of DNA sequences, aimed at resolving basal relationships in the *Apiales* and *Apioideae* (Plunkett & al., 1996; Downie & Katz-Downie, 1996; Plunkett & Downie, 1999), unfortunately did not include any representative of the *Pseudocarum* group.

Based on our experience of woody African *Apiaceae*, the following classification is proposed to accommodate the Madagascar species and to give formal taxonomic recognition to the remarkable diversity within the *Pseudocarum* group. This classification will hopefully contribute to a more natural grouping of the African and Madagascar *Apiaceae*. In comparison with other plant families, the seemingly low level of endemism in Madagascar *Apiaceae* is striking (see Pimenov & Leonov, 1993: 11). The treatment below thus also contributes to a more realistic view of the diversity and endemism of the family in Madagascar.

Key to the genera and species

1. Leaflets or leaf segments linear-filiform; margins entire; fruit surface tuberculate *Tana bojeriana*
- Leaflets or leaf segments narrowly lanceolate to ovate, margins serrate; fruit surface smooth and/or hairy 2
2. Leaves simple or ternately divided or palmate 3
- Leaves pinnate (bi- or tripinnately divided) 7
3. Calyx teeth inconspicuous or absent 4
- Calyx teeth prominent, deltoid 5
4. Pedicel up to 18 mm long; intervallecular vittae 6 per mericarp *Pseudocarum eminii*
- Pedicel 25 to 95 mm long; intervallecular vittae 12 to 14 per mericarp *Pseudocarum laxiflorum*
5. Leaves simple, subsessile *Andriana marojejensis*
- Leaves digitate or palmate, on long petioles 6
6. Leaf ternate, with 3 leaf segments fused at their bases *Andriana coursii*
- Leaf palmate, with 5 free leaflets *Andriana tsaratananensis*
7. Calyx teeth inconspicuous or absent; leaves tripinnately divided; inflorescence and mericarps glabrous; stem herbaceous ... *Pseudocannaboides andringitensis*
- Calyx teeth prominent, deltoid; leaves pinnately to bipinnately divided; inflorescence and mericarps usually densely hairy; stem woody 8
8. Leaf segments 2-3 mm wide; leaves usually glabrous *Cannaboides andohahelensis*
- Leaf segments 5-8 mm wide; leaves usually hairy, at least along the petiole and lower midrib *Cannaboides betsileensis*

Andriana B-E. van Wyk, **gen. nov.** – Type: *A. tsaratananensis* (Humbert) B-E. van Wyk (*Heteromorpha tsaratananensis* Humbert).

Heteromorphae et *Polemannieae* similis, sed ab iis foliis regularius compositis, palmatis, digitatis vel simplicibus (nec vario modo irregulariter lobatis), foliolis coriaceis margine serratis, mericarpis aequalibus perfecte isodiametricis (in *Polemanna* dorso complanatis; in *Heteromorpha* inaequalibus), praesentia constante vittarum vallecularium simulac intrajugali (in *Polemanna* et *Heteromorpha* vittae intrajugales raras nonnusquam observatur) differt. Ab aliis *Apiaceis* Madagascariensibus habitu magis ligneo, foliolis majoribus paucioribus uniformioribus, et glabritie differt.

The new genus is similar to *Heteromorpha* and *Polemanna* Eckl. & Zeyh. but differs in the more regularly divided or compound leaves (palmate, digitately divided, or simple, not irregularly and variably lobed as in the latter genera), the serrate leaflet margins, the equal, perfectly isodiametric mericarps (not dorsally flattened as in *Polemanna* or unequal as in *Heteromorpha*), the invariable presence of intrajugal oil ducts (within the fruit ribs) as well as vallecular oil ducts (between the fruit ribs) (oil ducts are rarely found in the ribs in *Polemanna* and in *Heteromorpha*). It differs from other Madagascar umbels in the more woody habit, the larger, fewer, more uniform leaflets, as well as in their thick and leathery texture, and in the absence of vestiture.

The generic name is formed from an abbreviation of the name of King Andriantsimitoviaminandriandehibe, who is said to have ruled in Antananarivo c. 1000 A.D. (“andrian” is the Malagasy word for “noble”). The length of Malagasy names used as specific epithets by Humbert (1955, 1956) pales in comparison!

Andriana coursii (Baker) B-E. van Wyk, **comb. nov.** \equiv *Heteromorpha coursii* Humbert in Notul. Syst. (Paris) 15: 118. 1956. – Lectotype (designated here): Madagascar, “massif de l’Anjanaharibe à l’Ouest d’Andapa (haute Andramonta, bassin de la Lokoho)...”, *Humbert & al.* 24702 (P, sheet 1!; isolectotypes: P!, K!).

Specimens examined. – *Humbert & al.* 24702 (P, 2 sheets; K); *s. coll.* ex Herbario de l’Alaotra No. 3825 (MO).

Andriana marojejyensis (Humbert) B-E. van Wyk, **comb. nov.** \equiv *Heteromorpha marojejyensis* Humbert in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 6: 120. 1955. – Lectotype (designated here): Madagascar, “sommet oriental du Marojejy”, 2137 m, *Humbert* 22710 (P, sheet 1 [with fruit]!; isolectotypes: P!, 2 sheets).

The epithet is derived from the type locality, Mount Marojejy, in north-eastern Madagascar.

Specimens examined. – *Humbert* 22710 (P, 3 sheets); *Humbert & Cours* 23800 (K); *Miller & Lowry* 4160 (MO); *s. coll.* ex Herbario de l’Alaotra No. 3475 (MO).

Andriana tsaratananensis (Humbert) B-E. van Wyk, **comb. nov.** \equiv *Heteromorpha tsaratananensis* Humbert in Notul. Syst. (Paris) 15: 120. 1956. – Lectotype (designated here): Madagascar, “massif du Tsaratanana”, 2300-2600 m, *Perrier de la Bâthie* 16411 (P, sheet 1!; isolectotypes: P!, K!).

Tsaratanana mountain is situated in the extreme north of Madagascar, about 100 km south-east of Nosy Be.

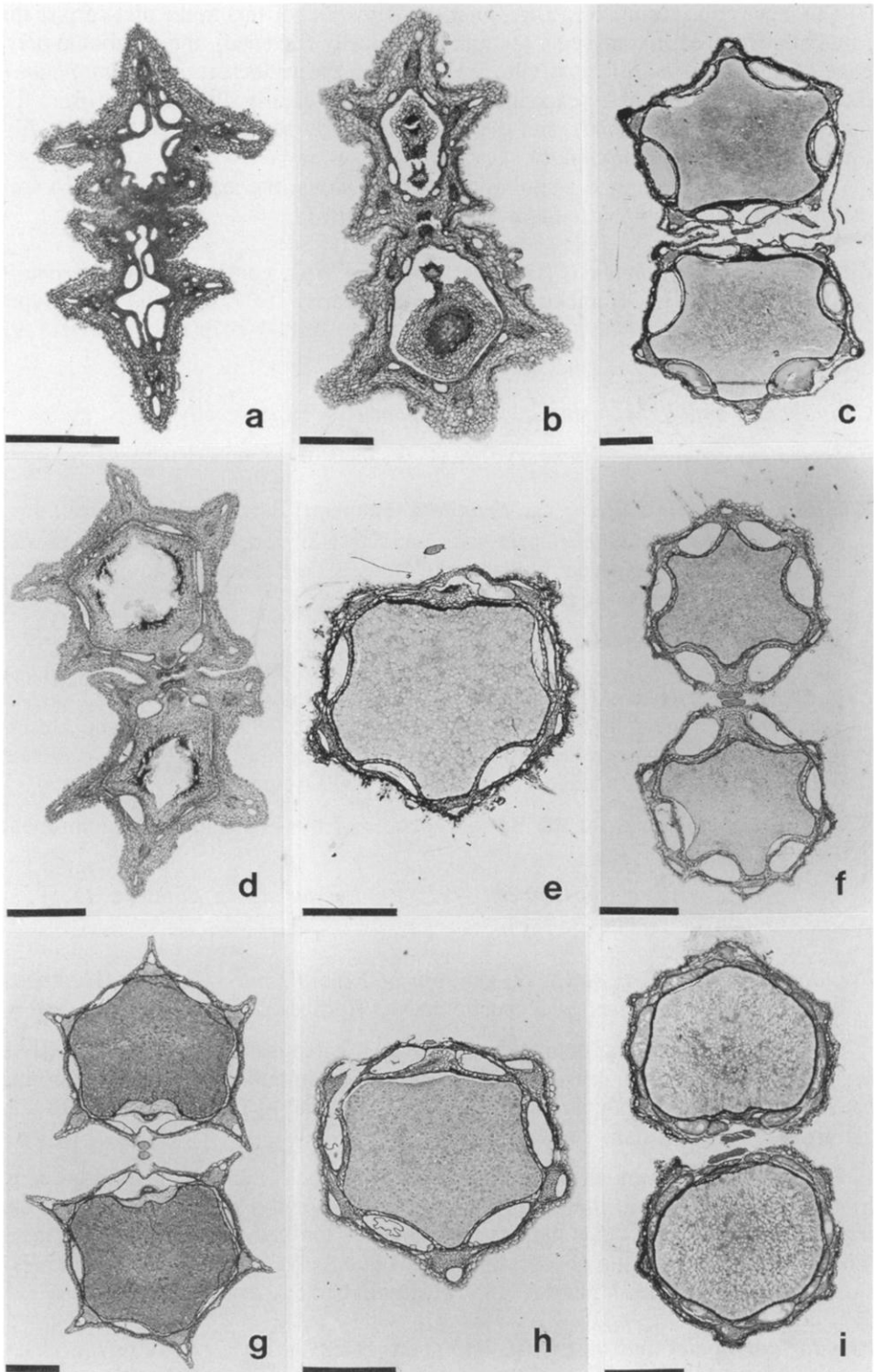
Specimens examined. – *Humbert* 18374 (P, 3 sheets; K); *Perrier de la Bâthie* 6806 (P, 2 sheets), 16411 (P, 2 sheets; K).

Cannaboides B-E. van Wyk, **gen. nov.** – Type: *C. andohahelensis* (Humbert) B-E. van Wyk (*Heteromorpha andohahelensis* Humbert).

Diplolophio simile, sed ab eo mericarpiis isodiametricis (nec dorso complanatis), praesentia constante vittarum intrajugalium (nec vittis ad valleculeas restrictis), foliarum basi angusta (nec expansa et vaginante, a parte superiore manifeste distincta), foliolis latis regulariter serratis (nec filiformibus integris) differt.

→

Fig. 1. Transverse sections of ovaries (a) and fruits (b-i) of the Madagascar species hitherto placed in *Heteromorpha*. – a, *Andriana coursii* (*Humbert & al.* 24702, P); b, *A. marojejyensis* (*Humbert* 22710, P; immature); c, *A. tsaratananensis* (*Humbert* 18374, P); d, *A. coursii* (*Humbert & al.* 24702, P); e, *Cannaboides andohahelensis* (*Humbert* 6192, P); f, *C. bet-sileensis* (*Perrier de la Bâthie* 6815, P); g, *Pseudocannaboides andringitrensis* (*Perrier de la Bâthie* 13741, P); h, *Tana bojeriana* (*Baron* 5185, P); i, *Pseudocarum laxiflorum* (*Humbert & Capuron* 25427, P). – Scale bar = 0.25 mm in a-b, 0.5 mm in c-i.



The new genus is similar to *Diplolophium* Turcz. but differs in the mericarp shape (perfectly rounded in transverse section, not dorsally flattened), the invariable presence of vittae in the fruit ribs (vittae restricted to the valliculae in *Diplolophium*), the non-enlarged leaf base (expanded and sheathing, clearly differentiated from the upper part in *Diplolophium*), and the broad, regularly serrate leaflets (leaflets filiform and entire in *Diplolophium*).

"*Cannaboides*" refers to a similarity with *Cannabis*; the leaflets of the two species are remarkably similar to those of *Cannabis sativa* L.

Cannaboides andohahelensis (Humbert) B-E. van Wyk, **comb. nov.** \equiv *Heteromorpha andohahelensis* Humbert in Notul. Syst. (Paris) 15: 121. 1956. – Holotype: Madagascar, "massif de l'Andohahela (Sud-Est)", 1800-1979 m, *Humbert 6192* (P!; isotypes: P!, K!).

Cannaboides andohahelensis var. *andohahelensis*. – Type as above.

Specimens examined. – *Humbert 6192* (P, 2 sheets; K), *13654* (P).

Cannaboides andohahelensis var. *denudata* (Humbert) B-E. van Wyk, **comb. nov.** \equiv *Heteromorpha andohahelensis* var. *denudata* Humbert in Notul. Syst. (Paris) 15: 122. 1956. – Holotype: Madagascar, "massif de Beampingaratra (Sud-Est)", c. 1500 m, *Humbert 6466* (P!).

Specimen examined. – *Humbert 6466* (P).

Cannaboides betsileensis (Humbert) B-E. van Wyk, **comb. nov.** \equiv *Heteromorpha betsileensis* Humbert in Notul. Syst. (Paris) 15: 122. 1956. – Lectotype (designated here): Madagascar, "mont Antety, près d'Ambrosita", c. 1600 m, *Perrier de la Bâthie 6815* (P [with leaves, flowers and fruits]!; isolectotypes: P!, 3 sheets).

The species is named for the Betsileo people of the Fianarantsoa region, about 200 km south of the capital.

Specimens examined. – *Humbert 3792* (P); *Perrier de la Bâthie 6815* (P, 4 sheets), *13605* (K); *s. coll. 4038* (P).

Pseudocannaboides B-E. van Wyk, **gen. nov.** – Type: *P. andringitrensis* (Humbert) B-E. van Wyk (*Heteromorpha andringitrensis* Humbert).

Cannaboidi similis, sed habitu herbaceo (nec suffrutescenti), pedunculis cavis (nec solidis lignosisque), foliis ad basim (nec ad apicem ramorum) congestis, tripinnatis (nec bipinnatis), calycis lobis nullis (nec evolutis) et fructibus valde costatis glabris (nec parum costatis dense pilosis) differt.

The new genus is similar to *Cannaboides*, from which it differs in its herbaceous (not suffrutescant) habit, the hollow (not solid and woody) peduncles, the leaf arrangement (crowded towards the base, not towards the branch ends), the tripinnate (not bipinnate) leaves, the absence of calyx lobes (calyx present in *Cannaboides*) and in the strongly ribbed, glabrous (not weakly ribbed and densely hairy) fruits.

Pseudocannaboides andringitrensis (Humbert) B-E. van Wyk, **comb. nov.** \equiv *Heteromorpha andringitrensis* Humbert in Notul. Syst. (Paris) 15: 126. 1956. – Holo-

type: Madagascar, “massif de l’Andringitra (Iratsy): vallées de la Riambava et de l’Antsifotra et montagnes environnantes”, 2000-2500 m, *Perrier de la Bâthie* 14430 (P!; isotypes: P!, 2 sheets).

Specimens examined. – *Perrier de la Bâthie* 6809 (P), 13741 (P, K), 14430 (P, 3 sheets).

Tana B-E. van Wyk, **gen. nov.** – Type: *T. bojeriana* (Baker) B-E. van Wyk (*Peucedanum bojerianum* Baker).

Cannaboidi et *Pseudocannaboidi* similis, sed habitu humili suffrutescente, foliis subpalmatim compositis segmentis integris filiformibus (nec pinnatim compositis segmentis latis serratis) et fructus epidermide tuberculata (in aliis generibus laevi vel pilosa) differt. Etiam speciebus *Pimpinellae* Africanis simile, a quibus differt vitta valleculari singula et intrajugali singula (nec vittis vallecularibus 2-3 et intrajugalibus ut videtur nullis) differt.

The new genus is similar to *Cannaboides* and *Pseudocannaboides* but differs in the low, suffrutescent habit, the almost palmately compound leaves with entire filiform segments (leaves pinnately compound, with broad serrate segments or leaflets in *Cannaboides* and *Pseudocannaboides*) and in the tuberculate epidermis of the fruit (smooth or hairy in the other genera). It is also similar to African species of *Pimpinella*, from which it differs in having single vallecular and intrajugal vittae (not 2-3 vallecular and apparently no intrajugal vittae). The heavily cutinised outer walls of the epidermis cells and their somewhat bottle-shaped appearance are characteristic for the fruit epidermis of *Anginon* Raf. (Van Wyk & al., 1997), but intrajugal vittae are not found in the latter genus.

“Tana” is a frequently used abbreviation for Antananarivo, the capital city of Madagascar.

Tana bojeriana (Baker) B-E. van Wyk, **comb. nov.** ≡ *Peucedanum bojerianum* Baker in J. Linn. Soc., Bot. 25: 319. 1890 ≡ *Heteromorpha bojeriana* (Baker) Humbert in Notul. Syst. (Paris) 15: 126. 1956. – Holotype: Madagascar, “Ankaratra”, *Baron 5185* (BM; isotype: P!).

The epithet commemorates Wenceslas Bojer (1797-1856), who collected the species for the first time. This Czech born explorer was director of the botanical garden in Port Louis, Mauritius.

Specimens examined. – *Baron 5185* (P, 2 sheets); *Bojer s.n.* (P); *Catat 332* (P); *Dorr & al. 2889* (MO).

Pseudocarum C. Norman in J. Bot. 62: 333. 1924. – Type: *Pseudocarum clematidifolium* C. Norman [= *P. eminii* (Engl.) H. Wolff].

Scrambling herb, climbing to more than 7 m high. Stems slender, glabrous, terete or striate. Leaves glabrous, ternate to bi- or subtrternate; petioles and petiolules sometimes prehensile; leaflets ovate to linear-lanceolate, margins serrate with setaceous-mucronate teeth. Umbels numerous, compound, with long slender peduncles and pedicels. Calyx teeth inconspicuous or absent. Fruit ovoid to elliptic, glabrous, smooth or with prominent ribs; intrajugal vittae small or absent, vallecular vittae shallow and broad, single or a few in each vallecule (Fig. 1i).

Pseudocarum eminii (Engl.) H. Wolff in Engler, Pflanzenr. 90: 184. 1927 ≡ *Peucedanum eminii* Engl., Pflanzenw. Ost-Afrikas C: 300. 1895. Holotype: Kenya, Ruwenzori, "Msussai-Schlucht", *Stuhlmann 2417* (B†).

= *Pseudocarum clematidifolium* C. Norman in J. Bot. 62: 333. 1924. – Lectotype (designated here): Kenya, Ruwenzori, Kivata, *Scott Elliot 7677* (BM!).

= *Heteromorpha scandens* Clark in Bull. Misc. Inform. Kew 1911: 229. 1911. – Holotype: Kenya, Aberdares, *Battiscombe 278* (K!; isotype: EA).

This species differs from the following by the relatively short pedicels and the single vitta in each vallecule of the fruit. It appears to be widely distributed in Uganda, Kenya, and Ethiopia (Townsend, 1989).

Specimens examined. – *Newbould 3697* (K); *Scott Elliot 7677* (BM); *Townsend 2432* (K); *Verdcourt 2058* (K).

Pseudocarum laxiflorum (Baker) B-E. van Wyk, **comb. nov.** ≡ *Pimpinella laxiflora* Baker in J. Linn. Soc., Bot. 21: 349. 1884 ≡ *Heteromorpha laxiflora* (Baker) Humbert in Notul. Syst. (Paris) 15: 124. 1956. – Lectotype (designated here): Madagascar, without locality, *Baron 2887* (P [as "*Pimpinella laxiflora*"]!).

Pseudocarum laxiflorum var. *laxiflorum*. – Type as above.

Specimens examined. – *Baron 290, 2887, 3887* (P); *Bosser 15975, 19846* (P); *Humbert 18503* (K); *Humbert & Capuron 24882, 25182* (K); *Keraudren 266* (P); *Leeuwenberg 13721* (P); *Schatz 2655* (MO); *Humbert & Capuron 25427* (K, P, "var. *angustifolia*"); *Perrier de la Bâthie 15168* (P, "var. *angustifolia*"), *s. coll. 174* (P, "var. *angustifolia*"); *Humbert & Capuron 25031* (K, P, "f. *unifoliolata*").

The names *Heteromorpha laxiflora* var. *angustifolia* Humbert and *H. laxiflora* f. *unifoliolata* Humbert, which appear on some herbarium labels (see above) and also in Humbert (1955: fig. 8), have apparently never been validly published.

Pseudocarum laxiflorum var. *alticola* (Humbert) B-E. van Wyk, **comb. nov.** ≡ *Pimpinella laxiflora* var. *alticola* Humbert in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 6: 122. 1955. – Holotype: Madagascar, "sommet oriental du Marojejy", 1850 m, *Humbert 22657* (P!).

Specimens examined. – *Humbert 22657* (P); *Humbert & Cours 23816* (P).

Pseudocarum laxiflorum is an unusual species so similar to *P. eminii*, a suffrutescent climber from east Africa with the same slender, almost hair-like pedicels, that the above transfer seems long overdue. *P. laxiflorum* may easily be distinguished from *P. eminii* by the pedicel length: up to 18 mm in *P. eminii* (Townsend, 1989) but 25-95 mm in *P. laxiflorum*. In the latter species, the pedicels are much longer than the rays, while the rays are much longer than the pedicels in *P. eminii*. The leaves and leaflets of *P. laxiflorum* also seem to be much more variable than those of *P. eminii*, but the exact relationship between the African and Madagascar species needs to be studied in detail. It is not clear whether the petioles of *P. laxiflorum* are also prehensile, as are those of *P. eminii* (see Townsend, 1989). Fruits of *P. eminii* appear to have only a single vitta in each vallecule, but the full range of variation of this character is not known.

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