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Studies in the tribe Spermacoceae (Rubiaceae-Rubioideae): the circumscriptions of *Amphiasma* and *Pentanopsis* and the affinities of *Phylohydrax*

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Abstract. Phylogenetic analysis of *rbc*L cpDNA sequences for 34 members of the tribe Spermacoceae s. lat. indicates that the African genera *Amphiasma, Conostomium, Manostachya, Pentanopsis* and *Phylohydrax* form a strongly supported clade, characterised by basal placentation and heterostyly. This is a new position for the sea shore genus *Phylohydrax* that has previously been associated with *Diodia* and *Spermacoce* in Spermacoceae s. str. *Amphiasma* is not monophyletic as the two samples of *A. gracilicaule* included form a strongly supported clade with *Pentanopsis fragrans*. A new taxonomy is therefore proposed, where the previously monotypic *Pentanopsis* is circumscribed as a genus of two species in north-eastern tropical Africa, whereas *Amphiasma* is treated in its original sense as a genus of about eight species confined to south-central tropical Africa. The new combination *Pentanopsis gracilicaulis* is made.

Key words: Rubiaceae, Spermacoceae, *Amphiasma, Conostomium, Hydrophylax, Manostachya, Pentanopsis, Phylohydrax*, chloroplast DNA, *rbc*L, morphology, phylogeny, taxonomy.

Fifty-two genera were included in the tribe Spermacoceae by Bremer and Manen (2000), 32 of these on the basis of molecular data, and the remaining 20 on the basis of morphological similarity. With this wide circumscription the tribe includes, for example, all investigated taxa of the formerly generally recognised tribes Hedyotideae and Knoxieae. However, in the published cladograms (Bremer and Manen 2000: Figs. 3, 4) only a small part of these genera are shown.

In the present study we include a relatively large sample of taxa from the Spermacoceae s. lat. and focus on a clade including the African genera *Amphiasma, Conostomium, Pentanopsis* (all formerly Hedyotideae), and *Phylohydrax* (formerly Spermacoceae s. str.). These four genera were included also in the analysis of Bremer and Manen (2000), but they were absent from the published cladograms. Here we add five further sequences from taxa belonging in this clade, with the particular aim of investigating the circumscriptions of *Amphiasma* and *Pentanopsis*, as well as the phylogenetic position of the enigmatic *Phylohydrax* that was segregated from *Hydrophylax* by Puff (1986).

Material and methods

The sampling strategy was to include representative taxa from different parts of the tribe Spermacoceae, but with a concentration on the *Amphiasma*/*Pentanopsis* clade, according to the analyses in Bremer and Manen (2000). Based on general morphological similarities and type of placentation we also included genera that we suspected could be close to *Amphiasma* and *Pentanopsis* (*Dibrachionostylus, Manostachya*, and *Mitrasacmopsis*). Two samples of *Amphiasma gracilicaule* were included, one from a plant closely similar to the type, and one from a more large-flowered form. We also added a sequence of *Hydrophylax*. Altogether 33 taxa representing 26 genera of Spermacoceae were sampled. As outgroup we used one taxon from outside the subfamily Rubioideae (*Luculia*) and five genera representing other tribes within Rubioideae (Bremer and Manen 2000). Silica gel-dried or herbarium material was used in the DNA investigations. DNA was extracted and amplified according to Bremer et al. (1995) and sequencing was performed with a MegaBACE 1000 (Amersham Biosciences) following the protocol of the manufacturer. The sequences of the coding gene *rbc*L were manually aligned by using the reading frames of the corresponding amino acid sequences. The *rbc*L matrix comprises 40 sequences. Eight of these have been produced for this study (Fig. 1), and the other sequences have been published before (Bremer et al. 1995, Manen and Natali 1995, Bremer 1996, Bremer and Manen 2000).

Phylogenetic relationships were obtained by parsimony analysis using PAUP* (Swofford 1998), version 4.0b10. Only informative characters were analysed. The search method was heuristic with 100 replications of RANDOM stepwise additions of sequences, the TBR branch swapping, and MULPARS options in effect. Support for the nodes was calculated with jackknife analysis with 1000 replicates and TBR branch swapping and MULPARS off.

Results

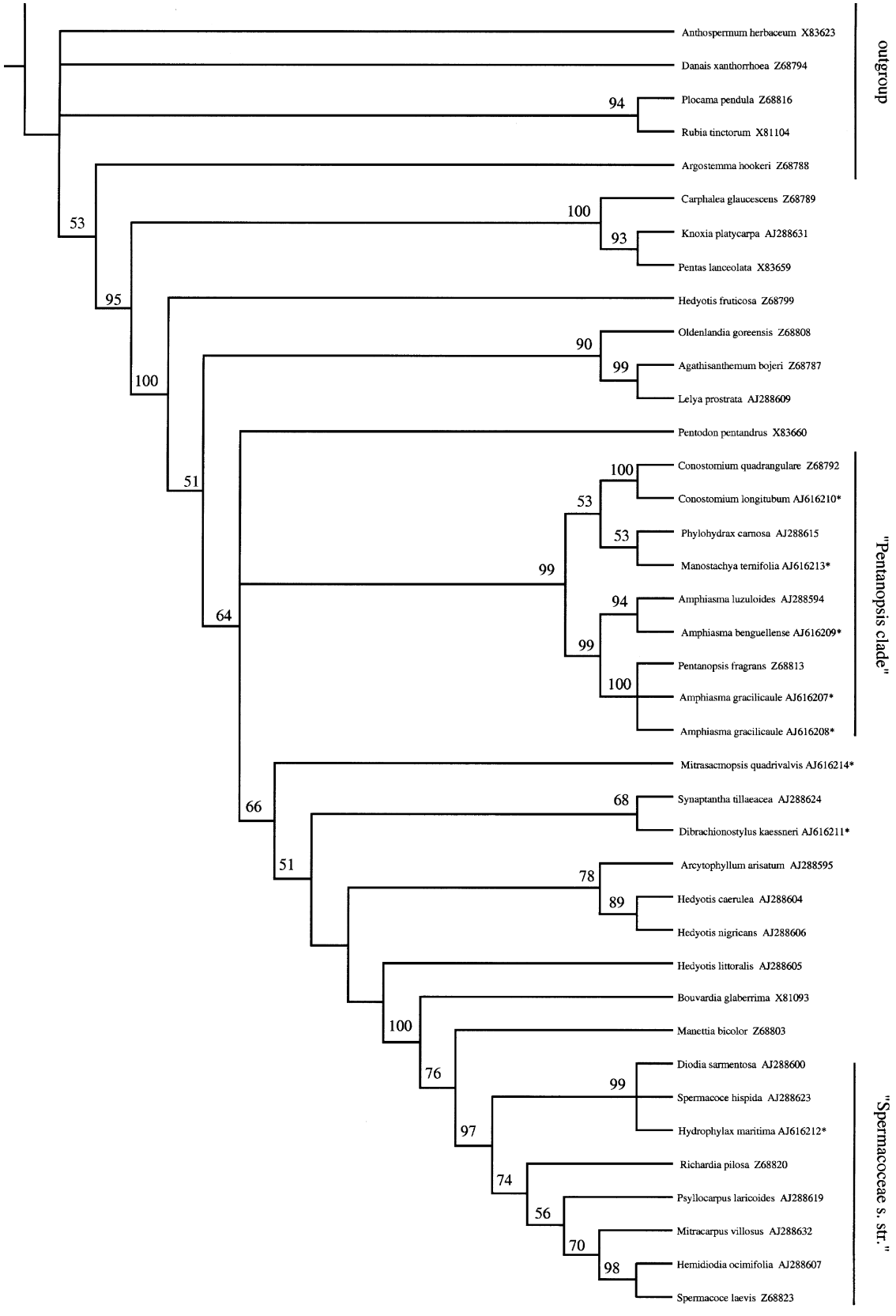
The data matrix comprises 39 species (one species, *Amphiasma gracilicaule*, is represented by two accessions) and 1402 positions, 187 of which are parsimony-informative. The heuristic analysis resulted in 18 most parsimonious trees 649 steps long with a consistency index CI = 0.604 and a retention index RI = 0.709. A strict consensus tree is shown in Fig. 1. The included taxa of *Conostomium, Phylohydrax, Manostachya, Amphiasma*, and *Pentanopsis*, form a strongly supported clade (99%), "the *Pentanopsis* clade". Further, *Conostomium* is strongly supported as monophyletic (100%), as is *Amphiasma* plus *Pentanopsis* (99%), but the two samples of *A. gracilicaule* form a strongly supported clade (100%) with *Pentanopsis*, whereas *A. benguellense* is strongly supported (94%) as sister to *A. luzuloides*.

Hydrophylax is nested with species of *Diodia* and *Spermacoce* in a strongly supported clade (99%) that is sister with strong support (97%) to a clade with other taxa with solitary ovules, these two clades together corresponding to the former Spermacoceae s. str. *Spermacoce* itself is, according to our analysis, biphyletic with *S. hispida* in the former and *S. laevis* in the latter of these clades.

Discussion

Puff (1986), when erecting the new genus *Phylohydrax* for *P. carnosa* (in South Africa and Mozambique) and *P. madagascariensis* (in Madagascar and Tanzania), suggested that this genus and *Hydrophylax* (with the remaining species *H. maritima* in southern Asia) are derived from different portions of "an ancestral *Diodia–Spermacoce-like* stock". Our results confirm that *Hydrophylax maritima* is indeed closely related to *Diodia* and *Sperma-*

Fig. 1. Strict consensus tree with jackknife values above branches. The asterisks (*) indicate new sequences (*Amphiasma benguellense*, Bamps et al. 4489 (UPS); *Conostomium longitubum*, Thulin 10855 (UPS); *Dibrachionostylus kaessneri*, Strid 2464 (UPS); *Hydrophylax maritima*, Lundqvist 8945 (UPS); *Manostachya ternifolia*, Malaisse & Robbrecht 2063 (K); *Mitra-sacmopsis quadrivalvis*, Richards 11069 (K); *Pentanopsis gracilicaulis* (*Amphiasma gracilicaule*), Thulin et al. 10608 (UPS) & Thulin et al. 10512 (UPS)


Anthospermum herbaceum X83623
Danais xanthorrhoea Z68794
Plocama pendula Z68816
Rubia tinctorum X81104
Argostemma hookeri Z68788
Carphalea glaucescens Z68789
Knoxia platycarpa AJ288631
Pentas lanceolata X83659
Hedyotis fruticosa Z68799
Oldenlandia goreensis Z68808
Agathisanthemum bojeri Z68787
Lelya prostrata AJ288609
Pentodon pentandrus X83660
Conostomium quadrangulare Z68792
Conostomium longitubum AJ616210*
Phylohydrax carnosa AJ288615
Manostachya ternifolia AJ616213*
Amphiasma luzuloides AJ288594
Amphiasma benguellense AJ616209*
Pentanopsis fragrans Z68813
Amphiasma gracilicaule AJ616207*
Amphiasma gracilicaule AJ616208*
Mitrasacmopsis quadrivalvis AJ616214*
Synaptantha tillaeacea AJ288624
Dibrachionostylus kaessneri AJ616211*
Arcytophyllum arisatum AJ288595
Hedyotis caerulea AJ288604
Hedyotis nigricans AJ288606
Hedyotis littoralis AJ288605
Bouvardia glaberrima X81093
Manettia bicolor Z68803
Diodia sarmentosa AJ288600
Spermacoce hispida AJ288623
Hydrophylax maritima AJ616212*
Richardia pilosa Z68820
Psyllocarpus laricoides AJ288619
Mitracarpus villosus AJ288632
Hemidiodia ocimifolia AJ288607
Spermacoce laevis Z68823
outgroup
"Pentanopsis clade"
"Spermacoceae s. str."

coce. As *Spermacoce* comes out as biphyletic, *Hydrophylax* may indeed even be nested within *Spermacoce*. The delimitations between *Spermacoce, Diodia, Hemidiodia*, and various other segregates in this complex, are weak (see, for example, Verdcourt 1976). Our sampling is too small to allow any conclusions to be drawn, but surely the clade corresponding to Spermacoceae s. str. is in need of further study. As pointed out by Puff (1986) several apparently unrelated species of *Spermacoce* and *Diodia* grow on tropical sea-shores and *Hydrophylax maritima*, with its creeping stems rooting at the nodes and indehiscent fruits, may represent an extreme case of adaptation in this respect.

The *Pentanopsis* clade has not previously been detected in phylogenetic analyses. Andersson and Rova (1999) showed a close relationship between *Conostomium* and *Amphiasma,* but also *Oldenlandia affinis* was nested in this clade. We are not able to contradict this position for *O. affinis*, but regard it as highly unlikely. Despite the strong support for the *Pentanopsis* clade in our molecular analysis, it is not easy to characterise the group morphologically. All members seem to be heterostylous, but heterostyly is found also elsewhere in Spermacoceae, for example in species of *Pentas* and *Oldenlandia*. The number of ovules per locule varies from numerous to one, but a unifying feature is that the placentation always is more or less basal, whereas in Spermacoceae s. str. the solitary ovules are attached near the middle of the septum. *Manostachya* was originally stated to have ovules attached to the middle of the septum (Bremekamp 1952), and this has been repeated by, e.g. Verdcourt (1989). However, in material studied by us, *Manostachya* has basal placentation as the other members of the *Pentanopsis* clade. Basal placentation is otherwise rare in Spermacoceae, and the only other instances may be *Carphalea, Chamaepentas, Mitrasacmopsis, Pseudonesohedyotis* and *Dibrachionostylus*. Of these genera *Carphalea, Mitrasacmopsis and Dibrachionostylus* are included in this study, and they do not belong in the *Pentanopsis* clade (see Fig. 1). The remaining taxa, *Chamaepentas* and *Pseudonesohedyotis*, are both monotypic African genera and, judging from morphology, they probably do not belong in the *Pentanopsis* clade either.

Phylohydrax is clearly nested in the *Pentanopsis* clade, even if its sister group relationship is uncertain. It is also, with its heterostylous flowers, filiform stigma lobes, and nearly basal attachment of the placenta, morphologically quite at home in this clade, although the solitary ovules and indehiscent fruits are unique. The superficially similar *Hydrophylax*, instead, has isostylous flowers, capitate or shortly 2-lobed stigma, and the placenta attached near the middle of the septum, all characters that are compatible with Spermacoceae s. str. Obviously the various similarities in habit between *Phylohydrax* and *Hydrophylax* can be attributed to convergent adaptations to a life on sea shores. For example, the indehiscent fruits of both these genera may be adapted to dispersal with water as proposed by Puff (1986).

The two species of *Conostomium* included, *C. quadrangulare* (type of genus) and *C. longitubum* (type of *C.* subgen. *Beckia*), form a strongly supported clade (100%). *Conostomium* is morphologically characterised by its pollen grains. Bremekamp (1952) described them as porate, but Lewis (1965) showed that short colpi are also present. The other members of the *Pentanopsis* clade, as far as known, all have colporate pollen with long and distinct colpi. A possible exception is *Phylohydrax*, the pollen grains of which were described as "plurizonocolpate" by Robbrecht in Puff (1986).

Amphiasma was proposed by Bremekamp (1952) as a genus in south-central tropical Africa with eight species from southern Tanzania in the north to Namibia in the south. Four of these were described as new, whereas the remaining species were previously placed in *Oldenlandia*. Since then, one further species has been described, *A. gracilicaule* (Verdcourt 1981). This was based on a single collection from central Somalia and, on account of its long-tubed, glabrous corolla and 4-colporate pollen it was placed in a subgenus of its own, *A.* subgen. *Stonocomium*. The other species of

Amphiasma have corollas with a very short tube, hairy in throat, and 3-colporate pollen (Bremekamp 1952). Comparisons were also made between *A. gracilicaule* on one hand and *Pentanopsis* and *Conostomium* on the other (Verdcourt 1981). In our analysis two forms of *A. gracilicaule* have been included, one corresponding to the type specimen in flower size and one with slightly larger flowers. Both these forms group with strong support (100%) with *Pentanopsis*, a monotypic genus also from the Horn of Africa region and actually partly sympatric with *A. gracilicaule*.

The type of *Amphiasma, A. luzuloides* from southern Tanzania and Malawi, forms a strongly supported clade (94%) with *A. benguellensis* from Angola. Morphological support for this clade is 3-colporate pollen, in contrast to the 4-colporate pollen in the clade with *P. fragrans* and *A. gracilicaule*. These two clades together have a strong support (99%) in the analysis and all members have dorsiventrally flattened seeds with thin walls of the testa cells. Of the other members of the *Pentanopsis* clade, *Conostomium* has angular seeds, *Phylohydrax* has seeds rounded in section, and *Manostachya* has dorsiventrally flattened seeds with thick outer walls of the testa cells (Bremekamp 1952).

Chromosome numbers are known for all genera in the *Pentanopsis* clade, except from *Pentanopsis* itself. *Conostomium and Amphiasma* have $x = 9$ (Lewis 1965, Kiehn 1985) and this base number characterises also many related genera, such as *Agathisanthemum, Dibrachionostylus, Lelya, Oldenlandia*, and *Pentodon*, and it is the most common number in the previous Hedyotideae. However, *Manostachya* is exceptional in having $x = 11$ (Lewis 1965, Kiehn 1985), a common number in other parts of Rubiaceae, and Lewis (1965) suggested its occurrence in *Manostachya* to be "a relic". In our view it is more likely that $x = 11$ in *Manostachya* is secondarily derived from $x = 9$, although we cannot suggest any particular mechanism for this. Most interesting is the report of $x = 14$ ($2n = 56$) in *Phylohydrax* (Kiehn 1985, Puff 1986). This base number is characteristic for Spermacoceae s. str., and has also been reported for *Hydrophylax* (Puff 1986). However, Kiehn (1985) gave the number as $2n = 56 \pm 2$, and we believe that further studies are needed to exclude the possibility that *Phylohydrax* is a hexaploid with $x = 9$.

Taxonomy of *Amphiasma* and *Pentanopsis*

With its present circumscription *Amphiasma* is obviously not monophyletic and some taxonomic change is necessary. We have considered the following three options, under the assumption that the two samples of *A. gracilicaule* are conspecific:

(1) to unite *Amphiasma* and *Pentanopsis* to create a genus of about 10 species, two in north-east tropical Africa and eight in south-central Africa (some of the latter are very similar according to Verdcourt 1976).
(2) to transfer *A. gracilicaule* to *Pentanopsis* to create a genus of two species in north-east tropical Africa. This would differ from *Amphiasma* not only in having 4-colporate (versus 3-colporate) pollen grains, but also in, for example, its much larger flowers. The corolla tube in such an extended *Pentanopsis* would be 12–37 mm long, whereas in *Amphiasma* s. str. it is only 2–4 mm long.
(3) to place *A. gracilicaule* in a genus of its own differing from *Pentanopsis* in its glabrous corolla. In *P. fragrans* the corolla-lobes are covered on the inside with short blunt hairs.

On balance we prefer the second option. By this we avoid monotypic entities and get two geographically confined genera that can be very easily recognised by the great difference in flower size. *Amphiasma* can then be circumscribed in the same way as it was before 1981, whereas for *Pentanopsis* we propose a new taxonomy that is outlined below.

PENTANOPSIS Rendle in J. Bot. 36: 28 (1898). Type: *P. fragrans* Rendle.

Amphiasma subgen. *Stonocomium* Verdc. in Kew Bull. 36: 498 (1981). Type: *A. gracilicaule* Verdc.

Slender shrubs or subshrubs. Leaves opposite, linear-subulate to lanceolate; stipules sheathing the stem, united with petiole, with fimbriate margin, becoming ± woody and persistent. Flowers fragrant, heterostylous, solitary or few together terminating short shoots; pedicels short. Calyx-tube obovoid; lobes 4, narrowly triangular to linear, not united at the base. Corolla white, with slender tube; lobes 4, induplicate-valvate in bud. Stamens 4, inserted in corolla-tube; anthers oblong; pollen grains 4-colporate. Ovary 2-locular with numerous ovules on peltate placentas inserted at the base of the septum; style with filiform stigma-lobes shortly exserted in long-styled flowers, included in short-styled flowers. Capsule obovoid or ellipsoid, with a short beak, loculicidally dehiscent. Seeds flat, elliptic; testa thin-walled, reticulate, with lumina of testa cells smooth.

Genus of two species in north-eastern tropical Africa.

Pentanopsis differs from *Amphiasma* in its much larger flowers (corolla tube 12–37 versus 2–4 mm long), 4-aperturate (versus 3-aperturate) pollen grains, and by its stipules becoming more or less woody and persistent. Also, the calyx-lobes are not united at the base, whereas this generally seems to be the case in *Amphiasma*.

1. Leaves ± scabrid; corolla-tube 18–37 mm long; corolla-lobes ± densely covered with short hairs on the inside.1. *P. fragrans*
– Leaves glabrous; corolla-tube 12–14 mm long; corolla-lobes glabrous on the inside. 2. *P. gracilicaulis*

1. ***Pentanopsis fragrans*** Rendle in J. Bot. 36: 29 (1898). Type: Somalia, ''Wagga'' Mt, Lort Phillips s.n. (BM holotype).

Conostomium brevirostrum Bremek. in Verh. Kon. Nederl. Akad. Wetensch., Afd. Natuurk., sect. 2, 48: 129 (1952), **syn. nov.** Type: Somalia/Ethiopia border, between Dolo (''Doloun'') and ''Batta'', Ruspoli & Riva 1094 (FT holotype).

Conostomium squarrosum Bremek. in Kew Bull. 11: 169 (1956). Type: Ethiopia, between Gorrahi and Wardere, Ellis 138 (K holotype).

Shrub, 0.3–2.5 m tall. Leaf-blades linear to lanceolate, 6–40 × 0.8–5 mm, acute at the apex, ± densely scabrid with short hairs above to subglabrous, usually with revolute margins; stipule sheath 2–7 mm long, with 1–4 up to c. 1 mm long fimbriae. Pedicels 1–4 mm long. Calyx-tube 1.5–2.5 mm long; lobes narrowly triangular to linear, 2–11 mm long, minutely ciliate. Corolla white or tinged purplish outside; tube 18–37 mm long, sparsely hairy inside; lobes 5–15 mm long, acute, sparsely to densely covered with short blunt hairs on the inside. Anthers 1–2 mm long in long-styled flowers, 2.1–3 mm long in short-styled flowers. Style 2-lobed, 16–22 mm long in short-styled flowers, 21–30 mm long in long-styled flowers. Capsule 4.5–7 mm long. Seeds 1.5–2 mm long.

Deciduous or evergreen bushland, usually on rocky ground; 145–1500 m. Somalia, eastern Ethiopia, northern Kenya.

Representative specimens. *Ethiopia*. Bale Region: 42 km SE of Ghinir on road to Imi, 6°55′N, 40°57′E, 31 May 1983, Gilbert, Ensermu & Vollesen 7978 (K, UPS). *Somalia*. Nugaal Region: 49 km SE of Sinujiif, 8°10′N, 49°10′E, 6 May 2001, Thulin, Abdi Dahir, Abdulkadir Khalid & Ahmed Osman 10463 (K, UPS). *Kenya*. Northern Frontier Prov.: Dandu, 14 Apr. 1952, Gillett 12789 (K).

2. ***Pentanopsis gracilicaulis*** (Verdc.) Thulin & B. Bremer, **comb. nov.**

Amphiasma gracilicaule Verdc. in Kew Bull. 36: 498 (1981). Type: Somalia, slopes E of Gawen village, 5°19′N, 48°18′E, Gillett, Hemming & Watson 22249 (K holotype, EA isotype not seen).

Shrub or subshrub, 0.5–1.5 m tall. Leaf-blades linear-subulate, 20–70 × 0.5–1 mm, acute at the apex, glabrous, with revolute margins; stipule-sheath 1–3 mm long with 2–4 up to c. 0.5 mm long fimbriae. Pedicels 1.5–4 mm long. Calyx-tube 1.5–2.5 mm long; lobes narrowly triangular, 1–4 mm long. Corolla white or tinged greyish-brownish outside, gla-

brous; tube 12–14 mm long; lobes 7–11 mm long, acute. Anthers c. 1.8–2 mm long in long-styled flowers, short-styled flowers not seen. Style 2-lobed, 11–14 mm long in long-styled flowers. Capsule 4–6 mm long. Seeds 1.2–1.5 mm long.

Acacia-Commiphora bushland or open plains, in shallow soil over limestone; 180–300 m. North-eastern and central Somalia.

Remarks. The plants from the northernmost locality (Thulin et al. 10608) have larger corollas and longer calyx-lobes than the other material. However, the difference is not great compared to the variation found within *P. fragrans*. Also, the *rbc*L sequences from large-flowered and small-flowered plants are practically identical. However, the *rbc*L sequence data is also inadequate to distinguish between *P. fragrans* and *P. gracilicaulis*, and would be compatible with a taxonomy recognising either one, two or three species of *Pentanopsis*. The taxonomy with two species proposed here is therefore ultimately based on the clear discontinuities found in the morphological variation.

Additional specimens. *Somalia*. Bari Region: 72 km from Qarxis on track to Marraya, 8°23′N, 50°08′E, 15 May 2001, Thulin et al. 10608 (K, UPS). Nugaal Region: 22 km on track from Gaalogod to Garadeen, 7°43′N, 49°36′E, 9 May 2001, Thulin et al. 10512 (UPS). Mudug Region: E of Gawen, c. 30 km on road from Hobyo to Wisil, 5°19N, 48°19′E, 28 May 1989, Thulin & Abdi Dahir 6673 (E, FT, K, UPS).

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