Phylogeny and generic delimitation in Molluginaceae, new pigment data in Caryophyllales, and the new family Corbichoniaceae

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Abstract The circumscription of Molluginaceae has changed radically in recent years, with *Corbichonia* being moved to Lophiocarpaceae, *Limeum* to Limeaceae, *Macarthuria* to Macarthuriaceae and all species of *Hypertelis*, except the type, to *Kewa* in Kewaceae. In a broad analysis of core Caryophyllales using plastid *trnK-matK* and *rbcL* sequences, the position of Molluginaceae in a strict sense as sister to the Portulacineae clade is corroborated, as are the positions of *Corbichonia*, *Limeum* and *Kewa* outside the family. The phylogeny of Molluginaceae is reconstructed based on *trnK-matK* and nuclear ITS sequences of about half of the currently recognized species in the family and with representatives from all recognized genera. *Mollugo* is found to be polyphyletic and a new taxonomy for the family with 11 genera is proposed. *Mollugo* in its new restricted sense is a mainly American genus of about 15 species, including *M. ulei* comb. nov., previously placed in the monotypic *Glischrothamnus*. The Australian and Asian genus *Trigastrotheca* is resurrected for *T. molluginea*, *T. pentaphylla* comb. nov. and *T. stricta* comb. nov. The name *Paramollugo* nom. nov. is proposed for the *Mollugo nudicaulis* group and the combinations *P. angustifolia* comb. nov., *P. cuneifolia* comb. nov., *P. decandra* comb. nov., *P. deltoidea* comb. nov., *P. navassensis* comb. nov. and *P. nudicaulis* comb. nov. are made. *Hypertelis* is expanded to include, besides the type *H. spergulacea*, also *H. cerviana* comb. nov., *H. fragilis* comb. nov., *H. umbellata* comb. nov. and *H. walteri* comb. nov. In *Pharnaceum*, the new combination *P. namaquense* comb. nov. is made, *Hypertelis longifolia* is treated as a synonym of *P. lineare* and *Mollugo tenella* as a synonym of *P. subtile*. *Corbichonia* is proposed to be treated as a family of its own, Corbichoniaceae fam. nov. Several names are lectotypified, including the Linnaean *Mollugo pentaphylla* and *M. stricta*. An anthocyanin is reported for the first time from Simmondsiaceae. The detection of anthocyanins in members of Kewaceae and Molluginaceae agree with previous reports and corroborate the view that these families represent reversals from betalains to anthocyanins. The report of an anthocyanin in Limeaceae, previously regarded as unpigmented, apparently represents a newly detected reversal from betalains to anthocyanins in this family.

Keywords anthocyanins; betalains; *Corbichonia*; *Hypertelis*; ITS; *Mollugo*; *Paramollugo*; taxonomy; *Trigastrotheca*; *trnK-matK*; typification

Supplementary Material The Electronic Supplement (Figs. S1–S11) is available in the Supplementary Data section of the online version of this article at http://www.ingentiaconnect.com/content/iapt/tax; DNA sequence alignment is available from TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S18909)

■ INTRODUCTION

Mollugo L. and its relatives were long treated as members of Aizoaceae, an early exception being Hutchinson (1926), who recognized Molluginaceae as distinct from Aizoaceae. However, the family Molluginaceae was not generally recognized until the later part of the 20th century, when it was demonstrated that some of its members did not have betalains as Aizoaceae and most other families of Caryophyllales. Instead they had anthocyanins as Caryophyllaceae, which led to the view that Molluginaceae and Caryophyllaceae are a pair of closely related families (e.g., Mabry, 1977).

In the overview of Molluginaceae by Endress & Bittrich (1993), 13 genera were included in the following order: *Corbichonia* Scop., *Limeum* L., *Macarthuria* Hügel ex Endl., *Psammotropha* Eckl. & Zeyh., *Adenogramma* Rchb.,

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Glischrothamnus Pilger, *Mollugo*, *Glinus* L., *Hypertelis* E.Mey. ex Fenzl, *Pharnaceum* L., *Suessenguthiella* Friedrich, *Coelanthum* E.Mey. ex Fenzl and *Polpoda* C.Presl. Endress & Bittrich (1993) regarded the anthocyanin-producing Molluginaceae as an early branch within Caryophyllales "as betalains must be considered as an advanced character common to most families of the order".

The molecular phylogenies that have appeared since the early 1990s (e.g., Cuénoud & al., 2002; Brockington & al., 2009, 2011; Christin & al., 2011) have led to a radically changed view of the circumscription of Caryophyllales, as well as of the circumscription of Molluginaceae and of its position within Caryophyllales. Currently available evidence indicates that Molluginaceae is sister to the Portulacineae clade within the core Caryophyllales and nested among betalain-producing families. Of the genera listed above for Molluginaceae, *Corbichonia* has been moved to Lophiocarpaceae, *Limeum* to Limeaceae, *Macarthuria* to Macarthuriaceae, and all species of *Hypertelis*, except the type, to Kewaceae (Christenhusz & al., 2014).

Within Molluginaceae, the results of Christin & al. (2011) strongly indicated that taxonomic changes are needed, particularly regarding the apparently grossly polyphyletic *Mollugo*. As for pigment data, Brockington & al. (2011) stated that the claim that Molluginaceae is an anthocyanic family "is not supported by any published data". The presence of anthocyanins in *Mollugo* (Mears, 1976) "was reported with no reference to experimental data" (Brockington & al., 2011), and the same applies to the report of anthocyanins in *Pharnaceum* (Clement & al., 1994). Otherwise, within Caryophyllales, the reports of anthocyanins in species of *Hypertelis* now placed in *Kewa* Christenh. in Kewaceae are surrounded by some doubt (Brockington & al., 2011), *Limeum* in Limeaceae is regarded as apparently unpigmented (Behnke & al., 1983), and some families, such as Simmondsiaceae, have not been examined for their pigments (Brockington & al., 2011). Brockington & al. (2015) showed that a single origin of betalain pigmentation in Caryophyllales is most likely and that, accordingly, anthocyanin-producing groups within the betalain clade are to be interpreted as evolutionary reversals.

The first aim of the present paper is to investigate the phylogenetic position and structure of Molluginaceae with a broader sampling than in previous studies, and to use the results to propose new generic delimitations and other taxonomic rearrangements in the family. The second aim is to add pigment data on members of Molluginaceae, Kewaceae, Limeaceae and Simmondsiaceae. Finally, we want to reconsider the current status of *Corbichonia* as a member of Lophiocarpaceae.

■ MATERIALS AND METHODS

Taxon sampling. — In total, 120 accessions from 75 currently recognized taxa (74 species and 1 variety in 43 genera) were included (Appendix 1), representing nearly all families within the core Caryophyllales. Approximately half of the recognized species of Molluginaceae were sampled, including 17 of the about 22 species currently recognized in *Mollugo* and at least one representative of all recognized genera. Eighty sequences were newly generated for this study, including in particular part of the nuclear ribosomal DNA (ITS).

DNA extraction, amplification and sequencing. — Dried leaf material (2–10 mg) from herbarium specimens was used for DNA extraction. Samples were extracted using the FastDNA SPIN kit (MP Biomedicals, Santa Ana, California, U.S.A.) following manufacturer's protocol except that two elution steps were generally used, with 50 µl of DES each time to maximize yield.

The nuclear ribosomal internal transcribed spacer (ITS) and chloroplast *trnK-matK* regions were amplified using PCR. The primers ITS4 and ITS5 (White & al., 1990) were used to amplify the ITS region, while various combinations of the forward primers trnKmatK_For H, M, G, and K and the reverse primers trnKmatK_Rev B, C, E, and I, all from Christin & al. (2011), except for trnKmatK_M (5′-ACTATGTATCATTGGT TAAGC-3′). The same PCR protocol was used for both regions, in 25 µl reactions including 1 unit GoTaq (Promega Corporation, Madison, Wisconsin, U.S.A.), 5× GoTaq Reaction Buffer (Promega), 0.5 mM $MgCl_2$, 0.15 mM each dNTP (New England Biolabs, Ipswich, Massachusetts, U.S.A.), 0.2 µM each primer, and approximately 0.6 ng extracted DNA. The following PCR program was used: initial denaturation of 3 min at 94°C; 37 cycles of 1 min denaturation at 94°C, 30 s annealing at 48°C or 51°C, 60 to 150 s extension at 72°C, and final extension of 10 min at 72°C.

PCR products were cleaned with the Exo-SAP PCR Product Pre-Sequencing Kit (USB Corporation, Cleveland, Ohio, U.S.A.). Cleaned PCR products were sequenced at the Rhode Island Genomics and Sequencing Center with either a 3130XL Genetic Analyzer or a 3500XL Genetic Analyzer (Applied Biosystems, Life Technologies, Grand Island, New York, U.S.A.). The same primers were used for PCR and sequencing, with additional internal primers being used to sequence samples for which *trnK-matK* could be amplified as a single fragment. Chromatograms were edited and contigs were constructed using ChromasPro v.1.7.5 (Technelysium, Tewantin, Queensland, Australia).

Sequence alignment and phylogenetic analyses. — Sequences were aligned using MUSCLE v.3.5 (Edgar, 2004) and alignments were checked by eye and manually adjusted in SeaView v.4.4.2 (Galtier & al., 1996; Gouy & al., 2010) and in AliView v.1.17.1 (Larsson, 2014). The alignments are available in TreeBase (study number S18909). Phylogenetic analyses were performed using RAxML-HPC2 v.8.1.11 (Stamatakis, 2014) on XSEDE or at the CIPRES Science Gateway (Miller & al., 2010) using RAxML v.8.0.22. Four separate analyses were performed. First a broad analysis of members of core Caryophyllales was made using *trnK-matK* and *rbcL* sequences and with *Simmondsia* as outgroup based on Christin & al. (2011). Then separate and combined analyses were made of *trnK-matK* and ITS sequences of members of Molluginaceae, along with representatives of families in the Portulacineae clade, and with *Limeum* as outgroup, the separate analyses being used to check for congruence. For each analysis, a search for the best tree was combined with 1000 bootstrap pseudoreplicates. The GTRCAT model was

used with 25 gamma rate categories. MrBayes v.3.2.6 (Ronquist & al., 2012) was run at the CIPRES Science Gateway on all four datasets. Models of nucleotide substitution were chosen according to the Akaike information criterion using jModelTest v.2.1.7 (Guindon & Gascuel, 2003; Darriba & al., 2012). Each analysis consisted of two runs of four chains each with 5 million generations, with the generations before the standard deviation of the split frequency reached 0.01 removed as burn-in (670,000 for core Caryophyllales, 685,000 for combined Molluginaceae, 510,000 for Molluginaceae *trnK-matK*, and 1,175,000 for Molluginaceae ITS). Substitution model parameters were estimated separately for the two genes when these were combined.

Chemical analysis of pigments. — Dried leaf samples of representatives of Simmondsiaceae, Limeaceae, Kewaceae and Molluginaceae (Appendix 2) were analyzed for presence of anthocyanins/betalains. The powdered plant material was extracted with acetone at room temperature three times with occasional stirring, filtered and evaporated. The macerate was then extracted three times with ethanol (EtOH) for three days each, filtered and evaporated, followed by extraction with EtOH/water (70 : 30), three days for each crop and freeze-drying of the aqueous part after evaporization. Pigments of each extract were investigated and identified using Liquid Chromatography-Mass Spectrometry² (LC-MS²) analysis.

For the LC-MS² analysis the crude extracts were dissolved in 50% acetonitrile (ACN), 0.1% formic acid (FA). The samples were injected by syringe through a PicoTip emittor at 0.3 µl/min connected to a Q-Tof Micro (Waters, Milford, Massachusetts, U.S.A.) with the voltage set at 1.4 kV. The analysis was carried out in positive ion mode and linear gradient from 10% (v/v) H_2O to 99% (v/v) ACN in 0.1% (v/v) FA at a flow rate of 0.3 µl/min over 75 min.

■ RESULTS

Core Caryophyllales dataset. — The best tree based on the core Caryophyllales dataset is shown in Fig. 1 (tree showing branch lengths in Electr. Suppl.: Fig. S1). *Macarthuria* (Macarthuriaceae) is strongly supported as sister to all other members of the ingroup. The position of *Limeum* (Limeaceae) is weakly supported. The sister-group relationship of *Lophiocarpus* and *Corbichonia* in Lophiocarpaceae is strongly supported and together they are sister to a clade with members of Kewaceae (*Kewa*), Barbeuiaceae (*Barbeuia*), Gisekiaceae (*Gisekia*), Aizoaceae (*Conicosia*, *Galenia*, *Gibbaeum*, *Mesembryanthemum*, *Sesuvium*, *Tetragonia*), Phytolaccaceae (*Phytolacca*), Sarcobataceae (*Sarcobatus*), Petiveriaceae (*Petiveria*, *Rivina*), and Nyctaginaceae (*Bougainvillea*, *Guapira*, *Mirabilis*). Molluginaceae s.str. is strongly supported as monophyletic, and as sister to a clade with members of Basellaceae (*Basella*), Montiaceae (*Lewisia*), Halophytaceae (*Halophytum*), Didiereaceae (*Alluaudia*), Talinaceae (*Talinum*), Anacampserotaceae (*Anacampseros*), Portulacaceae (*Portulaca*) and Cactaceae (*Opuntia*, *Pereskia*).

Molluginaceae dataset. — Separate analyses of the *trnK-matK* and the ITS data produced trees with very similar topology (Electr. Suppl.: Figs. S2, S3), and visual inspection revealed no well-supported conflict between them. This lack of conflict between nuclear and chloroplast markers was also evidenced with nuclear genes encoding PEPC (Christin & al., 2011). Therefore, the phylogenetic tree based on the combination of *trnK-matK* and ITS data was considered for further discussion.

The Molluginaceae s.str. clade (Fig. 2; tree showing branch lengths in Electr. Suppl.: Fig. S4) comprises two main well-supported clades (A and B), each resolved into generally well-supported branches. In Clade A, the type of *Mollugo*, *M. verticillata* L., is nested within a strongly supported clade, the *Mollugo* clade, which is sister to *Glinus*, and also comprises *M. enneandra* C.Wright from Cuba, *M. snodgrassii* B.L.Rob., *M. crockeri* J.T.Howell, *M. flavescens* Andersson and *M. floriana* (B.L.Rob.) J.T.Howell from the Galapagos Islands, *M. brasiliensis* Thulin & Harley and *Glischrothamnus ulei* Pilger from Brazil, and *M. disticha* (L.) Ser. from India and Sri Lanka. *Mollugo verticillata* is not monophyletic, with three samples from U.S.A., Canada and Italy forming a clade with *M. enneandra* from Cuba, and one sample from Bolivia being sister to the radiation of *Mollugo* on the Galapagos Islands. Also *M. brasiliensis* is not monophyletic, with two samples from Minas Gerais being sister to *Glischrothamnus ulei* and two from Bahia being sister to the clade with *M. verticillata* and its closest relatives.

The *Glinus* clade is strongly supported as monophyletic, with *G. oppositifolius* (L.) A.DC. sister to *G. setiflorus* Forssk., *G. radiatus* (Ruiz & Pav.) Rohrb. and *G. lotoides* L., the type of *Glinus*.

Finally in Clade A, there is a strongly supported clade, the *Trigastrotheca* clade, with *Mollugo molluginea* (F.Muell.) Druce, based on *Trigastrotheca molluginea* F.Muell., the type of *Trigastrotheca* F.Muell., as sister to a strongly supported clade with five samples of the widespread Asian *M. pentaphylla* L. Within *M. pentaphylla*, two samples from, respectively, India and Sri Lanka, come out together as strongly supported group sister to the rest. The *Trigastrotheca* clade is strongly supported as sister to the *Mollugo* clade and the *Glinus* clade together.

In Clade B, a clade with the widespread *Mollugo nudicaulis* Lam., *M. decandra* Scott Elliot from Madagascar, and *M. angustifolia* M.G.Gilbert & Thulin from Somalia is strongly supported as sister to the rest. Within this *Mollugo nudicaulis* clade, two samples of *M. nudicaulis* var. *navassensis* Ekman from the Caribbean are weakly supported as sister to the rest of the clade, in which the other samples of *M. nudicaulis* form a monophyletic group.

In the rest of Clade B, there is a clade with the southern African *Hypertelis spergulacea* E.Mey. ex Fenzl, the type of *Hypertelis*, the widespread *Mollugo cerviana* (L.) Ser., *M. fragilis* Wawra from Angola, and *M. walteri* Friedrich from Namibia as sister to the rest. Within this *Hypertelis* clade, the four samples of *Hypertelis spergulacea* form a strongly supported monophyletic group, as do the two samples of *Mollugo fragilis*. *Mollugo cerviana*, however, is polyphyletic. Seven samples of *M. cerviana* form a strongly supported clade that is sister to the rest of the *Hypertelis* clade, whereas six others are sister to *M. fragilis* plus two other samples of *M. cerviana* from Namibia. *Mollugo walteri* is strongly supported as sister to *Hypertelis spergulacea*.

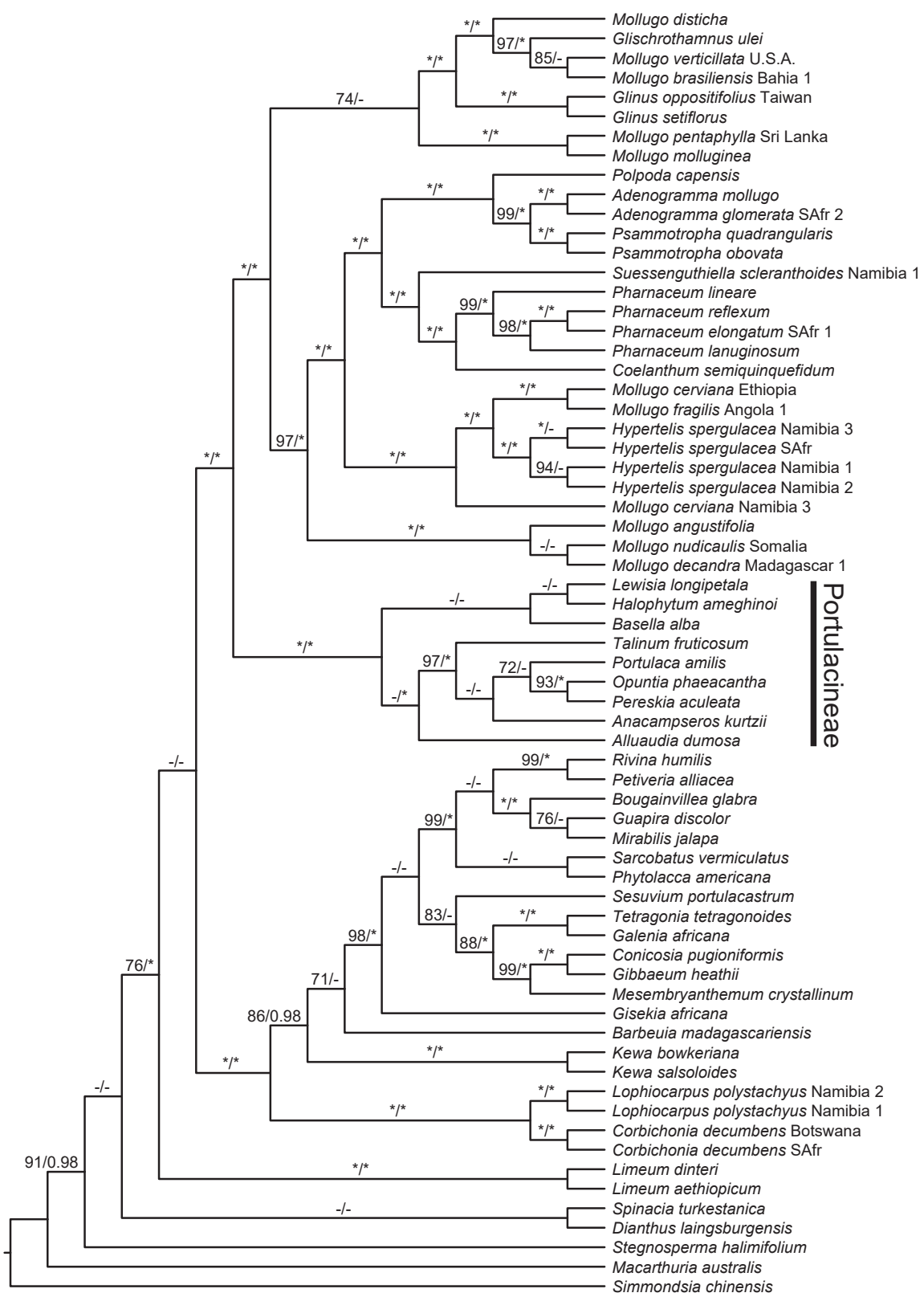


Fig. 1. Best tree from the RAxML analysis of the combined *trnK-matK* and *rbcL* core Caryophyllales dataset. Bootstrap values from 1000 bootstrap replicates and Bayesian posterior probabilities from the MrBayes analysis are above the branches. Bootstrap values of 100 and posterior probabilities of 1.0 are replaced by asterisks, while bootstrap values less than 70 and posterior probabilities less than 0.95 are replaced by dashes. When more than one accession per species was included, the localities after the names correspond to those in Appendix 1. SAfr refers to South Africa.

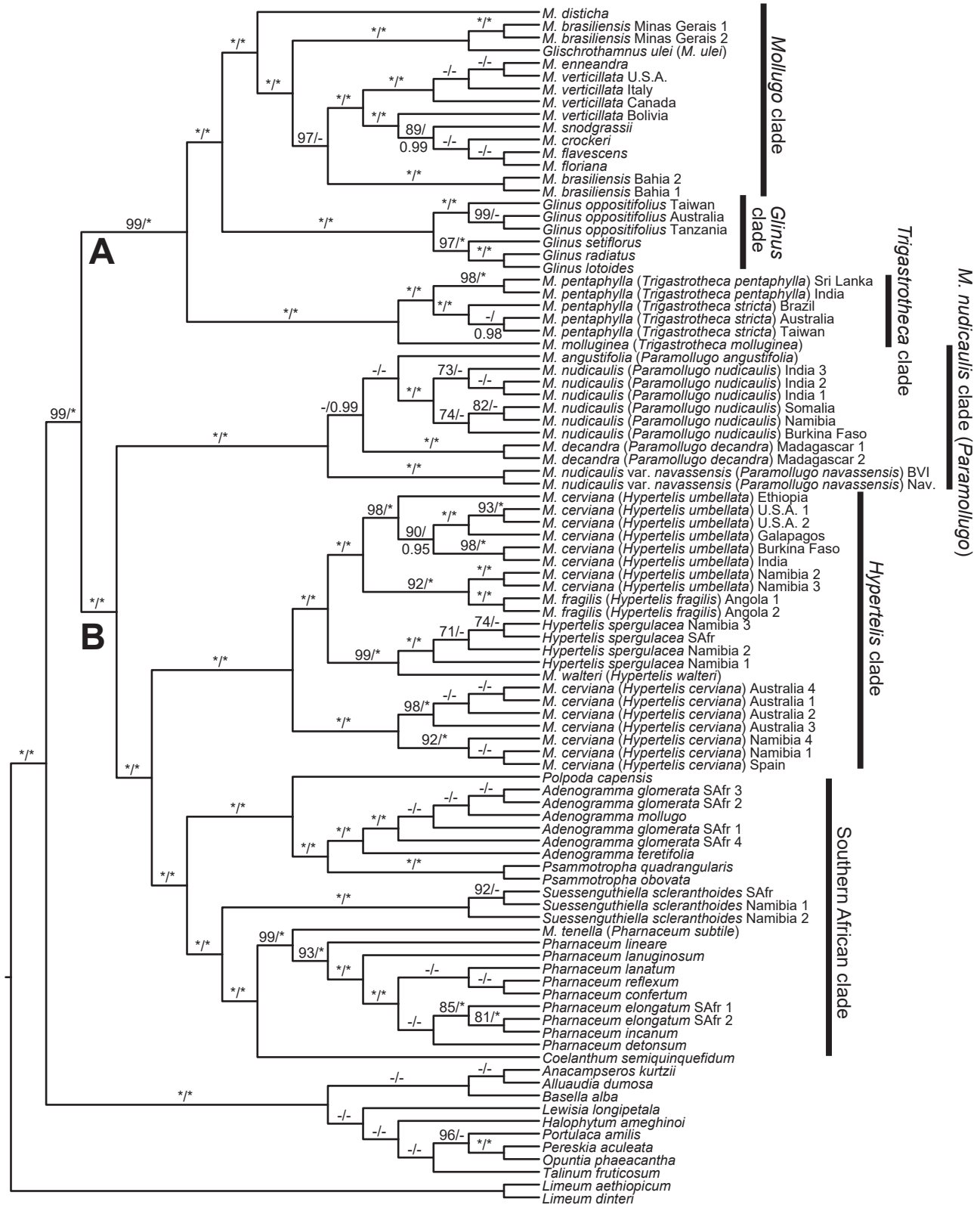


Fig. 2. Best tree from the RAxML analysis of the combined ITS and *trnK-matK* Molluginaceae dataset. Bootstrap values from 1000 bootstrap replicates and Bayesian posterior probabilities from the MrBayes analysis are above the branches. Bootstrap values of 100 and posterior probabilities of 1.0 are replaced by asterisks, while bootstrap values less than 70 and posterior probabilities less than 0.95 are replaced by dashes. When more than one accession per species was included, the localities after the names correspond to those in Appendix 1. Species names within parentheses are the new names proposed in this paper. The names to the right of the clades are the clade names used in the text. BVI refers to the British Virgin Islands, Nav. refers to Navassa Island, and SAfr refers to South Africa.

The *Hypertelis* clade is sister to a species-rich and strongly supported clade comprising samples of *Suessenguthiella*, *Coelanthum*, *Pharnaceum*, *Psammotropha*, *Adenogramma* and *Polpoda*, all almost entirely restricted to southern Africa. Within this southern African clade, *Mollugo tenella* Bolus ex Schltr. in Namibia and South Africa is sister to *Pharnaceum*. The southern African clade comprises two strongly supported clades, one with *Suessenguthiella*, *Coelanthum* and *Pharnaceum*, and the other with *Psammotropha*, *Adenogramma* and *Polpoda*.

Chemical analysis of pigments. — *Simmondsiaceae.* – The pyranoanthocyanin vitisin A was identified in the extract of *Simmondsia chinensis* (Link) C.K.Schneid. The compound was eluted at R_t 27.94 min and showed molecular ion of *m/z* 561.16 Da. The following MS² fragment peaks were recognized: *m/z* 399.01 Da (15%) due to loss of the glucose moiety (−162 Da) and *m/z* 267.07 Da (100%) due to the partial loss of aglycone (−132 Da; Flamini, 2013), as shown in Fig. S5 (Electr. Suppl.).

Limeaceae. – The anthocyanin malvidin-3-*O*-coumaroyl-glucoside-5-*O*-glucoside was detected in the extract of *Limeum aethiopicum* Burm.f. The peak was observed at molecular ion of *m/z* 801.159 Da and R_t 28.69 min. MS² fragmentation gave five signals: at *m/z* 801.21 Da (5%), *m/z* 656.25 Da (8%) (M +1), *m/z* 493.09 Da (6%), *m/z* 331.00 Da (8%) and *m/z* 213.06 Da (10%) (M +1), which are attributed to the loss of coumaroyl (−146 Da), glucose (−162 Da), glucose (−162 Da) and Diels-Alder fission of a malvidin unit (−120 Da) moieties, respectively (He & al., 2012), as shown in Fig. S6 (Electr. Suppl.).

Kewaceae. – The anthocyanins cyanidin-3-*O*-rutinoside and pelargonidin-3-*O*-rutinoside were identified in the *Kewa salsoloides* (Burch.) Christenh. extract at R_t 24.97 and 23.83 min, respectively. Cyanidin-3-*O*-rutinoside possessed molecular ion of *m/z* 595.16 Da. The MS² fragmentation resulted from loss of the glucose moiety (−162 Da) giving *m/z* 449.15 Da (80%) prior to Diels-Alder fission of a cyanidin-3-*O*-glucoside unit at *m/z* 329.68 Da (100%) (M +1) and at *m/z* 299.08 Da (45%) (M +1) (Tian & al., 2006), as shown in Fig. S7 (Electr. Suppl.).

The loss of a pelargonidin unit (−120 Da) and partial loss of a pelargonidin unit (−228 Da) were secondary to the cleavage of the glucose moiety (−162 Da), giving rise to a gradual decrease of the fragment mass as *m/z* 433.08 Da (7%), *m/z* 313.08 Da (100%) and *m/z* 85.02 Da (21%) (M +1). The compound was identified as pelargonidin-3-*O*-rutinoside at molecular ion of *m/z* 579.17 Da (Tian & al., 2006), as shown in Fig. S8 (Electr. Suppl.).

Molluginaceae. – The anthocyanin pelargonidin-3,5-*O*-diglucoside with molecular ion of *m/z* 595.14 Da and R_t 24.14 min was identified in the *Mollugo verticillata* extract. The MS² fragmentation peak at *m/z* 433.10 Da (47%) (−162 Da) justified the identification of the anthocyanin derivative. The fragmentation was due to loss of a glucose moiety (−120 Da), leading to formation of a *m/z* 313.07 Da (100%) mass, followed by Diels-Alder fission of a pelargonidin unit (−228 Da) and partial loss of a pelargonidin unit ending up with a mass of *m/z* 85.02 Da (10%) (Lin & al., 2008), as shown in Fig. S9 (Electr. Suppl.). Similarly, delphinidin-3-*O*-rutinoside, an anthocyanin analogue, was identified at *m/z* 611.14 Da and R_t 20.84 min. The loss of a rutinoside unit (−308 Da) corresponded to the fragmentation pattern of *m/z* 303.08 Da (100%) (Wu & Prior, 2005; Chen & al., 2014), as shown in Fig. S10 (Electr. Suppl.).

The anthocyanin cyanidin-3-*O*-rutinoside with molecular ion of *m/z* 595.16 Da and R_t 23.83 min was detected in the extract of *Hypertelis spergulacea*. The fragment ions at *m/z* 449.13 Da (72%) and *m/z* 287.06 Da (12%) were related to the loss of a rutinoside moiety (Tian & al., 2006), as shown in Fig. S11 (Electr. Suppl.). The precursor ion of *m/z* 287.06 Da (12%) showed that the anthocyanin contained cyanidin within its structure.

■ DISCUSSION

The topology of the strict consensus tree based on the core Caryophyllales dataset (Fig. 1) largely agrees with the results of Christin & al. (2011) and Brockington & al. (2011).

The position of *Limeum* (Limeaceae) is weakly supported, but it may be sister to the Globular Inclusion Clade (Brockington & al., 2013). *Lophiocarpus* and *Corbichonia* in Lophiocarpaceae are together sister to the rest of the Raphid Clade (Brockington & al., 2013). Molluginaceae in its new restricted sense is monophyletic and sister to the Portulacineae clade (Arakaki & al., 2011; Brockington & al., 2011). The topology of the strict consensus tree based on the Molluginaceae dataset (Fig. 2) in all essentials agrees with the results of Christin & al. (2011), the main difference being the increased sampling in our study. Our clades A and B correspond to the two major clades in figure 3 of Christin & al. (2011), and the topology and main groupings within these clades are also the same.

***Mollugo* clade. —** In this newly circumscribed *Mollugo* clade, *M. disticha* is strongly supported as sister to the rest of the species. This species, distributed in India and Sri Lanka, is the only species in the *Mollugo* clade that is not native to the Americas, and it also differs from all other members of this clade by having raceme-like (not umbel-like) inflorescences. This could be a reason for treating *M. disticha* in a genus of its own, but as it agrees with all other members of the *Mollugo* clade in having leaves without stipules in false whorls at the nodes and with most other members of the clade in having an indumentum of glandular hairs (otherwise found nowhere else in the family), we prefer to retain *M. disticha* in *Mollugo*.

Glischrothamnus ulei is firmly nested within the *Mollugo* clade and we propose that the name of this Brazilian endemic is transferred to *Mollugo*. The species is unique within the family by being dioecious. It is also unique in the *Mollugo* clade by being a shrub, but in other characters it agrees well with other species of this group.

Further work is needed on the biphyletic *Mollugo brasiliensis* (Thulin & Harley, 2015). The type collection of this species, *Poveda & Guedes PCD 515*, is from Bahia and falls within the clade that is sister to *M. verticillata* and its closest relatives. Apparently only material from Bahia should be included in *M. brasiliensis*, whereas material from Minas Gerais should be placed in a species of its own.

Further work is also needed as regards *Mollugo verticillata*. The type of this is Herb. Linn. 112.4 (Reveal & al., 1987), a specimen of unknown origin, but almost certainly from North America. The three samples from U.S.A., Canada and Italy that form a clade together with *M. enneandra* apparently represent "typical" *M. verticillata*, whereas the taxon represented by a single sample from Bolivia that is sister to the Galapagos radiation needs another name.

***Glinus* clade. —** The strongly supported *Glinus* is also well characterized morphologically by its seeds with a filiform-appendaged aril and its indumentum of often stellate hairs, features that are not found elsewhere in the family. Also the commonly present and sometimes petaloid staminodes in the flowers are unique for *Glinus* within Molluginaceae (Ronse De Craene, 2013).

***Trigastrotheca* clade. —** The clade with *Mollugo molluginea* and *M. pentaphylla* can no longer be retained in *Mollugo*, but the name *Trigastrotheca* based on *T. molluginea* is available. The members of this clade differ from *Mollugo* in a strict sense by having stipules and by having filaments that are filiform from a broader base. *Trigastrotheca molluginea*, endemic to Australia, is strongly supported as sister to the rest of the clade, and it is also morphologically unique in the family by having capitate stigmas and bladder-like capsules markedly notched at the apex. Therefore, *T. molluginea* could be treated in a genus of its own, but we prefer to include all the members of this clade in *Trigastrotheca*. This gives a more informative classification, and besides the characters listed above, all members of the clade also have, for example, a similar ornamentation of the seeds.

The mainly Asian *M. pentaphylla* is usually widely circumscribed to include *M. stricta* L. (e.g., Fosberg, 1995). However, Sivarajan & Usha (1983) argued that *M. pentaphylla* should be restricted to some of the material from India and Sri Lanka, whereas the name *M. stricta* should be reinstated for the widespread taxon. Our molecular phylogeny, with two samples from India and Sri Lanka as strongly supported sister to the rest, agrees with this view, and we therefore suggest that *M. stricta* be treated as a distinct species.

***Mollugo nudicaulis* clade. —** The members of this clade cannot be retained in *Mollugo*, and, as the only generic name available is the illegitimate *Lampetia* Raf., a new name is needed for them. They differ from *Mollugo* in a strict sense by having alternate leaves that are generally crowded at the base of the stem (not in false whorls at the nodes). The widespread *M. nudicaulis* is not monophyletic and *M. nudicaulis* var. *navassensis* from the Caribbean should be treated as a distinct species. *Mollugo decandra* from Madagascar differs markedly from the other members of the clade by being a small shrub with leaves either scattered along long shoots or clustered on short shoots, and by having flowers with ca. 10 (not 3–5) stamens.

***Hypertelis* clade. —** Most of the members of this clade were previously in *Mollugo*, but should now all be placed in *Hypertelis*. The 15 samples of *M. cerviana* that were sequenced fall out in three different places in this clade. Seven of the samples form a clade that is sister to the rest of the *Hypertelis* clade. They have linear basal leaves and five stamens and agree with the type of this widespread species. Six other samples form a clade that is sister to *M. fragilis* plus a clade with two samples from Namibia. These samples, which have obovate basal leaves and false whorls of linear leaves at the nodes, agree with the type of *Pharnaceum umbellatum* Forssk. Also the two samples from Namibia that form the clade sister to *M. fragilis* have obovate basal leaves and false whorls of linear leaves at the nodes, whereas *M. fragilis* is characterized by having obovate leaves throughout.

Mollugo walteri, with 10 stamens, is sister to *Hypertelis spergulacea* with 15–25 stamens, whereas all other members of the *Hypertelis* clade have 5 stamens. *Mollugo walteri* has sometimes been treated as a variety or form of *M. cerviana*, but is clearly a distinct species. In the key to the species of *Hypertelis* and *Kewa* published by Christenhusz & al. (2014), *H. spergulacea* is keyed out as having 20–30 stamens in bundles as opposed to the free stamens in *Kewa*. However, all members of the *Hypertelis* clade have free stamens too, although in *H. spergulacea* they tend to be arranged in five groups of about three to five stamens each.

The members of the *Hypertelis* clade are unique in Molluginaceae by having fully developed C_4 photosynthesis, with the exception of *H. spergulacea* that is a putative C_3–C_4 intermediate (Christin & al., 2011). *Hypertelis spergulacea* may represent a reversal from C_4 to C_3–C_4 or, alternatively, there may have been two independent transitions from C_3–C_4 to C_4 in this clade. Christin & al. (2011) strongly preferred the latter hypothesis based on analyses of C_4 genetic determinants. Duplication of the gene encoding a key C_4 enzyme in "the *fragilis* group" sensu Christin & al. (2011) preceded C_4 optimization of the gene, implying that the transition between C_3–C_4 intermediacy and C_4 occurred in this group after it separated from *M. cerviana* s.str., which underwent independent, non-homologous C_4 optimization. *Mollugo walteri*, the sister of *H. spergulacea*, has not been included in previous studies and its photosynthetic system is unknown.

Southern African clade. — The southern African clade is divided into two subclades. The members of the subclade with *Suessenguthiella*, *Coelanthum* and *Pharnaceum* all have ovaries with numerous ovules in each carpel (locule), whereas in the subclade with *Psammotropha*, *Adenogramma* and *Polpoda*, each carpel of the ovary has a single ovule only. *Mollugo tenella* cannot be retained in *Mollugo* and should be placed in *Pharnaceum*, where it also fits morphologically. With the inclusion of *M. tenella* in *Pharnaceum*, all of the genera in the southern African clade are monophyletic. *Suessenguthiella* is unique in the family by having tepals with a projecting mucro on the back, *Coelanthum* is unique in having the tepals united at the base for at least half their length, and *Pharnaceum* is unique in having a combination of many-seeded capsules and flowers almost always with a nectariferous disk. In the subclade with a single ovule in each carpel, *Psammotropha* differs from the other genera by having ovaries with 3–5 carpels, *Adenogramma* differs by having ovaries with a single carpel that develops into a 1-seeded nutlet, and *Polpoda* differs by having flowers with exserted stamens and styles and ovaries with two carpels.

All genera in the southern African clade therefore are both molecularly and morphologically well supported.

Taxonomic implications within Molluginaceae. — On the basis of the phylogenetic analyses numerous taxonomic changes within Molluginaceae are proposed below under Taxonomy. The new names for the species included in the trees are added within parentheses in Fig. 2. In Fig. S4 (Electr. Suppl.), with a tree showing branch lengths, only the new names are used. Figure S4 (Electr. Suppl.) also makes clear the remarkably long branches that characterize many of the clades within the family.

Chemical analysis of pigments. — The report of vitisin A in *Simmondsia chinensis* shows, for the first time, that Simmondsiaceae is an anthocyanin-producing family. This is also what could be expected from its phylogenetic position outside the betalain-producing clade within the core Caryophyllales. Brockington & al. (2015) showed that a single origin of betalain pigmentation in Caryophyllales is most likely, and that reversals to anthocyanins seem to have occurred in Kewaceae and Molluginaceae, Caryophyllaceae being a possible third case.

The detection of anthocyanins in *Kewa salsoloides* confirms old reports of unspecified anthocyanins in *K. salsoloides* and *K. bowkeriana* (Sond.) Christenh. (Beck & al., 1962, as *Hypertelis salsoloides* (Burch.) Adamson and *H. bowkeriana* Sond.), as well as in *K. angrae-pequenae* (Friedrich) Christenh. (Mabry, 1977, as *H. angrae-pequenae* Friedrich). As Kewaceae is nested among betalain-producing families, the view that it represents a reversal from betalains to anthocyanins (Brockington & al., 2011, 2015) is supported.

The report of anthocyanins in *Mollugo verticillata* and *Hypertelis spergulacea*, species representing the two major clades A and B in Molluginaceae (Fig. 2), is in agreement with previous findings of unspecified anthocyanins in *Mollugo* (Mears, 1976) and *Pharnaceum* (Clement & al., 1994). As Molluginaceae is nested among betalain-producing families, the view that it represents a reversal from betalains to anthocyanins (Brockington & al., 2011, 2015) is corroborated.

Limeum in Limeaceae has up to now been regarded as apparently unpigmented (Behnke & al., 1983; Endress & Bittrich, 1993). However, we here report an anthocyanin from *Limeum aethiopicum*. As Limeaceae, albeit with low support, is nested among betalain-producing families, it seems to represent a previously undetected reversal from betalains to anthocyanins. At least three such reversals are therefore now documented.

Status of *Corbichonia*. — The family Lophiocarpaceae was proposed by Doweld & Reveal (2008) to accommodate *Lophiocarpus* and *Corbichonia*, in accordance with the phylogenies presented by Cuénoud & al. (2002) and others. However, the validating description for the family is based entirely on *Lophiocarpus*. This is understandable as *Lophiocarpus* and *Corbichonia* morphologically are about as different as two plant groups can possibly be (Fig. 3). They both produce betalains (Cuénoud & al., 2002) and have alternate, simple, entire leaves without stipules, but these are trivial characters in core Caryophyllales and no morphological synapomorphies for the family in its current sense have been suggested. Instead, both *Lophiocarpus* and *Corbichonia* are morphologically unique within Caryophyllales, *Lophiocarpus* by its androecium of four stamens, three alternating with sepals and one opposite a sepal (Fig. 3A), and *Corbichonia* by its hypogynous flowers with ca. 20 stamens supplemented by outer whorls of 20–25 petals of staminodial origin (Fig. 3B). The two genera also differ markedly in leaf and inflorescence morphology, ovary structure, placentation, and in fruit and seed morphology (for micromorphological differences in pericarp and seed coat, see Sukhorukov & al., 2015). *Lophiocarpus* and *Corbichonia* are both small genera and their sister-group relationship seems well supported. Still, we argue that in this case taxonomy is better served by the recognition of two morphologically very distinctive families rather than having a single family without supporting characters.

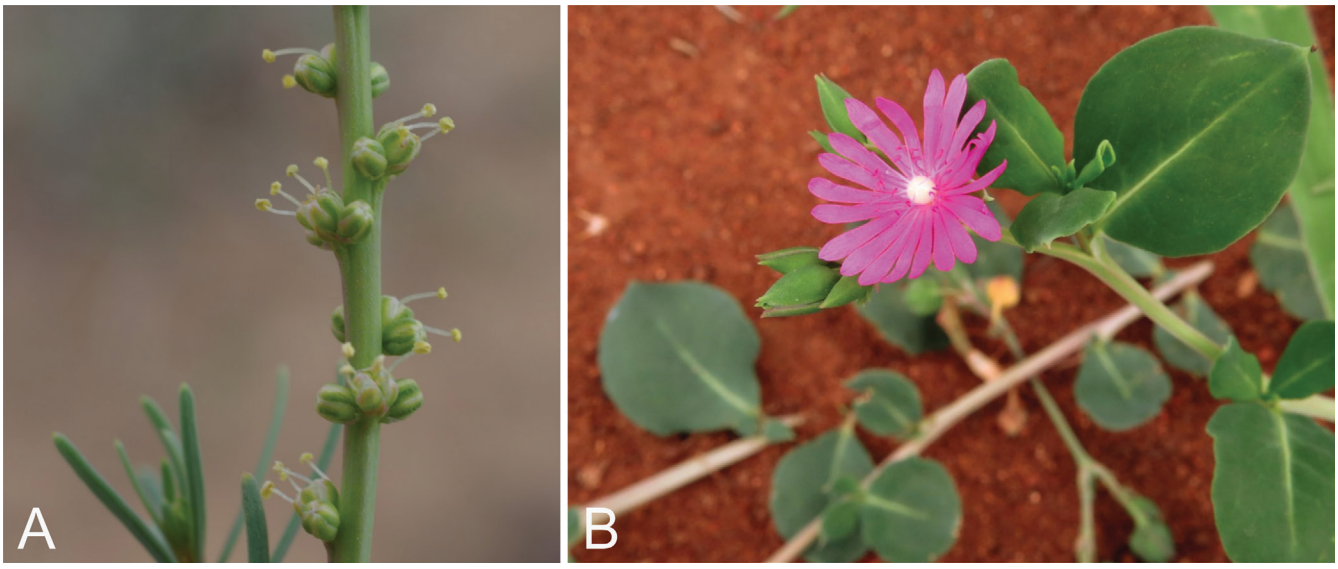


Fig. 3. Flowering shoots of: **A,** *Lophiocarpus polystachyus*, portion of inflorescence and leaves (photo by Mats Thulin); **B,** *Corbichonia decumbens*, inflorescence and leaves (photo by Kate Braun).

■ TAXONOMY

Molluginaceae Bartl. in Bartling & Wendland, Beitr. Bot. 2: 158. 1825 ("Mollugineae"), nom. cons. – Type: *Mollugo* L.
= Pharnaceaceae Martinov, Tekhno-Bot. Slovar: 477. 1820 ("Pharnaceae") – Type: *Pharnaceum* L.
= Glinaceae Mart., Consp. Regn. Veg.: 64. 1835 ("Glinoideae") – Type: *Glinus* L.
= Adenogrammaceae Nakai in J. Jap. Bot. 18: 101. 1942 ("Adenogrammataceae") – Type: *Adenogramma* Rchb.
= Polpodaceae Nakai in J. Jap. Bot. 18: 102. 1942 – Type: *Polpoda* C.Presl

Annual or perennial herbs, or sometimes small shrubs or subshrubs, bisexual or rarely (*Mollugo ulei*) dioecious, usually glabrous but glandular (*Mollugo*) or stellate (*Glinus*) hairs or papillae (*Paramollugo*) sometimes present. Leaves alternate, opposite, in false whorls, or crowded in a basal rosette, simple, entire, often mucronate to aristate at the apex; stipules membranous, often fimbriate-laciniate, but sometimes small, obsolete or absent. Flowers actinomorphic, small, in terminal or seemingly axillary, umbel-, panicle- or raceme-like or more or less dichotomously branching cymes, or flowers solitary; perianth simple; tepals (4–)5, free, or sometimes basally united, with membranous margins and with the upper surface often petaloid, with quincuncial aestivation; staminodes rarely present (*Glinus*), sometimes petaloid; nectariferous disc sometimes present; stamens 3–5, 10, 15 or rarely more (*Glinus*, *Hypertelis*), the filaments free or rarely connate at the base (*Polpoda*, *Suessenguthiella*); anthers dehiscing by longitudinal slits; pollen grains usually tricolpate, in *Mollugo* sometimes polypantocolpate or polypantoporate; carpels 2–5, connate, or carpel solitary (*Adenogramma*); ovules usually few to many per carpel, but sometimes only one (*Adenogramma*, *Polpoda*, *Psammotropha*), with axile or seemingly basal placentation; styles 1–5, sometimes (*Polpoda*, *Psammotropha*) ± connate at the base and forming a single 2–5-lobed style; stigmas linear or rarely (*Trigastrotheca molluginea*) capitate. Fruit a loculicidal capsule or a nutlet (*Adenogramma*). Seeds usually subreniform-suborbicular in outline; aril usually absent or obsolete, but sometimes prominent (*Glinus*); embryo peripheral, curved around perisperm. — Fig. 4.

Eleven genera and some 90 species, mainly in subtropical and tropical regions, but with some species extending into warm-temperate areas, most diverse in southern Africa.

Key to genera of Molluginaceae

1. Seeds arillate, the aril filiform-appendaged; indumentum often of stellate hairs; staminodes often present …… 2. ***Glinus***
1. Seeds exarillate or aril minute and without appendage; indumentum of glandular hairs, papillae or absent; staminodes absent …… 2
2. Tepals with a projecting mucro on the back …… 9. ***Suessenguthiella***
2. Tepals without mucro …… 3
3. Tepals united at the base for at least half their length …… 10. ***Coelanthum***
3. Tepals free or only slightly united at the base …… 4
4. Ovary of 1 carpel with a single ovule; fruit a 1-seeded nutlet …… 7. ***Adenogramma***
4. Ovary of 2–5 carpels; fruit a 2- to many-seeded capsule .. 5
5. Stamens and styles exserted; ovary of 2 carpels; styles 2 …… 6. ***Polpoda***
5. Stamens and styles not exserted; ovary of 3–5 carpels; styles 3–5 …… 6
6. Ovary of 3–5 carpels, each with a single ovule …… 8. ***Psammotropha***
6. Ovary of 3 carpels, each with few to numerous ovules . 7
7. Stipules absent …… 8
7. Stipules present, at least on upper leaves, sometimes small or forming a narrow rim ± clasping the node …… 9
8. Leaves in false whorls at the nodes …… 1. ***Mollugo***
8. Leaves alternate, either all crowded in a basal rosette, or leaves scattered along long shoots and crowded on short shoots …… 4. ***Paramollugo***
9. Flowers in umbel-like cymes …… 5. ***Hypertelis***
9. Flowers in panicle- or raceme-like cymes …… 10
10. Seeds papillose; disk absent; stipules entire or toothed .. …… 3. ***Trigastrotheca***
10. Seeds various but not papillose; lobed annular disk mostly present at base of ovary; stipules mostly fimbriate-laciniate …… 11. ***Pharnaceum***

1. ***Mollugo*** L., Sp. Pl.: 89. 1753 ≡ *Galiastrum* Fabr., Enum.: 108. 1759, nom. illeg. superfl. – Type (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 2: 35. 1913): *Mollugo verticillata* L.
= *Glischrothamnus* Pilger in Bot. Jahrb. Syst. 40: 396. 1908, **syn. nov.** – Type: *Glischrothamnus ulei* Pilger.

Annual or perennial herbs or small shrubs or subshrubs, rarely dioecious (*M. ulei*), glabrous or with indumentum of glandular hairs. Leaves in false whorls; stipules absent. Flowers in seemingly axillary, sessile or pedunculate, umbel- or raceme-like cymes, or flowers solitary; bracts small, membranous or partly herbaceous. Tepals 5, free. Stamens 3–9. Ovary of 3 carpels, with few to numerous ovules; styles 3. Capsule dehiscent with 3 valves. Seeds 3 to numerous, smooth to tuberculate or with curved parallel ridges. — Fig. 4A.

About 15 species, native in tropical to warm temperate parts of North and South America, *M. verticillata* occasionally introduced in Europe, Africa and Asia, *M. disticha* restricted to India and Sri Lanka. *Mollugo* differs from other members of Molluginaceae by having a combination of leaves in false whorls, no stipules, and ex-arillate seeds.

Apart from the nine species included in our phylogenetic study, also *M. brevipes* Urb., *M. cubensis* Urb. and *M. pinosia* Urb., all endemic on Cuba, belong here. Further work is needed as regards the non-monophyletic *M. brasiliensis* and *M. verticillata*. The following new combination is proposed:

Mollugo ulei (Pilger) Thulin, **comb. nov.** ≡ *Glischrothamnus ulei* Pilger in Bot. Jahrb. Syst. 40: 396. 1908 – **Lectotype (designated here):** Brazil, Bahia, Serra do São Ignacio, Feb 1907, *Ule 7211* (B barcode B 10 0242329 [digital

image!]; isolectotypes: G barcode G00301593 [digital image!], K barcode K000471682!).

2. ***Glinus*** L., Sp. Pl.: 463. 1753 ≡ *Rolofa* Adans., Fam. Pl. 2: 256. 1763, nom. illeg. superfl. – Type: *Glinus lotoides* L.

Annual herbs, with indumentum of often stellate hairs. Leaves opposite or in false whorls; stipules absent. Flowers in seemingly axillary, sessile umbel-like cymes; bracts membranous. Tepals 5, free. Staminodes mostly present, in various numbers, often with bifid tips, sometimes petaloid. Stamens 3–20(–30). Ovary of 3–5 carpels, with numerous ovules; styles 3–5. Capsule dehiscent with 3–5 valves. Seeds numerous, each with a long filiform-appendaged aril. — Fig. 4B.

About 10 species, some pantropical and some extending into temperate areas as weeds. *Glinus* differs from other members of Molluginaceae by its indumentum of often stellate hairs, presence of staminodes, and by the filiform-appendaged aril on the seeds.

3. ***Trigastrotheca*** F.Muell. in Hooker's J. Bot. Kew Gard. Misc. 9: 16. 1857 – Type: *Trigastrotheca molluginea* F.Muell.

Annual or perennial glabrous herbs. Leaves in false whorls; stipules present, membranous, often toothed. Flowers in terminal or leaf-opposed, panicle- or raceme-like cymes; bracts membranous. Tepals 5, free. Stamens 3–5; filaments filiform from a broader base. Ovary of 3 carpels, with numerous ovules; styles 3. Capsule with very thin and membranous wall, tardily dehiscent with 3 valves. Seeds few to numerous, orbicular-reniform, papillose. — Fig. 4C.

Three species, mainly in tropical parts of Asia and Australia. *Trigastrotheca* differs from *Mollugo* by having stipules and broad-based filaments. Mueller (l.c.) in the protologue of *Trigastrotheca* described the fruits as "indehiscens, irregulariter rumpens", but the capsules are loculicidally dehiscent, although the valves often remain more or less united at the tips and only tardily split apart.

Key to the species of *Trigastrotheca*

1. Leaves linear; styles with capitate stigmas . . ***T. molluginea***
1. Leaves lanceolate to narrowly elliptic or obovate; styles with linear stigmas 2
2. Lower leaves obovate, obtuse ..... ***T. pentaphylla***
2. Lower leaves lanceolate to narrowly elliptic, ± acute ..... ***T. stricta***

Trigastrotheca molluginea F.Muell. in Hooker's J. Bot. Kew Gard. Misc. 9: 16. 1857 ≡ *Mollugo trigastrotheca* F.Muell., Pl. Victoria 1: 201. 1862, nom. illeg. superfl. ≡ *Mollugo molluginea* (F.Muell.) Druce in Rep. Bot. Soc. Exch. Club Brit. Isles 4 (Suppl. 2): 636. 1917 ("*molluginis*") – Holotype: Australia, Victoria, "in planitiebus apricis præsertim subsalinis ad rivum Sturt's Creek", Feb 1856, *Mueller s.n.* (MEL barcode MEL 723998 [digital image!]).

Trigastrotheca molluginea (Fig. 4C) is known only from north-western Australia.

Trigastrotheca pentaphylla (L.) Thulin, **comb. nov.** ≡ *Mollugo pentaphylla* L., Sp. Pl.: 89. 1753 ≡ *Pharnaceum pentaphyllum* (L.) Spreng., Syst. Veg. 1: 949. 1824 – **Lectotype (designated here):** Sri Lanka, "Habitat in Zeylona", *Hermann s.n.* (BM barcode BM000621882 [digital image!]).

Tardieu-Blot (1967: 94) designated *Osbeck s.n.*, Herb. Linn. 112.8 (LINN) as lectotype of *Mollugo pentaphylla* and this was accepted by Jarvis (2007). However, this Osbeck specimen originates from "Canton sinensium" and therefore cannot be type material of *M. pentaphylla* that in the protologue is said to be from "Zeylona". According to *ICN* Art. 9.17 (McNeill & al., 2012) a lectotype can be superseded if "it is in serious conflict with the protologue and another element is available that is not in conflict with the protologue". The Chinese origin of the lectotype proposed by Tardieu-Blot (1967) is here regarded as serious conflict with the protologue. The phrase name of *Mollugo pentaphylla* used by Linnaeus in the protologue is taken from "Fl. Zeyl. 51". The specimen in Hermann's herbarium here designated as the new lectotype has the figure "51". Furthermore, the previous lectotype from China represents *Mollugo stricta*, and without change of lectotype the plant from Sri Lanka apparently would be without a name.

Trigastrotheca pentaphylla is known from India and Sri Lanka.

Trigastrotheca stricta (L.) Thulin, **comb. nov.** ≡ *Mollugo stricta* L., Sp. Pl., ed. 2: 131. 1762 ≡ *Pharnaceum strictum* (L.) Spreng., Syst. Veg. 1: 949. 1824 ≡ *Mollugo pentaphylla* var. *stricta* (L.) Hochr. in Candollea 2: 356. 1925 – **Lectotype (designated here):** "Habitat in Asia", Herb. Linn. 112.1 (LINN [digital image!]).

Herb. Linn. 112.1 is the only specimen cited as original material of *Mollugo stricta* by Jarvis (2007). It is a specimen of unknown origin that Linnaeus had acquired from Breynius.

Trigastrotheca stricta is widespread in tropical and subtropical Asia and Australia, and also occurs as an occasional introduction in Africa and South America. In India and Sri Lanka, where both *T. stricta* and *T. pentaphylla* occur, the two species can mostly be easily separated by the leaf-shape as indicated in the key. Sivarajan & Usha (1983) also mentioned differences in tepal and seed morphology, but these do not seem to hold true in a larger sample.

4. ***Paramollugo*** Thulin, **nom. nov.** ≡ *Lampetia* Raf., Fl. Tellur. 3: 34. 1837, nom. illeg., non K.D.Koenig, Icon. Foss. Sectiles: 2, t. 2, fig. 23. 1825 – Type: *Paramollugo nudicaulis* (Lam.) Thulin.

Annual or perennial glabrous or sometimes papillose herbs or small shrubs. Leaves alternate, mostly all crowded in a basal rosette or sometimes leaves scattered along long shoots and crowded on short shoots; stipules absent. Flowers in seemingly axillary, dichotomously branched or sometimes raceme-like cymes; bracts small, membranous. Tepals 5, free. Stamens 3–5 or ca. 10. Ovary of 3 carpels, with numerous ovules; styles 3, short. Capsule dehiscent with 3 valves. Seeds numerous, papillose. — Fig. 4D, E.

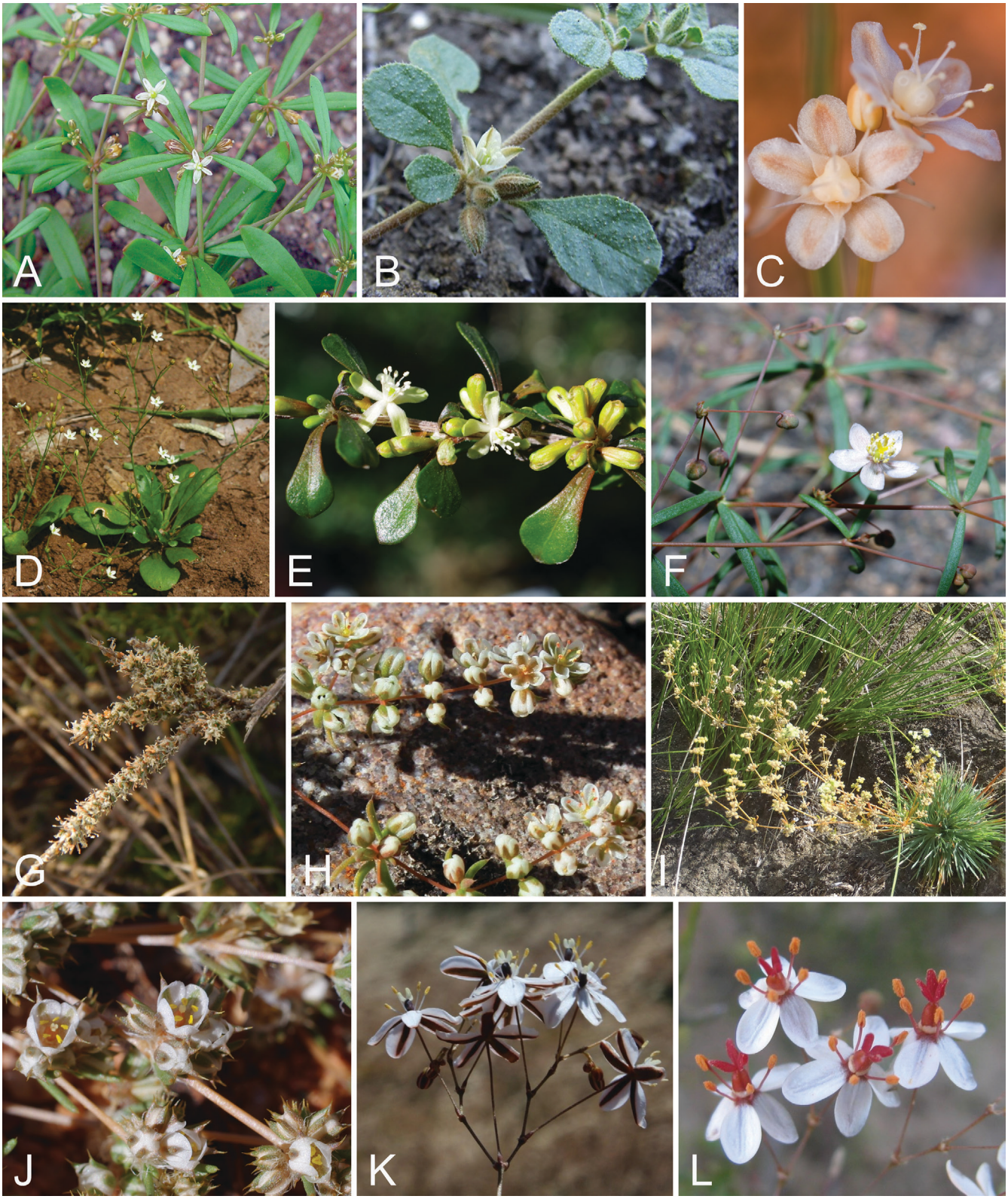


Fig. 4. Representative species of genera of Molluginaceae. **A,** *Mollugo verticillata* (photo by Arthur Haines, New England Wild Flower Society); **B,** *Glinus lotoides* (photo by Sara Gold, Wildflowers of Israel, http://www.wildflowers.co.il/English/); **C,** *Trigastrotheca molluginea* (photo by Farhan Bokhari); **D,** *Paramollugo nudicaulis* (photo by Bart Wursten); **E,** *Paramollugo decandra* (photo by Mats Thulin); **F,** *Hypertelis spergulacea* (photo by Mats Thulin); **G,** *Polpoda capensis* (photo by Melda Goets); **H,** *Adenogramma glomerata* (photo by Tony Rebelo); **I,** *Psammotropha myriantha* (photo by Nicky van Berkel); **J,** *Suessenguthiella scleranthoides* (photo by Mats Thulin); **K,** *Pharnaceum lineare* (photo by Tony Rebelo); **L,** *Pharnaceum elongatum* (photo by Douglas Euston-Brown).

Six species, one almost pantropical, one restricted to Somalia, one to Madagascar, and three to the West Indies. *Paramollugo* can be distinguished from other members of Molluginaceae by having a combination of mostly dichotomously branched inflorescences and ex-stipulate leaves that are alternate and either all crowded in a basal rosette or scattered along long shoots and crowded on short shoots. The distinctly papillose seeds are also characteristic.

Key to the species of *Paramollugo*

1. Leaves scattered along long shoots and crowded on short shoots; stamens ca. 10 …… ***P. decandra***
1. Leaves crowded in a rosette at base of plant; stamens 3–5 …… 2
2. Plant with a creeping woody rhizome; leaves obovate-cuneate, densely and distichously arranged at base of plant, marcescent …… ***P. cuneifolia***
2. Plant an annual or perennial herb; leaves not as above .. 3
3. Leaves linear, up to 1 mm wide …… ***P. angustifolia***
3. Leaves of varying shape but not linear, mostly well over 1 mm wide …… 4
4. Leaves with a ± triangular apical portion, abruptly narrowed below into a petiole-like base …… ***P. deltoidea***
4. Leaves obovate to narrowly oblanceolate, gradually narrowed at the base …… 5
5. Plant perennial; leaves narrowly oblanceolate, up to 3 mm wide …… ***P. navassensis***
5. Plant annual; leaves obovate-spathulate, mostly well over 3 mm wide …… ***P. nudicaulis***

Paramollugo angustifolia (M.G.Gilbert & Thulin) Thulin, **comb. nov.** ≡ *Mollugo angustifolia* M.G.Gilbert & Thulin in Nordic J. Bot. 13: 169. 1993 – Holotype: Somalia, Bay Region, ca. 3 km SW of Diinsoor, near Buur Diinsoor, 02°24′ N, 42°58′ E, 20 May 1990, *Thulin, Hedrén & Abdi Dahir 7606* (UPS No. V-051527!; isotypes: FT barcode FT001036!, K barcode K000232029!).

Paramollugo angustifolia is known only from the type collection from south-central Somalia.

Paramollugo cuneifolia (Griseb.) Thulin, **comb. nov.** ≡ *Mollugo nudicaulis* var. *cuneifolia* Griseb., Cat. Pl. Cub.: 22. 1866 ≡ *Mollugo cuneifolia* (Griseb.) Urb. in Ark. Bot. 22A(17): 14. 1929 – **Lectotype (designated here):** Cuba, "in litore pr. Baracoa", 1860, *Wright 2020* (K barcode K000471688!; isolectotypes: GH barcode 00037489 [digital image!], S Nos. 05-6834! & 05-6836!, YU barcode YU.001112 [digital image!]).

Paramollugo cuneifolia is known only from eastern Cuba.

Paramollugo decandra (Scott Elliot) Thulin, **comb. nov.** ≡ *Mollugo decandra* Scott Elliot in J. Linn. Soc., Bot. 29: 24. 1891 – Holotype: Madagascar, "sea-shore near Fort Dauphin", Apr, *Scott Elliot 2481* (K barcode K000232027!).

Paramollugo decandra (Fig. 4E) is known only from southern Madagascar.

Paramollugo deltoidea (Léon) Thulin, **comb. nov.** ≡ *Mollugo deltoidea* Léon in Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 9: 3. 1950 – Holotype: Cuba, Sabana de la Yaba, Yareyales, W of Holguín, 4 Jul 1932, *Léon 15715* (HAC [digital image!]).

Paramollugo deltoidea is known only from serpentine on eastern Cuba. It is close to *P. nudicaulis* and could possibly be a serpentine form of this species.

Paramollugo navassensis (Ekman) Thulin, **comb. nov.** ≡ *Mollugo nudicaulis* var. *navassensis* Ekman in Ark. Bot. 22A(17): 14. 1929 – **Lectotype (designated here):** "Insula Navassa (inter Haiti et Jamaica sita) in savannis ad partem septentrionali-occidentalem versus", 19 Oct 1928, *Ekman H 10810* (S No. R-3647!; isolectotypes: A barcode 00037491 [digital image!], B barcode B 10 0248713 [digital image!], C barcodes C10001454 & C10001455 [digital images!], G barcode G00356430 [digital image!], GH barcode 00037490 [digital image!], LE barcode LE 00006649 [digital image!], LL barcode 00370733 [digital image!], MO barcode MO-216413 [digital image!], NY barcode 00232982 [digital image!], S No. 13-8983!).

Paramollugo navassensis is known only from the Navassa Island and the British Virgin Islands in the Caribbean.

Paramollugo nudicaulis (Lam.) Thulin, **comb. nov.** ≡ *Mollugo nudicaulis* Lam., Encycl. 4: 234. Feb 1797 – Type: Mauritius, *Commerson s.n.* (?P, not located).

= *Pharnaceum spathulatum* Sw., Fl. Ind. Occid. 1: 568. Nov 1797 – **Lectotype (designated here):** Jamaica, *Swartz s.n.* (S No. 05-5804!).

= *Pharnaceum bellidifolium* Poir. in Lamarck, Encycl. 5: 262. 1804 ≡ *Mollugo bellidifolia* (Poir.) Ser. in Candolle, Prodr. 1: 391. 1824 – Type: not designated, in the protologue the species was said to occur in "la Guiane & la Jamaique".

= *Mollugo caespitosa* Scott Elliot in J. Linn. Soc., Bot. 29: 25. 1891, **syn. nov.** – Holotype: Madagascar, "from arid sandy country of the Antandroi, S.E. of Fort Dauphin", Jun–Jul, *Scott Elliot 2978* (K barcode K000232028!).

Jeffrey (1961) cited a "Hermann" specimen from Jamaica in the Sloane herbarium at BM as lectotype of *Pharnaceum spathulatum*. Swartz indeed cited "Sloan. Cat. 87. Hist. p. 203. t. 129. f. 2." in the protologue, and this figure, which could have served as a lectotype, is based on a specimen from Jamaica collected by Sloane (BM000589766 [digital image!]). However, the specimen itself was not seen by Swartz and cannot be a lectotype, and the specimen was also cited with wrong collector by Jeffrey. The specimen in S here designated as lectotype has a long description in Swartz's handwriting attached to the sheet.

Paramollugo nudicaulis (Fig. 4D) is widespread in tropical and subtropical parts of Africa, Asia and Australia, and is also common in the West Indies. However, it is very rare in North and South America, where it seems to be an occasional introduction only.

5. ***Hypertelis*** E.Mey. ex Fenzl in Ann. Wiener Mus. Naturgesch. 1: 352. 1836 – Type (designated by Phillips, Gen. S. Afr.

Fl. Pl., ed. 2: 291. 1951): *Hypertelis spergulacea* E.Mey ex Fenzl.

Annual or perennial glabrous herbs; lateral branches and pedicels mostly becoming markedly swollen at the base. Leaves in false whorls, mostly mucronate at the apex; stipules membranous, small, sometimes forming a narrow rim clasping the node. Flowers in axillary or terminal, sessile or pedunculate umbel-like cymes; bracts small or obsolete; pedicels often becoming ± deflexed. Tepals 5, free. Stamens ca. 5, 10 or 15–25. Ovary of 3 carpels, with numerous ovules; styles 3, short. Capsule dehiscent with 3 valves. Seeds numerous, very finely reticulate to almost smooth. — Fig. 4F.

Five species, two widespread and three mainly restricted to southern Africa. *Hypertelis* differs from other members of Molluginaceae by having a combination of leaves in false whorls, umbel-like inflorescences, and small and inconspicuous stipules. Also the mostly swollen bases of lateral branches and pedicels, and the very finely reticulate or almost smooth seeds are characteristic.

Key to the species of *Hypertelis*

1. Plant perennial; stamens 15–25 …… ***H. spergulacea***
1. Plant annual; stamens ca. 5 or 10 …… 2
2. Stamens 10 …… ***H. walteri***
2. Stamens ca. 5 …… 3
3. Basal leaves linear …… ***H. cerviana***
3. Basal leaves obovate or spathulate …… 4
4. Stem leaves obovate …… ***H. fragilis***
4. Stem leaves linear to narrowly oblanceolate ***H. umbellata***

Hypertelis cerviana (L.) Thulin, **comb. nov.** ≡ *Pharnaceum cervianum* L., Sp. Pl.: 272. 1753 ≡ *Mollugo cerviana* (L.) Ser. in Candolle, Prodr. 1: 392. 1824 – Lectotype (designated by Adamson in J. S. African Bot. 24: 14. 1957): Russia, "Habitat in Sibiria", *Ammann* in Herb. Linn. 387.1 (LINN [digital image!]).

Hypertelis cerviana is widespread in southern and eastern Europe, south-western and southern Asia, Africa and Australia. It is usually easily distinguished from *H. umbellata* by the shape of the basal leaves, but identification is sometimes difficult, particularly when the basal leaves have wilted.

Hypertelis fragilis (Wawra) Thulin, **comb. nov.** ≡ *Mollugo fragilis* Wawra in Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Cl. 38: 565. 1860 – **Lectotype (designated here):** Angola, "in littore maris prope Benguelam", *Wawra 296* (Z barcode Z-000000920 [digital image!]).

Wawra's types are normally in W, but as no material of *Wawra 296* seems to be present there, a specimen in Z is here designated as lectotype.

The distribution of *Hypertelis fragilis* has been thought to be restricted to Angola, but a single specimen from southern Ethiopia, *Corradi 8502* in FT, seems to be conspecific. This specimen was treated as "*Mollugo* sp. = Corradi 8502" by Gilbert (2000).

Hypertelis spergulacea E.Mey. ex Fenzl in Ann. Wiener Mus. Naturgesch. 2: 263. 1839 – Lectotype (designated by Adamson in J. S. African Bot. 24: 58. 1957): South Africa, "in lapidosis prope Verleptpram ad flumen Garip", *Drège 3020* (K barcode K000232009!; isolectotypes: W Nos. W0009849 & W0009850 [digital images!]).

Adamson (1957) stated that the type in W was lost and designated a lectotype in K. However, two sheets of *Drège 3020* are still extant in W, but as Adamson's typification is not in conflict with the protologue it has to stand.

Hypertelis spergulacea (Fig. 4F) is known only from southern Namibia and the Northern Cape Province in South Africa.

Hypertelis umbellata (Forssk.) Thulin, **comb. nov.** ≡ *Pharnaceum umbellatum* Forssk., Fl. Aegypt.-Arab.: 58. 1775 ≡ *Mollugo umbellata* (Forssk.) Ser. in Candolle, Prodr. 1: 393. 1824 – **Lectotype (designated here):** Yemen, "Lohajae", Jan 1763, *Forsskål s.n.*, Herb. Forsskål 1567 (C barcode C10002759 [digital image!]; isolectotype: S No. 05-5455!).

= *Mollugo cerviana* var. *spathulifolia* Fenzl in Ann. Wiener Mus. Naturgesch. 1: 379. 1836 ≡ *M. spathulifolia* (Fenzl) Dinter in Repert. Spec. Nov. Regni Veg. 19: 236. 1923 – Type: India, *Wight s.n.* (K-W, isolectotype, fide Jeffrey, 1961, n.v.).

Hypertelis umbellata is widespread in south-western Asia, India, Africa and America. It was previously mostly treated as a variety of *Mollugo cerviana*, but the latter is strongly supported as sister to all other members of *Hypertelis* in the analysis.

The accessions from Namibia that form the clade sister to *Hypertelis fragilis* are difficult to handle taxonomically. Similar collections from Namibia have previously been treated as *Mollugo spathulifolia* (Dinter, l.c.), but this is a synonym of *H. umbellata* with a type from India. As we have been unable to find any morphological characters that separate the Namibian plants from the fairly variable *H. umbellata*, we suggest that they are included there, even if this results in a paraphyletic species (Fig. 2). To avoid paraphyly we would either have to include *H. fragilis* in a more widely circumscribed *H. umbellata* or treat the Namibian plants as a distinct species. Both these solutions would be impractical, the first as *H. fragilis* is as morphologically distinct as any other species of *Hypertelis*, the second as there appears to be no morphological support for such a Namibian taxon.

Hypertelis walteri (Friedrich) Thulin, **comb. nov.** ≡ *Mollugo walteri* Friedrich in Mitt. Bot. Staatssamml. München 2: 65. 1955 ≡ *M. cerviana* var. *walteri* (Friedrich) Adamson in J. S. African Bot. 24: 15. 1957 – Holotype: Namibia, Karasburg, Farm Blinkoog, river NE of Wittsand, 3 Apr 1953, *Walter 2402* (M barcode M-0107822 [digital image!]; isotype: PRE barcode PRE0404944-0 [digital image!]).

Hypertelis walteri is known only from Namibia.

6. ***Polpoda*** C.Presl, Polpoda. 1829 – Type: *Polpoda capensis* C.Presl.

= *Blepharolepis* Nees in Lindl., Intr. Nat. Syst. Bot., ed. 2: 442. 1836 – Type: *Blepharolepis zeyheriana* Nees.

Small shrubs. Leaves small, alternate, appressed to the stem, mucronate at the apex; stipules membranous, fimbriate-laciniate, conspicuous. Flowers in numerous short 1- to few-flowered axillary cymes along the stem; bracts small, ovate. Tepals 4 or 5, sometimes fimbriate. Stamens 4 or 5, exserted; filaments sometimes connate at the base. Ovary of 2 carpels, each with a single seemingly basal ovule; styles 2, filiform, exserted. Fruit a compressed 2-seeded capsule; seeds orbicular-subreniform in outline, granular. — Fig. 4G.

Two species in the Western Cape Province of South Africa (Adamson, 1955). *Polpoda* differs from other Molluginaceae by its exserted stamens and styles. According to Adamson (1955) the flowers are protandrous and wind-pollinated.

7. ***Adenogramma*** Rchb., Iconogr. Bot. Exot. 2: 3. 1828 – Type: *Adenogramma mollugo* Rchb.

= *Steudelia* C.Presl, Steudelia. 1829, nom. illeg., non Spreng., Neue Entd. 3: 59. 1822 – Type: *Steudelia galioides* C.Presl.

Annual or perennial glabrous herbs or small shrubs or subshrubs, rarely aquatic. Leaves in false whorls or the lower ones sometimes alternate, linear to ovate or obovate, mucronate to aristate at the apex; stipules membranous, filiform or wanting. Flowers in seemingly axillary cymes or solitary; bracts filiform or wanting**.** Tepals (4–)5, free, ± hooded at the tip. Stamens (4–)5. Ovary of 1 carpel, with a single ovule; style 1, often asymmetrical. Fruit a 1-seeded nutlet. — Fig. 4H.

About 11 species in South Africa (Adamson, 1955; Manning & al., 2011). *Adenogramma* differs from other members of Molluginaceae by its indehiscent, 1-seeded fruits. The recently described *A. natans* J.C.Manning & Goldblatt is unique in the family by being aquatic.

8. ***Psammotropha*** Eckl. & Zeyh., Enum. Pl. Afric. Austral.: 286. 1836 – Type: *Psammotropha parvifolia* Eckl. & Zeyh. (= *P. marginata* (Thunb.) Druce).

Perennial glabrous herbs or shrublets, often cushion- or mat-forming. Leaves alternate, opposite or whorled, sometimes distinctly 4-ranked, mostly mucronate to aristate at the apex; stipules membranous or absent. Flowers in mostly umbel-like terminal or axillary cymes; bracts membranous. Tepals 5, free. Stamens 5; filaments mostly inserted on or just outside an annular disk. Ovary of 3–5 carpels, each with a single seemingly basal ovule; styles 3–5, mostly ± united at the base. Capsule dehiscent with 3–5 valves. Seeds orbicular-subreniform, granular. — Fig. 4I.

About 11 species (Adamson, 1959), mainly in South Africa, with one species, *P. myriantha* Sond., extending into tropical Africa, as far north as southern Tanzania. *Psammotropha* differs from other members of Molluginaceae by its ovary of 3–5 carpels, each with a single ovule.

9. ***Suessenguthiella*** Friedrich in Mitt. Bot. Staatssamml. München 2: 60. 1955 – Type: *Suessenguthiella scleranthoides* (Sond.) Friedrich.

Annual or perennial, mostly prostrate, glabrous herbs. Leaves linear-subulate, subterete, mucronate at the apex, in false whorls along the stem; stipules membranous, fimbriate-laciniate, persistent. Flowers in short, contracted, seemingly axillary cymes; bracts fimbriate-laciniate. Tepals 5, free, hooded at the tip and with a straight or somewhat outwards-curved mucro on the back. Stamens 5; filaments connate at the base into a low rim. Ovary of 3 carpels; ovules numerous; styles 3, short. Capsule dehiscent with 3 valves. Seeds numerous, orbicular-subreniform, finely granular. — Fig. 4J.

A single species in southern Namibia and the Northern and Western Cape Provinces in South Africa. *Suessenguthiella* differs from other members of Molluginaceae by its tepals with a projecting mucro on the back. The low rim at the base of the stamens was considered to be a disk by Adamson (1957), who treated *Suessenguthiella* as a monotypic section of *Pharnaceum*. Friedrich (1955, 1966), in contrast, stated that a hypogynous disk is lacking. In any case, the structure at the base of the stamens in *Suessenguthiella* seems to be morphologically different from the disk in *Pharnaceum* that is free from the stamens.

Suessenguthiella scleranthoides (Sond.) Friedrich in Mitt. Bot. Staatssamml. München 2: 60. 1955 ≡ *Pharnaceum scleranthoides* Sond. in Harvey & Sonder, Fl. Cap. 1: 143. 1860 – **Lectotype (designated here):** South Africa, Springbokkeel, *Zeyher 617* (S No. 05-4805!; isolectotype: TCD barcode TCD0002800 [digital image!]).

= *Suessenguthiella caespitosa* Friedrich in Mitt. Bot. Staatssamml. München 3: 616. 1960, **syn. nov.** – Holotype: Namibia, Aus, in crevices of granite rocks, 1400 m, 12 Jun 1922, *Dinter 3622* (M barcode M-0107813 [digital image!]; isotypes: B barcodes B 10 0153203 & B 10 0153204 [digital images!], Z barcode Z-000000201 [digital image!]).

Two specimens of *Suessenguthiella scleranthoides* collected by Zeyher in Springbokkeel are present in the Sonder Herbarium in S. Only one of them has the number 617 and this specimen is here designated as the lectotype.

One of the *Suessenguthiella caespitosa* specimens in B (B 10 0153203) is marked holotype by Friedrich, but it is the specimen in M that was cited as holotype in the protologue. Friedrich (1966) later cited *Dinter 3622 a* as type, whereas *Dinter 3622 b* was cited under *Suessenguthiella scleranthoides*. This indicates that Friedrich then considered *Dinter 3622* to be a mixture and therefore intended to lectotypify *S. caespitosa* with one part of the collection. However, no such subdivision of the collection *Dinter 3622* has been made by Friedrich or anybody else, so this apparently intended lectotypification is here left without consideration.

Suessenguthiella caespitosa was described from near Aus in southern Namibia and was said in the protologue to differ from *S. scleranthoides* by being a cushion-forming perennial with shorter and less conspicuous stipules. Friedrich (1966) later mentioned shorter stems and shorter capsules as additional differences. In April 2013 two of us, MT and AL, had the opportunity to study several populations of *Suessenguthiella* near Aus and according to our judgement the variation is continuous and only a single variable species should be recognized.

10. ***Coelanthum*** E.Mey. ex Fenzl in Ann. Wiener Mus. Naturgesch. 1: 353. 1836 – Type (designated by Phillips, Gen. S. Afr. Fl. Pl., ed. 2: 291. 1951): *Coelanthum grandiflorum* E.Mey. ex Fenzl.

Annual glabrous herbs. Leaves in a basal rosette and in false whorls along the stem, mucronate to aristate at the apex; stipules membranous, fimbriate-laciniate. Flowers in lax panicle- or raceme-like cymes; bracts laciniate-fimbriate. Tepals 5, united for at least half their length, hooded at the tip. Stamens 5; filaments adnate to the perianth-tube at the base. Ovary of 3 carpels; ovules numerous; styles 3, short. Capsule membranous, dehiscent with 3 valves. Seeds numerous, orbicular-subreniform, finely reticulate.

Three species in the Northern and Western Cape Provinces in South Africa (Adamson, 1957), one of them (*C. grandiflorum*) extending to southern Namibia (Friedrich, 1966). *Coelanthum* differs from other members of Molluginaceae by its tepals that are united into a distinct perianth-tube.

11. ***Pharnaceum*** L., Sp. Pl.: 272. 1753 ≡ *Ginginsia* DC., Prodr. 3: 362. 1828, nom. illeg. superfl. – Type (designated by Hitchcock in Sprague & al., Nom. Prop. Brit. Bot.: 143. 1929): *Pharnaceum incanum* L.

Annual or perennial herbs, or small shrubs or subshrubs, glabrous. Leaves alternate or in false whorls, linear to obovate, mostly mucronate to aristate at the apex; stipules membranous, mostly conspicuously fimbriate-laciniate. Flowers in mostly long-pedunculate panicle- to raceme-like cymes; bracts mostly ± fimbriate-laciniate. Tepals 5, free or almost so. Stamens 5, inserted outside a lobed annular disk, rarely disk wanting. Ovary of 3–5 carpels; ovules mostly numerous; styles 3–5. Capsule dehiscent with 3–5 valves. Seeds mostly numerous, orbicular-subreniform, finely granular, reticulate or almost smooth, sometimes bordered. — Fig. 4K, L.

About 25 species, mainly in South Africa (Adamson, 1957), a few extending into Namibia and one (*P. brevicaule* (DC.) Bartl.) into Zimbabwe.

Pharnaceum incanum, the type of *Pharnaceum*, was lectotypified by Adamson (1957: 28) with a specimen in the Linnean Herbarium, Herb. Linn. 387.5 (as "287.5"). However, as pointed out by Jarvis (2007), this specimen was not received by Linnaeus until ca. 1769 and therefore cannot be original material. Only with a new lectotypification the identity of *P. incanum* can be settled. Original material is available (Jarvis, 2007), but the situation is complex and needs careful study. A possible outcome is that *P. incanum* will become the name for the species currently treated as *P. elongatum* (DC.) Adamson (Adamson, 1957).

Pharnaceum can generally be distinguished from other members of Molluginaceae by the presence of a nectariferous disk in combination with fimbriate-laciniate stipules and more or less many-seeded fruits. *Mollugo tenella*, which is sister to all other included species of the genus, is here placed in synonymy of *Pharnaceum subtile*. It has an inconspicuous disk, whereas in *P. lineare*, which is sister to all other species except *P. subtile*, the disk is wanting. Mainly for this reason, *P. lineare* was placed in a section of its own, *P.* sect. *Spergulopsis* Adamson, by Adamson (1957). However, a disk is wanting also in *P. pusillum* (see below). We propose the following nomenclatural and taxonomic changes in the genus:

Pharnaceum lineare L.f., Suppl. Pl.: 185. 1782 – Holotype: South Africa, "Cap. b. spei", *Thunberg s.n.*, Herb. Thunberg 7533 (UPS-THUNB!).

= *Hypertelis longifolia* Gand. in Bull. Soc. Bot. France 59: 708. 1913, **syn. nov.** – Holotype: South Africa, "Cap. ad Stellensboch", Apr 1904, *Bonomi s.n.* (LY [digital image!]).

Adamson (1957) treated *Hypertelis longifolia* as an uncertain species, whereas Christenhusz & al. (2014), who stated that they failed to locate the type specimen, believed that it could be an older name for *Kewa trachysperma* (Adamson) Christenh. The type specimen is present in Gandoger's herbarium in LY, and clearly shows that *H. longifolia* is a synonym of *Pharnaceum lineare*. The distribution of *P. lineare* is restricted to the Northern and Western Cape Provinces in South Africa. *Pharnaceum lineare* (Fig. 4K) has tepals up to about 7 mm long, which probably makes it the member of Molluginaceae with the largest flowers.

Pharnaceum namaquense (Bolus ex Schltr.) Thulin, **comb. nov.** ≡ *Mollugo namaquensis* Bolus ex Schltr. in Bot. Jahrb. Syst. 27: 121. 1899 – **Lectotype (designated here):** South Africa, Namaland Minor, near Nababeep, Sep 1883, *Bolus 6641* (BOL barcode BOL128278 [digital image!]; isolectotypes: BOL barcode BOL128279 [digital image!], K barcode K000232024!, NBG barcode NBG0200323-0 [digital image!], Z barcode Z-000000215 [digital image!]).

Two collections were cited in the protologue of *Mollugo namaquensis*, *Bolus 6641* and *Schlechter 8714*, and Adamson (1957: 17) designated *Bolus 6641* in BOL as a "neotype". As two sheets of *Bolus 6641* are present in BOL, Adamson's action is here regarded as a first-step lectotypification according to *ICN* Art. 9.15 (McNeill & al., 2012), and one of these sheets is here designated as the lectotype.

Pharnaceum namaquense has previously been recorded only from the Northern and Western Cape Provinces in South Africa, but specimens have been seen also from southern Namibia. It has previously been treated as a *Mollugo*, but the raceme-like cymes and the presence of stipules and a tiny disk indicate that it is best placed in *Pharnaceum*. However, the stipules are small and almost entire and are not associated with the rosette leaves at the base of the plant, but only with the stem leaves. The seeds are reticulate as in *P. subtile* and these two small annual species are also similar in habit.

Pharnaceum pusillum Schltr. in Bot. Jahrb. Syst. 27: 123. 1899 ≡ *Mollugo pusilla* (Schltr.) Adamson in J. S. African Bot. 24: 17. 1957 – Lectotype (designated by Adamson, l.c.): South Africa, Boontjes Rivier, 25 Aug 1896, *Schlechter 8664* (BM barcode BM000902705!; isolectotypes: B barcode B 10 0159470 [digital image!], BR barcode 0000006861429 [digital image!], E barcode E00217681 [digital image!], PH barcode 00029562 [digital image!], S No. 05-4841!).

Pharnaceum pusillum is known only from the Northern and Western Cape Provinces of South Africa (Adamson, 1957). Adamson (1957) treated it as a *Mollugo* and mentioned the small, almost entire stipules, the lack of a disk, the very short stigmas and the seeds as differences from *Pharnaceum*. Being stipulate it is clearly not a *Mollugo* as defined here. It is reminiscent of *Hypertelis* in habit, but the raceme-like cymes would be anomalous in this genus, and it seems best retained in *Pharnaceum*. The stipules are somewhat fimbriate and the styles and seeds are also matched by other species in this genus, where it may be related to other small annual species, such as *P. namaquense* and *P. subtile*.

Pharnaceum subtile E.Mey. ex Fenzl in Ann. Wiener Mus. Naturgesch. 2: 259. 1839 – **Lectotype (designated here):** South Africa, *Drège 6214* (W No. W0009842 [digital image!]; isolectotype: W No. W0009841 [digital image!]).

= *Mollugo tenella* Bolus ex Schltr. in Bot. Jahrb. Syst. 27: 122. 1900, **syn. nov.** – Lectotype (designated by Adamson in J. S. African Bot. 24: 18. 1957): South Africa, "Namaland Minoris, in limosis prope Klipfontein, 3100 ped.", Aug 1883, *Bolus in Herb. Norm. Austr.-Afr. 1159* (BOL barcode BOL128282 [digital image!]; isolectotypes: B barcode B 10 0159477 [digital image!], BM barcode BM000902704!, GH barcode 00268178 [digital image!], K barcode K000232023!, NBG barcode NBG0200322-0 [digital image!], SAM barcode SAM0036898-0 [digital image!], UPS!).

Fenzl (l.c.) cited three syntypes of *Pharnaceum subtile* in the protologue and one of them, *Drège 6214* in B, was cited as the "type" by Adamson (1957: 42), although he admitted he had not seen it. This specimen is no longer extant, but two duplicates of *Drège 6214* are present in W. One of them is already indicated as type in the virtual herbarium of W, and this is here designated as a new lectotype.

Three syntypes of *Mollugo tenella* were cited by Schlechter (l.c.) in the protologue, *Bolus 6640*, *Bolus in Herb. Norm. Austr.-Afr. 1159*, and *Schlechter 8631*. Adamson (1957: 18) designated *Bolus 6640* (as "6646"), in B as type (destroyed) and *Bolus 1159* in BOL as "neotype". However, as *Bolus 1159* is part of the original material it cannot be a neotype, and Adamson's action is here regarded as a lectotypification in agreement with ICN Art. 9.9 (McNeill & al., 2012).

Friedrich (1966) recognized *Mollugo tenella*, but at the same time pointed to its similarity with *Pharnaceum subtile* and anticipated that it would become a synonym of the latter. *Pharnaceum subtile* is distributed in the Northern and Western Cape Provinces in South Africa and in southern Namibia.

Corbichoniaceae Thulin, **fam. nov.** – Type: *Corbichonia* Scop.

Differs from *Lophiocarpaceae* in its usually obovate to suborbicular (not linear to elliptic) leaves, lax (not densely spike-like) inflorescences, many petals (petals not absent), many (not 4) stamens, 5 (not 2) carpels forming a 5-locular (not 1-locular) ovary with axile (not basal) placentation and numerous ovules per carpel (not 1 ovule per ovary), loculicidally dehiscent capsule (fruit not a ridged or muricate nutlet), and arillate (not ex-arillate) seeds.

Annual or perennial glabrous to papillose herbs or subshrubs; stems angular, prostrate to ascending or erect. Leaves alternate, simple, usually obovate to suborbicular, entire, mucronate, somewhat succulent; stipules absent. Flowers actinomorphic, hermaphroditic, hypogynous, in terminal or seemingly axillary lax cymes; sepals 5, free, with membranous margins, with quincuncial aestivation; petals 20–25, reddish; stamens ca. 20; anthers dehiscing by longitudinal slits; pollen grains tricolpate; carpels 5, connate into a 5-locular ovary; ovules many per carpel, with axile placentation; styles 5, linear. Fruit a 5-valved loculicidal capsule. Seeds subreniform-suborbicular in outline; testa with concentric ridges; aril small, white; embryo peripheral, curved around perisperm. — Fig. 3B.

A single genus in drier parts of tropical Africa and southern Asia.

Corbichonia Scop., Intr. Hist. Nat.: 264. 1777 – Type: *Corbichonia decumbens* (Forssk.) Exell.

= *Axonotechium* Fenzl in Ann. Wiener Mus. Naturgesch. 1: 354. 1836 – Type: *Axonotechium trianthemoides* (Roth) Fenzl.

Two species, one widespread in drier parts of tropical and southern Africa and tropical Asia, one endemic to Namibia.

Key to the species of *Corbichonia*

1. Sepals 4–6 mm long; stems prostrate to erect, often somewhat woody; leaves broadly elliptic to obovate or sometimes almost orbicular …… ***C. decumbens***
1. Sepals 3–3.5(–4) mm long; stems prostrate, thin and herbaceous; leaves mostly orbicular or almost so …… …… ***C. rubriviolacea***

Corbichonia decumbens (Forssk.) Exell in J. Bot. 73: 80. 1935 ≡ *Orygia decumbens* Forssk., Fl. Aegypt.-Arab.: 103. 1775 ≡ *Portulaca decumbens* (Forssk.) Vahl, Symb. Bot. 1: 33. 1790 ≡ *Talinum decumbens* (Forssk.) Willd., Sp. Pl. 2: 864. 1799 – Lectotype (designated by Jeffrey in Hubbard & Milne-Redhead, Fl. Trop. E. Afr. Aizo.: 9. 1961): Yemen, "Musae", 1763, *Forsskål 541* (C barcode C10002703 [digital image!]; isolectotype: BM barcode BM000944675!).

= *Glinus trianthemoides* B.Heyne in Roth, Nov. Pl. Sp.: 231. 1821 ≡ *Axonotechium trianthemoides* (B.Heyne) Fenzl in Ann. Wiener Mus. Naturgesch. 1: 355. 1836 – Holotype: India, *Heyne s.n.* (B, destroyed).

= *Telephium laxiflorum* DC., Prodr. 3: 366. 1828 – Holotype: South Africa, Cape, 1812, *Burchell 2054* (G-DC barcode G00488203 [digital image!]; isotype: K!).

= *Orygia mucronata* Klotzsch in Peters, Naturw. Reise Mossambique 6: 140. 1861 ≡ *Glinus mucronatus* (Klotzsch) Klotzsch in Peters, Naturw. Reise Mossambique 6: 570. 1864 – **Lectotype (designated here):** Mozambique, Tette, *Peters s.n.* (K barcode K000232039!).

The citation of the Forsskål specimen of *Corbichonia decumbens* in C as a holotype by Jeffrey (1961) is here regarded as a lectotypification.

The type material of *Orygia mucronata* in B is destroyed and a syntype at K is therefore here designated as lectotype.

Corbichonia decumbens (Fig. 3B) is widespread in drier parts of tropical and southern Africa and tropical Asia.

Corbichonia rubriviolacea (Friedrich) C.Jeffrey in Kew Bull. 14: 235. 1960 ≡ *Orygia rubriviolacea* Friedrich in Mitt. Bot. Staatssamml. München 8: 340. 1953 – **Lectotype (designated here):** Namibia, Nambons, Friedenfelde, Blinkoog, 1953, *Walter 2366* (M barcode M-0107807 [digital image!]; isolectotype: M barcode M-0107808 [digital image!]).

Corbichonia rubriviolacea is endemic to Namibia. It is close to *C. decumbens* and its status should be further studied.

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Appendix 1. Taxa sampled for phylogenetic analyses with voucher information and GenBank accession numbers.

Accessions are grouped by family, with Molluginaceae first. Information is listed in the following order: taxon name, country and number (if more than one accession of that taxon was sampled in that country), collector and number (with herbarium acronym in parentheses), *trnK-matK*, ITS and *rbcL* GenBank numbers, when available. Sequences (*trnK-matK*, ITS) generated for this study are marked with an asterisk, most of the remaining sequences are from Christin & al. (2011).

Molluginaceae: ***Adenogramma glomerata*** (L.f.) Druce, South Africa 1, *Pillans 10706* (NY), FN825686, –, FN824405; South Africa 2, *Fries 25-9-20* (NY), FN825687.1, KT907380*, FN824406; South Africa 3, *Ogburn 146* (BRU), FN825688, –, FN824407; South Africa 4, *Ogburn 142* (BRU), FN825689, KT907379*, FN824408. ***Adenogramma mollugo*** Rchb., South Africa, *Pillans 10526* (NY), FN825690, –, FN824409. ***Adenogramma teretifolia*** (Thunb.) Adamson, South Africa, *Ogburn 156* (BRU), FN825691, KT907381*, FN824410. ***Coelanthum semiquinquefidum*** (Hook.) Druce, South Africa, *Wright 1853* (NY), FN825759, –, FN824411. ***Glinus lotoides*** L., U.S.A., *Errter 8854* (NY), FN825692, KT907409*, –. ***Glinus oppositifolius*** (L.) Aug.DC., Australia, *Barbidge 5949* (ANH), FN825696, –, FN824415; Taiwan, *Huang & Huang 14175* (NY), FN825695, KT907366*, FN824415; Tanzania, *Balslev 630* (NY), FN825694, –, FN824414. ***Glinus radiatus*** (Ruiz & Pav.) Rohrb., U.S.A., *Thomas 114677* (NY), FN825697, KT907410*, –. ***Glinus setiflorus*** Forssk., Kenya, *Burney & al. 146* (NY), FN825698, KT907367*, FN824418. ***Glischrothamnus ulei*** Pilger, Brazil, *Harvey 19007* (SPF), FN825699, –, FN824419. ***Hypertelis spergulacea*** E.Mey. ex Fenzl, Namibia 1, *Thulin & Larsson 11960* (UPS), KT950931*, KT907406*, –; Namibia 2, *Thulin & Larsson 11962* (UPS), KT950932*, KT907407*, –; Namibia 3, *Giess & al. 5366* (K), FN825700, KT907404*, FN824420; South Africa, *Acocks 19256* (K), FN825701, KT907405*, FN824421. ***Mollugo angustifolia*** M.G.Gilbert & Thulin, Somalia, *Thulin & al. 7606* (UPS), FN825702, KT907356*, –. ***Mollugo brasiliensis*** Thulin & Harley, Brazil: Bahia 1, *Guedes & al. PCD5162* (K), KT950938*, KT907373*, –; Brazil: Bahia 2, *Orlandi & al. PCD515* (K), KT950940*, KT907371*, –; Brazil: Minas Gerais 1, *Harley & al. 25029* (K), KT950939*, –, –; Brazil: Minas Gerais 2, *Harley & al. SPF36081* (K), KT950941*, –, –. ***Mollugo cerviana*** (L.) Ser., Australia 1, *Smyth 213* (CANB),

Appendix 1. Continued.

FN825706, KT907399*, FN824426; Australia 2, *Lazarides & Palmer 243* (CANB), FN825703, –, FN824423; Australia 3, *Jackson 5281* (CANB), FN825704, –, FN824424; Australia 4, *Leach 2008* (CANB), FN825705, KT907400*, FN824425; Burkina Faso, *Ataholo 1809* (FR), FN825715, KT907392*, FN824435; Ethiopia, *Thulin & al. 11211* (UPS), FN825713, KT907391*, FN824433; Galapagos, *Van der Werf 1008* (NY), FN825712, KT907395*, FN824432; India, n/a, FN825714, –, FN824434; Namibia 1, *Thulin & al. 11954* (UPS), KT950944*, KT907403*, –; Namibia 2, *Thulin & al. 11970* (UPS), KT950933*, KT907415*, –; Namibia 3, *Seydel 325* (NY), FN825709, KT907398*, FN824428; Namibia 4, *Potgieter 225* (K), FN825707, KT907402*, FN824427; Spain, *Sánchez Sánchez s.n.* (G), FN825708, KT907401*, FN824429; U.S.A. 1, *Reveal & Holmgren 1968* (NY), FN825710, KT907394*, FN824430; U.S.A. 2, *Atwood & Welsh 10684* (NY), FN825711, KT907393*, FN824431. ***Mollugo crockeri*** J.T.Howell, Galapagos, *Howell 10094* (NY), FN825716, KT907412*, –. ***Mollugo decandra*** Scott Elliot, Madagascar 1, *Croat 30852* (K), FN825718, KT907358*, FN824437; Madagascar 2, *Humbert & Swingle 5293* (NY), FN825717, KT907357*, FN824436. ***Mollugo disticha*** (L.) Ser., Sri Lanka, *Lundqvist 11379* (UPS), KT950942*, KT907378*, –. ***Mollugo enneandra*** C.Wright, Cuba, *Ekman 17848* (NY), FN825719, –, –. ***Mollugo flavescens*** Andersson, Galapagos, *Wheeler & al. 17* (NY), FN825720, KT907417*, –. ***Mollugo floriana*** (B.L.Rob.) J.T.Howell, Galapagos, *Eliasson 741* (K), FN825722, KT907413*, –. ***Mollugo fragilis*** Wawra, Angola 1, *Ward & Ward 79* (K), FN825724, KT907396*, FN824442; Angola 2, *Gossweiler 6* (K), FN825723, KT907397*, FN824441. ***Mollugo molluginea*** (F.Muell.) Druce, Australia, *Telford 11746* (CANB), FN825725, KT907408*, FN824443. ***Mollugo nudicaulis*** Lam., Burkina Faso, *Muller 257* (FR), FN825729, –, FN824447; India 1, n/a, FN825732, KT907362*, FN824450; India 2, *Devi s.n.* (CANB), FN825733, KT907365*, FN824451; India 3, n/a, FN825731, KT907361*, FN824449; Somalia, *Thulin & Bashir Mohamed 6759* (UPS), FN825730, KT907363*, FN824448; Namibia, *De Winter & Giess 6900* (K), FN825728, KT907359*, FN824446. ***Mollugo nudicaulis*** var. ***navassensis*** Ekman, British Virgin Islands, *Proctor 42517* (NY), FN825727, KT907360*, FN824445; Navassa Island, *Liogier 16585* (NY), FN825726, KT907364*, FN824444. ***Mollugo pentaphylla*** L., Australia, *Lazarides & Adams 326* (CANB), FN825736, KT907374*, FN824454; Brazil, *Nee 42741* (NY), FN825734, KT907376*, FN824452; India, n/a, FN825737, KT907377*, FN824455; Sri Lanka, *Jonsell 3885* (UPS), KT950929*, KT907418*, –; Taiwan, *Boufford & al. 25246* (NY), FN825735, KT907375*, FN824453. ***Mollugo snodgrassii*** B.L.Rob., Galapagos, *Howell 9450* (NY), FN825738, KT907411*, –. ***Mollugo tenella*** Bolus ex Schltr., Namibia, *Merxmüller & Giess 3316* (NY), FN825739, KT907414*, –. ***Mollugo verticillata*** L., Bolivia, *Nee 37372* (G), FN825743, KT907368*, FN824474; Canada, *Roy C-151-82* (G), FN825741, KT907370*, FN824460; Italy, *Cook & Gallucci 5430* (G), FN825742, KT907369*, FN824461; U.S.A., *Sage & Sage 8-2007* (TRT), FN825740, KT907372*, FN824459. ***Mollugo walteri*** Friedrich, Namibia, *Örtendahl 93* (UPS), KT950930*, KT907419*, –. ***Pharnaceum confertum*** Eckl. & Zeyh., South Africa, *Ogburn 163* (BRU), FN825744, –, FN824462. ***Pharnaceum detonsum*** Fenzl, South Africa, *Fries 764* (NY), FN825745, KT907416*, FN824463. ***Pharnaceum elongatum*** (DC.) Adamson, South Africa 1, *Ogburn 153* (BRU), FN825746, –, FN824464; South Africa 2, *Fellingham 238918* (CANB), FN825747, –, FN824465. ***Pharnaceum incanum*** L., South Africa, *Ogburn 148* (BRU), FN825748, KT907387*, FN824466. ***Pharnaceum lanatum*** Bartl., South Africa, *Venter 9568* (NY), FN825750, –, FN824468. ***Pharnaceum lanuginosum*** J.C.Manning & Goldblatt, South Africa, *Ogburn 161* (BRU), FN825752, KT907385*, FN824469. ***Pharnaceum lineare*** L.f., South Africa, *Helme 5887* (NBG), KT950943*, KT907386*, –. ***Pharnaceum reflexum*** Eckl. & Zeyh., South Africa, *Taylor 1162* (NY), FN825751, –, –. ***Polpoda capensis*** C.Presl, South Africa, *Acocks 17405* (CANB), FN825753, KT907384*, FN824470. ***Psammotropha obovata*** Adamson, South Africa, *Hilliard & Burtt 7045* (K), FN825754, KT907383*, FN824471. ***Psammotropha quadrangularis*** Fenzl, South Africa, *Ogburn 160* (BRU), FN825755, KT907382*, FN824472. ***Suessenguthiella scleranthoides*** (Sond.) Friedrich, Namibia 1, *Thulin & Larsson 11964* (UPS), KT950936*, KT907388*, –; Namibia 2, *Thulin & Larsson 11971* (UPS), KT950937*, KT907389*, –; South Africa, *Acocks 18950* (K), FN825756, KT907390*, FN824473. **Aizoaceae:** ***Conicosia pugioniformis*** (L.) N.E.Br., South Africa, *Klak 1570* (BOL, *trnK-matK* only), KF132628.1, –, JQ412345. ***Galenia africana*** L., JQ024963.1, –, JQ025048. ***Gibbaeum heathii*** (N.E.Br.) L.Bolus, South Africa, *Klak 1125* (BOL), KF132691.1, –, –. ***Mesembryanthemum crystallinum*** L., HM850877.1, –, HM850175. ***Sesuvium portulacastrum*** (L.) L., KC185420.1, –, FN868308. ***Tetragonia tetragonoides*** (Pall.) Kuntze, HM850882.1, –, HM850395. **Amaranthaceae:** ***Spinacia turkestanica*** Iljin, *Fuentes 181* (B), HE855620.1, –, –. **Anacampserotaceae:** ***Anacampseros kurtzii*** Bacigalupo, *Leuenberger & Eggli 4217* (ZSS, *trnk-matK* only), DQ855853.1, L78063.1, –. **Barbeuiaceae:** ***Barbeuia madagascariensis*** Steud., AY042552.1, –, GQ497673. **Basellaceae:** ***Basella alba*** L., JQ844148.1, L78018.1, M62564. **Cactaceae:** ***Opuntia phaeacantha*** Engelm., FN997327.1, JF786974.1, –. ***Pereskia aculeata*** Mill., HM041757.1, JF508526.1, AY875229. **Caryophyllacae:** ***Dianthus laingsburgensis*** S.S.Hooper, GU441169.1, –, –. **Didiereaceae:** ***Alluaudia dumosa*** (Drake) Drake, Madagascar, *Stone s.n.,* (DAV, ITS only), HQ620839.1, L78011.1, –. **Gisekiaceae:** ***Gisekia africana*** (Lour.) Kuntze, Namibia, *Thulin & al. 11955* (UPS), KT950945*, –, –. **Halophytaceae:** ***Halophytum ameghinoi*** Speg., *Chase 1753* (K, *rbcL* only), AY514852.1, EU410352.1, AJ403024. **Kewaceae:** ***Kewa bowkeriana*** (Sond.) Christenh., Namibia, *Giess 171* (NY), FN825761, –, FN824476. ***Kewa salsoloides*** (Burch.) Christenh., South Africa, *Zietsman 3833* (NY), FN825762, –, FN824477. **Limeaceae:** ***Limeum aethiopicum*** Burm.f., Namibia, *Thulin & Larsson 11957* (UPS), KT950934*, –, –. ***Limeum dinteri*** G.Schellenb., Namibia, *Thulin & Larsson 11959* (UPS), KT950935*, –, –. **Lophiocarpaceae:** ***Corbichonia decumbens*** (Forssk.) Exell, Botswana, *Aye 1074* (NY), FN825760, –, FN824475; South Africa, *Thulin & al. 11942* (UPS), KT950946*, –, –. ***Lophiocarpus polystachyus*** Turcz., Namibia 1, *De Winter 3156* (K), AY042611, –, –; Namibia 2, *Thulin & Larsson 11958* (UPS), KT950947*, –, –. **Macarthuriaceae:** ***Macarthuria australis*** Hügel ex Endl., Australia, *Lepschi & Brims 1943* (G), FN825765.1, –, FN824479.1. **Montiaceae:** ***Lewisia longipetala*** (Piper) S.Clay, *Edwards 141* (BRU, *trnk-matK* only), HQ620876.1, DQ498108, –. **Nyctaginaceae:** ***Bougainvillea glabra*** Choisy, JQ844141.1, –, M88340. ***Guapira discolor*** (Spreng.) Little, KJ522684.1, –, KJ522686. ***Mirabilis jalapa*** L., FN868307.1, –, HM850179. **Petiveriaceae:** ***Petiveria alliacea*** L., GQ429080.1, –, AJ402987. ***Rivina humilis*** L., AY514850.1, –, M62569. **Phytolaccaceae:** ***Phytolacca americana*** L., *Qiu 94109* (IND, *trnk-matK* only), DQ401362.1, –, HM850257. **Portulacaceae:** ***Portulaca amilis*** Speg., *Ogburn 11* (BRU, *trnK-matK* only), HQ620886.1, JF508528.1, –. **Sarcobataceae:** ***Sarcobatus vermiculatus*** (Hook.) Torr., AY042652.1, –, AF132088. **Simmondsiaceae:** ***Simmondsia chinensis*** (Link) C.K.Schneid., AF204863.1, –, AF093732. **Stegnospermataceae:** ***Stegnosperma halimifolium*** Benth., HQ878442.1, –, M62571. **Talinaceae:** ***Talinum fruticosum*** (L.) Juss., *Ferguson 848* (ZSS, *trnK-matK* only), DQ855844.1, KJ380908.1, KJ380905.

Appendix 2. Taxa sampled for pigment analysis with voucher information.

Kewaceae: ***Kewa salsoloides*** (Burch.) Christenh., Namibia, *Thulin & al. 11956* (UPS). **Limeaceae:** ***Limeum aethiopicum*** Burm.f., Namibia, *Thulin & Larsson 11957* (UPS). **Molluginaceae:** ***Hypertelis spergulacea*** E.Mey. ex Fenzl, Namibia, *Thulin & Larsson 11960* (UPS); ***Mollugo verticillata*** L., U.S.A., *Cronquist 6086* (UPS). **Simmondsiaceae:** ***Simmondsia chinensis*** (Link) C.K.Schneid., Mexico, *Thulin 11997* (UPS).