Phylogeny and systematics of Paramollugo (Molluginaceae)

Mats Thulin, Ehoarn Bidault, Vincent Boullet†, Nahid Heidari, Jean Hivert & Anders Larsson

Vincent Boullet tragically passed away in February 2024.
We dedicate this paper to his memory.

Abstract

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The genus *Paramollugo* Thulin (*Molluginaceae*) comprises herbs or small shrubs or subshrubs mainly distributed in the Madagascar region, but one species also widespread in the tropics and subtropics of the Old World, two restricted to the Caribbean and one to New Caledonia. In the revision presented here 11 species are recognized: *P. decandra* (Scott Elliot) Thulin, *P. caespitosa* (Scott Elliot) Thulin comb. nov., *P. compressa* Thulin sp. nov., *P. simulans* Sukhor. and *P. elliotii* Sukhor. endemic to Madagascar, *P. nudicaulis* (Lam.) Thulin in Madagascar and also widespread on neighbouring islands and in tropical and subtropical parts of Africa and Asia, *P. angustifolia* (M.G. Gilbert & Thulin) Thulin in Madagascar and Somalia, *P. digyna* (Montrouz.) Sukhor. endemic to New Caledonia, *P. nesophila* Thulin et al. sp. nov. endemic to Îles Éparses (Scattered Islands) in the Mozambique Channel, *P. spathulata* (Sw.) Sukhor. widespread in the Caribbean, and *P. cuneifolia* (Griseb.) Thulin endemic to Cuba. For each species descriptions and discussions are provided, as well as illustrations and distribution maps. New lectotypes are designated for *Mollugo caespitosa* Scott Elliot and *M. digyna* Montrouz. The phylogeny of the genus is reconstructed based on plastid *trnK-matK* and nuclear ITS sequences. Conflict between the datasets is seen as a result of the genus probably being a polyploid complex. Dating of the phylogeny resulted in two alternative topologies, both estimating the age of the stem clade to the Eocene, with a presumed origin in Africa, and mid-Miocene as the age of the crown clade, with a presumed origin in Madagascar and/or the Caribbean. The age of the crown clade is also the estimated date for a split between a Caribbean clade and the rest of the genus, long distance dispersal from Madagascar to the Greater Antilles being the most likely explanation.

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Résumé

THULIN, M., E. BIDAULT, V. BOULLET, N. HEIDARI, J. HIVERT & A. LARSSON (2024). Phylogénie et systématique du genre Paramollugo (Molluginaceae). *Candollea* 79: 179–228. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2024v792a1

Le genre *Paramollugo Thulin* (Molluginaceae) comprend des herbes ou de petits arbustes ou sous-arbrisseaux principalement distribués dans la région de Madagascar, mais une espèce est également répandue dans les régions tropicales et subtropicales de l'Ancien Monde, deux sont limitées aux Caraïbes et une à la Nouvelle-Calédonie. Dans la révision présentée ici, 11 espèces sont reconnues: *P. decandra* (Scott Elliot) Thulin, *P. caespitosa* (Scott Elliot) Thulin comb. nov., *P. compressa* Thulin sp. nov., *P. simulans* Sukhor. et *P. elliotii* Sukhor. endémiques de Madagascar, *P. nudicaulis* (Lam.) Thulin à Madagascar, mais également répandu dans les îles voisines et dans les parties tropicales et subtropicales d'Afrique et d'Asie, *P. angustifolia* (M.G. Gilbert & Thulin) Thulin à Madagascar et en Somalie, *P. digyna* (Montrouz.) Sukhor. endémique de Nouvelle-Calédonie, *P. nesophila* Thulin et al. sp. nov. endémique des Îles Éparses dans le canal du Mozambique, *P. spathulata* (Sw.) Sukhor. répandu dans les Caraïbes et *P. cuneifolia* (Griseb.) Thulin endémique de Cuba. Pour chaque espèce, des descriptions et des discussions sont fournies, ainsi que des illustrations et des cartes de répartition. De nouveaux lectotypes sont désignés pour *Mollugo caespitosa* Scott Elliot et *M. digyna* Montrouz. La phylogénie du genre est basée sur les marqueurs chloroplastiques *trnK-matK* et sur le marqueur nucléaire ITS. Les conflits entre les différents jeux de données sont vraisemblablement liés au complexe polyploïdique que constitue le genre. Deux topologies alternatives sont issues des analyses de datation moléculaire, toutes les deux estimant l'âge du groupe-souche à l'Eocène, avec une origine présumée en Afrique, et l'âge du groupe couronne à la mi-Miocène, avec une origine présumée à Madagascar et/ou dans les Caraïbes. L'âge du groupe couronne est également la date estimée pour la divergence entre le clade caribéen et le reste du genre, l'hypothèse d'une dispersion éloignée de Madagascar vers les Grandes Antilles étant l'explication la plus probable.

Keywords

MOLLUGINACEAE – *Mollugo* – *Paramollugo* – Madagascar – Biogeography – New combination – New species – Phylogenetic dating – Typification

Introduction

In the revised taxonomy of *Molluginaceae* proposed by Thulin et al. (2016), the genus *Paramollugo* Thulin was established with *P. nudicaulis* (Lam.) Thulin, based on *Mollugo nudicaulis* Lam., as type. In a subsequent paper (Thulin, 2017), the name *Paramollugo nudicaulis* was lectotypified with a specimen from Mauritius. *Paramollugo* is a genus of annual or perennial herbs or small shrubs with leaves mostly crowded in a basal rosette, small flowers and capsular fruits with mostly numerous minute seeds. Six species were recognized by Thulin et al. (2016), four of which were included in the phylogeny: *P. angustifolia* (M.G. Gilbert & Thulin) Thulin, *P. decandra* (Scott Elliot) Thulin, *P. navassensis* (Ekman) Thulin and *P. nudicaulis*. Since then, *P. elliotii* Sukhor. and *P. simulans* Sukhor. have been described from Madagascar, and *P. digyna* (Montrouz.) Sukhor. from New Caledonia has been resurrected and neotypified (Sukhorukov & Kushunina, 2016a). Also, *P. spathulata* (Swartz) Sukhor. (incl. *P. navassensis* (Ekman) Thulin) has been resurrected from the Caribbean (Sukhorukov & Kushunina, 2016b). Finally, Sukhorukov et al. (2016) discussed the identity of *Mollugo caespitosa* Scott Elliot from Madagascar and proposed an unfortunate lectotypification of the name, not with the extant original specimen, but with a plate that would make it a synonym of the Malagasy endemic *Paramollugo decandra*.

In this paper we present an expanded and dated phylogeny of *Paramollugo*, where samples of *P. spathulata* and *P. cuneifolia* (Griseb.) Thulin from Cuba, and of *P. digyna* from New Caledonia have been added, as well as further samples from Madagascar: from specimens that correspond to the original material of *Mollugo caespitosa* (*Paramollugo caespitosa* comb. nov., see below), from *P. angustifolia*, *P. elliotii*, *P. nudicaulis*, and *P. simulans*, and from a specimen representing a very distinctive new species, i.e., *P. compressa* Thulin. Finally, four samples from plants from Îles Éparses (Scattered Islands) in the Mozambique Channel have been included, also representing a new species, i.e., *P. nesophila* Thulin et. al. The aims of the present paper are to explore the taxonomic and biogeographic implications of this expanded phylogeny, to present a revised classification of the genus with typifications of all names, reconsidering the typifications of *M. caespitosa* and *P. digyna*, and to provide distribution maps for all accepted species.

Materials and methods

The present contribution is based on the study of herbarium collections, primarily from CBNM, E, G, K, MO, P, S and UPS, as well as on specimens from various other herbaria consulted online, mainly NOU, NY and US. All relevant type material has been examined. Field studies have been made in Madagascar (MT), Somalia (MT), Yemen (MT) and Îles Éparses (EB, VB and JH). For the preliminary conservation assessments, the geographical parameters Extent of Occurrence (EOO) and Area of Occupancy (AOO) were determined with the GeoCAT tool (Bachman et al., 2011). For SEM-images of seeds, a Zeiss Supra 35-VP microscope was used. Prior to study, the seeds were sputtered with gold-palladium alloy.

Taxon sampling for phylogenetic analysis. – Altogether 30 samples of *Paramollugo*, initially representing the 11 species recognized in this paper, *P. angustifolia*, *P. caespitosa*, *P. compressa*, *P. cuneifolia*, *P. decandra*, *P. digyna*, *P. elliotii* (however, the sample was found to be better placed in *P. simulans*, see below), *P. nesophila*, *P. nudicaulis*, *P. simulans*, and *P. spathulata* (incl. *P. navassensis*), were analyzed along with the members of *Molluginaceae* and the *Portulacineae* clade included in Thulin et al. (2016). *Kewa salsoloides* (Burch.) Christenh. is used as outgroup based on Thulin et al. (2018). Thirty-two sequences are newly generated for the present study, all for species of *Paramollugo*. For information on vouchers and GenBank accession numbers for the *Paramollugo* species, see Appendix 1. For information on vouchers and GenBank numbers for the included members of *Hypertelis* E. Mey. ex Fenzl, the Southern African clade (*Adenogramma* Rchb., *Coelanthum* E. Mey. ex Fenzl, *Pharnaceum* L., *Polpoda* C. Presl, *Psammotropha* Eckl. & Zeyh. and *Suessenguthiella* Friedrich), *Trigastrotheca* F. Muell., *Glinus* L. and *Mollugo* L., as well as of the *Portulacineae* clade and the outgroup, see Appendix 2.

DNA extraction, amplification and sequencing. – DNA was extracted from herbarium material or from leaf samples collected in silica gel, using a modified Carlson-Yoon protocol (Yoon et al., 1991). 0.01–0.03 g of plant material was added to a 2 mL tube with silica beads and grounded for 30 sec using a Mini-Beadbeater (BioSpec Products). 800 µl Carlson buffer and 8 µl 2-mercaptoethanol were added followed by incubation at 65° C for 60 min. 800 µl chloroform/isoamylalcohol 24:1 was added, followed by 30 min slow shake. Following 15 min of centrifugation, ⅔ volume of isopropanol was added to the water phase and the samples were left over night in -20° C for precipitation of DNA. The DNA pellets were collected after centrifugation and washed with buffer (76 % ethanol, 10 mM ammonium acetate), and dissolved in 100 µL 10 mM Tris-HCl (pH 8.0).

The nuclear ribosomal internal transcribed spacer (ITS) and chloroplast *trnK-matK* regions were used. PCR amplifications were performed using KAPA2G Robust DNA polymerase (Kapa Biosystems) according to the manufacturer's instructions. The PCR-program was performed as follows: an initial 3 min of denaturation at 95° C, followed by 35–37 cycles of 10 sec of denaturation at 95° C, 30 sec annealing at 50–60° C and 30 sec elongation at 72° C, ending with an additional elongation of 7 min at 72° C. The ITS region was amplified and sequenced with the primers ITS-P17 and

ITS-26S-82R (Popp & Oxelman, 2001). For the *trnK-matK* region we used the battery of different primers described by Christin et al. (2011: Fig. S1). Sequencing reactions were performed by Macrogen Europe, Amsterdam, Netherlands.

Sequence alignment, phylogenetic analyses, divergence time estimation and ancestral area reconstruction. – Sequence reads were assembled and edited with Staden package v. 2.0 (Staden et al., 1999) and Assseq v. 0.4 (Larsson & Ryberg, 2019). Sequences were aligned using MAFFT v. 7.453 (Katoh & Standley, 2013) and alignments were checked by eye and manually adjusted in AliView v. 1.25 (Larsson, 2014). Maximum likelihood bootstrap analyses were performed using RAxML-HPC-PTHREADS-AVX v. 8.2.12 (Stamatakis, 2014). Analyses were performed on the *trnK-matK* and ITS datasets separately, as well as on the two datasets concatenated into a combined dataset. A search for the best tree was combined with 1,000 bootstrap pseudoreplicates. Models of nucleotide substitution were choosen according to the corrected Akaike information criterion (AICc) as implemented with PartitionFinder v. 2.1.1 (Lanfear et al., 2016). The optimal model for both ITS and *trnK-matK* was GTR + I + G. In RAxML the GTRGAMMAI was selected for all datasets.

Divergence times for the stem and crown clade of *Paramollugo* were estimated using BEAST v. 1.10.4 (Suchard et al., 2018). We used secondary calibration points and the tree was calibrated using two normally distributed age priors: 51.9 Ma (with a standard deviation of 10 %) assigned to the node between *Molluginaceae* and the *Portulacineae* clade, based on Christin et al. (2011), and 25 Ma (with a standard deviation of 10 %) assigned to the node between *Opuntia* Mill. and *Pereskia* Mill., based on Arakaki et al. (2011). The analyses were performed with a relaxed molecular clock model with the following settings: birth-death tree prior, lognormal uncorrelated relaxed clock. Priors were set to default values except the previously described node age. GTR + I + G nucleotide substitution models were used. We ran the analysis for 100 million generations and sampled the posterior every 1,000 generations. Visual inspection in Tracer v. 1.7.1 (Rambaut et al., 2018) revealed that all runs converged within 10 million generations. Therefore, the first 10 million generations (10 %) of each run were removed as burn-in. We summarized the tree samples with TreeAnnotator v. 1.10.4 (Suchard et al., 2018).

In the RAxML analyses, bootstrap values of 95–100 % are regarded as strong support, of 75–94 % as moderate support, and 50–74 % as weak support. In the BEAST analyses, posterior probabilities of 1.0 are regarded as strong support, of 0.95–0.99 as moderate support and below 0.95 as weak support.

Ancestral area reconstruction was conducted with a Bayesian binary MCMC analysis (BBM) as implemented in RASP 4.1 (Yu et al., 2020). Starting tree was the the consensus tree of the BEAST analysis of the combined data set. The analysis was run for five million generations with 10 MCMC chains. Frequence of samples was 10,000 with 100 samples discarded as burnin. We used a fixed Jukes-Cantor model with equal among site rate variation. Maximum number of areas was set to four. The areas used for this study are listed in the legend of the BBM analysis. Distributions of taxa not treated in this paper are taken mainly from Thulin et al. (2016).

Supplementary figures (Fig. S1a–g) are available in the Supplementary material section of the online version of this article.

Results

The separate RAxML analyses of the *trnK-matK* (Fig. 1) and the ITS (Fig. 2) data produced trees where the species are mostly retrieved as monophyletic, but the relationships between them sometimes differ widely. Particularly as regards the relationships of *Paramollugo nudicaulis*, there is strong conflict between the trees. In the *trnK-matK* tree, *P. nudicaulis* is strongly supported as sister to *P. digyna*, whereas in the ITS tree, it is strongly supported as sister to *P. caespitosa* and *P. nesophila* together. In the *trnK-matK* tree, *P. caespitosa* is, in contrast, moderately supported as sister to *P. decandra*, a relationship that is not seen in the ITS tree, where *P. digyna* has an unsupported position within the genus as sister to all the species except *P. decandra*.

At species level, *Paramollugo nudicaulis*, *P. digyna*, *P. decandra*, *P. spathulata* and *P. angustifolia* are strongly supported as monophyletic in both *trnK-matK* and ITS trees, and *P. cuneifolia* (ITS only) is sister to *P. spathulata* with strong support. The new species *P. compressa* (ITS only) is strongly supported as a member of the genus *Paramollugo*, but its relationship to other species is uncertain. *Paramollugo nesophila* is moderately supported in the ITS tree, whereas in the *trnK-matK* tree the samples of *P. nesophila* appear in a strongly supported clade with *P. simulans* and *P. angustifolia*. In this clade, two collections previously identified as, respectively, *P. nudicaulis* (*De Block et al. 551*, *P. simulans* 3, only *trnK-matK*) and *P. elliotii* (*Jongkind et al. 3342*, *P. simulans* 4) also appear. In the ITS tree a similar clade with *P. simulans* and *P. angustifolia* is retrieved, but here without the samples of *P. nesophila*.

As there is no well supported conflict between the *trnK-matK* and the ITS trees as regards the monophyly of the species, we have made a combined analysis, where all samples included in the study can be used. The best tree of the combined RAxML analysis is shown in Fig. 3. The basic topology agrees with Fig. 1 in Thulin et al. (2016), the only difference being the better sampling in the *Paramollugo* clade. Here, there is a weakly supported basal split between a strongly supported clade with *P. spathulata* and *P. cuneifolia* and the rest of the genus. Another weakly supported clade comprises the strongly supported *P. nudicaulis* as sister to the strongly supported *P. caespitosa* and *P. nesophila* together. *Paramollugo simulans* appears in a moderately supported clade along with *P. angustifolia* and the two collections previously identified as *P. nudicaulis* and *P. elliotii* mentioned above.

After several runs with BEAST we have to conclude that two optima giving two different topologies are retrieved based on the combined dataset, one (Fig. 4, Fig. S1a–c) basically agreeing with the combined tree from the RAxML analysis and one (not shown but available as Fig. S1d–f) in some aspects agreeing more with the *trnK-matK* tree. Both topologies show a strongly supported basal split between two strongly supported clades, one with *Paramollugo spathulata* and *P. cuneifolia* in the Caribbean, centered in the Greater Antilles, and one with the rest of the genus, centered in Madagascar. *Paramollugo decandra* is weakly supported as sister to *P. digyna* in Fig. 4, whereas in the alternative topology *P. decandra*, *P. digyna* and *P. compressa* form a clade, albeit with weak support. In Fig. 4, *P. compressa* is instead weakly supported sister to *P. simulans* and *P. angustifolia* together. The topology in Fig. 4 shows a strongly supported clade with *P. nudicaulis* as sister to *P. caespitosa* and *P. nesophila* together, whereas in the alternative topology *P. nesophila* is strongly supported sister to *P. simulans* and *P. angustifolia* together.

The species of *Paramollugo* are all monophyletic and strongly supported in the BEAST analysis in Fig. 4, except for *P. simulans*, which is only weakly supported. In the alternative topology, *P. simulans* is paraphyletic with respect to *P. angustifolia*, whereas all other species are monophyletic and strongly supported.

The divergence time estimates with BEAST resulted in an age of (38.9–)47.5(–56.1) Ma (Eocene) for the *Paramollugo* stem clade and (10.4–)16.6(–23.8) Ma (mid-Miocene) for the crown clade (Fig. 4). The age of the crown clade would also be the estimated date for the split between the clades centered in the Caribbean and in Madagascar. The corresponding datings in the alternative topology are (37.9–)46.8(–55.5) Ma and (11.7–)18.4(–27.7) Ma. In the Caribbean clade, the date for the split between the widespread *P. spathulata* and *P. cuneifolia* in eastern Cuba is estimated to (2.2–)6.8(–12.3) Ma or (1.4–)6.9(–13.3) Ma, i.e., late Miocene in both cases. The estimated date for the split between *P. decandra* in Madagascar and *P. digyna* in New Caledonia is (4.2–)8.3(–13.0) Ma (Fig. 4), whereas in the alternative topology the split between *P. digyna* and *P. decandra* and *P. compressa* together is (5.2–)10.6(–16.9) Ma (late Miocene in both cases). The split between the widespread *P. nudicaulis* from *P. caespitosa* and *P. nesophila* together is estimated to (3.8–)6.9(–10.7) Ma (Fig. 4), whereas in the alternative topology, *P. nudicaulis* split from a clade with *P. caespitosa*, *P. nesophila*, *P. simulans* and *P. angustifolia* together at (6.3–)9.9(–14.8) Ma (late Miocene in both cases). The split between *P. nesophila* on Îles Éparses and *P. caespitosa* in Madagascar is estimated to (2.4–)4.9(–7.9) Ma in Fig. 4, whereas in the alternative topology the split between *P. nesophila* and *P. simulans* and *P. angustifolia* together in Madagascar is estimated to (4.1–)6.7(–10.2) Ma, i.e., late Miocene to Pliocene. Within *P. nesophila*, a split between the populations on Grand Glorieuse and Juan de Nova from those on Europa is estimated to (0.3–)1.2(–2.5) Ma in Fig. 4 and (0.3–)1.6(–3.3) Ma in the alternative topology, i.e., Pleistocene, and within *P. caespitosa*, a split between sample 1 from SE Madagascar and samples 2 and 3 from SW Madagascar is estimated to (0.6–)2.1(–3.9) Ma in Fig. 4 and to (0.7–)2.6(–5.5) Ma in the alternative topology, i.e., Pliocene/Pleistocene. Finally, the split between the populations of *P. angustifolia* in Madagascar and Somalia is estimated to (0.1–)0.8(–1.7) Ma in Fig. 4 and (0.1–)0.6(–1.4) Ma in the alternative topology, i.e., Pleistocene.

The result from the ancestral area reconstruction using BBM is shown in Fig. 5 (an uncollapsed tree in Fig. S1g). The ancestral area of the *Paramollugo* stem clade is Africa, whereas that of the crown clade most likely is Madagascar and/or the Caribbean. The ancestral area of *P. digyna* in New Caledonia and *P. nesophila* in Îles Éparses is Madagascar in both cases. The ancestral area of *P. nudicaulis* is Madagascar, from where it has spread to Africa and Asia, whereas *P. angustifolia* has spread from Madagascar to Africa.

Discussion

We assume that the conflict between the *trnK-matK* (Fig. 1) and the ITS (Fig. 2) trees, in particular as regards the position of *Paramollugo nudicaulis*, can be explained by the fact that this species is a hexaploid with $2n = 54$ (see below under generic description), presumably with an allopolyploid origin. Chromosome numbers are not known for any other species, but we suppose that the genus is a polyploid complex, where the relationships, at least in part, are in the form of a network rather than of a tree. The base number in *Molluginaceae* is $x = 9$ (Endress & Bittrich, 1993) and we assume that also diploids and tetraploids are found within *Paramollugo*. However, exploring this proposed network in more detail is beyond the scope of the present study, we can just point to instances of conflict between the trees and to a possibly allopolyploid origin of some of the species (apart from *P. nudicaulis*, also *P. caespitosa*, *P. nesophila* and *P. digyna* are candidates, see under these species in the taxonomic part). In the first place, chromosome numbers of more species would be needed for a fuller picture, as well as further phylogenetic analyses.

In all analyses, the *Paramollugo* clade is strongly supported as sister to the Southern African clade and the *Hypertelis* clade together, with the split estimated to the Eocene in the BEAST analysis (Fig. 4). The Southern African clade is entirely African, whereas the *Hypertelis* clade is centered in Africa, but with two of the species also occurring on other continents. This indicates an African origin of the *Paramollugo* clade, in agreement with the BBM analysis (Fig. 5), although none of the extant species are restricted to this continent. Therefore, dispersal from Africa to Madagascar and/or the Caribbean (Fig. 5) seems to have taken place sometime between the Eocene and mid-Miocene. Indeed, according to Samonds et al. (2022), dispersal has been the major force shaping the flora of Madagascar in general.

In the crown clade of *Paramollugo*, the sister group relationship between a Caribbean clade with two species, centered in the Greater Antilles, and the rest of the genus, centered in Madagascar (Fig. 5), is strongly supported in the BEAST analysis (Fig. 4). The split dates to the mid-Miocene and the distance between Madagascar and the Caribbean is roughly 13,000 km (Fig. 6). This apparently unparalleled disjunction could possibly be seen in the light of the boreotropics hypothesis (Tiffney, 1985; Lavin & Luckow, 1993; Lavin et al., 2000), according to which tropical plants occurred at higher latitudes than they do today during thermal maxima of the early Tertiary (Eocene). Such boreotropic plant groups later had to migrate southwards and may have ended up in distant regions such as Central America and the Horn of Africa (Lavin et al., 2000). However, the split seen in the crown clade of *Paramollugo* is too recent to make this interpretation tenable. Instead, long distance dispersal seems to be the only realistic alternative. The seeds of *Paramollugo* are small and light and transport by the easterly trade winds from Madagascar to the Greater Antilles, either in a single long jump or via stepping stones, is a possibility. As the seeds tend to be retained in the dry capsules after dehiscence, the dispersal unit may also be an entire capsule or a portion of a cyme (see below under the genus in the taxonomic part).

Paramollugo digyna, endemic to New Caledonia, split from its relatives in Madagascar during late Miocene (Fig. 4, 5). Also in this case, long distance dispersal by wind from Madagascar seems to be the only realistic alternative, the distance between Madagascar and New Caledonia being roughly 12,000 km (Fig. 6). Here, a parallel is found in the woody genus *Acridocarpus* Guill. & Perr. (*Malphigiaceae*), where *A. austrocaledonicus* Baill., the single species of the genus found in New Caledonia, is nested with strong support among *A. adenophorus* Adr. Juss. and *A. excelsus* Adr. Juss., two species endemic to Madagascar (Davis et al., 2002). This was considered as a perplexing biogeographical question by Davis et al. (2002), who suggested the dispersal of wing-fruited *Acridocarpus* from Madagascar to New Caledonia to be an instance of long-distance dispersal by wind "approximately 15–8 Mya", i.e., mid- to late Miocene, similar to the case of *Paramollugo*.

The species of *Paramollugo* in the Caribbean clade are ultramafic-tolerant, with many occurrences on serpentine, whereas *P. digyna* in New Caledonia is highly ultramafic-tolerant or possibly even ultramafic-obligate. The same applies to *Acridocarpus austrocaledonicus*, which generally occurs in bushland ("maquis") on serpentine. In Madagascar, the postulated source area, ultramafic substrates are rare (Pillon et al., 2019), and none of the Malagasy species of *Paramollugo* can be assumed to be ultramafic-tolerant. However, the capability of ultramafic tolerance may have evolved earlier in the stem clade of the genus.

Paramollugo nudicaulis is nested among species in Madagascar and also split from its relatives there in late Miocene (Fig. 4, 5). It still occurs in Madagascar and from there, at least three short out-of-Madagascar dispersals have apparently taken place to the Comoro Islands, Mauritius and Aldabra. Apart from that, *P. nudicaulis* is widespread in tropical and subtropical Africa and Asia and is the species of the genus that has by far gained the largest area of distribution. Within *P. nudicaulis* there is a split between the samples from Madagascar and India and those from Africa (Namibia, Burkina Faso and Somalia) that dates to the Pleistocene (Fig. 4). This indicates that independent dispersals have taken place, presumably by wind, from Madagascar to Africa and from Madagascar to Asia (Fig. 5).

Paramollugo nesophila, endemic to Îles Éparses in the Mozambique Channel, split from its relatives in Madagascar during late Miocene to Pliocene (Fig. 4, 5). The islands of Îles Éparses are low, about 125,000 years old, and mostly consist of coral reefs built on remnants of old volcanoes (Boullet et al., 2018). Therefore, *P. nesophila* represents an example of an island lineage that is much older than the islands where it occurs today. Possibly it evolved on the old volcanoes that previously existed in the region (Masters et al., 2022), as is also indicated by the split between the populations on Grand Glorieuse and Juan de Nova and those on Europe that is older than any of these islands. Other examples of lineages in the vicinity of Madagascar that are older than the islands where they occur today are *Monimia* Thouars (*Monimiaceae*) on Mauritius and Réunion (Renner et al., 2010), *Mathurina* Balf. f. (*Passifloraceae*) on Rodrigues Island (Thulin et al., 2012), and *Badula* Juss. (*Primulaceae*), also on Rodrigues (Strijk et al., 2014).

The most recent dispersal out of Madagascar in *Paramollugo* is found in *P. angustifolia*, a species nested among species in Madagascar, but also occurring in Somalia, from where it was first described (Gilbert & Thulin, 1993). In this case, the dispersal is dated to the Pleistocene (Fig. 4, 5), and the distance between the occurrences in Madagascar and Somalia is roughly 2,200 km. Again, long-distance dispersal by wind is the most likely explanation. The known area of distribution of *P. angustifolia*, restricted to Madagascar and a single locality in Somalia, is unique among flowering plants, but further localities of this inconspicuous species may remain to be discovered on the African continent.

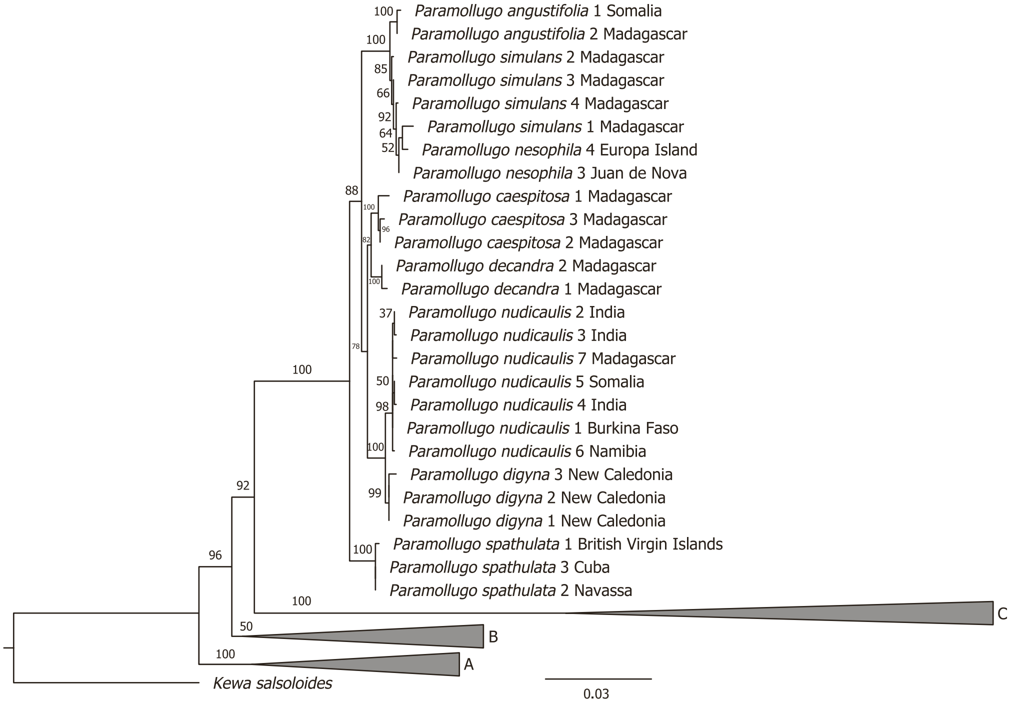

Fig. 1. – Best tree from the RAxML analysis of the *trnK-matK Molluginaceae* dataset. Bootstrap values from 1,000 bootstrap replicates are above the branches. When more than one accession per species was included, the numbers after the names correspond to those in Appendix 1. The clades with letters correspond to the *Portulacineae* clade (A), the *Glinus*, *Mollugo* and *Trigastrotheca* clade (B), and the *Hypertelis* and South African clade (C).

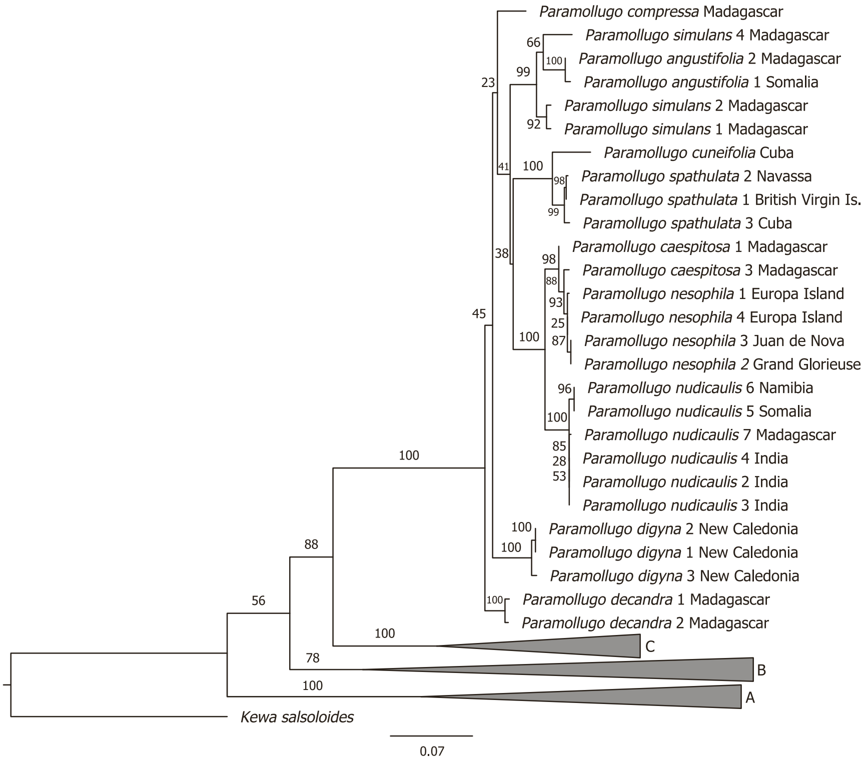

Fig. 2. – Best tree from the RAxML analysis of the ITS *Molluginaceae* dataset. Bootstrap values from 1,000 bootstrap replicates are above the branches. When more than one accession per species was included, the numbers after the names correspond to those in Appendix 1. The clades with letters correspond to the *Portulacineae* clade (A), the *Glinus*, *Mollugo* and *Trigastrotheca* clade (B), and the *Hypertelis* and South African clade (C).

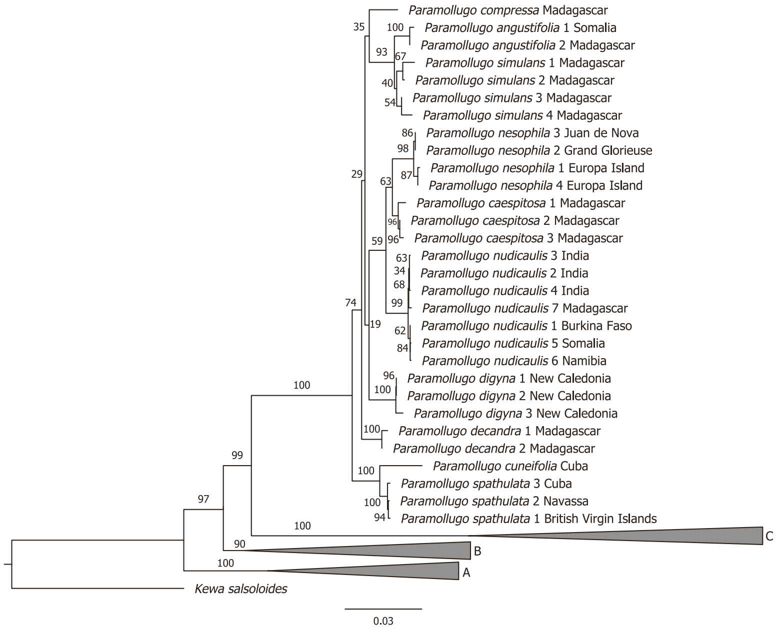

Fig. 3. – Best tree from the RAxML analysis of the combined *trnK-matK* and ITS *Molluginaceae* dataset. Bootstrap values from 1,000 bootstrap replicates are above the branches. When more than one accession per species was included, the numbers after the names correspond to those in Appendix 1. The clades with letters correspond to the *Portulacineae* clade (A), the *Glinus*, *Mollugo* and *Trigastrotheca* clade (B), and the *Hypertelis* and South African clade (C).

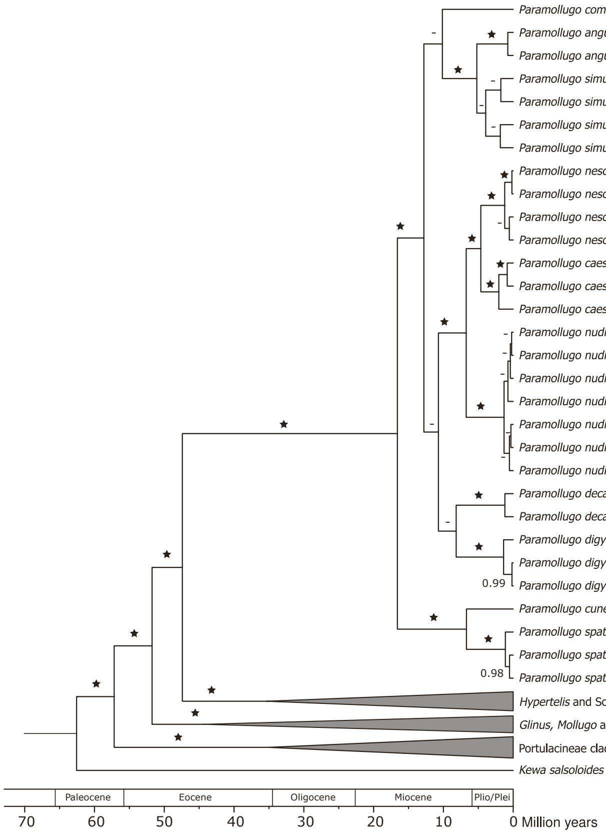

Fig. 4. – Dated phylogeny. Maximum clade credibility chronogram from BEAST analysis of the combined *Molluginaceae* dataset. Branch labels show Bayesian probablilities. Posterior probabilities of 1.0 are replaced by asterisks, whereas probabilities less than 0.95 are replaced by dashes. When more than one accession per species was included, the numbers after the names correspond to those in Appendix 1.

Dispersals out of Madagascar, apart from the case of *Acridocarpus* discussed above, have also been inferred for, e.g., *Exacum* L. (*Gentianaceae*) (Yuan et al., 2005), various members of *Rubiaceae* (Wikström et al., 2010), and *Psiadia* Jacq. ex Willd. (*Asteraceae*) (Strijk et al., 2012). An origin in Madagascar not before Eocene was suggested for *Exacum* by Yuan et al. (2005), and from there dispersals to India and Sri Lanka took place 8.2–35.6 Ma, followed by an extensive range expansion and radiation in Asia. More recent dispersals out of Madagascar took place to the Comoros and Mauritius, islands that share species of *Exacum* with Madagascar. A dispersal from Madagascar to Africa 4.7 Ma resulted in the the divergence of *E. oldenlandioides* (S. Moore) Klack., a species widespread in tropical Africa. According to Wikström et al. (2010), "Madagascar is the source origin for almost all *Rubiaceae* found on the neighbouring islands of the Comoros, Mascarenes and Seychelles". Also, a few dispersals from Madagascar to Africa were inferred in the four tribes of *Rubiaceae* studied. In the non-monophyletic *Psiadia*, two Malagasy clades were detected, both with an African origin, and both with an initial radiation in Madagascar followed by dispersals to surrounding islands (Strijk et al., 2012).

Taken altogether, the biogeography of *Paramollugo*, a genus centered in Madagascar and with disjunctions to the Caribbean and New Caledonia, along with dispersals to the neighbouring islands of the Comoros, Mauritius, Aldabra and Îles Éparses, as well as to Africa and Asia, is remarkable and seemingly unparalleled among flowering plants.

Taxonomy

Paramollugo Thulin in Taxon 65: 784. 2016.

≡ *Lampetia* Raf., Fl. Tellur. 3: 34. 1837 [nom. illeg., non K.D. Koenig, Icon. Foss. Sectiles: 2, tab. 2, fig. 23. 1825].

Typus: *Paramollugo nudicaulis* (Lam.) Thulin

Herbs or small shrubs or subshrubs, annual to perennial, glabrous or sometimes papillose or pubescent; stems terete or rarely compressed and phyllocladic, longitudinally ridged; nodes with 2–4 membranous scales, each node with 2–4 branches. *Leaves* alternate, mostly crowded in a basal rosette or sometimes scattered along long shoots and crowded on short shoots, sessile but often tapering below into a petiole-like base; stipules absent. *Flowers* in seemingly axillary, mostly lax, long-pedunculate dichotomously branched cymes, each node with 2–4 branches, sometimes with sessile or shortly pedunculate dense cymes borne on short shoots; bracts small, membranous. *Tepals* 5, free, apically hooded, white or rarely tinged with pink or green inside, greenish, brownish or purplish outside, with quincuncial aestivation. *Stamens* (2–)3–5(–6) or c. 10. *Ovary* of (2–)3 carpels, with mostly numerous ovules; styles (2–)3, short, papillose on the inner surface. *Capsule* loculicidally dehiscent with (2–)3 valves. *Seeds* mostly numerous, tuberculate to colliculate or finely reticulate, black to dark brown or rarely pale brown; testa cells sometimes with secondary ornamentation and small pits often present in the boundaries between them; hilum ± minutely strophiolate.

Notes. – *Paramollugo* is a genus of 11 species, seven of which are known from Madagascar (five restricted to Madagascar, one also widespread in the tropics and subtropics of the Old World, one also in Somalia), two species are restricted to the Caribbean, one to New Caledonia, and one to Îles Éparses in the Mozambique Channel (Fig. 6).

Paramollugo differs from other members of *Molluginaceae* by having alternate, ex-stipulate leaves that are either all crowded in a basal rosette or (in *P. decandra*) scattered along long shoots and crowded on short shoots. The small pits present in the boundaries between the testa cells of the seeds in species of *Paramollugo* was pointed to as a characteristic for this genus by Sukhorukov & Kushunina (2017) and Sukhorukov et al. (2018). We have found such pits to be present in all species, except *P. compressa*, *P. decandra*, *P. elliotii* and *P. simulans* (in part).

The seed surface of species of *Paramollugo* and other members of *Molluginaceae* has often been described as papillose (or papillate) when distinct protuberances are present and colliculate when the protuberances are low and only slightly convex. We prefer to use tuberculate instead of papillose in this account, as papillae are usually regarded as soft structures (Beentje, 2010), which is not the case here.

The chromosome number $2n = 54$ has been reported in material of *Paramollugo nudicaulis* from India (Raghavan & Srinivasan, 1940; Sanjappa, 1978). As the base number in *Molluginaceae* is $x = 9$ (Endress & Bittrich, 1993), *P. nudicaulis* is a hexaploid, presumably with an allopolyploid origin (see above under Discussion). Chromosome numbers for the other species are not known.

Pollen grains of *Paramollugo nudicaulis*, studied by LM and SEM and illustrated by SEM images, were described as 3-zonocolpate, subprolate and spinulate by Osman & Hassan (2015). This is in agreement with the pollen morphology in most other members of *Molluginaceae* (Endress & Bittrich, 1993). The embryology of *P. nudicaulis* was studied by Bhargava (1934).

Sulakshana & Raju (2019) studied floral biology and pollination ecology in *Paramollugo nudicaulis* in India. Flowers of *P. nudicaulis* were visited by forageing bees, flies and butterflies between 7:00 and noon, all effecting both self- and cross-pollination. Thrips were found to use the flowers for breeding and feeding, also effecting pollination. In the tepals of the simple perianth, the white upper surface attracts vistors and functions as corolla, whereas the greenish or brownish outside functions as calyx. Fruits mature within 8–12 days

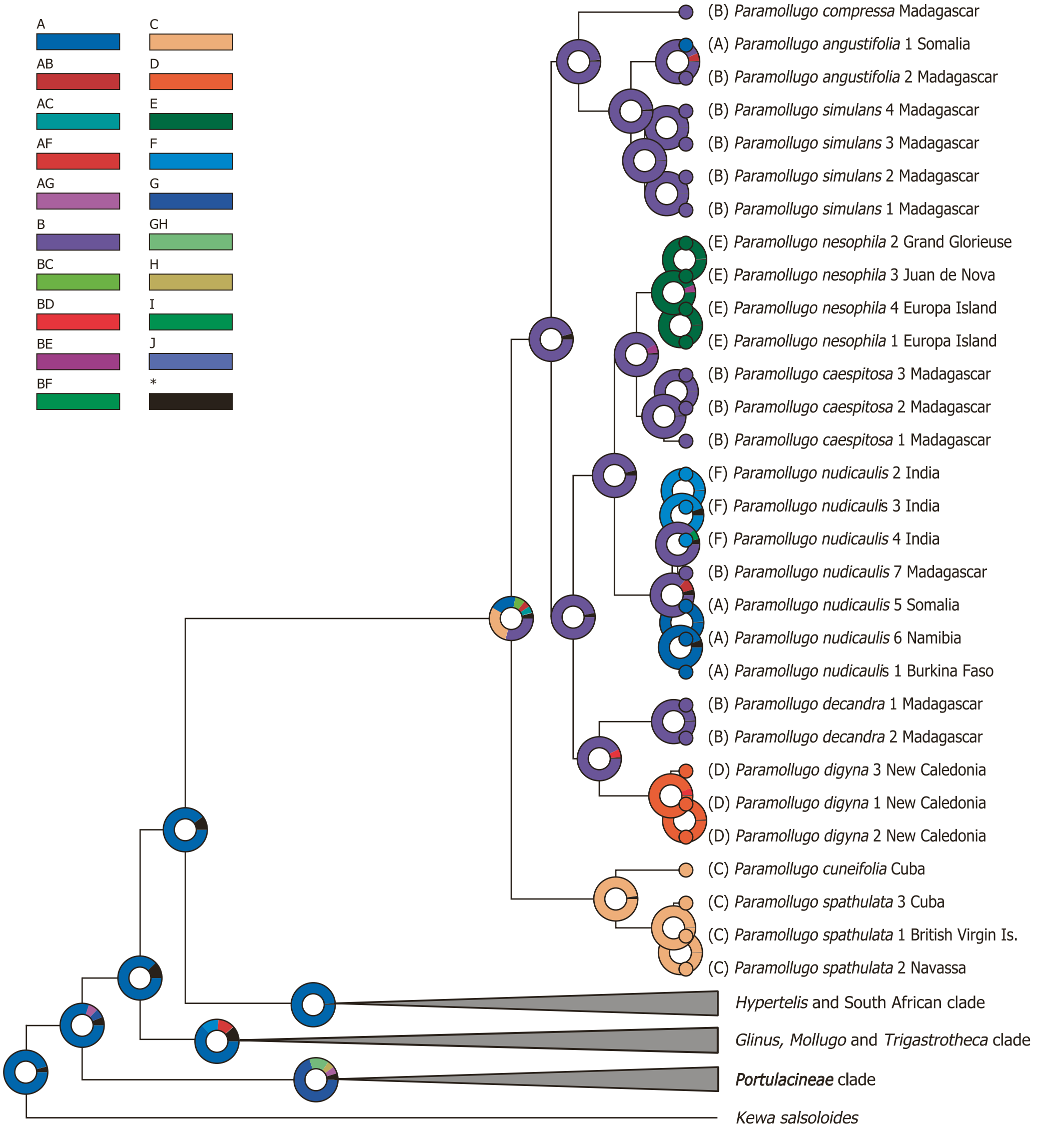

Fig. 5. – Ancestral area reconstruction of *Paramollugo* with BBM. Pie charts indicate the most likely distribution of the most recent common ancestor. The areas for species of *Paramollugo* are coded as follows: A, Africa; B, Madagascar; C, Caribbean; D, New Caledonia; E, Îles Éparses; F, Asia, and for other species included in the analysis also: G, North America; H, South America; I, Australia; J, Europe. Asterisk (in black) represents other ancestral ranges.

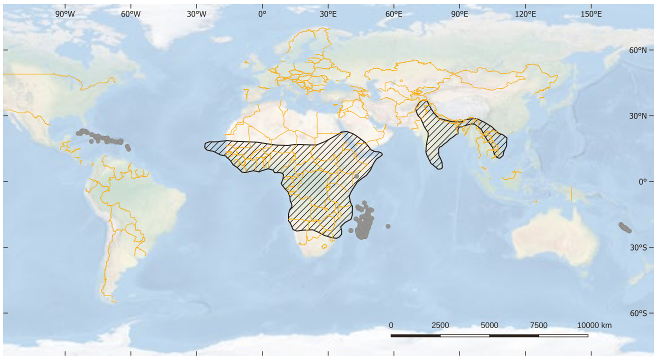

Fig. 6. – Geographic distribution of *Paramollugo*, with occurrences of the widespread *P. nudicaulis* in Africa and Asia hatched.

and seed set rate was found to be 86–89%. Capsules open when dry to expose the seeds that remain in the capsules until they gradually fall out or get washed out by rain. Seeds on the ground may be dispersed by rain water. Dehisced capsules or portions of cymes in fruit may be dispersed by wind, and retained seeds may gradually be released and fall to the ground.

Key to the species of Paramollugo

1\. Shrubs or subshrubs with leaves scattered along long shoots and crowded on short shoots; stamen-filaments very narrowly triangular .... 1. ***P. decandra***

1a. Herbs with leaves crowded at base; stamen-filaments filiform 2

2\. Stems compressed and phyllocladic; seeds finely reticulate, almost smooth .... 6. ***P. compressa***

2a. Stems terete; seeds colliculate or tuberculate 3

3\. Leaves linear to very narrowly oblanceolate, 0.7–1.5(–2) mm wide 4

3a. Leaves narrowly oblanceolate to obovate or spathulate, or with distal part reniform to ovate-triangular, (2–)3–30 mm wide 6

4\. Perennial; anthers 0.5–0.6 mm long; seeds 0.6–0.7 × c. 0.55 mm .... 9. ***P. elliotii***

4a. Annual or ephemeral; anthers 0.2–0.3 mm long; seeds c. 0.4–0.5 × 0.3–0.4 mm 5

5\. Testa cells with cross-striate secondary ornamentation; seeds c. 0.40–0.51 × 0.34–0.40 mm .... 4. ***P. nesophila***

5a. Testa cells smooth, without secondary ornamentation; seeds 0.39–0.43 × 0.28–0.36 mm .... 7. ***P. angustifolia***

6\. Stamens c. 10 .... 3. ***P. caespitosa***

6a. Stamens (3–)5(–6) 7

7\. Leaves succulent, marcescent, densely and ± distichously arranged at plant base .... 11. ***P. cuneifolia***

7a. Leaves herbaceous, not marcescent, arranged in basal rosette 8

8\. Annual or occasionally short-lived perennial; leaves with petiole-like part shorter than distal part 9

8a. Annual or perennial; leaves with petiole-like part about as long as or longer than distal part 10

9\. Leaves often > 12 mm wide; tepals (2–)2.5–3(–3.5) mm long; seeds ± distinctly tuberculate to sometimes colliculate, with cross-striate testa cells with small pits in boundaries between most of them .... 2. ***P. nudicaulis***

9a. Leaves 2–12 mm wide; tepals 1.5–2.5 mm long; seeds colliculate to finely tuberculate, with smooth to weakly striate testa cells without pits in boundaries between them or with pits between some cells only .... 8. ***P. simulans***

10\. Leaves with reniform or narrowly to broadly ovate-triangular distal part, ± abruptly tapering into a petiole-like part 1–4 times as long as distal part; styles 2–3 .... 5. ***P. digyna***

10a. Leaves with narrowly to broadly obovate or spathulate distal part, usually gradually tapering into a petiole-like part about as long as distal part; styles 3 .... 10. ***P. spathulata***

1\. ***Paramollugo decandra*** (Scott Elliot) Thulin in Taxon 65: 786. 2016 (Fig. 7, 8).

≡ *Mollugo decandra* Scott Elliot in J. Linn. Soc., Bot. 29: 24. 1891.

Lectotypus (designated by Sukhorukov & Belyaeva in Sukhorukov et al., 2016: 423)**: Madagascar. Reg. Anosy [Prov. Toliara]:** “sea-shore near Fort Dauphin”, IV.[?], fl. & fr., *Scott Elliot 2481* (K [K000232027]!; isolecto-: P [P00898406]!).

Shrubs or subshrubs, mostly 0.3–1 m tall, but occasionally up to 3 m (*Croat 31225*), glabrous in all parts or young stems and leaves papillose; stems terete, usually much branched, first pale brown, later dark brown or black. *Leaves* scattered along long shoots and crowded on short shoots, 5–30 × 2–12(–16) mm, oblanceolate to broadly obovate or spathulate, rounded or subacute to slightly emarginate at the apex, gradually to abruptly tapering below into a petiole-like base, the petiole-like part shorter than the distal part; midrib prominent beneath, lateral veins 2–4 pairs, indistinct. *Flowers* few to several in sessile or shortly pedunculate dense cymes; bracts 2–2.5 mm long, ovate, acute; pedicels up to 3 mm long. *Tepals* 2.5–3.5 × 1.2–1.6 mm, elliptic, rounded at the apex, with hyaline margins, 3–5-veined from the base, white or tinged with pink or green inside. *Stamens* 10(–12), 1–2 mm long; filaments very narrowly triangular; anthers c. 0.4 mm long, shortly oblong. *Ovary* 1.5–2 mm long, ellipsoid, 3-locular; styles 3, 0.3–0.4 mm long, spreading. *Capsules* 2–2.5 mm long, ellipsoid. *Seeds* 0.65–0.75 × 0.50–0.60 mm, subcircular-reniform in outline, flattened, finely tuberculate, black; testa cells without secondary ornamentation and without pits in the boundaries between them; hilum c. 0.1 mm long.

Vernacular names and uses. – “Alokantala” (*Sussman 230*), “Hazotaha” (*Humbert 12342*), “Jamaninjia” (*Koechlin 5*), “Tatavakibo” (*Humbert 12343*), “Vatolalaky” (*Koechlin s.n.*).

The plant is said to have medicinal uses (*Sussman 230*), but these are unspecified.

Distribution and ecology. – *Paramollugo decandra* is widespread in southern Madagascar (Fig. 9), where it occurs in dry deciduous bushland and forest, in sandy, gravelly or rocky places, at elevations from near sea level up to about 400 m.

Phenology. – Flowering and/or fruiting plants have been seen from all months except May.

Conservation status. – *Paramollugo decandra* is widespread in southern Madagascar with occurrences in, for example, the National Parks of Andohahela and Tsimanampetsotsa. It is listed as Near Threatened NT B2ab(iii) under the IUCN Red List Categories and Criteria (IUCN, 2012), based on an

Fig. 7. – *Paramollugo decandra* (Scott Elliot) Thulin, flowering branch.
[*Thulin & Razafindraibe 11820*] [Photo: M. Thulin]

assessment made by Ravololomanana (2018). This assessment is accepted here.

Notes. – The single collection cited in the protologue of *Mollugo decandra* (Scott Elliot, 1891) is *Scott Elliot 2481* and the specimen in K [K000232027] was cited as the holotype by Thulin et al. (2016 [30.VIII]). Soon thereafter, Sukhorukov & Belyaeva in Sukhorukov et al. (2016 [27.IX]) designated this specimen as the lectotype, arguing that a Scott Elliot specimen from Fort Dauphin in P is a syntype, making lectotypification necessary. Although the Scott Elliot specimen in P lacks collection number, it is assumed to be a duplicate of the type collection and the lectotypification is accepted here.

Paramollugo decandra is a strongly supported species in all the phylogenetic analyses (Fig. 3, 4). It is unique in the genus by being a small shrub or subshrub with the leaves scattered along long shoots and crowded on short shoots (Fig. 7). The inflorescences, which are sessile or shortly pedunculate, dense cymes borne on the short shoots, are also unique. Along with *P. caespitosa* and *P. compressa*, *P. decandra* is one of the few species in the genus with 10 stamens, but the stamens of *P. decandra* differ from those in *P. caespitosa*, *P. compressa* and all other species in the genus by having very narrowly triangular rather than filiform filaments. The comparatively large and finely tuberculate seeds of *P. decandra*, with testa cells without secondary ornamentation and without pits in the boundaries between them (Fig. 8), are characteristic. The only other species of *Paramollugo* that have testa cells lacking pits in the boundaries between them are *P. compressa*, *P. elliotii* and *P. simulans* (in part).

In the combined RAxML analysis (Fig. 3), *Paramollugo decandra* is unsupported sister to all species of the genus except *P. spathulata* and *P. cuneifolia* in the Caribbean clade. In the BEAST analysis (Fig. 4), it is instead weakly supported sister to *P. digyna*.

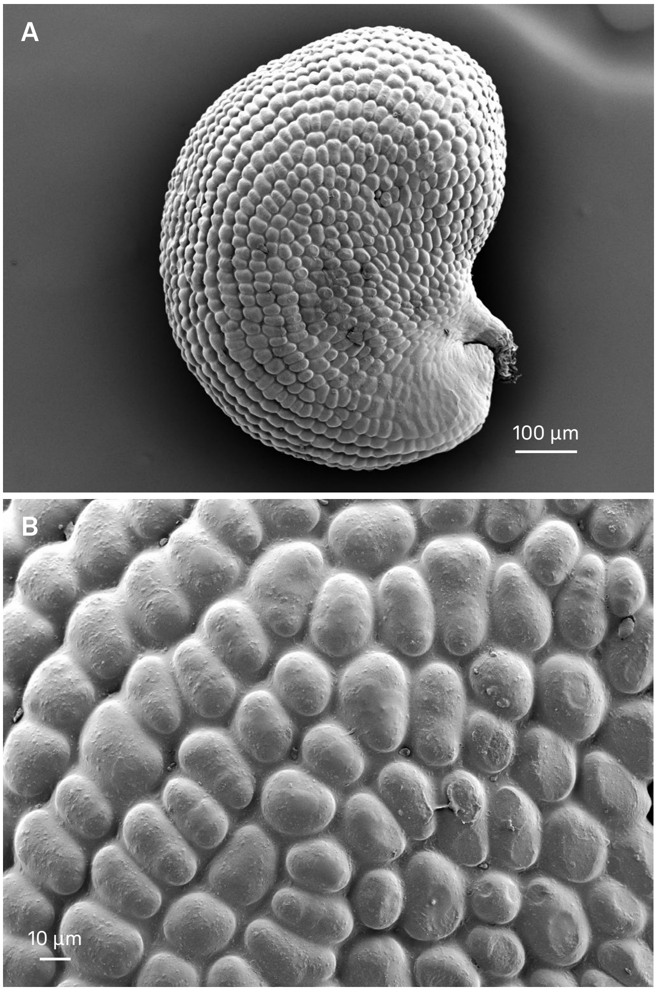

Fig. 8. – *Paramollugo decandra* (Scott Elliot) Thulin, SEM micrographs.
A. Seed; **B.** Detail of seed ornamentation.
[*Thulin & Razafindraibe 11820*, UPS]

Additional specimens examined. – Madagascar. **Reg. Androy [Prov. Toliara]:** near Ampanihy, 14.XI.1967, fl., *Bernardi 11457* (G, K, P); 1–10 km W of Ampanihy, 16.II.1975, fl., *Croat 31405* (MO); between Lavanono and Marovato, 17.II.1975, fl., *Croat 31576* (MO); Ambovombe Distr., 18.IV.1924, fl., *Decary 2585* (MO, P); Antanimora, 6.VIII.1924, fl., *Decary 2938* (K, MO, P); Ambovombe, 11.I.1925, fl., *Decary 3501* (P); Ambovombe, 12.III.1931, fl., *Decary 8588* (G, K, MO, P); E of Ambovombe, 29.VI.1931, fl., *Decary 9058* (P); from Beloha to Ampanihy, W of the village of Amborompotsy, 20.III.1985, fl., *Dorr et al. 4076* (BR, K, MO, P); from Ampanihy to the mouth of Menarandra, 10–11.III.1955, *Humbert & Capuron 29339* (MO, P, TAN); Tranoroa to Beloha, 6 km, III.1960, fl., *Keraudren 923* (P); Bevoalavo to Ampanihy, II.1962, fl., *Keraudren 1471* (P); between Itampolo and Bevoalavo, 28.XI.1960, fl., *Leandri 4114* (P); S of Antanimora, 24°51'05"S 45°40'14"E, 21.IV.2001, *Miles & Randriantarika 149* (K); Cape Ste. Marie Reserve, SW of Tsiombe, 25°35'S 45°09'E, 27.XII.1988, fl., *Phillipson 3010* (BR, MO, P); between Beloha and Ampanihy, 19.II.1949, fl., *Service Forestier 462* (MO, P); 10–15 km N of Itampolo, 14.IV.1961, fl., *Service Forestier 20274* (P). **Reg. Anosy [Prov. Toliara]:** road between Beraketa and Bevia, N of Amboasary, 24°55'56"S 46°25'11"E, 20.I.2007, fl. & fr., *Andriamihajarivo & Rakotoarivony 1197* (MO, P, TAN); Ifotaka (Mandrare), XI.1952, fl., *Bosser 3998* (P), *4182* (MO, TAN); Ranopiso, X.1956, fl., *Bosser 10482* (P); 16 km W of Manambaro, 21.II.1975, fl., *Croat 31942* (MO); 23–28 km W of Manambaro, 21.II.1975, fl.,

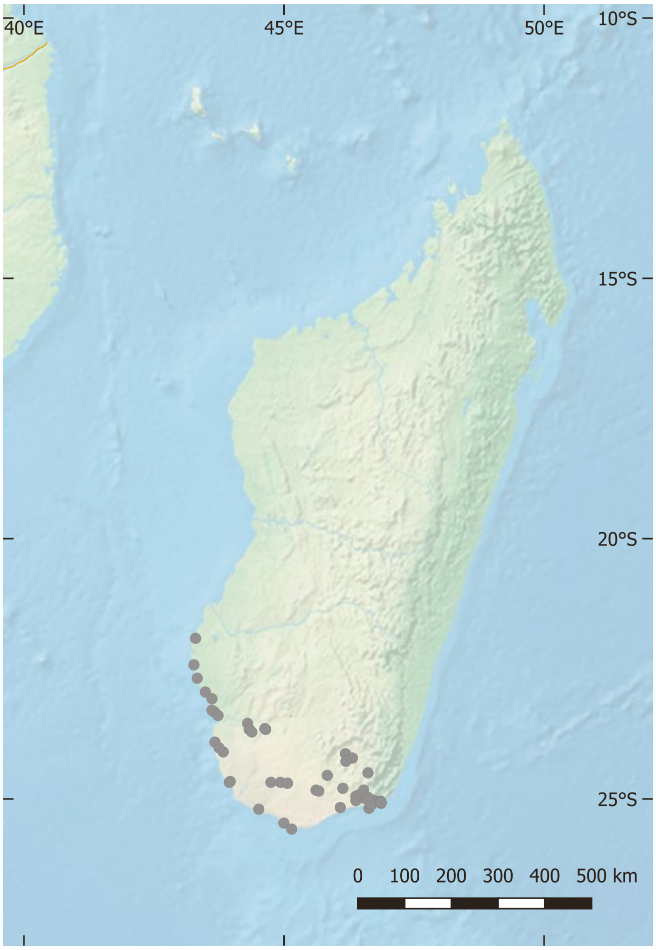

Fig. 9. – Geographic distribution of *Paramollugo decandra* (Scott Elliot) Thulin.

Croat 31979 (MO); Bevilany, 29.III.1924, fl., *Decary 2457* (G, P); Andrahomana, 17.VI.1926, fl., *Decary 4095* (P); Ifotaka, N of Ambovombe, 28.IX.1931, fl., *Decary 9217* (G, K, MO, P); Amboasary E of Ambovombe, 22.I.1932, fl., *Decary 9577* (K, MO, P); Bevilany, 23.IV.1932, fl., *Decary 9779* (P); Behara, 3.IX.1932, fl., *Decary 10456* (P); Petriky, 25°05'S 46°52'E, 30.X.1989, fl., *Dumetz et al. 819* (K, MO); near Bevilany, 14.IX.1928, fl., *Humbert & Swingle 5678* (P); between Tsivory and Anadabolava, XII.1933, fl., *Humbert 12342* (P), *12343* (G, K, P); near Anadabolava, XII.1933, fl., *Humbert 12421bis* (P); Manambolo valley, near Isomono, XII.1933–I.1934, fl., *Humbert 12868* (P); 30–35 km N of Ambia, 6–9.II.1955, fl., *Humbert & Capuron 28810* (MO, P); Mt. Vohitrandriana, S of Ranopiso, 27.II.1955, fl., *Humbert & Capuron 29158* (G, K, MO, P); lower Mandrare valley near Amboasary, 4.III.1955, fl., *Humbert 29210* (MO, P); Ifotaka, 17.XI.1938, fl., *Lam & Meeuse 5454* (L, P); upper Mananara valley, 2–7.XII.1960, fl., *Leandri & Saboureau 4213* (P); Petriky, 25°02'44"S 46°51'41"E, 13.III.1998, fl., *Lowry II et al. 5026* (K, MO, P, UPS); Petriky forest, 25°05'S 46°52'E, 16.X.1989, fl., *McPherson et al. 14115* (K, MO, P); Petriky, 25°05'S 46°52'E, 30.X.1989, fl., *McPherson & Dumetz 14318* (K, MO); Ranopiso, 23.XI.1959, fl., *Peltier 1480* (P); Petriky, 25°04'S 46°51'E, 25.XI.2004, fl., *Rabehevitra 1255* (G, MO, P); Petriky forest, 25°04'S 46°51'E, 13.IV.1989, fl., *Rabevohitra 1865* (MO); road towards Ambatohabo, 10 km from Ihazofotsy, 24°50'S 46°32'E, 10.XI.1994, fl., *Rakotomalaza 309* (MO); c. 1.8 km SW of Ankilivalo, 25°07'20"S 46°40'29"E, 20.VII.2010, fl., *Rakotovao et. al. 5468* (MO, P, TAN); 6 km S of Manambero, 25°05'00"S 46°49'36"E, 1.XII.2002, fl., *Randrainaivo et al. 873* (MO, P); Amboasary Sud, Ranobe, Betsingilo, 24°16'43"S 46°11'28"E, 11.II.2013, fl., *Randrianarivony et al. 516* (MO); Behara, 24.VI.1954, fl., *Service Forestier 6587* (P); Petriky forest, 25°03'45"S 46°52'01"E, 23.IV.2016, fl. & fr., *Swenson et al. 1708* (MO, P, S, TAN); E of Amboasary, 7 km after turning to Tsimelahy, 24°58'20"S 46°37'08"E, 9.IV.2010, fl. & fr., *Thulin & Razafindraibe 11820* (MO, TAN, UPS). **Reg. Atsimo-Andrefana [Prov. Toliara]:** Sakamalio near Manasoa Tanosy, 17.I.1913, fl., *Afzelius s.n.* (P); Ifaty, 10.IV.1996, *Bouharmont 26357* (BR); between Tongobory and Betioky, 14.II.1975, fl., *Croat 31225* (MO); Tulear, s.d., fl., *Homolle 1578* (P); Fiherenana delta, 14–26.IX.1924, fl., *Humbert & Perrier de la Bâthie 2400* (K, MO, P); delta of Fiherenana, 14–26.IX.1924, fl., *Humbert & Perrier de la Bâthie 2426* (P); near Beheloka, 17–24.VIII.1928, fl., *Humbert & Swingle 5293* (G, K, MO, P); Ankilibe, III.1960, fl., *Keraudren 609* (P); Tsiandamba, 20.XI.1967, fl., *Koechlin 5* (P); Bevato, 14.III.1968, 9.IV.1968 & 3.VI.1968, fl., *Koechlin s.n.* (P); Bevato Nord, 25.III.1968, fl., *Koechlin s.n.* (P); lac Tsimanampetsa, 23.XI.1960, fl., *Leandri & Saboureau 4440* (P); N of Betioky, Ankazoabo gorge, III.1971, fl., *Morat 3860* (P); lac Tsimanampetsotsa, 15–17.IV.1961, fl., *Peltier 3147* (P); lac Tsimanampetsa, VI.1910, fl., *Perrier de la Bâthie 5667* (P); Manombo, XIII.1919, fl., *Perrier de la Bâthie 12845* (P); Manampetsa, IV.1933, fl., *Perrier de la Bâthie 19018* (P), *19085* (P); Beza Mahafaly reserve, near Betioky, 23°40'S 44°39'E, 1.XI.1987, fl., *Phillipson 2498* (BR, K, MO, P); between Fiherenana and Manombo rivers, Ranobe forest, fl. & fr., 23°04'40"S 43°37'01"E, 15.III.2006, fl., *Phillipson et al. 5912* (G, K, MO, P); Efoetsy, 105 km W of Betioky, Tsimanampetsotse Reserve, 24°01'20"S 43°45'13"E, 13.III.2008, fl., *Randrianaivo et al. 1575* (G, MO); Tulear Distr., 11.XI.1952, fl., *Ravelonanahary 3647* (P); Betioky, VI.1952, fl., *Ravelonanahary 3935* (P); Soalary, 24.X.1952, fl., *Ravelonanahary 4290* (P); ibid., 31.XI.1952, *Ravelonanahary 4758* (P); ibid., 21.III.1953, fl., *Ravelonanahary 4999* (P); Betioky, Tongobory, XI.1964, *Service Forestier 21852* (P); 40 km NE of Betioky, E of Analafaly, 23°39'S 44°38'E, 24.VII.1987, fl., *Sussman 230* (MO). **Sine loco:** 6.II.1975, fl., *Croat 30852* (K, MO).

2. ***Paramollugo nudicaulis*** (Lam.) Thulin in Taxon 65: 786. 2016 (Fig. 10–12, 22A).

≡ *Mollugo nudicaulis* Lam., Encycl. 4: 234. 1797.

Lectotypus (designated by Thulin, 2017: 32): **Mauritius:** sine loco, s.d., fl. & fr., *Commerson s.n.* (MPU [MPU310690]!).

Herbs, annual, ephemeral or occasionally short-lived perennial, 5–30 cm tall, glabrous in all parts or very rarely pubescent towards the base; stems few to many, terete. *Leaves* crowded in a basal rosette, 10–80 × 3–30 mm, narrowly to broadly obovate, rounded to subacute at the apex, tapering ± gradually below into a petiole-like base, the petiole-like part shorter than the distal part; midrib prominent beneath, lateral veins 3–5 pairs. *Flowers* in much-branched lax cymes; bracts 1–1.5 mm long, ovate, acute; pedicels up to c. 20 mm long. *Tepals* (2–)2.5–3(–3.5) × 1–2 mm, elliptic, rounded at the apex, with hyaline margins, 3–5-veined from the base, white inside. *Stamens* (2–)3–5(–6), 1.5–2.5 mm long; filaments filiform; anthers c. 0.3 mm long, elliptic-oblong. *Ovary* 1–1.5 mm long, ellipsoid, 3-locular; styles 3, 0.2–0.3 mm long, spreading. *Capsules* 2–2.5 mm long, ellipsoid. *Seeds* 0.55–0.75 × 0.50–0.65 mm, subcircular-reniform in outline, flattened, ± distinctly tuberculate to sometimes colliculate, black; testa cells with cross-striate secondary ornamentation and with small pits in the boundaries between most of them; hilum c. 0.1 mm long.

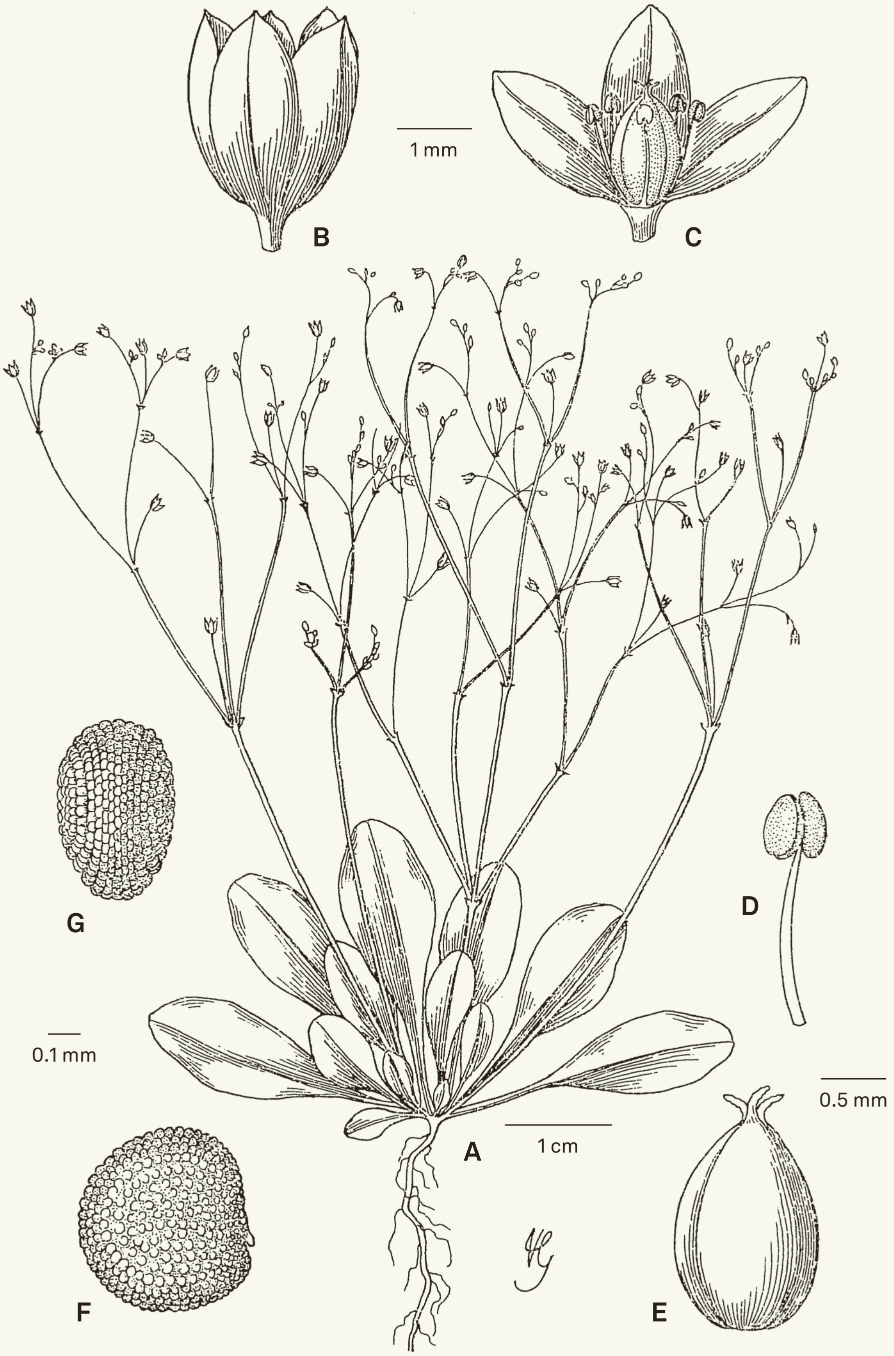

Fig. 10. – *Paramollugo nudicaulis* (Lam.) Thulin. **A.** Habit; **B.** Flower; **C.** Flower, with facing tepals removed; **D.** Stamen; **E.** Capsule; **F.** Seed, lateral view; **G.** Seed, posterior view. Drawing from *Fl. Zambesiaca* 4: 543 (1978) reproduced with permission from the artist V. Chesterman (née Goaman).

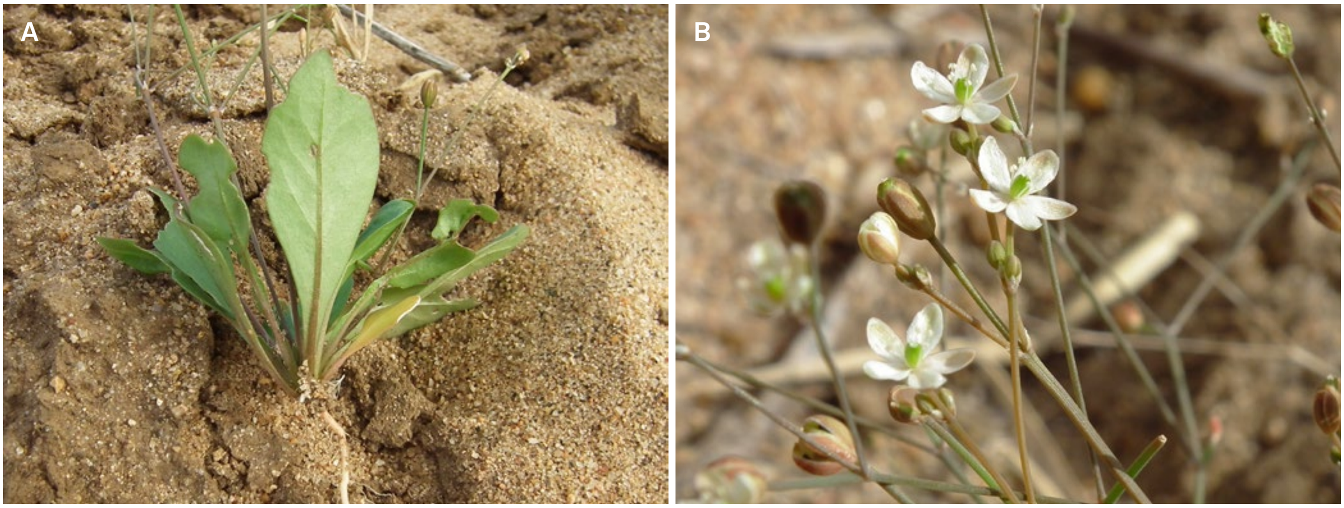

Fig. 11. – *Paramollugo nudicaulis* (Lam.) Thulin from Kruger National Park, South Africa. **A.** Basal parts of plant; **B.** Portion of inflorescence. [Photo: T. Marshall]

Vernacular names and uses. – "Aferontany" (*Boiteau 2154*, *Bosser 13399*, *Humbert 19775*, etc.), "Somitrora" (*Beaujard 4*).

Paramollugo nudicaulis has various medicinal uses in Madagascar, particularly for diseases among children. For example, infusions of the plant are used to treat cough, whooping cough and gastro-intestinal pains.

In southern India decoctions or powder of *Paramollugo nudicaulis* are used to treat fever, cough, headache, stomachache and veneral diseases In this region, the species has the vernacular name "Parpadagam" (Ayyanar & Ignacimuthu, 2011). According to Nagesh & Shanthamma (2011), the plant has wound-healing properties and is used in India also to cure whooping cough and jaundice.

Distribution and ecology. – *Paramollugo nudicaulis*, besides occurrences in Madagascar and the neighbouring Comoro Islands, Mauritius and Seychelles (Aldabra), is widespread in tropical and subtropical parts of Africa and Asia. From Africa, collections have been seen from Angola, Benin, Botswana, Burkina Faso, Burundi, Cameroon, Cape Verde Islands, Central African Republic, Chad, Côte d'Ivoire, Democratic Republic of Congo, Djibouti, Egypt, Eritrea, Ethiopia, Gabon, Ghana, Guinea, Kenya, Liberia, Malawi, Mali, Mauritania, Mozambique, Namibia, Niger, Nigeria, Republic of Congo, Rwanda, Senegal, Sierra Leone, Somalia, South African Republic, South Sudan, Sudan, Tanzania, Togo, Uganda, Zambia and Zimbabwe. From Asia, collections have been seen from Bhutan, China, India, Myanmar, Nepal, Pakistan, Saudi Arabia, Sri Lanka, Vietnam and Yemen. A distribution map showing the total distribution of the species, as well as a comprehensive list of collections, was provided by Sukhorukov & Kushunina (2016a). In the map presented here (Fig. 13), occurrences of *P. nudicaulis* in Madagascar and surrounding islands are shown in detail, whereas the areas of distribution in Africa and Asia are hatched. The species occurs in a wide variety of habitats in grasslands, woodlands and forests, where it is found in openings of bare soil, along roadsides or river beds, in waste places or as a weed in crop fields, at elevations from near sea level up to about 1800 m.

Phenology. – Flowering and fruiting plants have been seen from all months.

Conservation status. – *Paramollugo nudicaulis* is widespread over large areas in Africa and Asia and no particular threats to the species have been detected. It is therefore here preliminarily regarded as "Least Concern" [LC] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – *Paramollugo nudicaulis* is a strongly supported species in all phylogenetic analyses (Fig. 3, 4). It is a weakly supported sister to *P. caespitosa* and *P. nesophila* together in the combined RAxML analysis (Fig. 3), whereas this relationship is strongly supported in the BEAST analysis shown in Fig. 4. However, in the RAxML analysis based on *trnK-matK* only (Fig. 1), *P. nudicaulis* is strongly supported as sister to *P. digyna*, a conflict that is almost certainly a reflection of an allopolyploid origin of this hexaploid species (see above under Discussion).

Paramollugo nudicaulis is by far the most widespread and weedy species in the genus and is almost always an annual or ephemeral in contrast to the morphologically very similar *P. spathulata*, *P. digyna* and *P. caespitosa*, which all often perennate. However, occasional specimens, such as *Miller et al. 8637* (UPS) from Socotra, show plants with old dead stems along with new shoots and seem to be short-lived perennials. From the allopatric *P. spathulata* and *P. digyna*, the most easily seen additional difference is that of leaf shape, with the leaves in

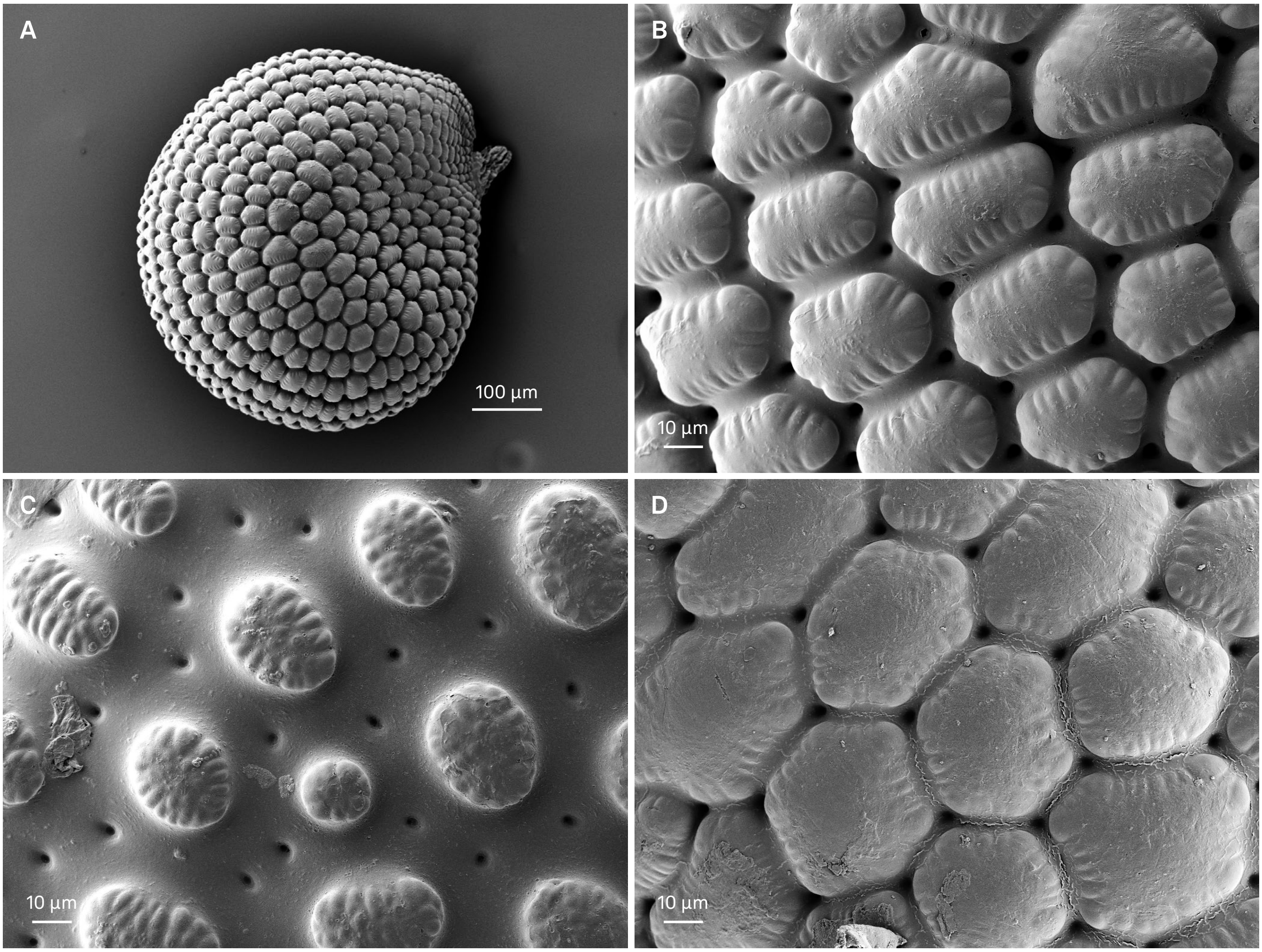

Fig. 12. – *Paramollugo nudicaulis* (Lam.) Thulin, SEM micrographs. **A.** Seed; **B–D.** Details of seed ornamentation. [**A, B:** *Thulin & Bashir Mohamed 6759*, UPS; **C:** *Phillipson 2800*, MO; **D:** *Peltier 4748*, P]

P. nudicaulis having the petiole-like part shorter than the distal part (about as long as the distal part in *P. spathulata* and longer than the distal part in *P. digyna*). From *P. caespitosa* it also differs by the 3–5 (not c. 10) stamens, and by the larger seeds (0.55–0.75 vs. 0.50–0.55 mm long).

In Madagascar, plants of *Paramollugo nudicaulis* are often difficult to separate from *P. simulans*, a species which is unrelated according to the phylogenetic analyses. Mostly, the broader leaves (often more than 12 vs. 2–12 mm) and longer tepals ((2–)2.5–3(–3.5) vs. 1.5–2.5 mm) in *P. nudicaulis* are diagnostic. Further differences are found in the seeds, which are usually more or less distinctly tuberculate with cross-striate testa cells with small pits in the boundaries between most of them in *P. nudicaulis* (Fig. 12), vs. colliculate to finely tuberculate, with smooth to weakly striate testa cells without pits in the boundaries between them or with pits between some cells only in *P. simulans*. However, seed variation is considerable in *P. nudicaulis*, and the tubercles vary from dense and prominent as in Fig. 12A, B to more scattered (e.g. in *Phillipson 2800*, Fig. 12C) or to low and only slightly convex (e.g. in *Madiomanana et al. 215* and *Peltier 4748*, Fig. 12D). Variation is particularly great in Madagascar.

Several specimens from Madagascar cited as *Paramollugo nudicaulis* by Sukhorukov & Kushunina (2016a) are here treated as *P. caespitosa*, *P. simulans* or *P. angustifolia* (see under these species).

The stamens in *Paramollugo nudicaulis* are normally three to five in number, but the occurrence of six stamens in plants in India was reported by Sulakshana & Raju (2019). Batenburg & Moeliono (1982) even recorded occasional flowers with only two stamens, and concluded that the reduction in stamen number in this species is likely to be effected by fusion of stamen primordia rather than abortion. Androecial oligomery is unique for *P. nudicaulis* within the genus.

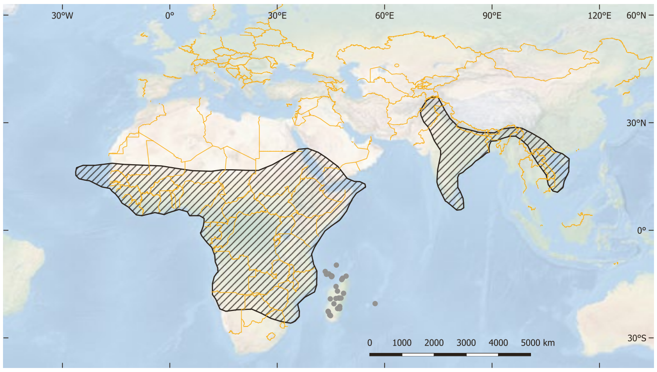

Fig. 13. – Geographic distribution of *Paramollugo nudicaulis* (Lam.) Thulin, with occurrences in Africa and Asia hatched.

Additional specimens examined. – Madagascar. **Reg. Alaotra-Mangoro [Prov. Toamasina]:** District d'Ambatondrazaka, Station Alaotra, X.1938, fl. & fr., *Cours 1262* (G, P); Lac Alaotra, 1918–19, fl. & fr., *Esperandieu 13* (P). **Reg. Anamalanga [Prov. Antananarivo]:** Nanisana, V.1905, fl. & fr., *d'Alleizette 97* (P); Manjankandriana, VI.1906, fl. & fr., *d'Alleizette 911* (P). **Reg. Androy [Prov. Toliara]:** Ampandrandava, XI.1942, fl. & fr., *Seyrig 339* (P). **Reg. Atsimo-Andrefana [Prov. Toliara]:** Analavelona, 15–19.XII.1946, fl. & fr., *Humbert 19775* (P); near Beza Mahafahy Reserve, near Betioky, ridge E of Sakamena, valley of the Analafaly river, 23°38'S 44°39'E, 5.I.1988, fl. & fr., *Phillipson 2800* (K, MO, P); Sakaraha, 22°48'10"S 44°17'54"E, 23.III.2013, fl. & fr., *Randrianarivony 553* (MO, P, TAN). **Reg. Betsiboka [Prov. Mahajanga]:** Belambo, III.1899, fl. & fr., *Perrier de la Bâthie 856* (P). **Reg. Boeny [Prov. Mahajanga]:** near Majunga, I.1908, fl. & fr, *Perrier de la Bâthie 5232*, *5232bis* (P). **Reg. Bongolava [Prov. Antananarivo]:** Kianjasoa, s.d., fl. & fr., *Boiteau 359* (P); ibid., 21.V.1937, fl. & fr., *Boiteau 2513* (P). **Reg. DIANA [Prov. Antsiranana]:** Nossibé, VI.1847, fl. & fr., *Boivin 2133* (G, P); S of Anivorano, near Ambalabao, 12°48'S 49°14'E, 13.III.1988, fl. & fr., *Cheek et al. 1471* (P); Nossi Bé, V.1879, fl. & fr., *Hildebrandt 2974* (BM, G, K, P); Ampasindava, Betsitsika forest, 13°46'02"S 48°00'03"E, 6.I.2009, fl. & fr., *Madiomanana et al. 215* (G). **Reg. Itasy [Prov. Antananarivo]:** Tsimbazaza, 15.XII.1935, fl. & fr., *Boiteau 1280* (P); near Tananarive, 6.VII.1970, fl. & fr., *Boiteau 2154* (P); Antongona, I.1960, fl. & fr., *Bosser 13399* (MO, TAN); ibid., 16.I.1960, fl. & fr., *Leandri 2598* (P). **Reg. Matsiatra-Ambony [Prov. Fianarantsoa]:** Ranomafana, chutes d'Ambodiriana, 20.II.1964, fl. & fr., *Peltier 4748* (P); Iarintsena, Tananomby, Ambalalova, 21°50'11"S 46°50'17"E, 15.III.2010, fl. & fr., *Rakotoarivelo et al. 241* (MO, P, TAN). **Reg. Melaky [Prov. Mahajanga]:** Tsingy de Bemaraha, N of Manambolo river, 19°09'S 44°49'E, 3.XII.1966, fl. & fr., *Jongkind et al. 3361* (BR, MO, P, WAG). **Reg. Menabe [Prov. Toliara]:** W of Janjina, 2.XII.1970, fl. & fr., *Keraudren-Aymonin & Aymonin 25808* (P). **Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa]:** Fort-Carnot, 1986, fl. & fr., *Beaujard 4* (P). **Sine loco:** *Baron 116* (K, P); *Chapelier s.n.* (P); *Du Petit-Thouars s.n.* (P); *Homolle 717* (P); 1932–1933, *Leandri 655bis* (P); *Parker s.n.* (K).

Comoro Islands. **Anjouan:** s.l., III. 1877, fl. & fr., *Bewsher 29* (K); s.l., 1875, fl. & fr., *Hildebrandt 1685* (P). **Grand Comore:** N'tsorale, 26.VIII.2006, fl. & fr., *Kaou s.n.* (P); s.l., XII.1848, fl. & fr., *Kirk s.n.* (K). **Mayotte:** Mtsamboro, 6.I.2002, fl. & fr., *Barthelat & Dufour 639* (P); Pamanzi, 1849, fl. & fr., *Boivin 3315* (G, P); Pointe Handrema, 22.IV.1999, fl. & fr., *Mas 57* (P); Saziley, 12°58'S 45°10'E, 11.IV.1999, fl. & fr., *Pignal et al. 1103* (P); Mtsamboro, Choazil, 17.II.2015, fl., *Valy s.n.* (MAO, P). **Moheli:** s.l., IX.1847, fl. & fr., *Boivin s.n.* (P). **Sine loco:** s.d., *Humblot 100* (P), *1438* (P).

Mauritius: Morne Brabant, 23.II.1973, fl. & fr., *Guého 15575* (K); "île de France", s.d., *Herb. Desvaux* (P [P04582925]).

Seychelles. **Aldabra:** Assumption, centre of island, 30.XI.1973, fl. & fr., *Frazier 742* (US).

3. ***Paramollugo caespitosa*** (Scott Elliot) Thulin, **comb. nov.** (Fig. 14, 15).

≡ *Mollugo caespitosa* Scott Elliot in J. Linn. Soc., Bot. 29: 25. 1891.

Lectotypus (designated here): **Madagascar. Reg. Anosy [Prov. Toliara]:** "from arid sandy country of the Antandroi, S.E. of Fort Dauphin", VI–VII.[?], fl., *Scott Elliot 2978* (K [K000232028]!).

Herbs, annual or perennial, 5–25 cm tall, glabrous in all parts except for stems sometimes pubescent with spreading hairs towards the base, with a slender tap-root when flowering in the first year or, when perennating, with a branched scaly rhizome; stems few to many, terete. *Leaves* crowded in a basal rosette, 10–40 × 4–15 mm, oblanceolate to broadly obovate, rounded or subacute and mucronate to slightly emarginate at the apex, tapering below into a 1–2 mm wide petiole-like base, the petiole-like part shorter than the distal part; midrib prominent beneath, lateral veins 3–4 pairs, indistinct. *Flowers* in much-branched lax cymes; bracts 0.5–2 mm long, lanceolate to ovate, acute; pedicels up to c. 10 mm long. *Tepals* 2.5–3 × 1.2–2 mm, elliptic, rounded at the apex, with hyaline margins, 3–5-veined from the base, white or tinged pink inside. *Stamens* c. 10, c. 1.5 mm long; filaments filiform; anthers 0.3–0.6 mm long, elliptic-oblong. *Ovary* c. 1.5 mm long, ellipsoid, 3-locular; styles 3, 0.3–0.5 mm long, spreading. *Capsules* 2–3 mm long, ellipsoid. *Seeds* 0.50–0.55 × 0.45–0.50 mm, subcircular-reniform in outline, flattened, tuberculate, black; testa cells with ± distinctly cross-striate secondary ornamentation and with small pits in the boundaries between most of them; hilum c. 0.1 mm long.

Vernacular name and uses. – "Aferontany" (*Humbert 19845*), used against cough. The vernacular name "Aferontany" has been recorded also for *Paramollugo nudicaulis* and *P. simulans*. See also under uses reported for these species.

Distribution and ecology. – *Paramollugo caespitosa* is known only from southern Madagascar (Fig. 16). Most localities are in the Ambovombe-Tolagnaro area in the southeast, but the species has also been found in a few places close to and south of Toliara in southwestern Madagascar. *Paramollugo caespitosa* occurs in arid bushland or thicket on dunes or sandy ground, among rocks or along roadsides, at elevations from near sea level up to about 400 m.

Phenology. – Flowering and fruiting collections have been seen from January to June, and from September and December.

Conservation status. – *Paramollugo caespitosa* is known from 16 collections made between 1924 and 2010, representing 11 occurrences. The EOO is calculated at 24,162 km^2,

Fig. 14. – *Paramollugo caespitosa* (Scott Elliot) Thulin, notice branched rhizome in uppermost plant. [*Humbert & Capuron 29035*, P04582854] [© Muséum national d'Histoire naturelle, Paris]

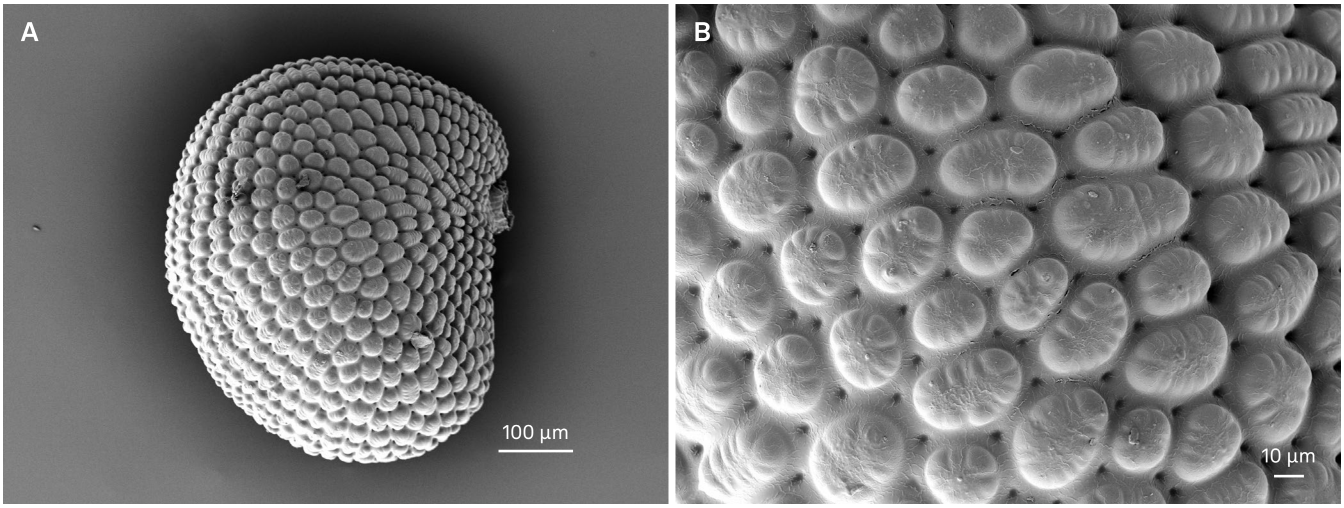

Fig. 15. – *Paramollugo caespitosa* (Lam.) Thulin, SEM micrographs. **A.** Seed; **B.** Detail of seed ornamentation. [*Larsson et al. L078*, UPS]

above the threshold for the "Vulnerable" category following criterion B1. The AOO is estimated at 44 km^2, below the threshold for the "Endangered" category following criterion B2. Two occurrences are located within the National Parks of Andohahela and Tsimanampetsotsa. Thirteen of the 16 occurrences are old (1955 and before) and may be considered as extirpated. The species is threatened by urbanization, fire events, small-scale wood collecting and grazing, all of which inducing a decline in the quality of the habitat of this species. We estimate that the 11 occurrences likely represent between 5 and 10 locations. The species is therefore preliminarily assessed as "Vulnerable" [VU B2ab(iii,v)] according to the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – The single collection cited in the protologue of *Mollugo caespitosa* (Scott Elliot, 1891) is *Scott Elliot 2978* from Madagascar, and the only specimen known of this collection (K000232028) was cited as the holotype (Thulin et al., 2016 [30.XIII]). This specimen also agrees well with the protologue and apparently is the specimen upon which the description of the species was based. Another typification was soon thereafter made by Sukhorukov & Belyaeva in Sukhorukov et al. (2016 [27.IX]), who designated "plate 7 in Scott Elliot (1893), J. Linn. Soc. London (Botany) 29(1)" as the lectotype, an action that would instead make *M. caespitosa* a synonym of *Paramollugo decandra* (≡ *Mollugo decandra* Scott Elliot), a species published in the same paper by Scott Elliot in 1891 (not 1893 as stated by Sukhorukov et al.). However, as cited specimens always take precedence over illustrations in lectotype designations (Turland et al., 2018: ICN Art. 9.12), the lectotypification proposed by Sukhorukov & Belyaeva has no standing. Also, the citation of plate 7 in the protologue of *M. caespitosa* was clearly made just by mistake. The plate agrees in every respect with the description of the simultaneously published *M. decandra*. At the same time, it is in strong conflict with the description of *M. caespitosa* and, although cited in the protologue, it would be highly unsuitable as a type of that name. For example, the statements in the protologue that the plant is a perennial with rosulate leaves, 1–1.5 cm wide are in conflict with plate 7 that shows a shrub with narrow leaves in alternate clusters along the branches. The specimen deposited at K is therefore treated as the type, in accordance with Thulin et al. (2016). However, its status is changed from holotype to lectotype, as it cannot be ruled out that duplicates are present elsewhere.

When checked in 2018, the envelope with loose plant parts of *Scott Elliot 2987* contained a fruit and a few seeds of *Paramollugo nudicaulis*. These were not there when the specimen was checked some years earlier and must have been added recently by mistake. They are also absent in the scan of the specimen [K000232028] and are not part of the original material.

Paramollugo caespitosa and *P. nesophila* together are strongly supported as sister to *P. nudicaulis* in the ITS RAxML tree (Fig. 2). The same pattern is found in the combined tree, but with less support (Fig. 3). In this tree, *P. caespitosa* is a strongly supported species, sister to *P. nesophila* with weak support. However, in the *trnK-matK* tree (Fig. 1), it is moderately supported as sister to *P. decandra*.

In the BEAST analysis (Fig. 4), *Paramollugo caespitosa* is a strongly supported species, sister to *P. nesophila* with strong support. However, in the alternative BEAST analysis, it is weakly supported sister to *P. nesophila*, *P. simulans* and *P. angustifolia* together, a conflict that may indicate an allopolyploid origin of the species.

Paramollugo caespitosa differs from both *P. nudicaulis* and *P. nesophila* by having flowers with about 10 stamens (vs. 3–5 stamens in *P. nudicaulis*, 5 in *P. nesophila*) and by being able

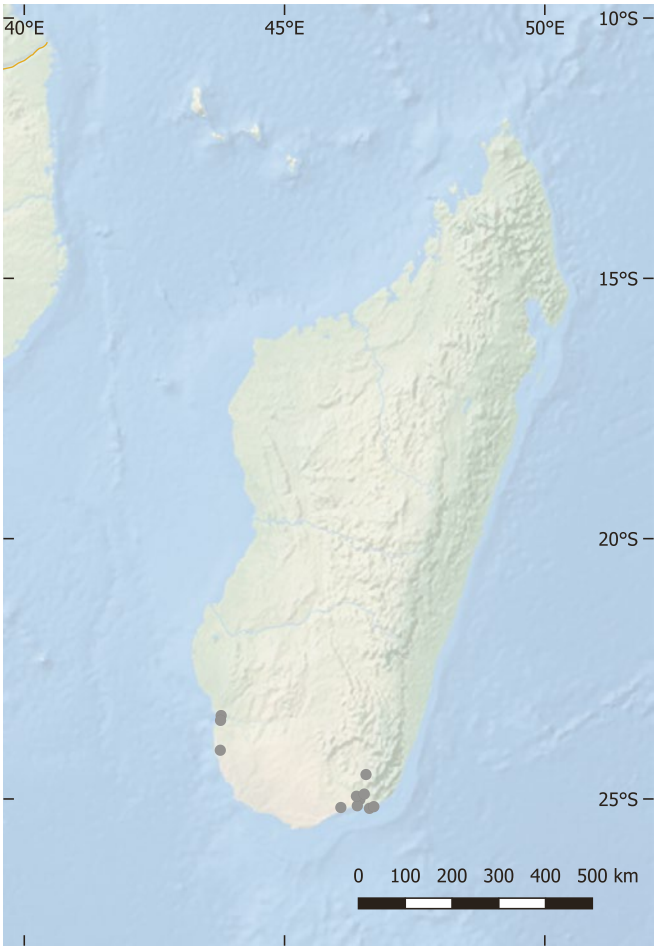

Fig. 16. – Geographic distribution of *Paramollugo caespitosa* (Scott Elliot) Thulin.

to perennate. Most collections comprise at least some plants that are distinctly perennial (Fig. 14), whereas *P. nudicaulis* and *P. nesophila* are annual or ephemeral. Furthermore, the seeds of *P. caespitosa* (Fig. 15) are smaller than those of *P. nudicaulis* (0.50–0.55 × 0.45–0.50 vs. 0.55–0.75 × 0.50–0.65 mm), and *P. caespitosa* also differs markedly from *P. nesophila* by having broader leaves (4–15 vs. 1–2 mm).

Paramollugo caespitosa and *P. decandra* are both confined to southern Madagascar and are, along with *P. compressa*, the only species in the genus with 10 stamens. However, *P. caespitosa* is easily separated from *P. decandra* by being a herb with the leaves crowded in a basal rosette and with flowers in lax, long-pedunculate cymes, whereas *P. decandra* is a shrub or subshrub with the leaves scattered along long shoots and crowded on short shoots and with flowers in sessile or shortly pedunculate, dense cymes borne on the short shoots. *Paramollugo caespitosa* also has stamens with filiform filaments, whereas *P. decandra* is unique in the genus by having very narrowly triangular filaments. *Paramollugo compressa*, also confined to southern Madagascar, differs from all other species in the genus by having compressed, phyllocladic stems.

Several of the collections in P here included in *Paramollugo caespitosa* were cited as *P. nudicaulis* by Sukhorukov & Kushunina (2016a): *Decary 9074* and *10491*, *Humbert 12403*, *12836* and *19845*, and *Humbert & Capuron 29035*. However, most of the collections treated here as *P. caespitosa* were not cited at all by Sukhorukov & Kushunina (2016a).

Additional specimens examined. – Madagascar. **Reg. Androy [Prov. Toliara]:** Distr. Ambovombe, 16.IV.1924, fl. & fr., *Decary 2612* (HBG, MO, P, TAN); Ambovombe (Antanimora), 12.V.1925, fl. & fr., *Decary 3800* (P, S); Ambovombe, 12.VII.1931, fl. & fr., *Decary 9074* (MO, P). **Reg. Anosy [Prov. Toliara]:** Ampasimpolaka, 5.IX.1924, fl. & fr., *Decary 3124* (P); N of Behara, s.d., fl. & fr., *Decary 3141* (P); Andrahomana, 18.VI.1926, fl. & fr., *Decary 4007* (P); Behara, 3.IX.1932, fl. & fr., *Decary 10451* (P); Mandrare valley, near Anadabolava, XII. 1933, fl. & fr., *Humbert 12403* (P); Manambolo valley, near Isomono, Kotriha and Isomonobe Mts., XII.1933–I.1934, fl. & fr., *Humbert 12836* (P); Baie des Galions (Ranofotsy), SW of Fort Dauphin, 18–21.II.1955, fl. & fr., *Humbert & Capuron 29035* (P, TAN); Andrahomana (Cap Andavaka), 22–26.II.1955, fl. & fr., *Humbert & Capuron 29119* (P); "basse vallée de la Mananara, affluent du Mandrare", 1–2.III.1955, fl. & fr., *Humbert & Capuron 29173* (P); 8 km E of Amboasary, 25°00'45"S 46°26'57"E, 9.IV.2010, fl. & fr., *Thulin & Razafindraibe 11800* (TAN, UPS). **Reg. Atsimo-Andrefana [Prov. Toliara]:** near La Table, 10–12.I.1947, fl. & fr., *Humbert 19845* (P); along the coast between Toliara and Anantsono, 17.I.2006, fl. & fr., *Larsson et al. L078* (UPS); Reserve de Tsimanampetsotsa, NW corner of Reserve, 24°04'S 43°46'E, 11.I.1989, fl. & fr., *Phillipson & Rabesihanaka 3159* (MO).

4. ***Paramollugo nesophila*** Thulin, E. Bidault, Boullet & Hivert, **sp. nov.** (Fig. 17, 18).

Holotypus: Îles Éparses. Île Europa: centre of island, 22°22'11"S 40°21'10"E, 9.IV.2019, fl. & fr., *Bidault et al. 4592 (CBNM-IE 888)* (MO [MO-3532500]!; iso-: CBNM!, G!, MAO!, P [P01085463]!, TAN!).

Paramollugo nesophila Thulin, E. Bidault, Boullet & Hivert differs from P. caespitosa (Scott Elliot) Thulin by being annual and often ephemeral (vs. often perennating), by having 5 (vs. c. 10) stamens and by having narrower leaves (1–2 vs. 4–15 mm). From P. nudicaulis (Lam.) Thulin, it differs by its narrower leaves (1–2 vs. 3–30 mm) and smaller seeds (0.40–0.51 × 0.34–0.40 vs. 0.55–0.75 × 0.50–0.65 mm). From P. angustifolia, it differs by its mostly larger seeds (0.40–0.51 × 0.34–0.40 vs. 0.39–0.43 × 0.28–0.36 mm) with testa cells with distinctly cross-striate secondary ornamentation (vs. without secondary ornamentation).

Herbs, annual, often ephemeral, 5–15(–20) cm tall, glabrous in all parts; stems few to several, terete. *Leaves* in dense basal rosette, 10–40(–50) × 1–2 mm, linear to very narrowly oblanceolate, obtuse to subacute at the apex; midrib prominent beneath, lateral veins indistinct. *Flowers* in lax cymes; bracts c. 1 mm long, ovate, acute; pedicels up to c. 10 mm long. *Tepals* 1.8–2.5 × c. 1 mm, elliptic, rounded at the apex, with hyaline margins, 3-veined from the base, white inside. *Stamens* 5,

Fig. 17. – *Paramollugo nesophila* Thulin et al. **A.** Basal portion of plant, showing leaves and parts of inflorescences; **B.** Portion of inflorescence, showing flowers; **C.** Portion of inflorescence, showing fruit. Notice that the seeds are retained in the dehisced capsule.
[**A, C:** *Bidault et al. 4616*, CBNM; **B:** Juan de Nova, 19.III.2013] [Photos: **A, C:** E. Bidault; **B:** J. Hivert]

1–1.5 mm long; filaments filiform; anthers 0.2–0.3 mm long, shortly oblong. *Ovary* c. 1.5 mm long, ellipsoid, 3-locular; styles 3, c. 0.3 mm long, spreading, reflexed against ovary. *Capsule* 1.5–2 mm long, ellipsoid. *Seeds* 0.40–0.51 × 0.34–0.40 mm, subcircular-reniform in outline, flattened, tuberculate, black; testa cells with cross-striate secondary ornamentation and with small pits in the boundaries between most of them; hilum c. 0.1 mm long.

Etymology. – The epithet *nesophila* (from Greek, transliterated into Latin, island-loving) refers to the distribution of the species on the islands of Îles Éparses.

Distribution and ecology. – *Paramollugo nesophila* is endemic to the islands of Îles Glorieuses, Juan de Nova and Europa (part of the Îles Éparses or Scattered Islands) in the Mozambique Channel (Fig. 19). These islands fall into a climatic gradient spanning from a semiarid and thermotropical bioclimate in Europa to a more humid and warm bioclimate, dry and infratropical, of Juan de Nova and Glorieuses (Boullet et al., 2018). *Paramollugo nesophila* generally occurs in pioneer and ephemeral vegetation on sand deposits or in shallow stony soils, in Europa particularly in the sandstone and coral plateau system of the island, but sometimes also in the gaps of *Sclerodactylon macrostachyum* (Benth.) A. Camus steppes on dry coral mud. In Juan de Nova and Glorieuses mainly on ruderal sands, in Juan de Nova also on coral limestone or sand-limestone table more or less mixed with guanic materials. All occurrences are at very low elevations, the islands being only up to 12 m (Europa), 10 m (Juan de Nova) and 14 m (Glorieuses) (Boullet et al., 2018).

Phenology. – Flowering and fruiting plants have been seen from February to June, and from August.

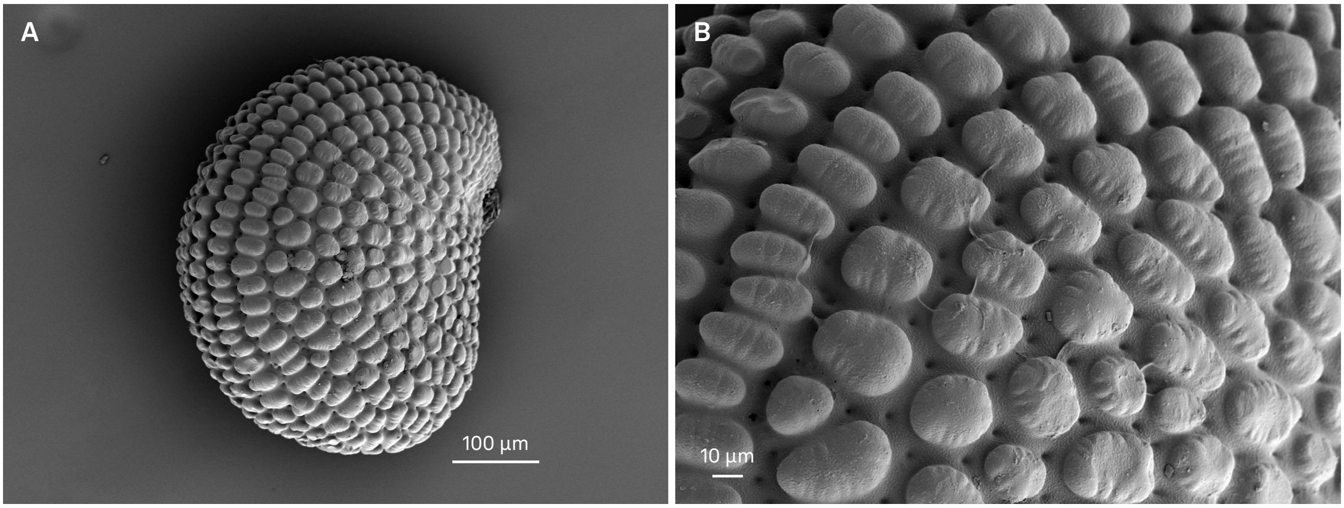

Fig. 18. – *Paramollugo nesophila* Thulin et al., SEM micrographs. **A.** Seed; **B.** Detail of seed ornamentation. [*Bidault et al. 4592*, CBNM]

Conservation status. – *Paramollugo nesophila* is known from 14 collections, collected between 1921 and 2019. Five collections could not be located precisely, the 14 collections thus representing nine occurrences and three subpopulations. The EOO of this species is calculated at 78,739 km^2, above the upper threshold for the category "Vulnerable", following criterion B1. The AOO is estimated at 28 km^2, below the upper threshold for the category "Endangered", following criterion B2. The islands of Îles Éparses are currently uninhabited apart from a limited military presence, and access is strictly regulated (Boullet et al., 2018). Nevertheless, all three islands were inhabited in the past, and their landscape profoundly changed due to phosphate extraction (in Juan de Nova), and *Cocos nucifera* L. plantation (Glorieuses). In addition, Filao trees (*Casuarina equisetifolia* L.) were massively planted on both Juan de Nova and Glorieuses. Finally, the military presence as well as the establishment and maintenance of weather stations have had, in the past (and still have today, even though to a much lesser extant) a significant impact on the habitats of the islands. According to observation data made by CBNM, *P. nesophila* is more abundant on Europa, where in a single favourable season several thousand individuals can be observed, than on Juan de Nova and Glorieuses, where it is not found in degraded habitats dominated by Filao or coconut trees. Nevertheless, the species has recently been observed in habitats previously affected by military activities and phosphate extraction, indicating that any possible past threats from these activities may have ceased today. Therefore, the nine occurrences represent three locations sensu IUCN, with regards to the most important threats (Filao and coconut plantations). As a consequence, *P. nesophila* is here preliminarily assessed as "Endangered" [EN B2ab(iii,v)] following the IUCN Red List Categories and Criteria (IUCN, 2012, 2022), at a global scale. In addition, *P. nesophila* was assessed by CBNM (under the name *Mollugo nudicaulis*) at a regional scale in 2018 (Hivert et al., 2018) as "Least Concern". The assessments were made for each of the three islands individually where it occurs, and at the scale of the whole Îles Éparses, following categories and criteria inspired and adapted from those of the IUCN Red List, to allow for evaluating the extinction risk of plant species at very restricted scales.

Notes. – *Paramollugo nesophila* and *P. caespitosa* together are strongly supported as sister to the widespread *P. nudicaulis* in the RAxML ITS tree (Fig. 2). The same pattern is found in the combined tree (Fig. 3), but with less support. In the combined tree, *P. nesophila* is a well-supported species, sister to *P. caespitosa* but with weak support. However, in the *trnK-matK* tree (Fig. 1), the samples of *P. nesophila* appear in a strongly supported clade with *P. simulans* and *P. angustifolia*.

In the BEAST analysis (Fig. 4), *Paramollugo nesophila* is a strongly supported species sister to *P. caespitosa* with strong support, whereas in the alternative topology, it is a strongly supported sister to *P. simulans* and *P. angustifolia* together. This conflict in the datasets, which is obvious in both the RAxML and the BEAST analyses, probably is a reflection of an allopolyploid origin of *P. nesophila*.

As stated under Results and Discussion, the split between *Paramollugo nesophila* on Îles Éparses and its inferred relatives in Madagascar is estimated to late Miocene or Pliocene. As these islands are about 125,000 years old, *P. nesophila* apparently represents a lineage that is much older than the islands where it occurs today (see above under Discussion).

The islands of Îles Éparses have a total of 250 taxa of vascular plants, with the highest number, 147 taxa, on Juan de Nova, according to Boullet et al. (2018), and since then these numbers have increased to, respectively, 257 and 152. *Paramollugo nesophila* was recorded from the islands (Europa,

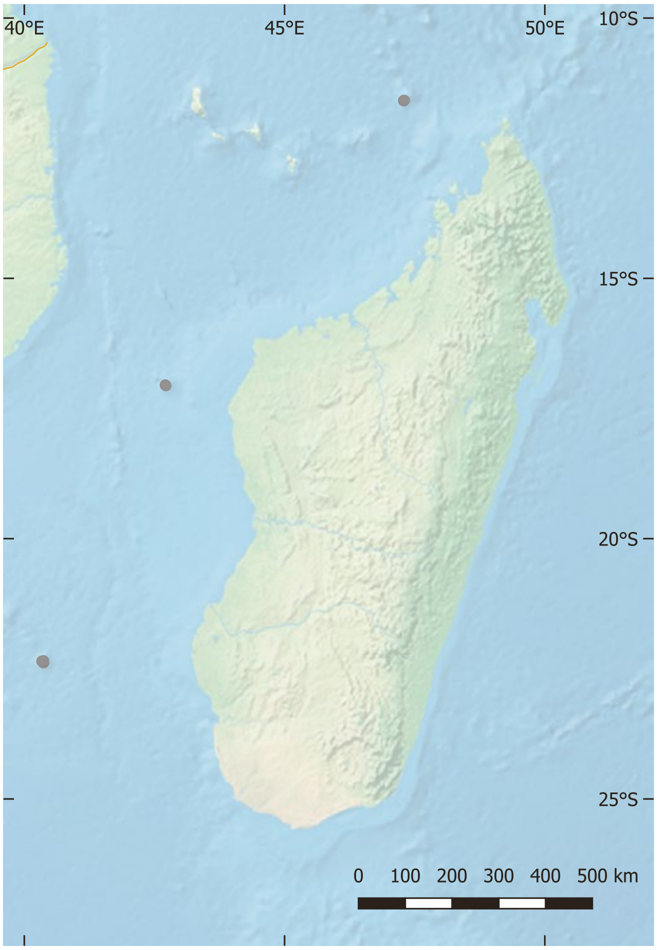

Fig. 19. – Geographic distribution of *Paramollugo nesophila* Thulin et al. The islands are, from north to south, Îles Glorieuses, Juan de Nova and Europa.

Juan de Nova and Îles Glorieuses) as *Mollugo nudicaulis* by Boullet et al. (2018). However, the first record was made by Perrier de la Bâthie (1921) on Europa as "*Mollugo* sp.". Perrier de la Bâthie cited his specimen n. 13807 and placed the plant in a group of species on the island with small seeds that had probably been transported from southern Madagascar by birds. However, from Madagascar there are no records of this species. We assume that *P. nesophila* is mainly dispersed by wind as other species in the genus (see above under Discussion), but also seabirds, such as the sooty tern, may be agents of dispersal for this plant.

Endemism on Îles Éparses is very limited and includes two previously described species, *Hypoestes juanensis* Benoist on Juan de Nova and *Perrierophytum glomeratum* Hochr. on Juan de Nova and Grande Glorieuse. A few further, potential but still undescribed endemics are found in the genera *Achyranthes* L., *Boerhavia* L., *Euphorbia* L. and *Nellica* Raf. (Boullet et al., 2018). None of these species has been included in a phylogenetic analysis and, furthermore, they occur only on one or two of the islands.

Panicum voeltzkowii Mez is a perennial grass that, like *Paramollugo nesophila*, occurs on Europa, Juan de Nova and Les Glorieuses (Boullet et al., 2018). However, it is also found in Madagascar, from where it was described (Vorontsova, 2018), and it is also known from a single coastal locality on Réunion, where it is most probably a recent introduction (Grondin & Boullet, 2006; Bosser & Renvoize, 2018; as *Panicum pseudowoelzkowii* A. Camus). It is certainly not "common on the coast of La Réunion" as stated by Vorontsova (2018). Samples of *P. voeltzkowii* from Europa, Les Glorieuses, Réunion and Madagascar were included in a molecular phylogenetic study by Hackel et al. (2018). The species appeared as paraphyletic in the analysis, with the populations on Îles Éparses and Réunion in a clade with an estimated split from the populations in Madagascar in the Pliocene. Therefore, also in this case, the lineage is much older than the islands of Îles Éparses, but the age is compatible with that of Réunion.

Paramollugo nesophila differs markedly from *P. caespitosa* by being annual and often ephemeral (vs. often perennating), by having 5 (vs. c. 10) stamens and by having narrower leaves (1–2 vs. 4–15 mm). From *P. nudicaulis* it differs by its narrower leaves (1–2 vs. 3–30 mm) and smaller seeds (0.40–0.51 × 0.34–0.40 vs. 0.55–0.75 × 0.50–0.65 mm). In being an annual with very narrow leaves, *P. nesophila* much resembles *P. angustifolia*, and they are difficult to separate by morphology, although the molecular results strongly indicate that they are different species (Fig. 3, 4). The seeds of *P. nesophila* are 0.40–0.51 mm long and have testa cells that are distinctly cross-striated (Fig. 18B). Instead, in *P. angustifolia*, the seeds are 0.39–0.43 mm long and the testa cells lack a secondary ornamentation (Fig. 29B).

Capuron s.n. and *Service Forestier s.n.* are two enigmatic collections, undated and of unknown provenance, which are included here with hesitation. In agreement with *Paramollugo nesophila*, they have linear, very narrow leaves and seeds 0.40–0.42 mm long, with testa cells with cross-striate secondary ornamentation and with small pits in the boundaries between most of them. Apparently due to this cross-striation, *Capuron s.n.* was cited as *P. nudicaulis* by Sukhorukov & Kushunina (2016a: 95), but with seeds only c. 0.4 mm long and linear leaves, this is not an option. Capuron did visit Europa in 1964 (Capuron, 1966; Boullet et al., 2018) and could then have made these collections. *Paramollugo nesophila* is often an ephemeral with more than one generation per year when conditions are favourable. However, *Service Forestier s.n.* is anomalous, as one of the plants appears to have a somewhat perennial base.

Additional specimens examined. – **Îles Éparses.** Île Europa: sentier Sud, 22°23'14"S 40°22'17"E, 5.IV.2011, fl. & fr., *Hivert et al. CBNM-IE 47 (EUR09)* (CBNM, MO, P); sentier du lagon, 22°20'54"S 40°22'16"E, 6.IV.2011, fl. & fr., *Hivert & Gigord CBNM-IE 63 (EUR21)* (CBNM, MO, P); sentier Baie des Congres, 22°21'14"S 40°20'17"E, 7.VI.2016, fl. & fr., *Hivert CBNM-IE 705* (CBNM); s.l., 3.VI.1921, fl. & fr., *Perrier de la Bâthie 13807* (P); s.l., 17.II.1923, fl. & fr., *Poisson 653* (P); s.l., 10.IV.1948, fl. & fr., *Saboureau 1700* (P). **Juan de Nova:** towards western point, 17°02'56"S 42°42'37"E, 13.IV.2019, fl. & fr., *Bidault et al. 4616 (CBNM-IE 913)* (CBNM, G, MAO, MO, P, TAN); sentier du Charbonnier, 17°03'42"S 42°43'10"E, 11.IV.2011, fl. & fr., *Hivert CBNM-IE 125* (CBNM). **Les Glorieuses:** Grand Glorieuse, sentier Sud, 11°35'11"S 47°17'30"E, 17.IV.2011, fl. & fr., *Hivert & Fontaine CBNM-IE 220* (CBNM); ibid., 11°35'07"S 47°17'29"E, 25.V.2012, fl. & fr., *Hivert & Beaurepaire CBNM-IE 437* (CBNM, MO); secteur Est, 11°34'47"S 47°18'08"E, 16.VIII.2017, fl. & fr., *Hivert et al. CBNM-IE 776* (CBNM, P). **Sine loco:** s.d., fl. & fr., *Capuron s.n.* (P [P04582819]); s.d., fl. & fr., *Service Forestier s.n.* (P [P04582823]).

5. ***Paramollugo digyna*** (Montrouz.) Sukhor. in PhytoKeys 73: 104. 2016 (Fig. 20, 21, 22C).

≡ *Mollugo digyna* Montrouz. in Mém. Acad. Roy. Sci. Lyon, Sect. Sci. 10: 179. 1860.

Lectotypus (designated here): **New Caledonia:** île Art, s.d., fl. & fr., *Montrouzier 169* (MPU [MPU310526]!) (Fig. 20).

Herbs, annual or perennial, 5–25 cm tall, glabrous in all parts, with a slender tap-root when flowering in the first year or, when perennating, with a branched scaly rhizome; stems few to many, terete. *Leaves* crowded in a basal rosette, 10–40 × 3–10 mm, the distal part reniform to narrowly to broadly ovate-triangular, obtuse to acute at the apex, sometimes shortly mucronate, tapering ± abruptly below into a c. 1 mm wide petiole-like base, the petiole-like part one to four times as long as the distal part that is often wider than long and sometimes cordate; midrib prominent beneath, lateral veins 2–4 pairs, indistinct. *Flowers* in much-branched lax cymes; bracts 0.5–1 mm long, ovate, acute; pedicels up to c. 20 mm long. *Tepals* 2–3 × c. 1 mm, elliptic, rounded at the apex, with hyaline margins, c. 3-veined from the base, white inside, outside of tepal with dark tip. *Stamens* 5, 1–2 mm long; filaments filiform; anthers c. 0.3 mm long, elliptic-oblong. *Ovary* 1–1.5 mm long, ellipsoid, 2–3-locular; styles 2–3, c. 0.3 mm long, spreading. *Capsules* 1.5–2.5 mm long, ellipsoid. *Seeds* c. 0.60–0.68 × 0.5–0.6 mm, few, subcircular-reniform in outline, flattened, tuberculate, black; testa cells with ± warty secondary ornamentation and with small pits in the boundaries between most of them; hilum c. 0.1 mm long.

Distribution and ecology. – *Paramollugo digyna* is widespread on the main island of New Caledonia (Grand Terre) and is also found on a number of neighbouring islands in the New Caledonia archipelago to which it is endemic (Fig. 23). The species is found in bushland or scrub (“maquis”), often in open places on rocky or stony ground at elevations from near sea level up to 460 m. According to many collectors, the occurrences of *P. digyna* are associated with ultramafic rocks (serpentines) and soils derived from them. The distribution of *P. digyna* also agrees well with the map of the distribution of “maquis on ultramafic soils” in New Caledonia in Isnard et al. (2016: 55). According to these authors, the ultramafic-obligate flora comprises about 50 % of the endemic flora of New Caledonia. Whether *P. digyna* can be included in this category is uncertain, but it can surely be regarded as highly ultramafic-tolerant.

Phenology. – Flowering and fruiting plants have been seen from all months except September.

Conservation status. – *Paramollugo digyna* is widespread in New Caledonia and no particular threats to the species have been detected, apart from mining and quarrying. It is listed as “Least Concern” [LC] under the IUCN Red List Categories and Criteria (IUCN, 2012), based on an assessment made by Amice et al. (2021). This assessment is accepted here.

Notes. – Sukhorukov & Kushunina (2016a) stated that *Montrouzier 169* in MPU was dated 1866 and therefore cannot be considered as original material. Sukhorukov in Sukhorukov & Kushunina (2016a) instead designated *Green 1287* (K) from the mainland of New Caledonia as neotype.

However, according to Guillaumin & Beauvisage (1914), the year 1866 printed on the Montrouzier specimens in MPU refers to the year when this material was sent to MPU and has nothing to do with the year of collection. Guillaumin & Beauvisage (1914) in their enumeration of plants collected by Montrouzier cited two specimens for *Mollugo digyna*, n. 87 “in herb. Lugd.” (Lyon) and n. 169 “in herb. Monsp.” (Montpellier). The Montrouzier herbarium in Lyon was destroyed sometime between 1955 and 1970 (M. Thiébaut, pers. comm.), and the specimen in MPU therefore is the only one that is still extant. The MPU specimen (Fig. 20) has, as also mentioned by Sukhorukov & Kushunina (2016a), a note saying “Stylos binos semper capsulamque bivalvam vidi!” This is signed with the initials “GB”, i.e., G. Beauvisage. However, the upper part of the specimen also has the annotation “*Mollugo bellidifolia* Seringe *digyna* (mihi) Art” in Montrouzier’s hand. This is a clear link to the protologue that starts: “*Mollugo digyna* (mihi.) omnia ut in *M. bellidifolia* (Ser.) exceptis stylis qui duo tantum sunt”. “Art” refers to l’île Art, a small island northwest of the mainland of New Caledonia that is the type locality for *M. digyna* according to Montrouzier (1860), a paper entitled “Flore de l’île Art (près de la Nouvelle Calédonie)”. These circumstances leave no doubt that *Montrouzier 169* in MPU is original material of *Paramollugo digyna*. The specimen is here designated as lectotype and supersedes the neotype previously designated by Sukhorukov.

Paramollugo digyna is a strongly supported species in all the phylogenetic analyses (Fig. 3, 4). It is strongly supported

Fig. 20. – Lectotype of *Mollugo digyna* Montrouz. (≡ *Paramollugo digyna* (Montrouz.) Sukhor.).
[*Montrouzier 169*, MPU310526] [© Université de Montpellier – Herbier MPU (SPH)]

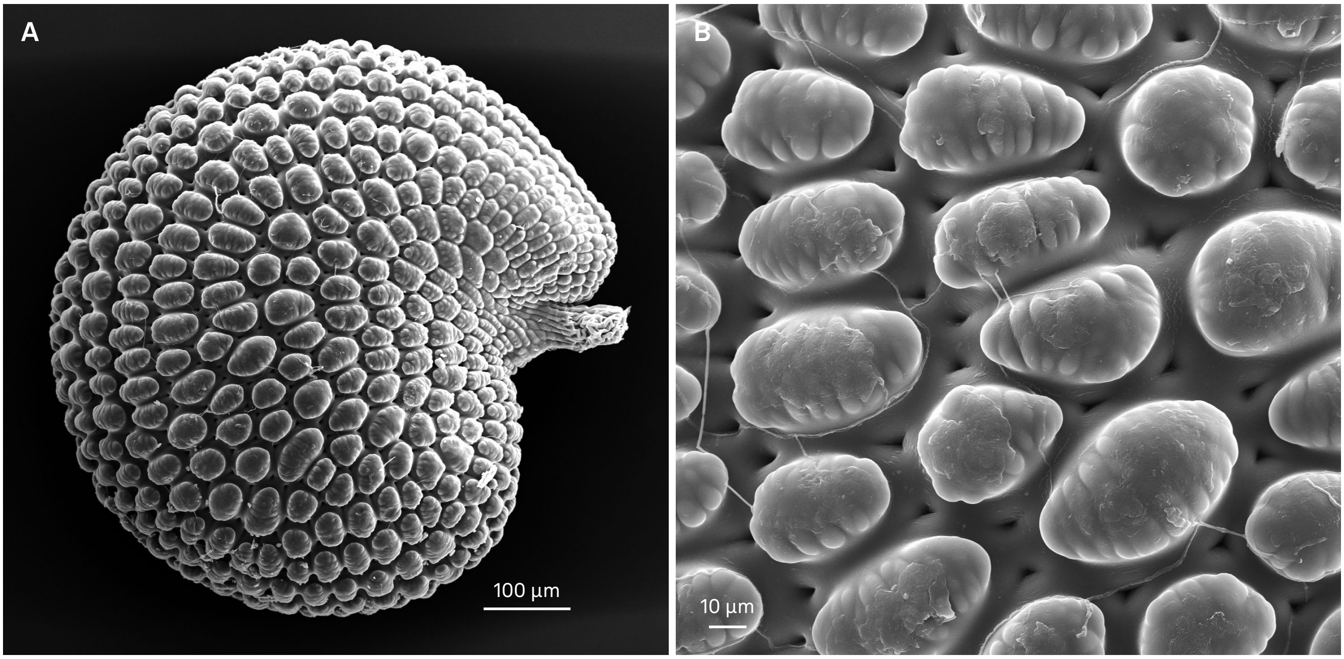

Fig. 21. – *Paramollugo digyna* (Montrouz.) Sukhor., SEM micrographs. **A.** Seed; **B.** Detail of seed ornamentation. [*Vieillard 120*, UPS]

as sister to *P. nudicaulis* in the *trnK-matK* tree (Fig. 1), whereas in the ITS tree (Fig. 2), it is unsupported sister to all species of *Paramollugo* except *P. decandra*. It is estimated to have split from its Malagasy relatives during late Miocene (see under Results and Discussion). The conflict in the datasets, which is obvious in both the RAxML and the BEAST analyses, probably reflects an allopolyploid origin of *P. digyna*.

Guillaumin & Beauvisage (1914) noted that the material of *Mollugo* from New Caledonia available to them varied in style number, some collections having two styles as the type of *M. digyna*, whereas other, otherwise identical collections, have three styles. They also noted the characteristic leaves of the New Caledonian plants, with narrow petioles abruptly widened into a subcordate limb, more similar to plants of *M. nudicaulis* from the Caribbean (now *Paramollugo spathulata*) than to plants from Africa. The difference in leaf shape between plants from New Caledonia, the Caribbean and Africa was illustrated in Guillaumin & Beauvisage (1914: Fig. 3), redrawn here in Fig. 22. The conclusion made by Guillaumin & Beauvisage (1914) was that *M. digyna* could hardly be considered as anything more than a variety or form of *M. nudicaulis*. Guillaumin (1948) treated the New Caledonian plant as *M. nudicaulis* without any reservations, and this is how it has been treated until the resurrection of *P. digyna* by Sukhorukov & Kushunina (2016a).

According to Sukhorukov & Kushunina (2016a), *Paramollugo digyna* has “a tendency to become a short-lived perennial” in contrast to the annual *P. nudicaulis*. We agree with this observation. Many specimens, including the lectotype designated here, appear to be annual, whereas several others, such as *Green 1287*, the neotype previously designated by Sukhorukov, are rhizomatous perennials.

Paramollugo digyna is unique in the genus by often having 2-locular ovaries and two styles, but presence of 3-merous ovaries is equally common. The species is usually easily recognized by the leaves with a reniform to narrowly to broadly ovate-triangular distal part that is more or less abruptly tapering into a petiole-like part that is one to four times as long as the distal part (Fig. 22C). In *P. nudicaulis* and *P. spathulata* the petiole-like part of the leaves is shorter than to about as long as the distal part (Fig. 22A, B). From the annual *P. nudicaulis*, *P. digyna* also differs in being able to perennate. Other differences from *P. nudicaulis* are the dark tips to the outside of the tepals in *P. digyna*, and the warty (not cross-striate) ultrastructure of the tubercles of the seed surface (Fig. 21B).

The similarity between the geographically very distant *Paramollugo digyna* in New Caledonia and *P. spathulata* in the Caribbean is striking, both species, for example, being able to perennate, having more or less spathulate leaves, having dark tips to the outside of the tepals, and having tubercles of the seeds with a warty ultrastructure. The most notable differences are the 2-locular ovaries often found in *P. digyna*, as well as the usually very clear difference in leaf-shape, with a proportionally longer petiole-like part of the leaves in *P. digyna* (Fig. 22).

Additional specimens examined. – **New Caledonia. Prov. Nord:** Voh, 24.I.1950, fl. & fr., *Baumann et al. 5969* (P); Mt. Panudala, 20.XII.1950, fl., *Baumann et al. 9423* (P); Mt Koniambo, 21.XII.1950, fl. & fr., *Baumann et al. 9540* (P, US), *9575* (P); Mt Kafiaté, 22.XII.1950, fl. & fr., *Baumann et al. 9664*

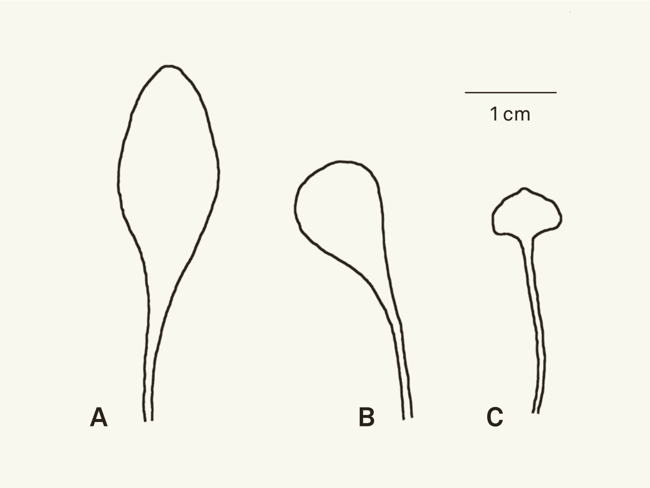

Fig. 22. – Outlines of leaves of species of *Paramollugo*.
A. *Paramollugo nudicaulis*, specimen from Angola;
B. *Paramollugo spathulata*, specimen from U.S. Virgin Islands, Saint Croix; **C.** *Paramollugo digyna*, specimen from New Caledonia. Redrawn from Guillaumin & Beauvisage (1914).

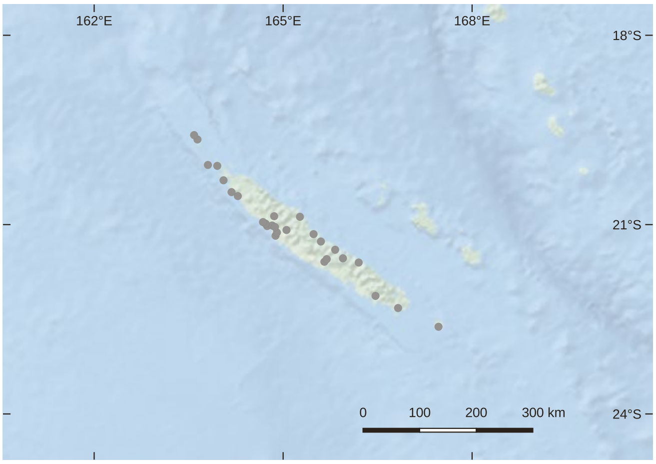

Fig. 23. – Geographic distribution of *Paramollugo digyna* (Montrouz.) Sukhor.

(P); Oua Tilou, 13.IV.1951, fl. & fr., *Baumann et al. 12305* (P); Néaria, III.1901, *Bernier 1141* (P); Kouaoua, VII.1977, fl. & fr., *Bourret 1354* (NOU); Tiéa, 27.III.2017, fl., *Bruy & Hattermann 627* (NOU); Canala, IV–V.1869, fl. & fr., *Delacour s.n.* (P); Mt. Koniambo, 14.I.1925, fl. & fr., *Däniker 878* (P); between Thio and Houailou, 1910, fl. & fr., *Fetscherin s.n.* (P); Keyani in northern part of l'île Art, 27.IV.2017, fl. & fr., *Gâteblé 922* (NOU); W face of Massif de Koniambo, 11.X.1963, fl. & fr., *Green 1287* (K, NOU, P); Massif de Koniambo, 20.XII.1972, fl. & fr., *Jaffré 1035* (NOU, P); Mt. Kafiate between Koné and Voh, 30.III.1956, fl. & fr., *MacKee 4228* (E, K, L, P); Monéo, 31.XII.1960, fl. & fr., *McKee 7875* (L); Mt. Koniambo, 5.I.1961, fl. & fr., *MacKee 7972* (L, P, US); upper Boghen river, 23.I.1965, fl. & fr., *MacKee 12062* (NOU, P); île Pott, Panane, 29.VIII.1968, fl. & fr., *MacKee 19358* (NOU, P); île Yandé, Pouagone, 6.X.1970, fl. & fr., *MacKee 22609* (G, NOU, P); Baaba, Tiomatch, 6.I.1971, fr., *MacKee 23162* (NOU, P); S of Tiébaghi and Paagoumene on road to Koumac, 15.VII.1952, fl. & fr., *McMillan 5093* (L, P); road to Plateau de Tiéa, c. 5 km S of Pouembout, 2.III.1983, fl. & fr., *McPherson 5531* (NOU, P); Paagoumène, 21.VIII.1967, fl. & fr., *Nothis 569* (NOU); Kanala, s.d., fl. & fr., *Pancher 236* (BM, K, P); Ourai, s.d., fl. & fr., *Pancher s.n.* (P); Massif de Poum, 24.VII.2007, fr., *Pillon, Barrière & Rigault 768* (NOU, P); Mé Mwanahea, 7.IV.2009, fl., *Pillon & Hoveureux 1369* (NOU); Boghen river, 1965, fl. & fr., *Schmid 380* (NOU, P); upper Palo river, N of Forêt-Plate, 24.III.1981, fl. & fr., *Suprin 1065* (NOU); île Yandé, 23.VIII.1978, fr., *Veillon 3643* (NOU); Kanala and Gatope, s.d., fl. & fr., *Vieillard 120* (L, P, UPS); Wagap, s.d., fl. & fr., *Vieillard 2331* (P); Massif de Boulinda, E of Muéo, 21°20'S, 165°05'E, 12.XII.1973, fl. & fr., *Webster & Jaffré 19221* (P). **Prov. Sud:** Mt. Mi, 20.II.1869, fl. & fr., *Balansa 1372* (P); Ouroué, V.1872, fl. & fr., *Balansa 3540* (MO, P); Thio valley, IV.1872, fl. & fr., *Balansa 3541* (P); Moyenne Couvélée, 9.V.1951, fl. & fr., *Baumann et al. 13166* (P); Prony, 20.I.1915, fl. & fr., *Franc 1931* (P); île de Pins, XII.1900, fl. & fr., *Le Rat 193* (P); ibid., 1.IV.1971, fl. & fr., *MacKee 23548* (NOU, P); ibid., 7.XI.1966, fl. & fr., *Nothis 317* (NOU).

6. *Paramollugo compressa* Thulin, sp. nov. (Fig. 24–26).

> **Holotypus: Madagascar. Reg. Atsimo-Andrefana [Prov. Toliara]:** Plateau calcaire Mahafaly, II.1962, fl. & fr., *Keraudren 1386* (P [P04999571]!) (Fig. 24).
>
> *Paramollugo compressa Thulin differs from all other species in the genus by having compressed, phyllocladic (vs. terete) stems and finely reticulate (vs. tuberculate or colliculate) seeds.*

Herbs, perennial, 7–25 cm tall, glabrous; stems few to many, compressed, phyllocladic, up to 2.5 mm wide; internodes up to 9 cm long, conspicuously longitudinally ridged; nodes with a pair of c. 0.5 mm long membranous scales, ovate, acute, each node with up to 4 branches. *Leaves* crowded in a basal rosette, apparently soon wilting; blade 5–35 × 3–10 mm, oblanceolate to obovate, rounded to emarginate at the apex, tapering below into a petiole-like base, the petiole-like part shorter than the distal part; midrib prominent beneath, lateral veins indistinct. *Flowers* in few-flowered cymes, white; bracts c. 0.5 mm long, membranous, ovate, acute, with denticulate margin; pedicels up to 5 mm long, ± flattened, longitudinally ridged. *Tepals* 2–2.8 × 1–1.5 mm, elliptic, obtuse, with hyaline margins. *Stamens* c. 10, c. 1 mm long; filaments filiform; anthers elliptic-oblong, c. 0.4 mm long. *Ovary* 1.5–1.8 mm long, oblong, 3-locular, many-ovulate; styles 3, c. 0.4 mm long, spreading. *Capsules* c. 2 mm long, splitting into 3 broad valves. *Seeds* 0.44–0.50 × 0.38–0.42 mm, subcircular-reniform in outline, flattened, almost smooth and only finely reticulate, pale brown; testa cells without secondary ornamentation and without pits in the boundaries between them; hilum 0.10–0.15 mm long.

Etymology. – The epithet of the new species refers to the compressed, phyllocladic stems, a unique feature in *Paramollugo* and in *Molluginaceae*.

Distribution and ecology. – *Paramollugo compressa* is known only from southwestern Madagascar (Fig. 27), where it occurs in arid bushland on limestone at elevations approximately between 200 and 300 m.

Phenology. – A flowering and fruiting collection has been seen from February, and one with flowers only from April.

Fig. 24. – Holotype of *Paramollugo compressa* Thulin.
[*Keraudren 1386,* P04999571] [© Muséum national d'Histoire naturelle, Paris]

Fig. 25. – *Paramollugo compressa* Thulin. **A.** Portion of stem showing flattened segments and buds; **B.** Portion of stem with flowers.
[**A:** *Bosser & Viennot-Bourgin 16124*, P; **B:** *Keraudren 1386*, P]

Conservation status. – *Paramollugo compressa* is known from three collections, representing three occcurrences and between one and three subpopulations. The EOO is calculated at 541 km^2, below the upper threshold for the category "Endangered" following criterion B1. The AOO is estimated at 12 km^2, also below the upper threshold for the category "Endangered", following criterion B2. None of the occurrences seems to be situated within a protected area, and no collection of the plant has been made since 1962. The species is threatened by small-scale agriculture, grazing and wood gathering for fuel, all of which inducing a decline in the quality and extent of its habitat. *Paramollugo compressa* is therefore here preliminarily assessed as "Endangered" [EN B1ab(iii)+B2ab(iii)] according to the IUCN Red List Categories and Criteria (IUCN, 2012, 2022).

Notes. – The relationships of *Paramollugo compressa* are uncertain, but in the BEAST analysis (Fig. 4), it is weakly supported sister to *P. simulans* and *P. angustifolia* together. Its compressed phyllocladic stems (Fig. 25) are unique in the genus and in *Molluginaceae* as a whole. Phylloclades are generally seen as a feature of xeromorphic plants, in which the stems become the main photosynthetic organs at the same time as transpiration is lessened through the reduced leaf area (Metcalfe, 1983). There are many other examples of plants with phylloclades in the flora of Madagascar, a common species that may co-occur with *P. compressa* in southwestern Madagascar is *Indigofera compressa* Lam. (*Fabaceae*). In *Paramollugo compressa* young plants have a basal leaf rosette, but this seems to soon wilt, whereas the rigid, flattened stems remain and perennate.

The seeds of *Paramollugo compressa* are unique in the genus by being finely reticulate (Fig. 26) and having a pale brown colour. The other species of the genus have tuberculate or colliculate seeds that are black or dark brown when ripe. Also, the complete lack of pits in the boundaries between the testa cells is unusual. Elsewhere in the genus, this is only found in *P. decandra*, *P. elliotii* and sometimes in seeds of *P. simulans*.

Despite its deviating features, the results of the phylogenetic analyses (Fig. 3, 4) clearly show that *Paramollugo compressa* belongs to this genus, and that it is nested among the species in Madagascar. However, there is no support for any particular sister group relationship.

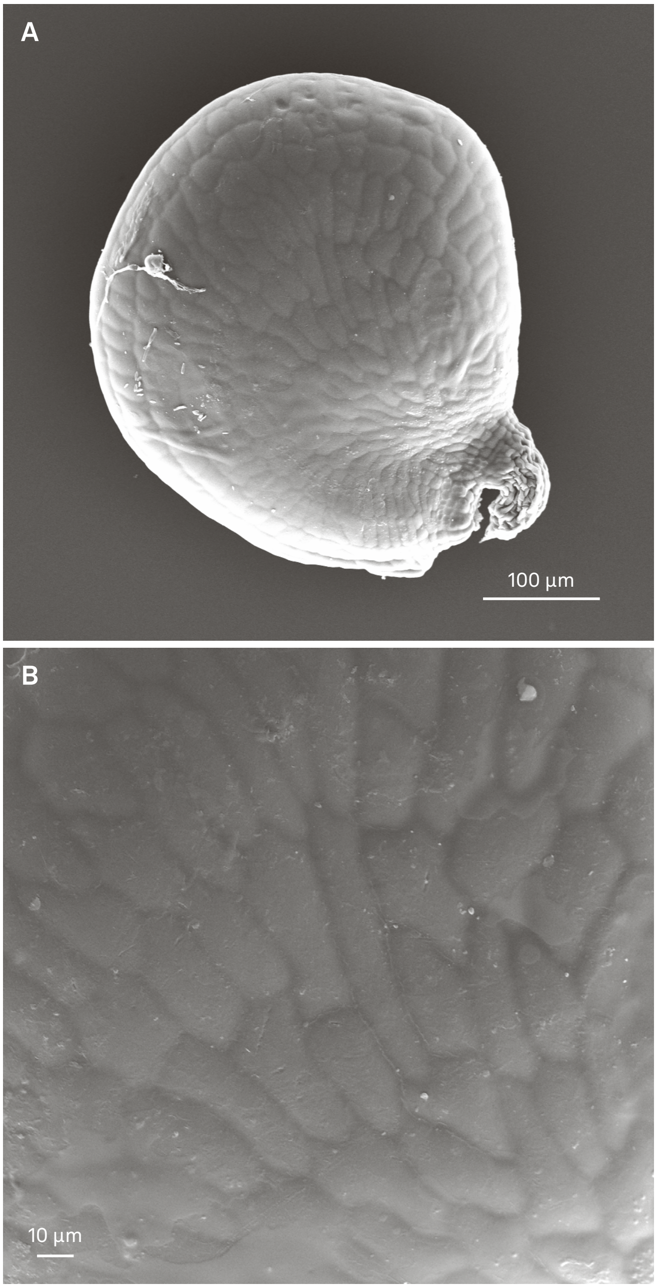

Fig. 26. – *Paramollugo compressa* Thulin, SEM micrographs. **A.** Seed; **B.** Detail of seed ornamentation. [*Keraudren 1386*, P]

Additional specimens examined. – **Madagascar. Reg. Atsimo-Andrefana [Prov. Toliara]:** Plateau Mahafaly, near Beomby, III.1962, ster., *Bosser & Viennot-Bourgin 16124* (P); Plateau Mahafaly, VI.1910, ster., *Perrier de la Bâthie 9901* (P); road from Ankazomanga to Betioky, "tombeau de chef d'Anakatsamby", 8.IV.1922, fl., *Poisson 405* (P).

7. ***Paramollugo angustifolia*** (M.G. Gilbert & Thulin) Thulin in Taxon 65: 786. 2016 (Fig. 28, 29).

≡ *Mollugo angustifolia* M.G. Gilbert & Thulin in Nordic J. Bot. 13: 169. 1993.

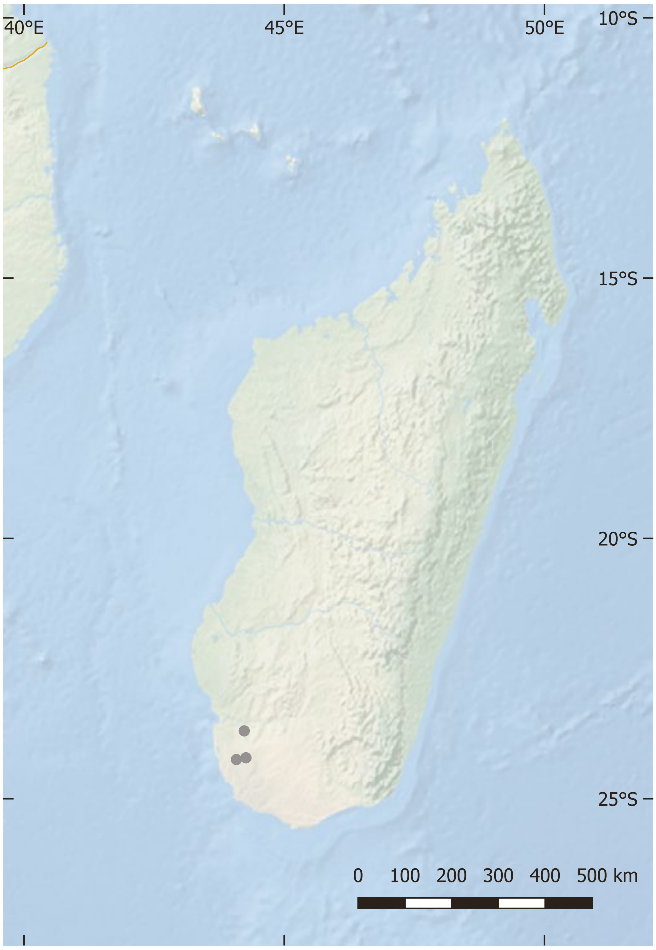

Fig. 27. – Geographic distribution of *Paramollugo compressa* Thulin.

Holotypus: Somalia. Bay Region: c. 3 km SW of Diinsoor, near Buur Diinsoor, 2°24'N 42°58'E, 20.V.1990, fl. & fr., *Thulin, Hedrén & Abdi Dahir 7606* (UPS Nº V-051527!; iso-: FT [FT001036]!, K [K000232029]!).

Herbs, annual or ephemeral, up to 15 cm tall, glabrous in all parts; stems few to several, terete. *Leaves* in dense basal rosette; juvenile leaves up to 1.5 mm wide, narrowly oblanceolate; adult leaves up to 35 × 0.7–1.2(–2) mm, linear, subacute at the apex; midrib prominent beneath, lateral veins indistinct. *Flowers* in lax cymes, white; bracts c. 1 mm long, ovate, acute; pedicels 3–10(–12) mm long. *Tepals* 1.8–2 × 1–1.2 mm, elliptic, rounded at the apex, with hyaline margins, 3(–4)-veined from the base. *Stamens* 5, 1–1.5 mm long; filaments filiform; anthers 0.25–0.30 mm long, shortly oblong. *Ovary* c. 1.5 mm long, ellipsoid, 3-locular; styles 3, c. 0.2 mm long, spreading, reflexed against ovary. *Capsules* 1.5–2 mm long, ellipsoid. *Seeds* 0.39–0.43 × 0.28–0.36 mm, subcircular-reniform in outline, flattened, finely tuberculate to colliculate, dark brown to black; testa cells without secondary ornamentation and with small pits in the boundaries between most of them; hilum c. 0.05 mm long.

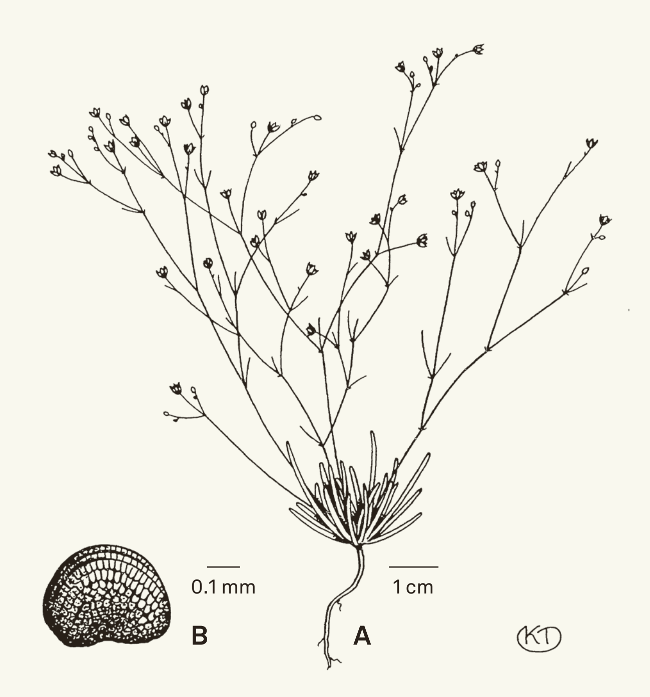

Fig. 28. – *Paramollugo angustifolia* (M.G. Gilbert & Thulin) Thulin. **A.** Habit; **B.** Seed. Reproduced with permission from *Nordic J. Bot.* 13: 170 (1993). Drawn by K. Thunberg. [*Thulin et al. 7606*, UPS]

Distribution and ecology. – *Paramollugo angustifolia* was previously known only from the type locality in south-central Somalia (Gilbert, 1993; Gilbert & Thulin, 1993), where it occurs in open places of bushland on sand at an elevation of c. 300 m. To this, a number of localities in western Madagascar can now be added based on collections made in dry deciduous forest at elevations from near sea level to about 300 m (Fig. 30).

Phenology. – Flowering and fruiting plants seen in May in Somalia and in January to March and in May in Madagascar.

Conservation status. – *Paramollugo angustifolia* is known from seven collections made between 1869 and 2018, representing seven occurrences and three to five subpopulations. The EOO is calculated at 440,312 km², above the upper threshold for the category "Vulnerable" following criterion B1, and the AOO is estimated at 28 km², below the upper threshold for the category "Endangered" following criterion B2. None of the occurrences is located within a protected area. The species is threatened by wood collecting, grazing and urbanization in both Somalia and Madagascar, inducing a decline in the extent and quality of its habitat and in the number of mature individuals. *Paramollugo angustifolia* is here preliminarily assessed as "Vulnerable" [VU B2ab(iii,v)], but a complete assessment following the IUCN Red List Categories and Criteria (IUCN, 2012) would be necessary, as three occurrences made before 1950 may be considered extirpated.

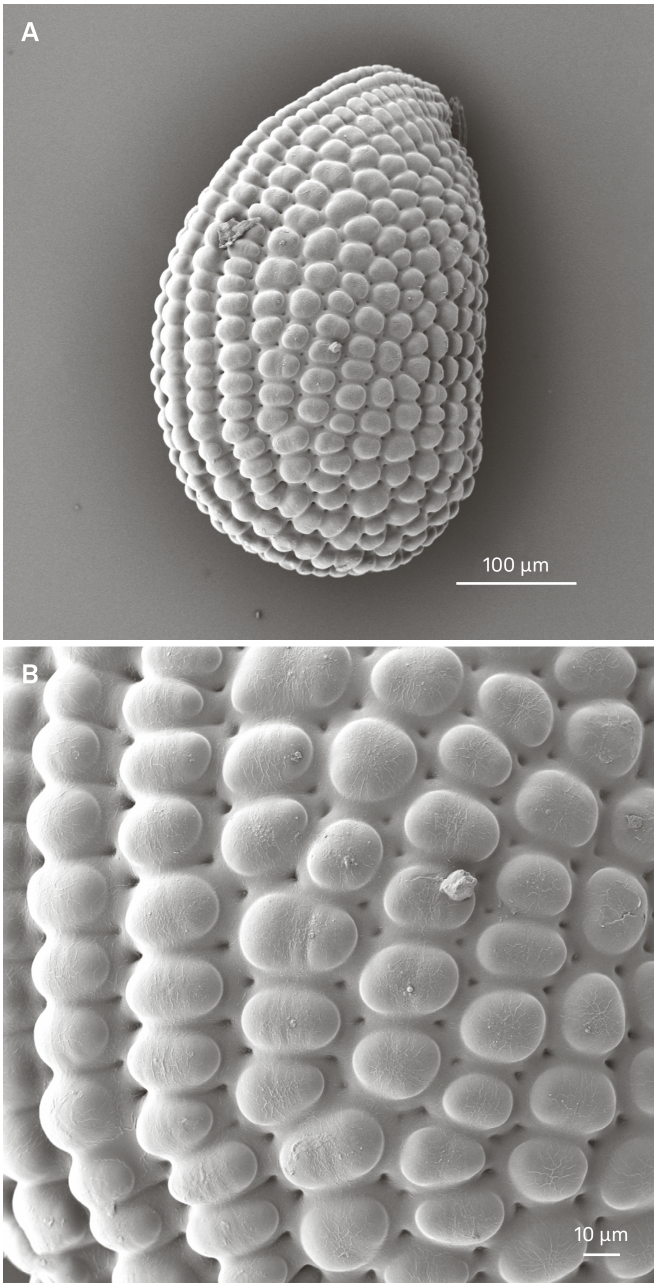

Fig. 29. – *Paramollugo angustifolia* (M.G. Gilbert & Thulin) Thulin, SEM micrographs. **A.** Seed; **B.** Detail of seed ornamentation. [*Razafimandimbison et al. 2222*, S]

Notes. – *Paramollugo angustifolia* is a strongly supported species, closely related to *P. simulans* in the phylogentic analyses. In the BEAST analysis in Fig, 4, the split between these two species is estimated at (2.7–)5.3(–8.4) Ma, whereas the dispersal from Madagascar to Somalia took place during the Pleistocene (see under Discussion).

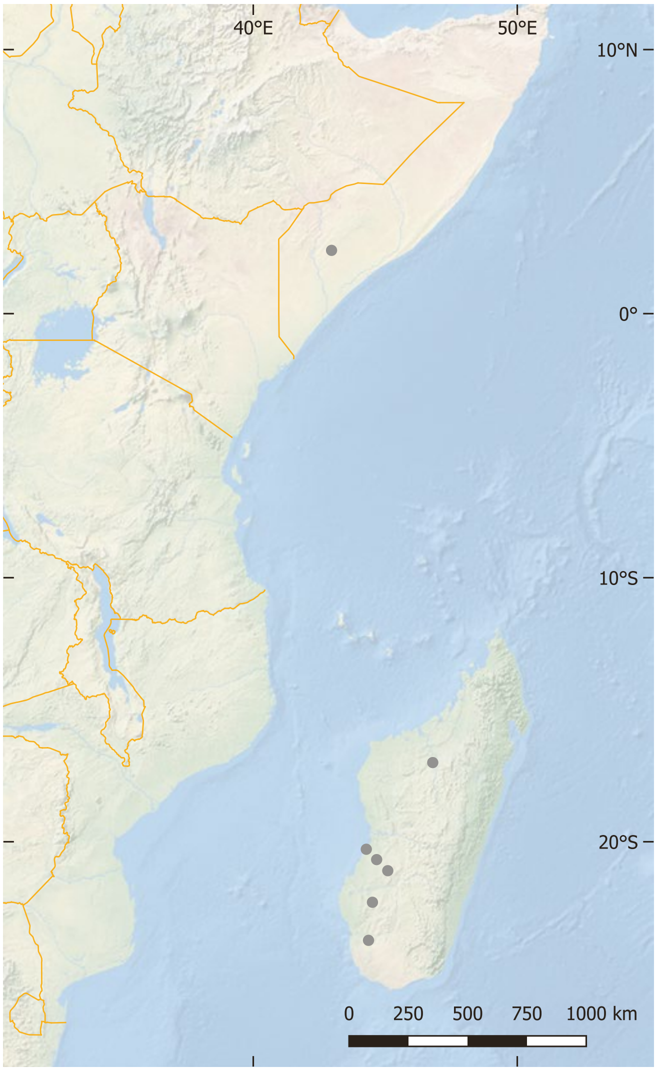

Fig. 30. – Geographic distribution of *Paramollugo angustifolia* (M.G. Gilbert & Thulin) Thulin.

Paramollugo angustifolia differs markedly from *P. simulans* in its narrower leaves 0.7–1.2(–2) mm (vs. 2–12 mm) and smaller seeds (0.39–0.43 × 0.28–0.36 vs. 0.55–0.65 × 0.45–0.60 mm) with small pits in the boundaries between most of the testa cells (vs. without pits or with pits between some cells only).

Instead, it is morphologically very difficult to separate *Paramollugo angustifolia* from the allopatric *P. nesophila*, but the molecular results strongly indicate that they are different species (Fig. 3, 4). The seeds of *P. angustifolia* are 0.39–0.43 mm long vs. 0.40–0.51 mm in *P. nesophila*. Further, the testa cells lack a secondary ornamentation in *P. angustifolia* (Fig. 29B), whereas they are distinctly cross-striate in *P. nesophila* (Fig. 18B).

Morat 2550, a collection with very narrow leaves and small seeds here treated as *Paramollugo angustifolia*, was cited under *P. nudicaulis* by Sukhorukov & Kushunina (2016a), although the testa cells are not cross-striate.

Additional specimens examined. – Madagascar. **Reg. Atsimo-Andrefana [Prov. Toliara]:** limestone plateau W of Betioky, 17.II.1947, fl. & fr., *Humbert 20281* (P); Ankazoabo, II.1967, fl. & fr., *Morat 2550* (P); Beroroha, Antsoa, Antanamary village, Androsy, 21°05'43"S 45°05'48"E, 9.I.2011, fl. & fr., *Razakamalala 5901* (MO, P, TAN). **Reg. Betsiboka [Prov. Mahajanga]:** near Maevatanana, Suberbieville, V.1897, fl. & fr., *Perrier de la Bâthie 230* (P). **Reg. Menabe [Prov. Toliara]:** Morondava, III.1869, fl. & fr., *Grandidier s.n.* (P); Morondava District, Kirindy forest, 20°40'30"S 44°40'30"E, 20.II.2018, fl. & fr., *Razafimandimbison et al. 2222* (S).

8. ***Paramollugo simulans*** Sukhor. in PhytoKeys 73: 97. 2016 (Fig. 31, 32).

Holotypus: Madagascar. Reg. Atsimo-Andrefana [Prov. Toliara]: Belananda, Ranobe, 4 km E of Andrevo village, 22°58'20"S 43°36'56"E, 17.III.2006, fl. & fr., *Ranaivojaona et al. 1442* (K [K000607662]!; iso-: BR [BR0000000514054]!, G [G00418734]!, MO [MO3065761]!, P [P05196698]!, TAN) (Fig. 31).

Herbs, annual or short-lived perennial, 5–35 cm tall, glabrous in all parts or leaves papillose; stems few to several, terete. *Leaves* in dense basal rosette, 15–50 × 2–12 mm, narrowly oblanceolate to obovate, obtuse to subacute at the apex, gradually to abruptly tapering below into a petiole-like base, the petiole-like part shorter than the distal part; midrib prominent beneath, lateral veins 3–4 pairs. *Flowers* in much-branched lax cymes; bracts 1–1.5 mm long, ovate, acute; pedicels 2–15(–20) mm long. *Tepals* 1.5–2.5 × 1–1.5 mm, elliptic, rounded at the apex, with hyaline margins, c. 3-veined from the base, white or pale pink inside. *Stamens* 5, 1–1.6 mm long; filaments filiform; anthers 0.25–0.40 mm long, shortly oblong. *Ovary* 1.2–1.5 mm long, ellipsoid, 3-locular; styles 3, c. 0.2 mm long, spreading, reflexed against ovary. *Capsules* 2–2.5 mm long, ellipsoid. *Seeds* 0.55–0.65 × 0.45–0.60 mm, subcircular-reniform in outline, flattened, colliculate to finely tuberculate, dark brown to black; testa cells without secondary ornamentation or weakly striate, without pits in the boundaries between them or with small pits between some cells only; hilum c. 0.1 mm long.

Vernacular name and uses. – "Aferontany" (*Antilahimena et al. 3464*, *Bogner 2084*, *Humbert 28729*, *Lefèvre & Mily 17*, *Stiefel 104*, etc.). The vernacular name "Aferontany" has been recorded also for *Paramollugo caespitosa* and *P. nudicaulis*. *Paramollugo simulans* is a medicinal plant, used against, for example, cough and stomachache. A decoction of the whole plant is used to treat diarrhoea in newborn babies 2–3 days after childbirth (*Lefèvre & Mily 17*). See also under uses reported for *P. caespitosa* and *P. nudicaulis*.

Isotype of: Paramollugo simulans Sukhor.

Ref. PhytoKeys 73:97, figs. 4&5. 2016

Missouri Botanical Garden (MO)

(R. Ranaivojaona, N.M. Andrianjafy,
Peter B. Phillipson & R.A. Lubke 1442)
MOLLUGINACEAE
Paramollugo simulans Sukhor.
det. A. Sukhorukov (at K) 2016

MADAGASCAR

AIZOACEAE
Mollugo nudicaulis Lam.

det. P. B. Phillipson, 2006
Toliara
Toliara II, Belalanda, Ranobe. 4 km
à l'Est du village Andrevo. Forêt
dégradée sur sable roux.
Echantillons préservés en alcool.
Récolté avec M. Andrianjafy, P.
Phillipson & R. Lubke.
22°58'20"S 43°36'56"E 135 m
Plante herbacée dressée 30 cm de
haut. Feuilles etalées en rosette
à la base du touffe des
inflorescences. Fleurs blanches.
Fruits verts.
17 mar 2006

R. Ranaivojaona et al. 1442
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 31. – Isotype of *Paramollugo simulans* Sukhor.
[*Ranaivojaona et al. 1442*, MO3065761] [© Missouri Botanical Garden, St. Louis]

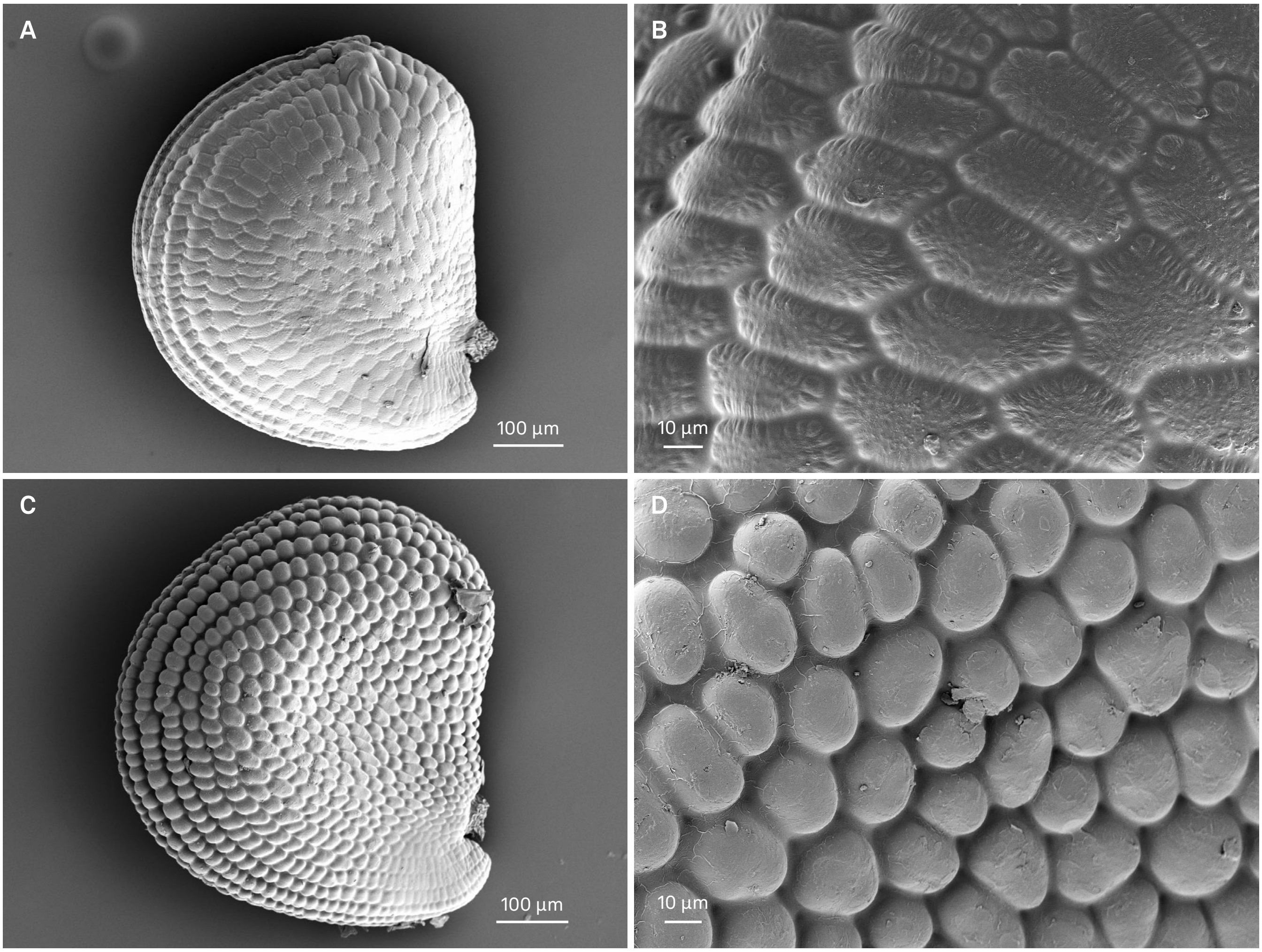

Fig. 32. – *Paramollugo simulans* Sukhor., SEM micrographs. **A, C.** Seeds; **B, D.** Details of seed ornamentation. [**A, B:** *Pettersson & Nilsson 108*, UPS; **C, D:** *Ranaivojaona et al. 1442*, MO]

Distribution and ecology. – *Paramollugo simulans* is widespread in Madagascar (Sukhorukov & Kushunina, 2016a), where it is the most common species in the genus (Fig. 33). It occurs in a wide variety of habitats, such as coastal dunes, littoral forests, and various types of woodland and bushland, often in open sandy or stony places, at elevations from near sea level up to about 1500 m.

Phenology. – Flowering and fruiting plants seen from all months except August.

Conservation status. – *Paramollugo simulans* is widespread in Madagascar and no particular threats to the species have been detected. It is therefore here preliminarily regarded as “Least Concern” [LC] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – *Paramollugo simulans* is an unsupported or only weakly supported species, sister to *P. angustifolia* in the combined phylogenetic analyses (Fig. 3, 4). However, it can be easily separated from *P. angustifolia* by its broader leaves (2–12 vs. 0.7–1.2(–2) mm) and larger seeds (0.55–0.65 × 0.45–0.60 vs. 0.39–0.43 × 0.28–0.36 mm), without pits in the boundaries between the testa cells (Fig. 32) or with small pits between some cells only (vs. with pits in the boundaries between most of the testa cells).

Instead, *Paramollugo simulans* is morphologically more similar to *P. nudicaulis*, a species that is not closely related according to the phylogenetic analyses. In most cases, the narrower leaves, 2–12 mm vs. often more than 12 mm, and shorter tepals, 1.5–2.5 vs. (2–)2.5–3(–3.5) mm, in *P. simulans* are distinctive. Other differences are found in the seeds, which in *P. simulans* are colliculate (Fig. 32A, B) to finely tuberculate (Fig. 32C, D), with smooth (Fig. 32D) to weakly striate (Fig. 32B) testa cells without pits in the boundaries

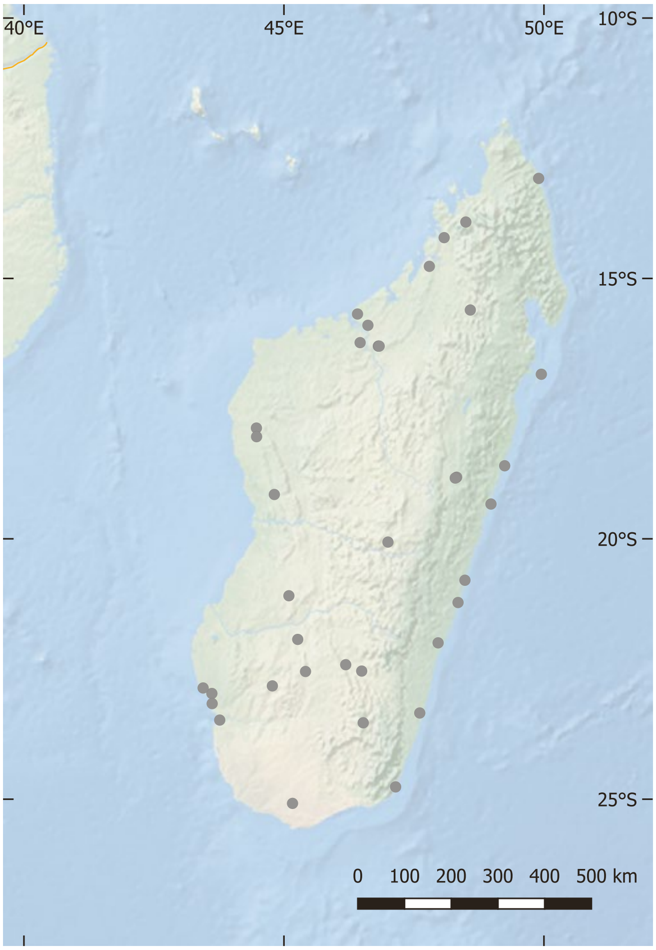

Fig. 33. – Geographic distribution of *Paramollugo simulans* Sukhor.

between them (Fig. 32B) or with pits between some cells only (Fig. 32D), whereas in *P. nudicaulis* the seeds are usually more distinctly tuberculate, with cross-striate testa cells with small pits in the boundaries between most of them (Fig. 12).

Sukhorukov & Kushunina (2016a) stated the number of stamens in *Paramollugo simulans* to be 5–10, but in the present study only 5 stamens have been counted. According to this study, the only species of *Paramollugo* with 10 stamens are *P. caespitosa*, *P. compressa* and *P. decandra*.

The specimen *Afzelius s.n.* (K), here treated as *Paramollugo simulans*, was cited under both *P. simulans* and *P. elliotii* by Sukhorukov & Kushunina (2016a). Several other collections here treated as *P. simulans* were cited by Sukhorukov & Kushunina (2016a) as *P. elliotii* (see further under this species). One of these, *Jongkind et al. 3342*, which was included in the phylogenetic analyses as *P. simulans* 4, consistently falls within the *P. angustifolia/P. simulans* clade (Fig. 3, 4).

Furthermore, two collections cited under *Paramollugo nudicaulis* by Sukhorukov & Kushunina (2016a), *Andrianjafy et al. 977* and *De Block et al. 551*, are here treated as *P. simulans*. A sample from *De Block et al. 551* was included in the phylogenetic analyses as *P. simulans* 3, and consistently groups with the *P. angustifolia/P. simulans* clade (Fig. 3, 4).

Paramollugo simulans is mostly an annual, but in some specimens the plants have a fairly well-developed tap-root and seem to have a somewhat longer lifespan. *Jongkind et al. 3342*, for example, seems to be a short-lived perennial.

Additional specimens examined. – Madagascar. **Reg. Alaotra-Mangoro [Prov. Toamasina]:** Moramanga, Andasibe, Berano, Ambatovy forest, Analamay, 18°49'05"S 48°19'25"E, 24.II.2005, fl. & fr., *Antilahimena et al. 3464* (G, MO, P, TAN); Moramanga, Apitambe, Ambatovy, 18°50'04"S 48°17'46"E, 15.II.2005, fl. & fr., *Razanatsoa 121* (G, MO, P, TAN). **Reg. Analanjirofo [Prov. Toamasina]:** Ste. Marie and Port Lewen de l'île Sata, III–IV.1849, fl. & fr., *Boivin 2577* (P); Ste. Marie, Lokintsy, Ambohidena, 16°50'25"S 49°57'09"E, 19.II.2004, fl. & fr., *Razakamalala et al. 898* (MO, P). **Reg. Androy [Prov. Toliara]:** Ampanihy–Beloha, 91 km, 25°05'S 45°10'E, 1.XII.1989, fl. & fr., *Cheek 2448* (K). **Reg. Anosy [Prov. Tulear]:** Ste. Luce, 24°46'S 47°09'E, 1.V.1989, fl. & fr., *Dumetz 720* (MO, P). **Reg. Antsinanana [Prov. Toamasina]:** Andranokoditra, 7.II.1990, fl. & fr., *Bogner 2084* (US); District de Vatomandry, 1.II.1904, fl. & fr., *Guillot 69* (G, P). **Reg. Atsimo-Andrefana [Prov. Toliara]:** 35 km E of Sakaraha, 4.II.1975, fl. & fr., *Croat 30640* (MO); 16–18 km N of Tulear along road to Morombe, 6.II.1975, fl. & fr., *Croat 30876* (MO, P, TAN); 6 km from St. Augustin on road to Tuléar, 23°28'59"S 43°45'59"E, 5.I.1999, fl., *De Block et al. 551* (BR, MO, P, TAN); Manombo, 22°51'59"S 43°26'49"E, 16.II.2002, fl. & fr., *Lefèvre & Mily 17* (P, TAN); Beroroha, Antsoa, Antanamary, 21°05'43"S 45°05'48"E, 9.I.2011, fl. & fr., *Razakamalala 5858* (MO, P, TAN). **Reg. Atsimo-Antsinanana [Prov. Fianarantsoa]:** Vangaindrano, s.d., fl. & fr., *Scott Elliot 2257* (BM, E, K). **Reg. Boeny [Prov. Mahajanga]:** Majunga, 27.IV.1912, fl. & fr., *Afzelius s.n.* (K, S); 5 km NNW of field station c. 4 km W of Ankarafantsika, 7.II.2000, fl. & fr., *Bremer et al. 4053-B53* (UPS); Majunga, 5.III.1924, fl. & fr., *Decary 2416* (P); Ambato-Boeni, 24.IV.1943, fl. & fr., *Decary 19088* (MO, P); Poste Forestier d'Ampijoroa, 16°14'S 46°28'E, 25.II.1985, fl. & fr., *Dorr et al. 3810* (BR, K, MO, P); near Majunga, 27–29.VII.1924, fl. & fr., *Humbert & Perrier de la Bâthie 2020* (P), 28–30.XII.1924, fl. & fr., *Humbert 4020* (K, P, US), *4079* (G, P); Majunga, 20.X.1912, fl. & fr., *Kaudern s.n.* (G, S); Majunga, II.1915, fl. & fr., *Perrier de la Bâthie 5183* (P); near Majunga, I.1908, fl. & fr., *Perrier de la Bâthie 5233* (P); near Lake Ampijoroa, 16°18'S 46°49'E, 27.XI.1986, fl. & fr., *Pettersson & Nilsson 108* (UPS); Majunga, 24.XII.1920, fl. & fr., *Poisson 44* (P); Ankarafantsika Integrated Nature Reserve, Abemena area, 16°18'S 46°50'E, 7.II.2000, fl. & fr., *Thulin et al. 10399* (TAN, UPS); between Antetikala forest and Baie de Bombetoke, 7.IX.1912, fl. & fr., *Viguier & Humbert 65* (P). **Reg. DIANA [Prov. Antsiranana]:** Antanambao, along Sambirano river, 13°55'S 48°30'E, 3.IX.1999, fl. & fr., *Stiefel 104* (G, MO, P). **Reg. Ihorombe [Prov. Fianarantsoa]:** Iakora, Begogo, Bekora, 23°32'08"S 46°03'35"E, 7.II.2005, fl. & fr., *Andrianjafy et al. 977* (MO, P, TAN); Isalo, Ranohira, 4.III.1943, fl. & fr., *Decary 18969* (P); Malio basin near Ambalabe, 23–27.XI.1946, fl. & fr., *Humbert 19430* (P); upper valley of Menarahaka, E of Ihosy, 1955, fl. & fr., *Humbert 28574bis* (P); plateau and valleys of Isalo, W of Ranohira, 1955, fl. & fr., *Humbert 28729* (MO, P); Ambia, Vohidava, bifurcation towards Farafangana, 22°25'10"S 46°11'23"E, 19.III.2010, fl. & fr., *Razafindraibe et al. 335* (MO, P, TAN). **Reg. Melaky [Prov. Mahajanga]:** Beanka forest, Ambatosoa, 17°52'25"S 44°28'19"E, 26.I.2012, fl. & fr., *Bolliger et al. 136* (G, K, MO, P); along Manambolo river, 19°09'S 44°49'E, 2.XII.1996, fl. & fr., *Jongkind et al. 3342* (BR, G, MO, WAG); Beanka, Ambinda Est, 18°02'24"S 44°28'31"E, 2.IV.2013, fl. & fr., *Ranaivoarisoa 54* (BR, G, MO, P). **Reg. SAVA [Prov. Antsiranana]:** Vohémar, Nosibe, Anjiabe, Anaborano, 13°04'43"S 49°54'04"E, 23.II.2003, fl. & fr., *Rabenantoandro et al. 1314* (MO). **Reg. Sofia [Prov. Mahajanga]:** 25 km E of Analalava towards Antsohihy, 14°46'03"S 47°47'53"E, 21.VI.2008, fl. & fr., *Andriamahay & Rakotoarison 2071* (K); Maromandia, 27.XII.1922, fl. & fr., *Decary 1352* (G, P); 4 km SW of Boriziny, Bongolava forest, 15°36'24"S 47°35'11"E, 21.I.2012, fl. & fr., *Rakotoarison & Andriamahay 2859* (K). **Reg. Vakinankaratra [Prov. Antananarivo]:** Antsirabe, Ibity, 20°03'51"S 47°00'07"E, 26.II.2008, fl. & fr., *Andriamahay & Rakotoarisoa 1890* (K). **Reg. Vatovavy-Fitovinany [Prov. Fianarantsoa]:** Ambila, 7.V.1928, fl. & fr., *Decary 6422* [in part] (K); Nosy Varika, Ambahy, 20°47'49"S 48°28'58"E, 23.IV.2004, fl. & fr., *Razakamalala et al. 1208* (MO, P); Mananjary Prov., III–IV.1909, fl. & fr., *Geay 7636*, *7790*, *7968* (P). **Sine loco:** *Gerrard 120* (K); *Humblot 100* (P); *Lyall 328* (K).

9. ***Paramollugo elliotii*** Sukhor. in PhytoKeys 73: 102. 2016 (Fig. 34, 35).

Holotypus: Madagascar. Reg. Melaky [Prov. Mahajanga]: "province du Mailaka" (Melaky), II.1892, fl. & fr., *Douliot s.n.* (P [P04582888]!).

Herbs, perennial, up to 40 cm tall, glabrous in all parts, with a branched rhizome from a tap-root; stems few to several, terete. *Leaves* in dense basal rosette, 20–60 × 1–1.5 mm, linear, obtuse to subacute at the apex; midrib prominent beneath, lateral veins indistinct. *Flowers* in much-branched lax cymes; bracts 1–1.5 mm long, ovate, acute; pedicels 3–15(–30) mm long. *Tepals* 2.5–3.5 × 1.5–1.8 mm, elliptic, rounded at the apex, with hyaline margins, c. 3-veined from the base, white inside. *Stamens* 5, 1.5–2 mm long; filaments filiform; anthers 0.5–0.6 mm long, elliptic-oblong. *Ovary* 1.5–2 mm long, ellipsoid, 3-locular; styles 3, c. 0.3 mm long, spreading, reflexed against ovary. *Capsules* c. 2.5 mm long, ellipsoid to ovoid. *Seeds* 0.60–0.70 × c. 0.55 mm, subcircular-reniform in outline, flattened, colliculate, black; testa cells without secondary ornamentation and without pits in the boundaries between them; hilum c. 0.1 mm long.

Distribution and ecology. – The collections here referred to *Paramollugo elliotii* are from western Madagascar, the three Douliot specimens from near Maintirano in the Melaky Region, where Douliot collected in January–February 1892 (Dorr, 1997), and *Perrier de la Bâthie 9211* from Baie de Baly near Soalala in the Boeny Region (Fig. 36). They were apparently all made on coastal sand dunes. In the map of the distribution of *P. elliotii* presented by Sukhorukov & Kushunina (2016a: 101), an occurrence of the species in southeastern Madagascar is shown. This is based on *Pervillé 643* that is said to originate from the Atsimo-Antsinanana Region. However, this is a mistake and the locality, Ambongo, is located in the Boeny Region in western Madagascar, where Pervillé collected in 1840–41 (Dorr, 1997). The Ambongo area includes Baie de Baly (see Fig. 36, the northern locality), and Pervillé's locality could be the same as or close to that of *Perrier de la Bâthie 9211*.

Phenology. – Flowering and fruiting plants seen from January and February.

Conservation status. – *Paramollugo elliotii* is known from five collections made between 1841 and 1905, representing two occurrences, one of them possibly located within the Baie de Baly National Park. The EOO cannot be calculated, and the AOO is estimated as 8 km^2, below the upper threshold for the category "Critically Endangered" following criterion B2. However, the species has not been collected since 1905 and should be searched for in suitable habitats in western Madagascar. A complete assessment following the IUCN Red List categories and criteria may not consider one or both of these two occurrences as still extant. We are reluctant to assign a category, as with the very scarce information available on its distribution and the threats the occurrences are facing, *P. elliotii* may either be assessed as "Vulnerable" [VU D2], "Endangered" [EN], "Critically Endangered" [CR], or even possibly "Extinct in the Wild" [EW].

Notes. – The collector of the holotype of *Paramollugo elliotii* is H.L. Douliot (not M. Douillot as stated by Sukhorukov & Kushunina, 2016a), and the collection was made in 1892 (not 1890).

Among the collections cited under *Paramollugo elliotii* by Sukhorukov & Kushunina (2016a), only *Jongkind 3342* from 1996 is relatively recent. A sample from this collection was included in the phylogenetic analyses as *P. simulans* 4, and grouped with the *P. angustifolia/P. simulans* clade (Fig. 3, 4). This collection, which appears to be a short-lived perennial, otherwise agrees well with *P. simulans* and is here included in this species. Although it has not been possible to include *P. elliotii*, as circumscribed here, in the phylogenetic analyses, it is assumed that it is a close relative of *P. simulans* that can be distinguished on morphological grounds.

The seeds of *Paramollugo elliotii*, with testa cells without secondary ornamentation and without pits in the boundaries between them (Fig. 35), resemble the seeds of *P. simulans* and suggest a relationship with this species. However, *P. elliotii* differs from *P. simulans* by its clearly perennial habit and narrower leaves (1–1.5 vs. 2–12 mm), and longer anthers (0.5–0.6 vs. 0.25–0.40 mm). The linear leaves (Fig. 34) agree with *P. angustifolia*, but *P. elliotii* differs from this, apart from by the perennial habit, also by the longer anthers (0.5–0.6 vs. 0.25–0.30 mm) and the larger seeds (0.60–0.70 × c. 0.55 vs. 0.39–0.43 × 0.28–0.36 mm), without pits in the boundaries between the testa cells.

Sukhorukov & Kushunina (2016a) listed several collections under *Paramollugo elliotii* that are here treated as *P. simulans*: *Afzelius s.n.* (cited under both *P. elliotii* and *P. simulans* by Sukhurukov & Kushunina, 2016a), *Jongkind 3342*, *Humbert & Perrier de la Bâthie 2020*, *Humbert 4020* and *Poisson 44*. These all have leaves more than 2 mm wide, short anthers, and also appear to be annuals or short-lived perennials, although sometimes with a fairly well developed tap-root.

Fig. 34. – *Paramollugo elliotii* Sukhor.
[*Douliot s.n.*, P04582869] [© Muséum national d'Histoire naturelle, Paris]

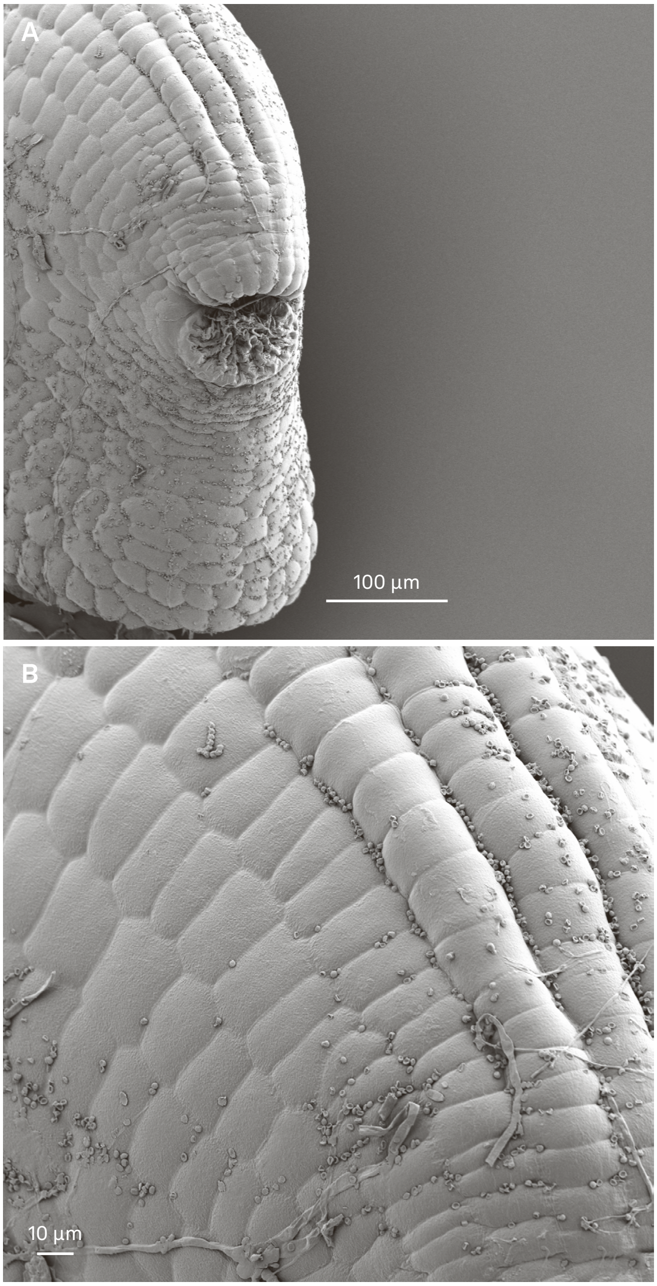

Fig. 35. – *Paramollugo elliotii* Sukhor., SEM micrographs. **A.** Seed, from hilar end; **B.** Detail of seed ornamentation. [*Douliot s.n.*, P04582886]

Additional specimens examined. – MADAGASCAR. **Reg. Boeny [Prov. Mahajanga]:** Baie de Baly, I.1905, fl. & fr., *Perrier de la Bâthie 9211* (P); Ambongo, 16.II.1841, fl. & fr., *Pervillé 643* (G, K, L, P). **Reg. Melaky [Prov. Mahajanga]:** "province de Mailaka, Namela", II.1892, fl. & fr., *Douliot s.n.* (P [P04582869]); "province de Mailaka", II.1892, fl. & fr., *Douliot s.n.* (P [P04582886]).

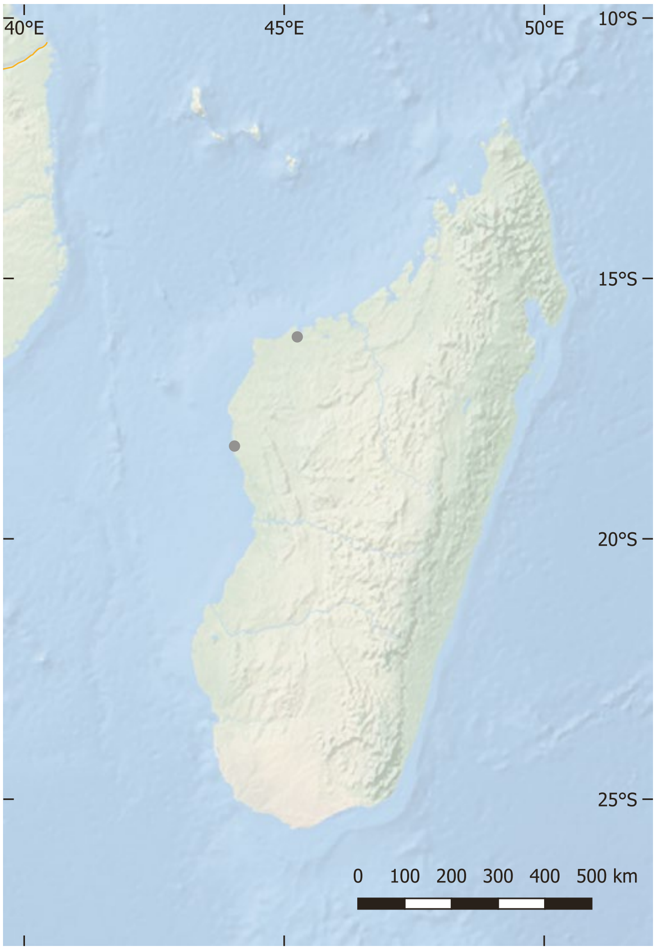

Fig. 36. – Geographic distribution of *Paramollugo elliotii* Sukhor.

10. ***Paramollugo spathulata*** (Sw.) Sukhor. in Skvortsovia 3: 51. 2016 (Fig. 22B, 37, 38).

≡ *Pharnaceum spathulatum* Sw., Fl. Ind. Occid. 1: 568. 1797.

≡ *Pharnaceum bellidifolium* Poir. in Lamarck, Encycl. 5: 262. 1804 [nom. illeg.].

≡ *Mollugo bellidifolia* (Poir.) Ser. in DC., Prodr. 1: 391. 1824 [nom. illeg.].

≡ *Mollugo nudicaulis* var. *bellidifolia* Fenzl in Ann. Wiener Mus. Naturgesch. 1: 383. 1836.

Lectotypus (designated by THULIN et al., 2016: 786): JAMAICA: s.l., s.d., fl. & fr., *Swartz s.n.* (S-05-5804!).

= *Mollugo nudicaulis* var. *gracilis* Fenzl in Ann. Wiener Mus. Naturgesch. 1: 383. 1836. **Holotypus: CUBA. Prov. Matanzas:** "montis Sabanasso", II [?], *Poeppig*? (B†).

= *Mollugo nudicaulis* var. *navassensis* Ekman in Ark. Bot. 22A(17): 14. 1929. ≡ *Paramollugo navassensis* (Ekman) Thulin in Taxon 65: 786. 2016. **Lectotypus** (designated

Fig. 37. – *Paramollugo spathulata* (Sw.) Sukhor.
[*Proctor 42517*, NY01510588] [© The New York Botanical Garden]

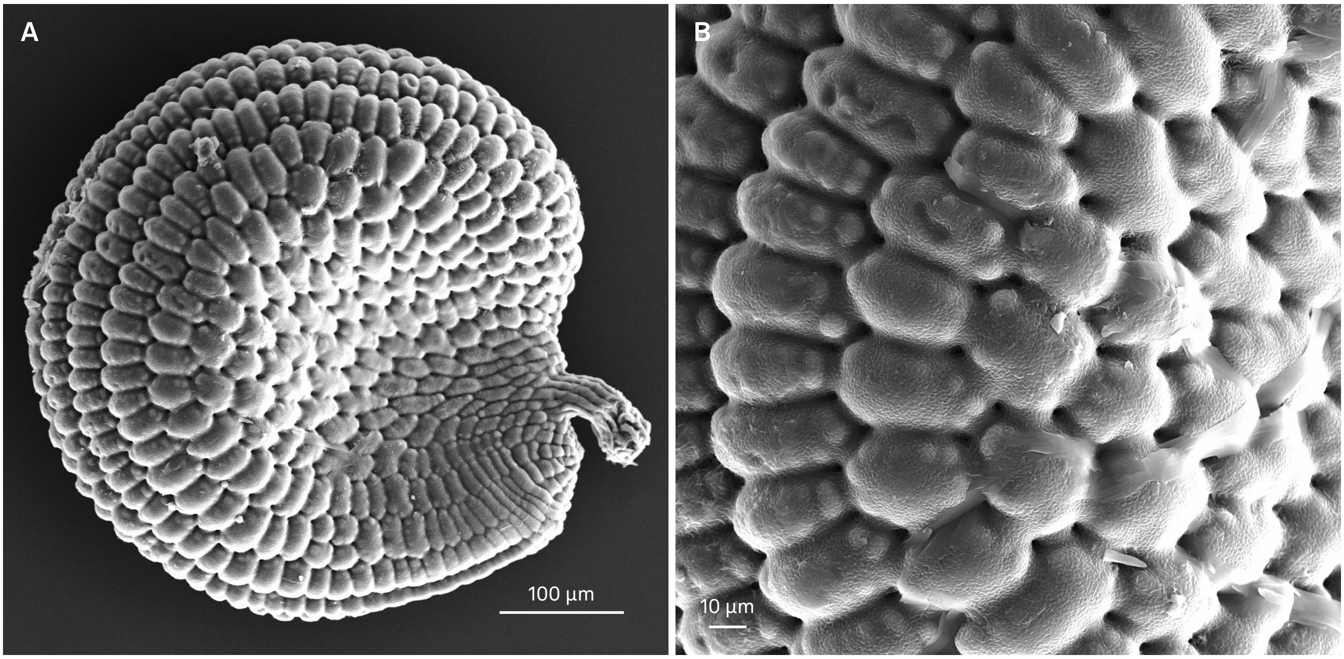

Fig. 38. – *Paramollugo spathulata* (Sw.) Sukhor., SEM micrographs. **A.** Seed; **B.** Detail of seed ornamentation. [*Eggers 169,* UPS]

by Thulin et al., 2016: 786): **Navassa Island:** "Insula Navassa (inter Haiti et Jamaica sita) in savannis ad partem septentrionali-occidentalem versus", 19.X.1928, fl. & fr., *Ekman H 10810* (S-R-3647!; isolecto-: A [A00037491]!, B [B100248713]!, C [C10001454, C10001455]!, G [G00356430]!, GH [GH00037490]!, K, LE [LE00006649]!, LL [LL00370733]!, MO [MO216413]!, NY [NY00232982]!, S-13-8983!, US [US00848205]!).

= *Mollugo deltoidea* Léon in Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 9: 3. 1950. ≡ *Paramollugo deltoidea* (Léon.) Thulin in Taxon 65: 786. 2016. **Holotypus: Cuba. Prov. Holguín:** Sabana de la Yaba, Yareyales, W of Holguín, 4.VII.1932, fl. & fr., *Léon 15715* (HAC image!).

Herbs, annual or perennial, 5–40 cm tall, glabrous in all parts, with a slender tap-root when flowering in the first year or, when perennating, with a branched scaly rhizome; stems few to many, terete. *Leaves* crowded in a basal rosette, 10–50(–70) × 3–18(–25) mm, the distal part narrowly to broadly obovate or spathulate, rounded to subacute or truncate at the apex, sometimes shortly mucronate, tapering gradually to ± abruptly below into a petiole-like base, the petiole-like part about as long as the distal part; midrib prominent beneath, lateral veins 3–5 pairs. *Flowers* in much-branched lax cymes; bracts 0.5–1 mm long, ovate, acute; pedicels up to c. 10 mm long. *Tepals* 1.5–2.5 × 1–1.5 mm, elliptic, rounded at the apex, with hyaline margins, c. 3-veined from the base, white or pinkish inside, midrib with dark tip. *Stamens* 5, 1.2–1.5 mm long; filaments filiform; anthers 0.3–0.4 mm long, elliptic-oblong. *Ovary* c. 1.5 mm long, ellipsoid, 3-locular; styles 3, c. 0.2 mm long, spreading. *Capsules* c. 2 mm long, ellipsoid. *Seeds* 0.48–0.52 × 0.40–0.46 mm, subcircular-reniform in outline, flattened, finely tuberculate, black; testa cells with ± warty secondary ornamentation, with small pits in the boundaries between most of them; hilum c. 0.1 mm long.

Distribution and ecology. – *Paramollugo spathulata* is widespread in the Caribbean, where it is known from British Virgin Islands, Cuba, Dominican Republic, Guadeloupe, Haiti, Jamaica, Martinique, Navassa Island, Puerto Rico and U.S. Virgin Islands (Fig. 39). According to Urban (1920), it also occurs in Guyana, but this has not been confirmed. A specimen from Pará in Brazil (*Poeppig s.n.*, P040601600) has to be wrongly labeled. Instead, it is almost certainly from Cuba, where Poeppig also collected (see Notes below).

The species is found in forest, various shrub formations including coastal thicket, and savanna, and it often occurs in open rocky or stony places, but also on naked earth, mud, sandy river banks or in fallow or cultivated fields, at elevations from near sea level up to about 750 m. Several collections from Cuba, Dominican Republic and Puerto Rico have been made in areas with ultramafic rocks (serpentine) or soils derived from them. Ultramafic substrates cover about 7% of Cuba and includes areas of ancient origin (10–30 Ma), as well as areas exposed more recently (Pillon et al., 2019). As for the Dominican Republic, some areas where ultramafic materials (serpentines) are particularly noticeable were pointed out by Cano et al. (2014), whereas in Puerto Rico the serpentine outcrops of the Guanajibo area in the southwestern part of the country are prominent. *Paramollugo spathulata* is found in all these areas of ultramafic substrates, but as the species is not confined to them, it is probably best characterized as ultramafic-tolerant.

Phenology. – Flowering and fruiting plants have been seen from all months.

Conservation status. – *Paramollugo spathulata* is widespread in the Caribbean and no particular threats to the species have been detected. It is therefore here preliminarily regarded as "Least Concern" [LC] following the IUCN Red List Categories and Criteria (IUCN, 2012).

Notes. – In the protologue of *Pharnaceum bellidifolium*, "*Pharnaceum spathulatum* Vahl" is cited in synonymy. Therefore, *P. bellidifolium* is superfluous according to ICN Art. 52.1, even if the author name given for *P. spathulatum* was a slip of the pen.

In the protologue of *Mollugo nudicaulis* var. *gracilis*, material in B from "montis Sabanasso" in Cuba was cited. Probably this refers to material collected by Poeppig, who visited Cuba 1822–1824. One of his collecting localities is "mons Sabanossa" just NE of Coliseo in Prov. Matanzas (Moya López, 2021).

Paramollugo spathulata, including *P. navassensis* (as *P. spathulata* 2), is strongly supported in the phylogenetic analyses (Fig. 3, 4) and is also strongly supported as sister to *P. cuneifolia*, endemic to eastern Cuba, in a clade restricted to the Caribbean. The estimated time for the split between *P. spathulata* and *P. cuneifolia* is (2.2–)6.8(–12.3) Ma (Fig. 4). *Paramollugo spathulata* was resurrected by Sukhorukov & Kushunina (2016b) for the widespread Caribbean plant that was previously long treated as a form of *P. nudicaulis*. Sukhorukov and Kushunina mainly pointed to the difference in the seed coat between *P. spathulata* and *P. nudicaulis* (tubercles with warty ultrastructure in *P. spathulata* vs. striate ultrastructure in *P. nudicaulis*), and also mentioned the ability of *P. spathulata* to perennate as a similarity to *P. digyna* rather than to *P. nudicaulis*.

Mollugo deltoidea (≡ *Paramollugo deltoidea*), described from near Holguín in Cuba, is here included in *P. spathulata* with which it intergrades. It is a perennial dwarf form growing on serpentine with the distal more or less triangular portion of the leaves narrowed more abruptly into the petiole-like base than in most other material of the species. However, in "Lista roja de la flora de Cuba" (González Torres et al., 2016), *Mollugo deltoidea* is recognized and included as a "Critically Endangered" [CR] taxon, due to its very limited EOO and AOO.

Paramollugo spathulata differs from *P. cuneifolia* by its herbaceous leaves arranged in a basal rosette (vs. leaves succulent, marcescent and densely and more or less distichously arranged at the base of the plant). Further, the seeds in *P. spathulata* are smaller (0.48–0.52 × 0.40–0.46 vs. 0.6–0.7 × 0.5–0.6 mm) and have testa cells with a more or less warty secondary ornamentation (Fig. 38B), vs. without secondary ornamentation in *P. cuneifolia* (Fig. 42B).

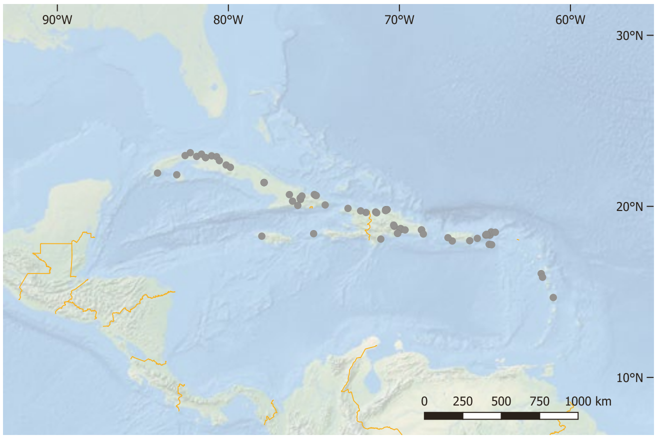

Fig. 39. – Geographic distribution of *Paramollugo spathulata* (Sw.) Sukhor.

However, the species that are morphologically most similar to *Paramollugo spathulata* are the allopatric *P. nudicaulis* and *P. digyna*, none of which is close to *P. spathulata* in the phylogenetic analyses. The difference in leaf shape between these three species (Fig. 22) is the easiest way to recognize them. *Paramollugo digyna* in New Caledonia is, as *P. spathulata*, often perennial and has testa cells with a warty ultrastructure, but also differs by often having 2-locular ovaries and two styles. The widespread *P. nudicaulis* also differs by being annual and by having testa cells with a cross-striate ultrastructure (Fig. 12B).

Additional specimens examined. – **British Virgin Islands. Guana Island:** SE of White Bay, 17.XI.1986, fl. & fr., *Proctor 42517* (NY). **Virgin Gorda:** 14.I.1919, fl. & fr., *Fishlock 301* (NY).

Cuba. Prov. Camagüey: Camagüey to Santayana, 4.IV.1909, fl. & fr., *Britton 2378* (NY, US); near Camagüey, 2–7.IV.1912, fl. & fr., *Britton et al. 13169* (NY, US); Queen City to Riverside, 31.III.1909, fl. & fr., *Shafer 1135* (NY, US). **Prov. Guantánamo:** Jauco, S. Baracoa, V.1940, fl. & fr., *Léon 17745* (US); Río Yamuri, XII.1910, fl. & fr., *Shafer 7883* (NY, US). **Prov. Holguín:** Moa, Mina Cromita, 24.VII.1944, fl. & fr., *Clemente & Alain 4090* (US); Moa, Playa la Vaca, 14.IV.1946, fl. & fr., *Clemente 4906* (US); Sierra de Nipe, base of Loma Mensura, 19.X.1914, fl. & fr., *Ekman 3140* (S); Moa, Mina Franklin, VII.1947, fl. & fr., *Léon & Clemente 23226* (US); crest of Sierra de Nipe, 16–18.X.1941, fl. & fr., *Morton & Acuna 3069* (US); Río Matamoros S of Holguín, 14.IV.1909, fl. & fr., *Shafer 1380* (NY, US). **Prov. Isla de la Juventud:** from Santa Ana to Santa Bárbara, 29.X.1920, fl. & fr., *Ekman 11961* (NY, S, UPS). **Prov. La Habana:** Lomas de las Jatas, 1.V.1914, fl. & fr., *Ekman 570* (S, US); ibid., 22.V.1914, fl. & fr., *Ekman s.n.* (S); Guanabacoa, 6.VI.1914, fl. & fr., *Ekman 1278* (S); Hoyo Colorado, 11.X.1917, fl. & fr., *Léon 7528* (NY); Guanabacoa, 8.VII.1907, fl. & fr., *Léon 63* (NY, P); Robles Regla, 8.IV.1903, fl. & fr., *Shafer 541* (NY); Loma de la Jata, 4.I.1912, fl. & fr., *Wilson 11647* (NY, US). **Prov. Matanzas:** San Miguel de los Baños, 17–18.XII.1931, fl. & fr., *Killip 13884* (US); Sabanilla de la Palma, 4.I.1921, fl. & fr., *Léon et al. 9668* (NY). **Prov. Mayabeque:** Madruga, 25.III.1903, fl. & fr., *Britton et al. 650*

(NY). **Prov. Pinar del Río:** Las Martinas to the coast, 19.XII.1911, fl. & fr., *Shafer 11091* (NY, US). **Prov. Santiago de Cuba:** Santiago, Punta Sal, 10–25.III.1912, fl. & fr., *Britton et al. 12854* (NY, US); Sierra de Nipe, at Río Piloto, 25.VII.1914, fl. & fr., *Ekman 2244* (S); Sierra Maestra, El Cobre, 6.X.1916, fl. & fr., *Ekman 7836* (S). **Prov. Villa Clara:** Santa Clara, 29–31.III.1910, fl. & fr., *Britton et al. 6060* (NY, US); ibid., 21–22.III.1911, fl. & fr., *Britton et al. 10168* (NY, US); 10 km W of Santa Clara, VI.1941, fl. & fr., *Howard 5038* (P, S, US); 4 km E of Cascajal, VII.1941, fl. & fr., *Howard 5526* (NY); Motembo, 9–10.VIII.1920, fl. & fr., *Léon 9370* (NY); ibid., 28.VIII.1922, fl. & fr., *Léon 11381* (NY); 6 km W of Santa Clara, 15.VII.1936, fl. & fr., *Smith et al. 3148* (S, US); between Santa Clara and Guaracabulla, 3.VII.1953, fl. & fr., *Webster et al. 134* (NY). **Sine loco:** *de la Sagra s.n.* (P); *Wright 25* (K, P, US).

Dominican Republic: Guayubín, 13–21.II.1921, fl. & fr., *Abbott 960* (US); vicinity of Piedra Blanca, 14.X.1947, fl. & fr., *Allard 16063* (NY, S, US); Higüey, banks of Río Duey, 10.IV.1929, fl. & fr., *Ekman H12114* (S, US); Barahona, Bahoruco, VI.1911, fl. & fr., *Fuertes 859* (US), *1087* (E, L, NY, P, S, US); near Higüey, 3–7.XI.1946, fl. & fr., *Howard 9718* (NY, US); San Cristóbal, 17.X.1957, fl. & fr., *Jiménez 3606* (US); Cafemba, 25.III.1961, fl. & fr., *Jiménez 4347* (US); Sierra Prieta, 9.X.1965, fl. & fr., *Lavastre 1970* (NY); Vila Mella, 26.III.1966, fl. & fr., *Lavastre 2097* (NY); Higüey, Boca de Yuma, 22.VIII.1968, fl. & fr., *Liogier 12292* (NY): Arroyo Francés, 4 mls. W of Puerto Plata, 28–29.X.1969, fl. & fr., *Liogier 16585* (NY, P, US); 6 mls. N of Villa Mella, 12.IX.1970, fl. & fr., *Liogier 17406* (NY); Laguna el Toro, Guerra, 20.II.1971, fl. & fr., *Marcano 5883* (NY); Loma Sierra Prieta, 18°39'N 69°53'W, 13.VIII.1980, fl. & fr., *Mejía & Zanoni 7845* (NY, S); Villa Mella, Río Guanuma, 14.IV.1977, fl. & fr., *Melo 161* (NY); Barrabás, 20.IV.1906, fl.& fr., *Raunkiaer 800* (US); SE of Bonao, 18°54'N 70°20'W, 21.IV.1981, fl. & fr., *Zanoni et al. 12701* (NY); between Villa Mella and Yamasá, 18°39'N 69°58'W, 8.VII.1981, fl. & fr., *Zanoni et al. 15302* (NY), 16.X.1984, fl. & fr., *Zanoni & Mejía 31917* (NY).

Gouadeloupe: Terre de Bas, 13.XI.1967, fl. & fr., *Le Gallo 3138* (US).

Haiti: Massif du Nord, Morne Haut-du-Cap Bay, 16.XII.1924, fl. & fr., *Ekman H2906* (S, US); Port-de-Paix to Jean-Rabel, N of Cabaret, 28.III.1925, fl. & fr., *Ekman H3608* (S); Plaine du Nord, Terrier-Rouge, 26.IV.1928, fl. & fr., *Ekman H9887* (K, S).

Jamaica: s.l., s.d., fl. & fr., *Sloane s.n.* (BM).

Martinique: s.l., s.d., fl. & fr., *Richard s.n.* (B-W).

Navassa Island: N of lighthouse, 18°24'N 75°01'E, 25.VII.1998, fl. & fr., *Buck & Zanoni 34161* (NY, S, US); near the lighthouse, 20–23.VI.1956, fl. & fr., *Proctor 15462* (US).

Puerto Rico: Guanajibo, near Mayagüez, II.1915, fl. & fr., *Britton et al. 4065* (NY, US); Guanajibo, 26.XII.1929, fl. & fr., *Britton 9398* (NY); Guanica, 2.II.1886, fl. & fr., *Sintenis 3596* (P, S, US); Maunabo, Punta de la Tuna, 18.IX.1886, fl. & fr., *Sintenis 5083* (L, P, US); Vieques, XI.1970, fl. & fr., *Woodbury s.n.* (NY, US).

U.S. Virgin Islands. **Saint Croix:** Teague Bay, 11.I.1979, fl. & fr., *Fosberg 58899* (US); s.l., s.d., fl. & fr., *Ravn s.n.* (S); s.l., s.d., fl. & fr., *Richard s.n.* (P); Judith's Fancy, 21.VIII.1896, fl. & fr., *Ricksecker 499* (E, NY, US). **Saint John:** VIERS [Virgin Islands Environmental Resource Station], 11.I.1990, fl. & fr., *Acevedo Rodríguez & Aleman 3202* (NY, US); Johns Folly, 11.I.1991, fl. & fr., *Acevedo Rodríguez & Siaca 3934* (NY, US). **Saint Thomas:** Water Island, 31.I–4.II.1913, fl. & fr., *Britton et al. 114* (NY, US); Nadir, 1–9.III.1924, fl. & fr., *Britton 186* (NY, US); s.l., XI.1880, fl. & fr., *Eggers 169* (K, L, P, UPS); Bovoni Valley, IX.1881, fl. & fr., *Eggers s.n.* (US); s.l., 2.III.1874, fl. & fr., *Kuntze 196* (NY); Mariendahl Road, 5.III.1913, fl. & fr., *Marble 1481* (US); s.l., s.d., fl. & fr., *Oersted s.n.* (NY, S); Smith Bay, 6.II.1914, fl. & fr., *Ostenfeld 260* (P); Løvenlund, XII.1905, fl. & fr., *Raunkiaer s.n.* (US); s.l., 28.III.1906, fl. & fr., *Raunkiaer s.n.* (US).

11. ***Paramollugo cuneifolia*** (Griseb.) Thulin in Taxon 65: 786. 2016 (Fig. 40–42).

≡ *Mollugo nudicaulis* var. *cuneifolia* Griseb., Cat. Pl. Cub.: 22. 1866. ≡ *Mollugo cuneifolia* (Griseb.) Urb. in Ark. Bot. 22A(17): 14. 1929.

Lectotypus (designated by Thulin et al., 2016: 786): **Cuba. Prov Guantánamo:** "in litore pr. Baracoa", 1860, fl. & fr., *Wright 2020* (K [K000471688]!; isolecto-: GH [GH00037489]!, HAC image!, S-05-6834!, S-05-6836!, YU [YU001112]!) (Fig. 40).

Herbs, perennial, or *dwarf subshrubs*, 5–15 cm tall, glabrous in all parts, from a branched scaly ± woody rhizome; stems few to several, terete. *Leaves* densely and distichously arranged at base of plant, 6–20 × 4–14 mm, succulent, marcescent, obovate-cuneate to obtriangular or spathulate, rounded to truncate and often mucronate at the apex, tapering below into a petiole-like base, the petiole-like part shorter than to about as long as the distal part; midrib prominent beneath, lateral veins indistinct. *Flowers* in much-branched lax cymes; bracts 0.5–1.5 mm long, ovate, acute; pedicels up to c. 10 mm long. *Tepals* 2–2.5 × 1–1.5 mm, elliptic, rounded at the apex, with hyaline margins, c. 3-veined from the base, white inside, with dark tips. *Stamens* 5, 1.5–2 mm long; filaments filiform; anthers c. 0.4 mm long, elliptic-oblong. *Ovary* c. 1.5 mm long, ellipsoid, 3-locular; styles 3, 0.2–0.3 mm long, spreading. *Capsules* 2–2.5 mm long, ellipsoid. *Seeds* 0.6–0.7 × 0.5–0.6 mm, subcircular-reniform in outline, flattened, finely tuberculate, black; testa cells without secondary ornamentation, with small pits in the boundaries between most of them; hilum c. 0.1 mm long.

Distribution and ecology. – *Paramollugo cuneifolia* is known only from easternmost Cuba (Fig. 43), where it is found on coastal cliffs, coral reefs or in sand, at elevations from near sea level to 100 m.

Phenology. – Flowering and fruiting plants have been seen from January, July, September, November and December.

Conservation status. – The few collections seen of *Paramollugo cuneifolia* are all old, the most recent ones being *Alain & López 4217* from Macambo in 1954 and *Morton & Alain 9206* from near Imías in 1956. In the same area of the Guantánamo Province, it was found in September 2016 by Lisbet González-Oliva and Ramona Oviedo Prieto (Fig. 41), and should be searched for in other suitable localities in coastal areas of eastern Cuba. In "Lista roja de la flora de Cuba" (González Torres et al., 2016), the species was not included. However, González-Oliva & Oviedo (2020) assessed it as "Endangered" [EN B1ab(i,ii,iii,iv)+B2ab(i,ii,iii,iv)], due to its limited EOO and AOO, few locations and continuing decline.

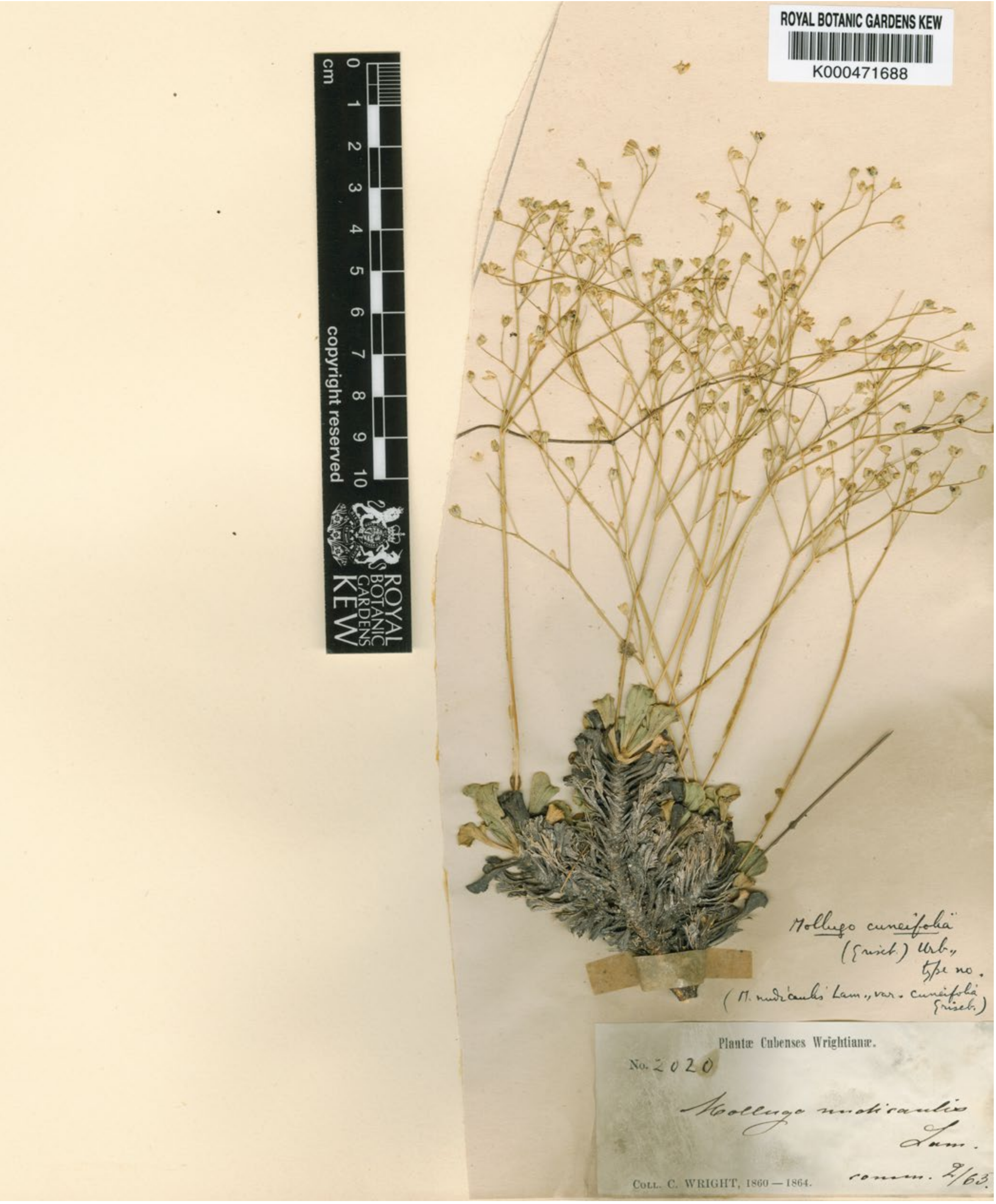

Fig. 40. – Lectotype of *Paramollugo cuneifolia* (Griseb.) Thulin [*Wright 2020*, K000471688] [© Royal Botanic Gardens, Kew]

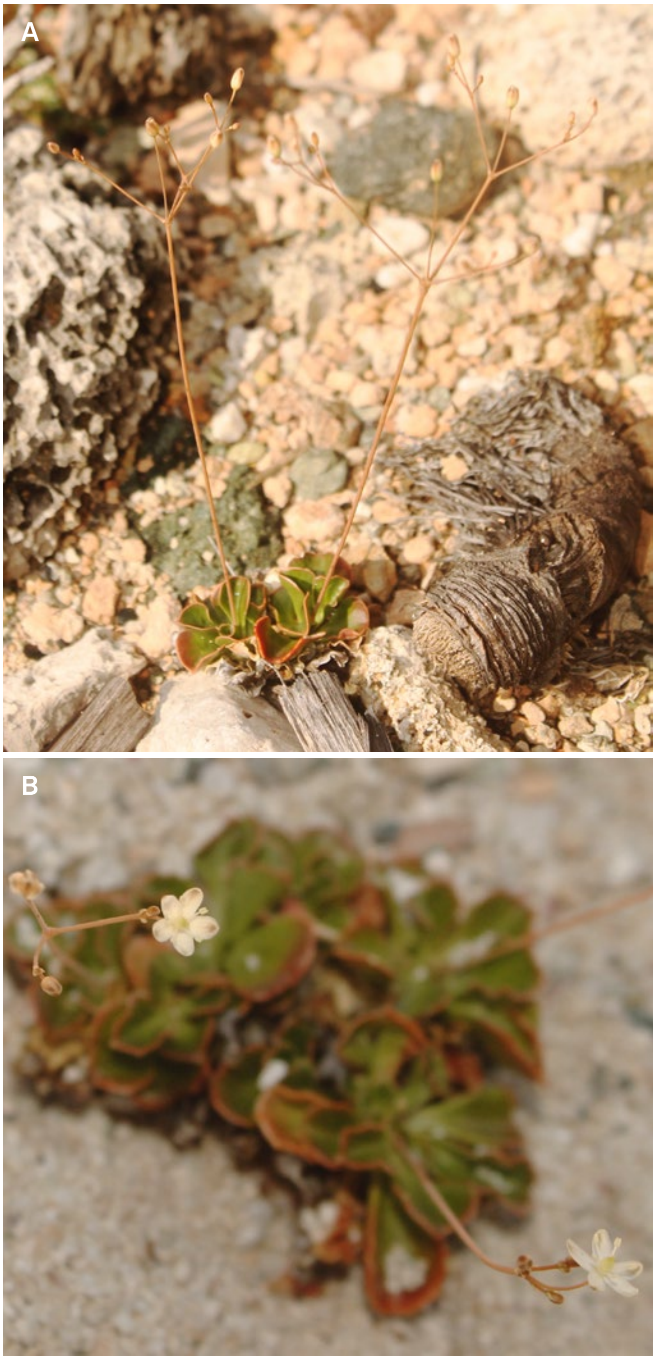

Fig. 41. – *Paramollugo cuneifolia* (Griseb.) Thulin from the Guantánamo Province, Cuba. **A.** Plant in habitat; **B.** Plant from above, showing flowers. [Photos: Lisbet González-Oliva]

Threats to the habitat of the species include urbanization, camping tourism and sheep-farming.

Notes. – *Paramollugo cuneifolia* is sister to *P. spathulata* (Fig. 3, 4) and is easily distinguished from this and all other species in the genus by its obovate-cuneate to obtriangular, succulent and marcescent leaves that are densely and distichously arranged at the base of the plant (Fig. 40). From *P. spathulata*, it also differs by its larger seeds (0.6–0.7 × 0.5–0.6 vs. 0.48–0.52 × 0.40–0.46 mm), with testa cells without secondary ornamentation (Fig. 42B), vs. with a more or less warty secondary ornamentation (Fig. 38B).

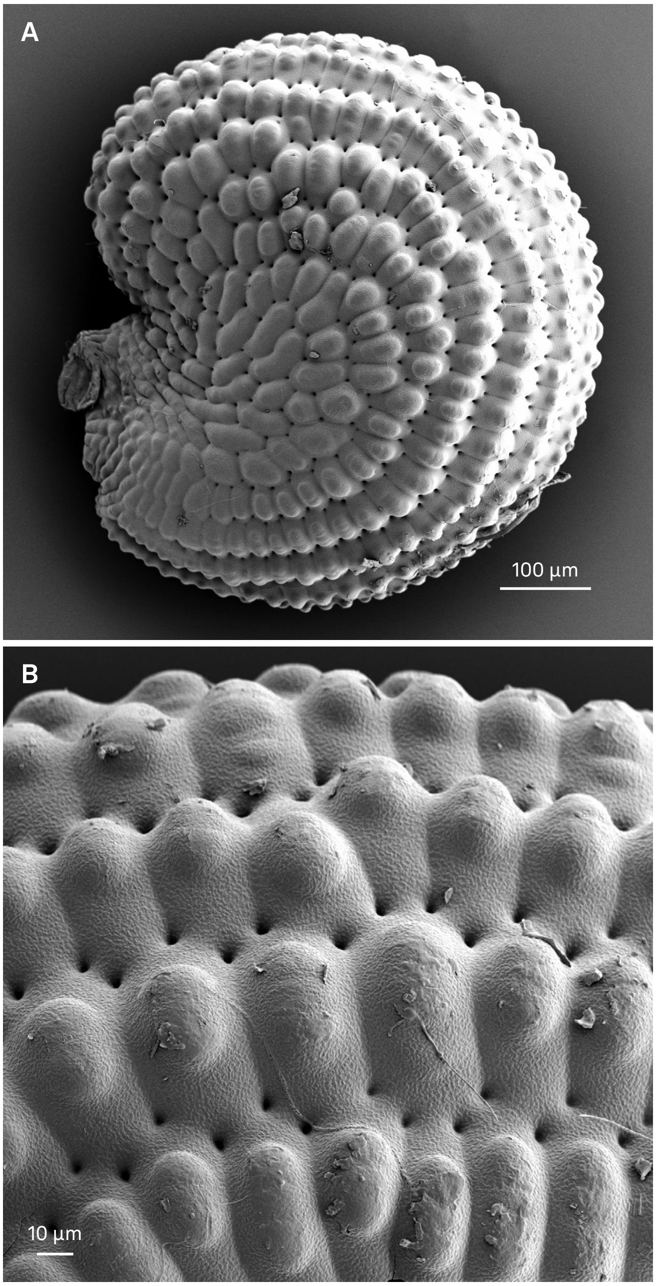

Fig. 42. – *Paramollugo cuneifolia* (Griseb.) Thulin, SEM micrographs. **A.** Seed; **B.** Detail of seed ornamentation. [*Ekman 8431,* UPS]

Additional specimens examined. – **Cuba. Prov. Guantánamo:** near Macambo, Vía Azul, 28.XII.1954, fl. & fr., *Alain & López 4217* (HAC); Cai-

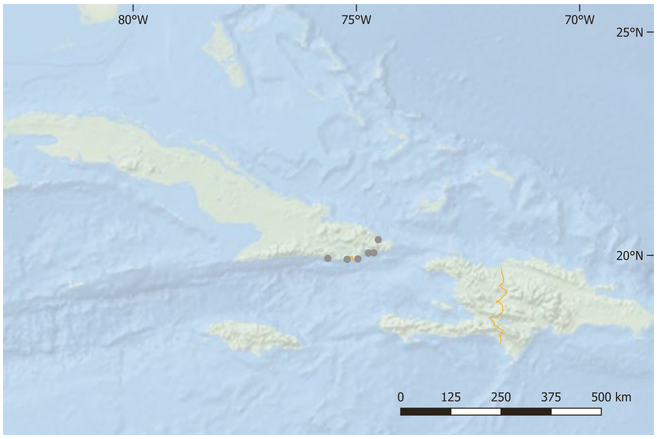

Fig. 43. – Geographic distribution of *Paramollugo cuneifolia* (Griseb.) Thulin.

manera, Leeward Point, 23.XI.1922, fl. & fr., *Ekman 15759* (B, NY, S, US); beach E of Imías, 16.I.1956, fl. & fr., *Morton & Alain 9206* (US); vicinity of Uvero Beach, between Escondido Bay and Río Yateras, 19°55'N 74°58'W, 28.VII.1951, fl. & fr., *Webster 3967* (US). **Prov. Santiago de Cuba:** Daiquiré, coral reef W of the harbour, 23.XI.1916, fl. & fr., *Ekman 8431* (NY, S, UPS).

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Appendix 1. – Species of *Paramollugo* included in the phylogenetic analysis with voucher information and GenBank accession numbers (new sequences in bold).

Taxon	Voucher	*trnK-matK*	ITS
Paramollugo angustifolia 1	Somalia, *Thulin et al. 7606* (UPS)	FN825702	KT907356
Paramollugo angustifolia 2	Madagascar, *Razafimandimbison et al. 2222* (S)	**OR962075**	**OR914178**
Paramollugo caespitosa 1	Madagascar, *Thulin & Razafindraibe 11800* (UPS)	**OR962076**	**OR914179**
Paramollugo caespitosa 2	Madagascar, *Larsson et al. L078* (UPS)	**OR962077**	
Paramollugo caespitosa 3	Madagascar, *Phillipson & Rabesihanaka 3159* (MO)	**OR962078**	**OR914180**
Paramollugo compressa	Madagascar, *Bosser & Viennot-Bourgin 16124* (P)		**OR914181**
Paramollugo cuneifolia	Cuba, *Ekman 8431* (UPS)		**OR914182**
Paramollugo decandra 1	Madagascar, *Croat 30852* (K)	FN825718	KT907358
Paramollugo decandra 2	Madagascar, *Humbert & Swingle 5293* (NY)	FN825717	KT907357
Paramollugo digyna 1	New Caledonia, *Mac Kee 23548* (P)	**OR962079**	**OR914183**
Paramollugo digyna 2	New Caledonia, *Pillon 1369* (NOU)	**OR962080**	**OR914184**
Paramollugo digyna 3	New Caledonia, *Bruy 627* (NOU)	**OR962081**	**OR914185**
Paramollugo nesophila 1	Europa Island, *Hivert*, no voucher		**OR914186**
Paramollugo nesophila 2	Grand Glorieuse, *Hivert et al. CBNM-IE 776* (CBNM)		**OR914187**
Paramollugo nesophila 3	Juan de Nova, *Bidault et al. 4616* (CBNM)	**OR962082**	**OR914188**
Paramollugo nesophila 4	Europa Island, *Hivert CBNM-IE 705* (CBNM)	**OR962083**	**OR914189**
Paramollugo nudicaulis 1	Burkina Faso, *Muller 257* (FR)	FN825729	
Paramollugo nudicaulis 2	India, no voucher	FN825732	KT907362
Paramollugo nudicaulis 3	India, *Devi s.n.* (CANB)	FN825733	KT907365
Paramollugo nudicaulis 4	India, no voucher	FN825731	KT907361
Paramollugo nudicaulis 5	Somalia, *Thulin & Bashir Mohamed 6759* (UPS)	FN825730	KT907363
Paramollugo nudicaulis 6	Namibia, *De Winter & Giess 6900* (K)	FN825728	KT907359

Taxon	Voucher	*trnK-matK*	ITS
Paramollugo nudicaulis 7	Madagascar, *Phillipson 2800* (MO)	**OR962084**	**OR914190**
Paramollugo simulans 1	Madagascar, *Pettersson & Nilsson 108* (UPS)	**OR962085**	**OR914191**
Paramollugo simulans 2	Madagascar, *Thulin et al. 10399* (UPS)	**OR962086**	**OR914192**
Paramollugo simulans 3 ("*P. nudicaulis*")	Madagascar, *De Block et al. 551* (MO)	**OR962087**	
Paramollugo simulans 4 ("*P. elliotii*")	Madagascar, *Jongkind et al. 3342* (MO)	**OR962088**	**OR914193**
Paramollugo spathulata 1	British Virgin Islands, *Proctor 42517* (NY)	FN825727	KT907360
Paramollugo spathulata 2	Navassa Island, *Liogier 16585* (NY)	FN825726	KT907364
Paramollugo spathulata 3	Cuba, *Ekman 11961* (UPS)	**OR962089**	**OR914194**

Appendix 2. – Voucher information and GenBank accession numbers for the outgroup of the phylogenetic analyses, as well as for the taxa sampled in the *Portulacineae* clade, the Southern African clade, the *Hypertelis* clade, the *Glinus* and *Mollugo* clade, and the *Trigastrotheca* clade. The sequences (*trnK-matK*, ITS) of the outgroup are from THULIN et al. (2018), and most of the remaining sequences are from CHRISTIN et al. (2011) and THULIN et al. (2016). A dash indicates a missing sequence. When information on country of origin and/or collector is not given, this information is missing in GenBank. A number is given after a country if there is more than one accession of the species from that country.

Outgroup

Kewaceae: Kewa salsoloides (Burch.) Christenh., Namibia, *Thulin et al. 11956* (UPS), MH019266, MH018128.

Portulacineae clade

Anacampserotaceae: Anacampseros kurtzii Bacigalupo, *Leuenberger & Eggli 4217* (ZSS), DQ855853.1, –. ***Basellaceae: Basella alba*** L., JQ844148.1, L78018.1. ***Cactaceae: Opuntia phaeacantha*** Engelm., FN997327.1, JF786974.1. ***Pereskia aculeata*** Mill., HM041757.1, JF508526.1. ***Didiereaceae: Alluaudia dumosa*** (Drake) Drake, Madagascar, *Stone s.n.* (DAV), HQ620839.1, L78011.1. ***Halophytaceae: Halophytum ameghinoi*** Speg., *Chase 1753* (K), AY514852.1, EU410352.1. ***Montiaceae: Lewisia longipetala*** (Piper) S. Clay, *Edwards 141* (BRU), HQ620876.1, DQ498108. ***Portulacaceae: Portulaca amilis*** Speg., *Ogburn 11* (BRU), HQ620886.1, JF508528.1. ***Talinaceae: Talinum fruticosum*** (L.) Juss., *Ferguson 848* (ZSS), DQ855844.1, KJ380908.1.

Southern African clade

Molluginaceae: Adenogramma glomerata (L. f.) Druce, South Africa 1, *Pillans 10706* (NY), FN825686, –; South Africa 2, *Fries 25-9-20* (NY), FN825687.1, KT907380; South Africa 3, *Ogburn 146* (BRU), FN825688, –; South Africa 4, *Ogburn 142* (BRU), FN825689, KT907379. ***Adenogramma teretifolia*** (Thunb.) Adamson, South Africa, *Ogburn 156* (BRU), FN825691, KT907381. ***Coelanthum semiquinquefidum*** (Hook.) Druce, South Africa, *Wright 1853* (NY), FN825759, –. ***Pharnaceum confertum*** Eckl. & Zeyh., South Africa, *Ogburn 163* (BRU), FN825744, –. ***Pharnaceum detonsum*** Fenzl, South Africa, *Fries 764* (NY), FN825745, KT907416. ***Pharnaceum elongatum*** (DC.) Adamson, South Africa 1, *Ogburn 153* (BRU), FN825746, –; South Africa 2, *Fellingham 238918* (CANB), FN825747, –. ***Pharnaceum incanum*** L., South Africa, *Ogburn 148* (BRU), FN825748, KT907387. ***Pharnaceum lanatum*** Bartl., South Africa, *Venter 9568* (NY), FN825750, –. ***Pharnaceum lanuginosum*** J.C. Manning & Goldblatt, South Africa, *Ogburn 161* (BRU), FN825752, KT907385. ***Pharnaceum lineare*** L. f., South Africa, *Helme 5887* (NBG), KT950943, KT907386. ***Pharnaceum reflexum*** Eckl. & Zeyh., South Africa, *Taylor 1162* (NY), FN825751, –. ***Pharnaceum subtile*** E. Mey. ex Fenzl, Namibia, *Merxmüller & Giess 3316* (NY), FN825739, KT907414. ***Polpoda capensis*** C. Presl, South Africa, *Acocks 17405* (CANB), FN825753, KT907384. ***Psammotropha obovata*** Adamson, South Africa, *Hilliard & Burtt 7045* (K), FN825754, KT907383. ***Psammotropha quadrangularis*** Fenzl, South Africa, *Ogburn 160* (BRU), FN825755, KT907382. ***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.

Hypertelis clade

Molluginaceae: Hypertelis cerviana (L.) Thulin, Australia 1, *Smyth 213* (CANB), FN825706, KT907399; Australia 2, *Lazarides & Palmer 243* (CANB), FN825703, –; Australia 3, *Jackson 5281* (CANB), FN825704, –; Australia 4, *Leach 2008* (CANB), FN825705, KT907400; Namibia 1, *Thulin et al. 11954* (UPS), KT950944, KT907403; Namibia 2, *Potgieter 225* (K), FN825707, KT907402; Spain, *Sánchez Sánchez s.n.* (G), FN825708, KT907401; ***Hypertelis fragilis*** (Wawra) Thulin, Angola 1, *Ward & Ward 79* (K), FN825724, KT907396; Angola 2, *Gossweiler 6* (K), FN825723, KT907397. ***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 et al. 5366* (K), FN825700, KT907404; South Africa, *Acocks 19256* (K), FN825701, KT907405. ***Hypertelis umbellata*** (Forssk.) Thulin, Burkina Faso, *Ataholo 1809* (FR), FN825715, KT907392; Ethiopia, *Thulin et al. 11211* (UPS), FN825713, KT907391; Galápagos, *Van der Werf 1008* (NY), FN825712, KT907395; India, FN825714, –; Namibia 1, *Thulin et al. 11970* (UPS), KT950933, KT907415; Namibia 2, *Seydel 325* (NY), FN825709, KT907398; USA 1, *Reveal & Holmgren 1968* (NY), FN825710, KT907394; USA 2, *Atwood & Welsh 10684* (NY), FN825711, KT907393. ***Hypertelis walteri*** (Friedrich) Thulin, Namibia, Örtendahl 93 (UPS), KT950930, KT907419.

Glinus and *Mollugo* clade

Molluginaceae: Glinus lotoides L., USA, *Errter 8854* (NY), FN825692, KT907409. ***Glinus oppositifolius*** (L.) Aug. DC., Australia, *Barbidge 5949* (ANH), FN825696, –; Taiwan, *Huang & Huang 14175* (NY), FN825695, KT907366; Tanzania, *Balslev 630* (NY), FN825694, –. ***Glinus radiatus*** (Ruiz & Pav.) Rohrb., USA, *Thomas 114677* (NY), FN825697, KT907410. ***Glinus setiflorus*** Forssk., Kenya, *Burney et al. T46* (NY), FN825698, KT907367. ***Mollugo brasiliensis*** Thulin & Harley, Brazil 1, *Guedes et al. PCD5162* (K), KT950938, KT907373; Brazil 2, *Orlandi et al. PCD515* (K), KT950940, KT907371. ***Mollugo crockeri*** J.T. Howell, Galápagos, *Howell 10094* (NY), FN825716, KT907412. ***Mollugo disticha*** (L.) Ser., Sri Lanka, *Lundqvist 11379* (UPS), KT950942, KT907378. ***Mollugo enneandra*** C.Wright, Cuba, *Ekman 17848* (NY), FN825719, –. ***Mollugo flavescens*** Andersson, Galápagos, *Wheeler et al. 17* (NY), FN825720, KT907417. ***Mollugo floriana*** (B.L. Rob.) J.T. Howell, Galápagos, *Eliasson 741* (K), FN825722, KT907413. ***Mollugo snodgrassii*** B.L. Rob., Galápagos, *Howell 9450* (NY), FN825738, KT907411. ***Mollugo ulei*** (Pilger) Thulin, Brazil, *Harvey 19007* (SPF), FN825699, –. ***Mollugo verticillata*** L., Bolivia, *Nee 37372* (G), FN825743, KT907368; Canada, *Roy C-151-82* (G), FN825741, KT907370; Italy, *Cook & Gallucci 5430* (G), FN825742, KT907369; USA, *Sage & Sage 8-2007* (TRT), FN825740, KT907372. ***Mollugo viscosa*** Thulin & Harley, Brazil 1, *Harley et al. 25029* (K), KT950939, –; Brazil 2, *Harley et al. 6481 [SPF36081]* (K), KT950941, –.

Trigastrotheca clade

Molluginaceae: Trigastrotheca molluginea F. Muell., Australia, *Telford 11746* (CANB), FN825725, KT907408. ***Trigastrotheca pentaphylla*** (L.) Thulin, India, FN825737, KT907377; Sri Lanka, *Jonsell 3885* (UPS), KT950929, KT907418. ***Trigastrotheca stricta*** (L.) Thulin, Australia, *Lazarides & Adams 326* (CANB), FN825736, KT907374; Brazil, *Nee 42741* (NY), FN825734, KT907376; Taiwan, *Boufford et al. 25246* (NY), FN825735, KT907375.

Supplementary material
The Supplementary material for this article can be found online at: http://dx.doi.org/10.15553/c2024v792a1.s1

Supplementary material S1a. – Tree from BEAST analysis of combined *Molluginaceae* dataset showing posterior probabilities.

Supplementary material S1b. – Tree from BEAST analysis of combined *Molluginaceae* dataset showing dating in Ma.

Supplementary material S1c. – Tree from BEAST analysis of combined *Molluginaceae* dataset showing dating uncertainties in Ma.

Supplementary material S1d. – Alternative tree from BEAST analysis of combined *Molluginaceae* dataset showing posterior probabilities.

Supplementary material S1e. – Alternative tree from BEAST analysis of combined *Molluginaceae* dataset showing dating in Ma.

Supplementary material S1f. – Alternative tree from BEAST analysis of combined *Molluginaceae* dataset showing dating uncertainties in Ma.

Supplementary material S1g. – Ancestral area reconstruction of *Paramollugo* and related taxa with BBM. Pie charts indicate the most likely distribution of the most recent common ancestor. The areas are coded as follows: A, Africa; B, Madagascar; C, Caribbean; D, New Caledonia; E, Îles Éparses; F, Asia; G, North America; H, South America; I, Australia; J, Europe. Asterisk (in black) represents other ancestral ranges.