

**CIRCUMSCRIPTION AND PHYLOGENETIC
RELATIONSHIPS OF *GYMNOCARPOS*
(*CARYOPHYLLACEAE-PARONYCHIOIDEAE*)**

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A molecular phylogenetic study based on nuclear ribosomal internal transcribed spacer sequences and plastid *rps16* intron sequences on the status of the genus *Gymnocarpus* (*Paronychioideae*, *Caryophyllaceae*) is presented. *Gymnocarpus decandrus* and *Sclerocephalus arabicus* form a strongly supported clade within a well-supported group consisting also of *G. przewalskii*, and the rest of *Gymnocarpus*. Re-examination of morphological characters also supports this conclusion. *Paronychia* is found to be polyphyletic, with the subgenera *Paronychia* and *Siphonychia* forming a strongly supported sister group to *Gymnocarpus*, whereas *P. kapela* and *P. chlorothyrsa* (representing subgen. *Anoplonychia*) are found to be related to *Herniaria* and *Philippiella*. A key to the 10 species recognized in *Gymnocarpus* is presented, as well as synoptical information on nomenclature and distributions.

Keywords. *Gymnocarpus*, ITS, *Paronychia*, *Paronychioideae*, *rps16* intron, *Sclerocephalus*.

INTRODUCTION

The genus *Gymnocarpus* was described by Forsskål (1775, 1776), who discovered the first species, *G. decandrus*, in Egypt during the ill-fated 'Arabia Felix' expedition in 1761–63. A second species, *G. przewalskii*, was described from Central Asia by Maximowicz (1880). Both these species are small shrublets with succulent, mucronate leaves growing in arid regions. Chaudhri (1968) treated *Gymnocarpus* as a genus with two species (those mentioned above) and closely related to *Paronychia*, the main distinguishing character being the 3-merous gynoeceum in *Gymnocarpus* versus the 2-merous gynoeceum in *Paronychia*.

In more recent treatments the genus has either been included in *Paronychia*, e.g. Bittrich (1993), or been recognized as distinct with up to eight species, most of them in the Horn of Africa region (Petrusson & Thulin, 1996). However, Petrusson & Thulin (1996) excluded *G. przewalskii* from the genus, and this species was left in limbo pending further studies. All previous treatments have been based on morphology only, and the aim of the present study is to use molecular data also to elucidate the circumscription and phylogenetic relationships of *Gymnocarpus*.

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TAXONOMIC BACKGROUND

The subfamily *Paronychioideae sensu* Bittrich (1993) is distinguished from the other two subfamilies generally recognized in *Caryophyllaceae*, *Alsinoideae* and *Caryophylloideae*, by having stipules and by its often apetalous flowers. In Bittrich's classification *Paronychioideae* was further subdivided into three tribes, *Polycarpeae*, *Paronychieae* and *Corrigioleae*. *Paronychieae* and *Corrigioleae* have perigynous flowers and 1-seeded indehiscent fruits and have sometimes been treated together as the separate family *Illecebraceae*. The following genera were included in *Paronychieae* by Bittrich: *Cometes* (2 spp.), *Dicheranthus* (1 sp.), *Pteranthus* (1 sp.), *Sphaerocoma* (2 spp.), *Sclerocephalus* (1 sp.), *Lochia* (2 spp.), *Paronychia* (c.110 spp.), *Herniaria* (c.45 spp.), *Philippiella* (1 sp.), *Chaetonychia* (1 sp.), *Achyronychia* (2 spp.), *Illecebrum* (1 sp.), *Cardionema* (6 spp.), *Scopulophila* (1 sp.), and *Pollichia* (1 sp.). The tribe *Corrigioleae* is distinguished from *Paronychieae* essentially by its alternate, instead of opposite, uppermost leaves.

A notable feature of Bittrich's classification is that *Gymnocarpus* is included in *Paronychia*. This obviously goes back to a paper by Rohweder & Urm-König (1975), who made a morphological and anatomical comparison between *Gymnocarpus decandrus*, *G. przewalskii* and *Paronychia argentea* (the type species of *Paronychia*). They concluded that *Gymnocarpus* should be included in *Paronychia* as the two species of *Gymnocarpus* are more similar to *P. argentea* than are other species of the variable genus *Paronychia*. Moreover, flowers with 3-merous gynoecia were said to be occasionally present also in *Paronychia*. However, their conclusions were apparently based on the study of only one specimen each of the three species mentioned.

Petrusson & Thulin (1996) resurrected *Gymnocarpus* and included eight species in the genus, apart from the type, *G. decandrus*, as well as three species previously treated as the genus *Lochia* (*L. bracteata*, the type, *L. kuriensis* from the Socotra archipelago, and *L. parvibractea* from Somalia), and four new species, all from the southern part of the Arabian Peninsula. However, the geographically isolated *G. przewalskii* (from Mongolia and north-western China) was excluded on the basis of postulated differences in the arrangement of the bracts and in leaf morphology.

In the present study we use DNA sequence data from five species of *Gymnocarpus sensu* Petrusson & Thulin, *G. przewalskii*, eight species of *Paronychia*, two species of *Herniaria*, and the mono- or bitypic genera *Dicheranthus*, *Illecebrum*, *Philippiella*, *Sclerocephalus* and *Sphaerocoma* to elucidate the phylogenetic relationships within the tribe *Paronychieae*, the circumscription of *Gymnocarpus*, and particularly the position of *G. przewalskii*.

MATERIALS AND METHODS

The 21 taxa from tribe *Paronychieae* selected for the molecular analysis are listed by their taxonomic position *sensu* Chaudhri (1968), together with voucher details and GenBank accession numbers for new sequences, in Table 1. *Gymnocarpus przewalskii*

was analysed from two different collections, because both of them yielded DNA with only weak results in PCR. Table 1 also includes the four outgroup taxa, *Corrigiola litoralis* in the tribe *Corrigioleae*, *Spergularia rubra* in the tribe *Polycarpeae*, *Atocion armeria* (= *Silene armeria*, see Oxelman *et al.*, 2001) in subfam. *Caryophylloideae* tribe *Sileneae*, and *Stellaria media* in subfam. *Alsinoideae* tribe *Alsineae*. The taxa in the ingroup include the types of the genera *Dichranthus*, *Gymnocarpus*, *Herniaria*, *Lochia*, *Paronychia*, *Philippiella* and *Sclerocephalus*. Furthermore, the selection of taxa in the large genera *Herniaria* and *Paronychia* was designed to include representatives from as many as possible of the subgenera, sections and subsections recognized in the latest revision of these genera (Chaudhri, 1968). Of these taxa, we failed to find usable material from the monotypic section *Nyachia* (subgen. *Paronychia*) and the ditypic subsection *Fasciculatae* (subgen. *Paronychia*).

For the phylogenetic analysis, we primarily used the internal transcribed spacer sequence (ITS) regions and the intervening 5.8S gene of the nuclear ribosomal DNA. This region has been successfully used for phylogenetic problems at putatively comparable levels in the *Caryophyllaceae* (*Sileneae*, Oxelman & Lidén, 1995; Desfeux & Lejeune, 1996) and many other plant groups (e.g. Baldwin *et al.*, 1996).

The DNA was extracted, amplified and sequenced following the description in Oxelman *et al.* (1999). For PCR of the ITS region we used the P17/26S-82R primer pair (Popp & Oxelman, 2001) and the nested primers P16 and P25 for sequencing of both strands (Popp & Oxelman, 2001). The ITS region turned out to be more variable than expected, with uncorrected pairwise 'p' distances (Swofford, 2000) ranging from 0.00% between the two *Gymnocarpus przewalskii* sequences up to 22.67% in the ingroup (*Herniaria glabra* vs. *Paronychia suffruticosa*) and 28.36% between outgroup and ingroup (*Atocion armeria* vs. *Paronychia suffruticosa*). The average pairwise distance was 15.96%. Therefore, and because we wanted an independent check on the results obtained from the nuclear locus, we sequenced a subset of 21 taxa for the chloroplast gene *rps16* intron, using the primers for PCR and sequencing described by Oxelman *et al.* (1997).

Multiple alignment and gap-coding was performed with the criteria described in Oxelman *et al.* (1997) and Popp & Oxelman (2001) as guidelines. However, for some regions, especially in the ITS sequences, it was difficult to align the sequences unambiguously. In those cases, the outgroup sequences and/or single ingroup sequence regions which could not be reliably homologized with regions in the other taxa were substituted with question marks (missing data) for the phylogenetic analyses. The alignments can be found at <http://www3.ebi.ac.uk/Services/align/listali.html>.

Most parsimonious trees for the ITS (26 sequences), *rps16* (21 sequences) and combined data sets were searched for heuristically using PAUP* (Swofford, 2000) performing 100 random addition sequences, with TBR swapping and multrees on. Bootstrap analyses of the same data sets, with 1000 constant characters added (see Harshman, 1994), were performed with 1000 replicates, each with 10 random additions, TBR swapping, and multrees on. For each replicate, the strict consensus tree was saved and the bootstrap majority rule consensus was constructed from these

TABLE 1. Taxa used in the DNA sequence analyses with voucher information, literature references, and GenBank accession numbers. *Paronychia* is arranged according to the supra-specific classification of Chaudhri (1968). Abbreviations of herbaria are according to Holmgren *et al.* (1990)

Higher taxon	Species	Voucher	GenBank number
<i>Gymnocarpus</i> Forssk.			
	<i>G. decandrus</i> Forssk.	Anderberg 475 (S)	AJ310975 (ITS), AJ310948 (<i>rps16</i>)
	<i>G. przewalskii</i> Bunge ex Maxim.	Valkova & Pachovskaya 7380 (LE) Valkova & Pachovskaya 7393 (LE)	AJ310972 (ITS) AJ310971 (ITS)
	<i>G. argenteus</i> Petruss. & Thulin	Thulin 8330 (UPS)	AJ310973 (ITS)
	<i>G. mahranus</i> Petruss. & Thulin	Thulin 9572 (UPS)	AJ310970 (ITS), AJ310946 (<i>rps16</i>)
	<i>G. rotundifolius</i> Petruss. & Thulin	Thulin 9931 (UPS)	AJ310974 (ITS)
	<i>G. bracteatus</i> (Balf.f.) Petruss. & Thulin	Miller 11148 (UPS)	AJ310969 (ITS), AJ310945 (<i>rps16</i>)
<i>Paronychia</i> Mill.			
	subgen. <i>Siphonychia</i> (Torr. & Gray) Chaudhri		
	<i>P. americana</i> (Nutt.) Fenzl	Tehler 108 (S)	AJ310961 (ITS), AJ310943 (<i>rps16</i>)
	subgen. <i>Paronychia</i>		
	sect. <i>Nyachia</i> Pax & K. Hoffm.	No material available	
	sect. <i>Paronychia</i>		
	subsect. <i>Fasciculatae</i> Chaudhri	No material available	
	subsect. <i>Polygonoideae</i> (DC.) Chaudhri		
	<i>P. suffruticosa</i> (L.) DC.	Thulin 4840 (UPS)	AJ310964 (ITS), AJ310944 (<i>rps16</i>)
	subsect. <i>Anychia</i> (Michx.) Chaudhri		
	<i>P. fastigiata</i> (Raf.) Fernald	Ahlgren 29 ix 1998 (UPS)	AJ310962 (ITS), AJ310941 (<i>rps16</i>)
	subsect. <i>Chartaceifoliae</i> Chaudhri		
	<i>P. depressa</i> Nutt. ex Torr. & Gray	Porter 10538 (UPS)	AJ310960 (ITS), AJ310940 (<i>rps16</i>)
	subsect. <i>Paronychia</i>		
	<i>P. argentea</i> Lam.	Julin 2 iii 1986 (UPS)	AJ310958 (ITS), AJ310942 (<i>rps16</i>)
	<i>P. canariensis</i> (L.f.) Juss.	Julin 5 iii 1976 (UPS)	AJ310959 (ITS), AJ310939 (<i>rps16</i>)
	subgen. <i>Anoplonychia</i> (Fenzl) Chaudhri		
	sect. <i>Anoplonychia</i>		
	<i>P. kapela</i> (Hacq.) Kerner	Ahlgren x 1998 (UPS)	AJ310967 (ITS), AJ310952 (<i>rps16</i>)
	sect. <i>Heterosepalae</i> Chaudhri		
	<i>P. chlorothyrsa</i> Murb.	Thulin 7952 (UPS)	AJ310963 (ITS), AJ310951 (<i>rps16</i>)

TABLE 1. (Cont'd)

Higher taxon	Species	Voucher	GenBank number
<i>Herniaria</i> L.			
subgen. <i>Herniaria</i>	<i>H. glabra</i> L.	<i>Lundqvist</i> 12656 (UPS)	AJ310965 (ITS), AJ310949 (<i>rps16</i>)
subgen. <i>Heterochiton</i> Maire & Weiller	<i>H. hemistemon</i> Gay	<i>Boulos</i> 5 v 1992 (UPS)	AJ310966 (ITS), AJ310950 (<i>rps16</i>)
<i>Sphaerocoma</i> T. Anderson			
	<i>S. aucheri</i> Boiss.	<i>Thulin</i> 8215 (UPS)	AJ310979 (ITS), AJ310955 (<i>rps16</i>)
<i>Sclerocephalus</i> Boiss.			
	<i>S. arabicus</i> Boiss.	<i>Hedberg</i> 92219 (UPS)	AJ310968 (ITS), AJ310947 (<i>rps16</i>)
<i>Philippiella</i> Speg.			
	<i>P. patagonica</i> Speg.	<i>Skottsberg</i> 1 i 1909 (UPS)	AJ310978 (ITS)
<i>Dicheranthus</i> Webb			
	<i>D. plocamoides</i> Webb	<i>Thulin</i> 9950 (UPS)	AJ310976 (ITS), AJ310953 (<i>rps16</i>)
<i>Illecebrum</i> L.			
	<i>I. verticillatum</i> L.	<i>Anderberg et al.</i> 45 (S)	AJ310977 (ITS), AJ310956 (<i>rps16</i>)
Outgroups			
<i>Paronychioideae, Corrigioleae</i>			
	<i>Corrigiola litoralis</i> L.	<i>Julin</i> 26 iii 1975 (UPS)	AJ310980 (ITS), AJ310954 (<i>rps16</i>)
<i>Paronychioideae, Polycarpeae</i>			
	<i>Spergularia rubra</i> (L.) J. & C. Presl	<i>Danielsson</i> 10 vii 1988 (UPS)	AJ310981 (ITS), AJ310957 (<i>rps16</i>)
<i>Alsinoideae, Alsineae</i>			
	<i>Stellaria media</i> L.	<i>Oxelman</i> 2231 (GB)	X86899 (ITS), Z83152 (<i>rps16</i>)
<i>Caryophylloideae, Sileneae</i>			
	<i>Atocion armeria</i> (L.) Raf.	<i>Oxelman</i> 2289 (GB)	X86880 (ITS), Z83159 (<i>rps16</i>)

trees. Note that this approach is more conservative than the traditional implementation.

RESULTS

The size of the ITS/5.8S region ranged from 570bp (*Paronychia fastigiata*) to 621bp (*Philippiella patagonica*) in the ingroup. The outgroup sequences ranged from 642bp (*Stellaria media*) to 650bp (*Spergularia rubra*). The alignment of the sequences

included 976 positions of which 359 were variable. Of these, 219 were parsimony-informative, and 29.45% of the entries in the matrix were gaps. Thirteen gap regions were parsimony-informative. The aligned ITS matrix analysis of the ITS data set resulted in 24 most parsimonious trees, 896 steps long, with a consistency index (CI, autapomorphies excluded) of 0.53 and a retention index (RI) of 0.71. One of the most parsimonious trees with branch lengths, bootstrap frequencies, and branches not present in the strict consensus indicated, is shown in Fig. 1. There is a strongly supported clade, hereafter named the *Gymnocarpus* clade, with all the species of *Gymnocarpus*, including *G. przewalskii*, as well as *Sclerocephalus*. Sister to this clade is a moderately well-supported clade (*Paronychia s. str.*, 80%) with all the included species of *Paronychia* except *P. kapela* and *P. chlorothyrsa*. *Paronychia suffruticosa* also belongs to this larger clade, but it is not resolved whether it is related to *Gymnocarpus* or the *Paronychia s. str.* clade. It is notable that a large proportion (80 of 250 bases) of *P. suffruticosa* ITS1 had to be omitted from the analysis because of alignment ambiguities.

Within the *Gymnocarpus* clade, *G. decandrus* and *Sclerocephalus arabicus* form a strongly supported clade that is weakly resolved as sister to the rest of the species. *G. przewalskii* is sister to a clade with *G. bracteatus* (Socotra) and *G. mahranus*, *G. rotundifolius* and *G. argenteus* (all from the southernmost part of the Arabian Peninsula).

Outside the *Gymnocarpus* and the *Paronychia s. str.* clades together, there is a *Herniaria* clade with the two species of *Herniaria*, *Philippiella*, *Paronychia kapela* and *P. chlorothyrsa*. The positions of *Corrigiola*, *Dicheranthus*, *Sphaerocoma* and the other outgroups are unresolved in the strict consensus. Again, it is notable that the alignment of these taxa is more or less ambiguous in certain parts, with portions (95–123 bases) of the ITS1 sequence omitted from the analysis.

The length of the *rps16* intron ranged from 769bp (*Paronychia fastigiata*) to 848bp (*Herniaria hemistemon*). The alignment of the *rps16* sequences included 1154 positions of which 400 were variable. Of these, 203 were parsimony-informative. Some 28.25% of the entries in the matrix were gaps. Twelve gap regions were parsimony-informative.

The analysis of the *rps16* data set resulted in one most parsimonious tree, 667 steps long, with a CI of 0.65 and a RI of 0.79 (Fig. 2). The *rps16* tree corroborates most of the principal findings from the *rps16* data. However, the position of *P. suffruticosa* is resolved (80% bootstrap fraction) with the *Paronychia s. str.* clade, and the *Herniaria*, *Gymnocarpus* and *Paronychia s. str.* clades are together supported with a 75% resampling frequency. *Dicheranthus*, *Sphaerocoma* and *Illecebrum* together form a clade with 86% support. The ingroup is resolved with 98% bootstrap support. It is notable that the alignment of the *rps16* sequences was much more straightforward than the alignment of the ITS sequences. However, given the morphological similarity of the taxa, it is remarkable how diverse their DNA sequences are. Uncorrected pairwise 'p' distances (Swofford, 2000) range from 1.19% (*Paronychia kapela* vs. *P. chlorothyrsa*) up to 18.47% (*Spergularia rubra* vs.

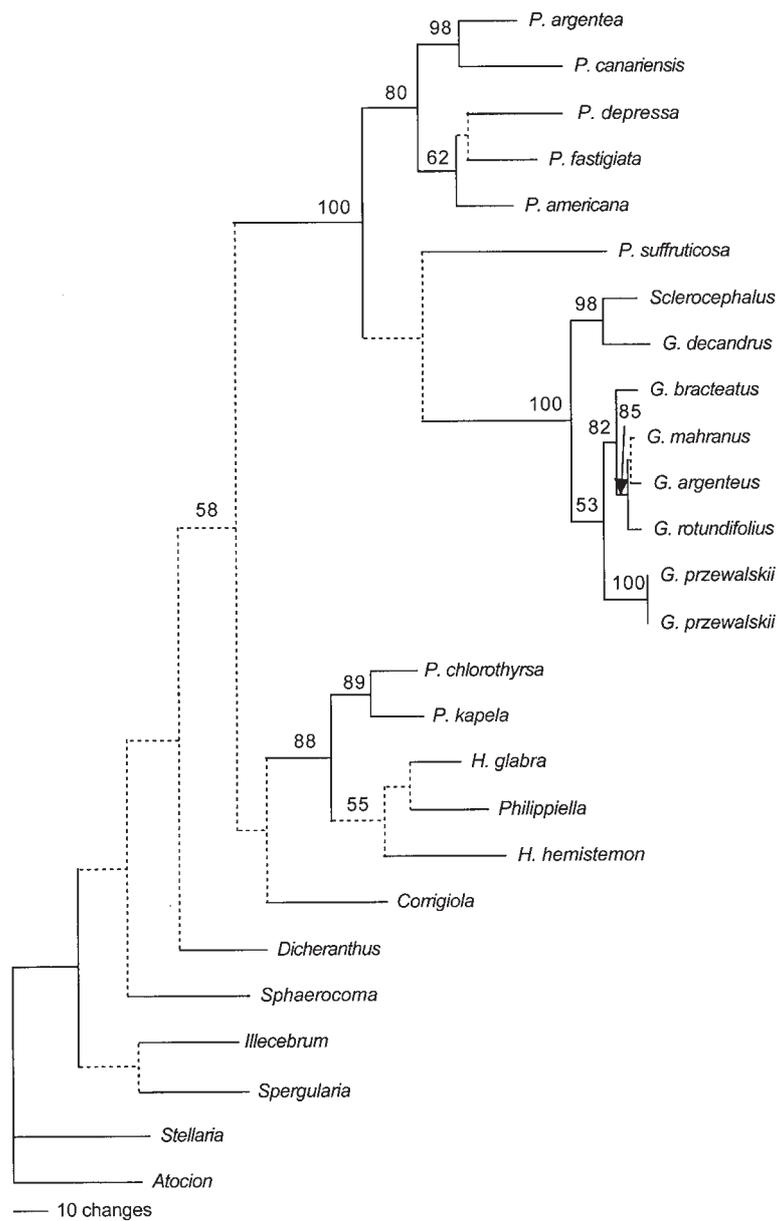


FIG. 1. Phylogram of one of the 24 most parsimonious trees found for the ITS matrix. Dashed lines indicate clades which collapsed in the strict consensus tree. Numbers above branches indicate bootstrap resampling percentages from 1000 replicates. Only support values above 50% are indicated.

Paronychia depressa). The average pairwise distance in the entire matrix was 11.23%. In fact, the magnitude of differences among the *rps16* intron sequences within the *Paronychieae* is comparable to what is found within the whole of the order *Lamiales* (Oxelman *et al.*, unpublished data).

The analysis of the combined data resulted in one most parsimonious tree 1523 steps long, with a CI of 0.58 and a RI of 0.71 (Fig. 3). The topology of this tree largely repeats that of *rps16* data alone (Fig. 2), but the resolution is slightly better. *Corrigiola* is resolved as sister group to the *Herniaria*, *Gymnocarpus* and *Paronychia s. str.* clades, and together these are supported with 87% bootstrap support.

DISCUSSION

The results of the analyses strongly indicate that the members of *Gymnocarpus sensu* Petrusson & Thulin (1996) constitute a monophyletic group if *G. przewalskii* and *Sclerocephalus arabicus* are added. The results also indicate that various other genera, superficially more or less similar to *Gymnocarpus*, such as *Dicheranthus* on the Canary Islands and *Sphaerocoma* in north-eastern Africa, southern Arabia, and Iran, are not closely related to *Gymnocarpus*. There are also morphological characters that indicate a distant relationship between *Gymnocarpus* and these two genera. *Dicheranthus*, for example, differs from all other members of the ingroup in having partial inflorescences with hermaphrodite central and male outer flowers, whereas *Sphaerocoma* is unique in *Paronychieae sensu* Bittrich in having a 2-ovulate ovary.

When *G. przewalskii* was excluded from *Gymnocarpus* by Petrusson & Thulin, differences in the arrangement of the bracts as well as differences in leaf morphology were emphasized. A study of many more specimens of *G. przewalskii* now shows that the presence of inner narrow lateral flowerless bracts indeed seems to be apomorphic for this species. However, the postulated difference in leaf morphology does not hold true. In fact, the leaves in *G. przewalskii* are normally terete and cylindrical-subcylindrical as in the other species of *Gymnocarpus*.

Sclerocephalus was published by Boissier (1843) and has since then always been treated as a distinct monotypic genus. It is distributed in arid areas from the Cape Verde Islands and the Canary Islands in the west, across northern Africa to Somalia, the Arabian Peninsula and southern Iran in the east. It has generally been regarded as closely related to *Paronychia*, *Gymnocarpus* and *Lochia*, the main differences being that it is an annual herb, with flowers and bracts fused together in spherical heads that become hardened and spinose in fruit. Obviously these characters are best interpreted as autapomorphic. Another, earlier proposed characteristic of *Sclerocephalus*, lack of petals/staminodes, is obviously erroneous (see below under *G. sclerocarpus*). The close relationship with *G. decandrus* as indicated in the molecular data is reflected also in morphological similarity in that both *G. decandrus* and *Sclerocephalus arabicus* have herbaceous, leaf-like, non-scarious bracts. All other species of *Gymnocarpus*, as well as all species of *Paronychia*, have more or less conspicuously scarious bracts.

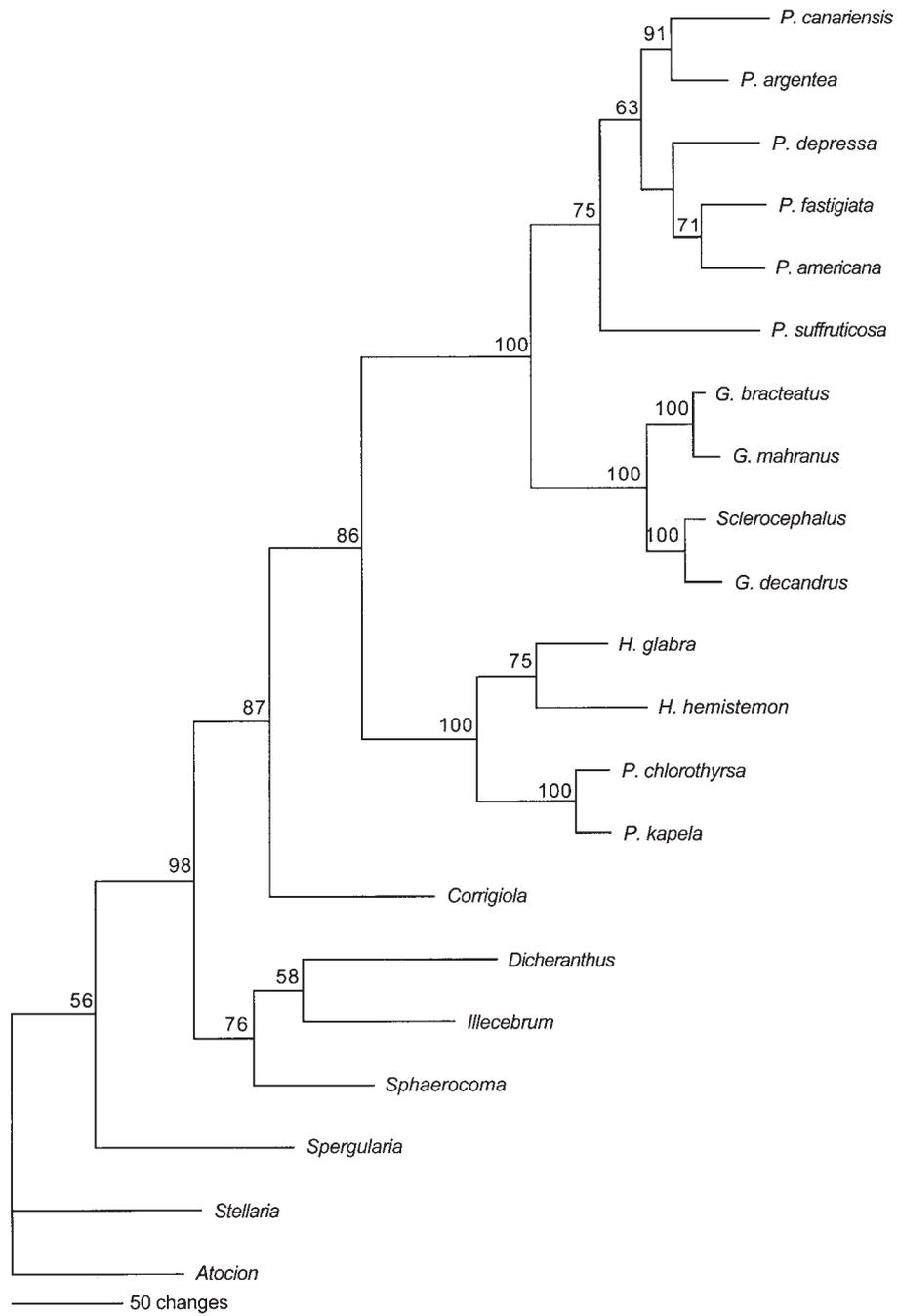


FIG. 3. Phylogram of the most parsimonious tree found for the combined data matrix. Numbers above branches indicate bootstrap resampling percentages from 1000 replicates. Only support values above 50% are indicated.

The *Gymnocarpus* clade is supported by the morphological characters 3-merous gynoecium, and cylindrical to subcylindrical leaves with the vascular bundles arranged in an arch-shaped fashion. This seems to be consistent in all taxa including *Sclerocephalus*. In the literature *Sclerocephalus* is often said to have a 2-merous gynoecium, but this could not be confirmed in the material studied by us (see below under *G. sclerocephalus*). In *Paronychia*, *Herniaria* and *Philippiella* the gynoecium is generally 2-merous, although occasional flowers with 3-merous gynoecia may be found in various members of *Paronychia*, and the leaves are flattened with more or less parallel vascular bundles.

The monophyly of *Paronychia* is supported in the present study with the exception of *P. kapela* and *P. chlorothyrsa* that are instead included in the clade with the two representatives of the large and widespread genus *Herniaria*, and with *Philippiella*. *Paronychia kapela* is a southern European species that is the type of *Paronychia* subgen. *Anoplonychia*. *Paronychia chlorothyrsa* is a North African species representing the other section (*sensu* Chaudhri, 1968) of the subgen. *Anoplonychia*, sect. *Heterosepalae*, which is chiefly Mediterranean. *Philippiella patagonica* is endemic in Patagonia. *Paronychia kapela*, *P. chlorothyrsa* and *Philippiella* agree with *Herniaria* in having non-mucronate leaves and sepals, whereas in all members of *Gymnocarpus*, as well as in all members of the *Paronychia s. str.* clade, the leaves and sepals are more or less distinctly mucronate-aristate at the apex.

TAXONOMIC CONCLUSIONS

The results indicate that taxonomic changes may be necessary in *Paronychia*, *Herniaria* and *Philippiella* in order to achieve monophyletic entities, but our sample of species in *Paronychia* and *Herniaria* is far too limited for any formal changes to be made. However, for the *Gymnocarpus* clade there is now both molecular and morphological evidence supporting the recognition of an extended genus *Gymnocarpus* with 10 species, including *G. przewalskii* and *Sclerocephalus arabicus*. This new taxonomy is summarized below. For the two species not treated in Petrusson & Thulin (1996) a more detailed treatment is given, whereas the other species are just listed, in some cases with the addition of new information.

Gymnocarpus Forssk., Fl. Aegypt.-Arab.: 65 (1775). Type: *G. decandrus* Forssk.

Syn.: *Sclerocephalus* Boiss., Diagn. Pl. Orient. 1, 1(3): 12 (1843). Type: *S. arabicus* Boiss.

Lochia Balf.f. in Proc. Roy. Soc. Edinb. 12: 409 (1884). Type: *L. bracteata* Balf.f.

Shrublets or herbs with glabrous, much-branched, erect to prostrate stems. *Leaves* opposite, often fascicled on younger branches, sessile or shortly petiolate, fleshy, terete or with a \pm shallow groove, linear-oblongate to subcircular in outline, acute to obtuse, mucronate, entire. *Stipules* interpetiolar, scarious, ovate-triangular, acute at the apex, subentire to \pm frayed at the margin, first connate, later splitting into two.

Inflorescences dichasial or partly monochasial, sometimes forming dense spherical heads; bracts scarious, stipule-like to conspicuous and equalling or exceeding the flowers, or leaf-like with \pm well-developed lamina. *Flowers* sessile or sometimes the middle ones pedicelled, with a distinct obconical receptacle that is sometimes concrescent with the bracts. *Sepals* 5, with a membranous margin, shortly hooded and mucronate at the apex; petals absent. *Stamens* 5, opposite the sepals, alternating with 5 filiform to triangular staminodes; anthers broadly oblong. *Ovary* papillose above, free or \pm sunken into the receptacle; style slender; stigma 3-lobed; ovule single, basal. Fruit oblong, papillose above, rupturing irregularly. *Seed* ovate to \pm reniform in outline, somewhat compressed, brown; embryo horseshoe-shaped to annular; radicle superior.

Distribution. A genus of 10 species distributed in arid regions from the Cape Verde Islands and the Canary Islands in the west to Mongolia and north-western China in the east, with a centre of diversity in the Horn of Africa region.

Key to the species

- 1a. Annual herb; inflorescences spherical with partly concrescent flowers and bracts _____ **2. G. sclerocephalus**
- 1b. Shrublets; inflorescences \pm densely congested but not spherical heads, concrescent flowers and bracts _____ 2
- 2a. Bracts small, stipule-like _____ 3
- 2b. Bracts large, equalling or exceeding the flowers, or bracts leaf-like with stipules and lamina _____ 4
- 3a. Bracts mostly brown, except for a white margin, glabrous; leaves sessile, cylindric or almost so _____ **9. G. mahranus**
- 3b. Bracts mostly white, except for a brown base, minutely pubescent; leaves petiolate, globose-ovoid to fusiform _____ **10. G. parvibractus**
- 4a. Bracts leaf-like, with small stipules and 2–4mm long lamina __ **1. G. decandrus**
- 4b. Bracts large, scarious, only the lowermost sometimes with a vestigial to well-developed lamina _____ 5
- 5a. Style about as long as the sepals; distal flowers with an outer pair of large bracts and an inner pair of lateral narrower bracts _____ **3. G. przewalskii**
- 5b. Style much shorter than the sepals; flowers with a single pair of bracts only 6
- 6a. Leaves sessile _____ 7
- 6b. Leaves with a 0.25–1.5mm long petiole _____ 8
- 7a. Sepals glabrous or with some short hairs only at the base; bracts glabrous, brown with a \pm broad white margin; leaves linear-oblong to fusiform or almost globose _____ **7. G. dhofarensis**

- 7b. Sepals with long hairs at the base; bracts puberulous, white with a brown base only; leaves always linear-oblongate in outline _____ **8. *G. argenteus***
- 8a. Leaves narrowly linear-oblongate in outline; bracts brown throughout or with narrow white margin in upper part only _____ **4. *G. bracteatus***
- 8b. Leaves broadly linear-oblongate in outline to almost globose _____ 9
- 9a. Bracts white with a brown base only; staminodes 0.8–1mm long _____ **5. *G. rotundifolius***
- 9b. Bracts mainly brown with a \pm narrow white margin; staminodes 0.4–0.6mm long _____ **6. *G. kuriensis***

1. *G. decandrus* Forssk. (see Petrusson & Thulin, 1996: 11–13).

Additional synonym: *Paronychia decandra* (Forssk.) Rohweder & Urmi-König in Bot. Jahrb. Syst. 96: 407 (1975).

2. *G. sclerocephalus* (Decne.) Ahlgren & Thulin, **comb. nov.**

Type: Egypt, Sinai, 'près de Tor', *Bové* (holo. P).

Syn.: *Paronychia sclerocephala* Decne. in Ann. Sci. Nat., sér. 2, 3: 262 (1835). *Sclerocephalus arabicus* Boiss., Diagn. Pl. Orient. 1, 1(3): 12 (1843); *S. aucheri* Walpers, Repert. 5: 75 (1845), nom. illeg.

Sclerocephalus arabicus f. *leianthus* Murb., Contr. Fl. Nord-Ouest de l'Afrique 1: 50 (1897); *S. arabicus* var. *leianthus* (Murb.) Maire, Études Fl. Vég. Sahara Central: 96 (1933). Type: Algeria, 'Chetma in ditone Biskra', *Kralik* 38 (holo. LD, n.v.; iso. UPS).

Annual herb; stems erect to decumbent, c.3–25cm tall; internodes to c.22mm long. *Leaves* sessile, linear, cylindrical or almost so, c.5–20 \times 1–2mm, slightly narrowed to the base, acute at the apex; mucro 0.3–0.6mm long, pale brown, rigid. *Stipules* 3–4 \times 1.5–2mm, white, glabrous, not keeled, subentire. *Inflorescence* a compact spherical head, usually 4–7-flowered and 7–12mm in diam.; peduncle to c.5mm long, glabrous; bracts leaf-like, subulate, c.4–7mm long, strongly mucronate, fused at base with stipules. *Flowers* 4–5mm long, the receptacle concrescent with the bracts and forming a hardened structure eventually shed with the peduncle. *Sepals* slightly unequal, narrowly oblong, 2.5–3mm long, fleshy, with a narrow membranous margin, \pm densely covered with woolly hairs near the apex and base; mucro 0.25–1mm long, pale brown, rigid. *Stamens* with up to 0.8mm long linear filaments; anthers 0.25–0.3 \times 0.2mm; staminodes linear, 0.2–0.3mm long, hyaline. *Ovary* ovoid, c.1.5 \times 1mm, the basal part sunken into and fused with the receptacle; style 0.5–0.8mm long, 3-lobed at the tip, \pm equalling the stamens. *Fruit* 2.5–3 \times 1.5–2mm, papillose at the top, rupturing irregularly above. *Seed* c.2.25 \times 1.5mm.

Distribution and habitat. *Gymnocarpos sclerocephalus* is known from the Cape Verde Islands in the west through northern Africa to southern Arabia, Iraq and western Iran in the east. It is found in sandy or rocky places up to about 1100m altitude.

For an extensive list of collections of *G. sclerocephalus*, see Chaudhri (1968: 63). In addition to the countries listed by Chaudhri this species has now also been found in Djibouti, Somalia, Qatar and the United Arab Emirates (Lebrun *et al.*, 1989; Gilbert, 1993; Chamberlain, 1996).

The name *Sclerocephalus arabicus* var. *leianthus* has been given to forms with a more sparse indumentum on the sepals, but the variation is continuous, as was also pointed out by Chaudhri (1968: 63).

The annual habit and the dense globose heads with conrescent flowers and bracts of *G. sclerocephalus* are unique in *Gymnocarpus*. The mature head, which is eventually shed with the peduncle, simulates a several-seeded fruit and represents an extreme case of synaptospermy. Synaptospermy, in various degrees, is also found in all the other species of *Gymnocarpus*, in which the mostly large and scarious bracts are probably an adaptation to wind dispersal (Petrusson & Thulin, 1996). By contrast, the globose heads with almost spinescent bracts and sepals in *G. sclerocephalus* are clearly an adaptation to zoochory.

In the original description of *Paronychia sclerocephala* (Decaisne, 1835), as well as in the original description of *Sclerocephalus* (Boissier, 1843), the style was described as bifid. This appears to have been copied by all subsequent authors, although in later works the style has often been said to have two or three stigma lobes. In the material studied by us, from different parts of the range of the species, the style has always been three-lobed and we assume that the bifid style of early authors is a mistake. *Sclerocephalus* has also always been said to lack petals or staminodes, which would be unique in *Gymnocarpus*. However, this statement also seems to be erroneous as minute staminodes are generally present in the material studied by us.

Gymnocarpus sclerocephalus is the sister species of *G. decandrus* in the phylogenetic analysis. This relationship is supported by the leaf-like bracts, a feature found only in these two species. In the other species of *Gymnocarpus* the bracts are either small and stipule-like (*G. mahranus*, *G. parvibractus*) or large and scarious (*G. przewalskii*, *G. argenteus*, *G. dhofarensis*, *G. bracteatus*, *G. rotundifolius*, *G. kuriensis*).

3. *G. przewalskii* Bunge ex Maxim. in Bull. Acad. Imp. Sci. St. Pétersbourg 26: 502 (1880). Type: China, 'Mongolia occidentalis', Kansu, Huangho, 15–17 v 1872, *Przewalski* 45 (holo. LE, n.v.; iso. K, LE).

Syn.: *Paronychia przewalskii* (Bunge ex Maxim.) Rohweder & Urmi-König in Bot. Jahrb. Syst. 96: 407 (1975).

Gymnocarpus przewalskii var. *scabrida* Chaudhri in Med. Bot. Mus. Rijksuniv. Utrecht 285: 58 (1968). Type: China, Sinkiang, 'Turkestan sinensis', Dochanart valley, 14–17 vi 1903, *Merzbacher* 781 (holo. LE, n.v.; iso. LE).

Shrublet, erect or ascending, to c.0.5m tall; young stems purplish brown, glabrous or pubescent; internodes to c.20mm long; bark of older stems whitish. *Leaves* linear,

cylindrical and often with a distinct groove, to $c.20 \times 1.5$ mm, attenuate at the base, acute and mucronate at the apex; petiole to $c.1$ mm long, whitish; mucro 0.2 – 0.5 mm long. *Stipules* to $c.3 \times 2$ mm, white with a brownish base, glabrous or almost so, subentire. *Inflorescences* of densely congested 3–15-flowered clusters; peduncles 5 – 10 mm long, pubescent to subglabrous; bracts scarious, white with a brownish base, \pm frayed at the apex, elliptic to broadly ovate or suborbicular, to 7×5 mm, distal flowers also with an inner pair of lateral narrower bracts. *Flowers* 5 – 7 mm long, sessile; receptacle 2 – 3 mm long, pubescent, papillose or subglabrous. Sepals narrowly oblong with broader base, 3 – 4 mm long, with a membranous margin, pubescent all along, near apex and base only, or subglabrous; mucro 0.2 – 0.5 mm long, glabrous or puberulous. *Stamens* with 1.5 – 2.2 mm long filaments; anthers $c.0.5$ – 0.3 mm; staminodes filiform, 1.2 – 2.2 mm long, whitish or brown. *Ovary* $c.1 \times 0.5$ mm, papillose; style 3 – 4 mm long, shortly 3-lobed at the apex, much longer than the stamens. *Fruit* $c.2 \times 1.5$ mm, narrowly ellipsoid, papillose, light brown. *Seed* $c.1.6 \times 1.2$ mm.

Distribution and habitat. *Gymnocarpus przewalskii* is known from Mongolia and north-western China, where it grows in semi-desert steppe areas in stony or gravelly places up to about 2600m altitude. For an extensive list of collections of *G. przewalskii* see Chaudhri (1968: 58). We have studied $c.25$ collections in LE, K and S.

Chaudhri (1968) recognized two varieties of *G. przewalskii*, var. *przewalskii* with sepals more or less glabrous on the back but with a patch of short hairs near the apex just below the mucro, and var. *scabrida* with sepals almost entirely covered with short appressed hairs. However, the variation is quite continuous and these varieties are not recognized here.

The presence in distal flowers of an inner pair of narrow, lateral bracts is a unique feature for *G. przewalskii*. These bracts probably represent the bracts of an aborted lateral flower. The long style, more or less equal to the length of the sepals and much longer than the stamens, is another unique feature of this species. In the phylogenetic analysis *G. przewalskii* comes out as the sister to a clade containing *G. bracteatus*, *G. mahranus*, *G. rotundifolius* and *G. argenteus*, all species in the Horn of Africa region. However, this sister group relationship is not strongly supported.

4. ***G. bracteatus*** (Balf.f.) Petrus. & Thulin (see Petrusson & Thulin, 1996: 17–19).

5. ***G. rotundifolius*** Petrus. & Thulin (see Petrusson & Thulin, 1996: 19–20, and Thulin *et al.*, 2001).

6. ***G. kuriensis*** (Radcl.-Sm.) Petrus. & Thulin (see Petrusson & Thulin, 1996: 20–22).

7. ***G. dhofarensis*** Petrus. & Thulin (see Petrusson & Thulin, 1996: 15–17).

8. ***G. argenteus*** Petrus. & Thulin (see Petrusson & Thulin, 1996: 13–15).

9. *G. mahranus* Petrus. & Thulin (see Petrusson & Thulin, 1996: 22–24).

When originally published *G. mahranus* was known only from the type, but the following collections have been made since then.

Additional specimens examined. YEMEN. Mahrah: 35km E of Itab along road to Qishn, 15°24'N, 51°35'E, 5 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9572 (UPS); Ras Fartak, above Al Wadi, 15°40'N, 52°11'E, 7 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9632 (UPS); Ras Fartak, 15°40'N, 52°13'E, 9 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9652 (UPS); 28km from Al Wadi along road to Tabut, 15°47'N, 52°00'E, 9 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9667 (K, UPS); along road between Al Ghaydah and Al Fatk, 16°30'N, 52°40'E, 10 xi 1998, *Thulin, Beier & Mohammed A. Hussein* 9678 (UPS).

10. *G. parvibractus* (M. Gilbert) Petrus. & Thulin (see Petrusson & Thulin, 1996: 24–25).

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