Phylogenetic position of *Canaridiscus* and reestablishment of *Gonyodiscus* (Gastropoda: Discidae)

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Abstract. The genus *Canaridiscus* M.R. Alonso & Ibáñez, 2011, endemic to the Canary Islands, has a curious taxonomic history and is currently defined based only on the peculiar anatomy of its genital organs. Its relationship to European *Discus* species and other members of the family Discidae is unclear and its status as a distinct genus remains tentative. In the present study we include a species of *Canaridiscus*, *C. textilis* (Shuttleworth, 1852), in a molecular phylogenetic framework of the Discoidea to investigate its position in the superfamily's tree. *Canaridiscus* is retained as a distinct genus in Discidae, but *Discus* is shown to be polyphyletic. Thus, the genus *Gonyodiscus* Fitzinger, 1833 is here resurrected to include 2 European species, reclassified as *G. perspectivus* (Megerle von Mühlfeld, 1816) and *G. rotundatus* (O.F. Müller, 1774). *Discus* Fitzinger, 1833 is restricted to a clade containing mostly North American species.

Key words. Discoidea, *Discus*, land snails, molecular phylogenetics, Stylommatophora.

Introduction

The families Discidae (disc snails and tiger snails) and Oreohelicidae (mountain snails) have traditionally been classified within the superfamily Punctoidea. Recent molecular evidence (SALVADOR et al. 2020), however, has shown that these families form a distinct group, the superfamily Discoidea, unrelated to Punctoidea. While the Oreohelicidae are an exclusively North American family, Discidae also has representatives in Europe (including various fossil species), Macaronesia, northern Japan, and northeastern Russia (SCHILEYKO 2002). The extant species outside North America are presently classified in either *Discus* Fitzinger, 1833 or *Canaridiscus* M.R. Alonso & Ibáñez, 2011 (HOLYOAK et al. 2011, WELTER-SCHULTES 2012).

Canaridiscus, as its name implies, is endemic to the Canary Islands in the Atlantic Ocean and has a curious taxonomic history. It was first described as a subgenus of *Atlantica* Ancey, 1887 in the family Discidae (YANES et al. 2011), but also included species previously classified in *Discus* and its subgenus/synonym *Gonyodiscus* Fitzinger, 1833 (HOLYOAK et al. 2011). However, *Atlantica* (*Atlantica*) was later discovered to be a member of the Gastrodontidae instead and was transferred to that family (CAMERON et al. 2013). *Canaridiscus*, however, was considered a group of Discidae species based on conchological and anatomical characters (HOLYOAK et al. 2011). The reclassification of *Atlantica* thus made *Canaridiscus* an "orphan" subgenus in Discidae, so it was raised to genus level, mainly on the basis of the peculiar genital anatomy (i.e., extremely long penes) of its various species. *Canaridiscus* consists of some 12 different species on the islands of Tenerife, La Gomera, El Hierro, and La Palma (HOLYOAK et al. 2011).

In the absence of molecular data, the relationship of *Canaridiscus* to *Discus* is unclear and its status as a distinct genus remains tentative. In the present study we include *Canaridiscus* in a molecular phylogenetic framework of the Discoidea to investigate its position in the superfamily's tree.

Materials and Methods

Three species of *Canaridiscus* are known from La Palma, of which the morphology of the soft parts is unknown. All these were considered to be extinct, but fresh material of
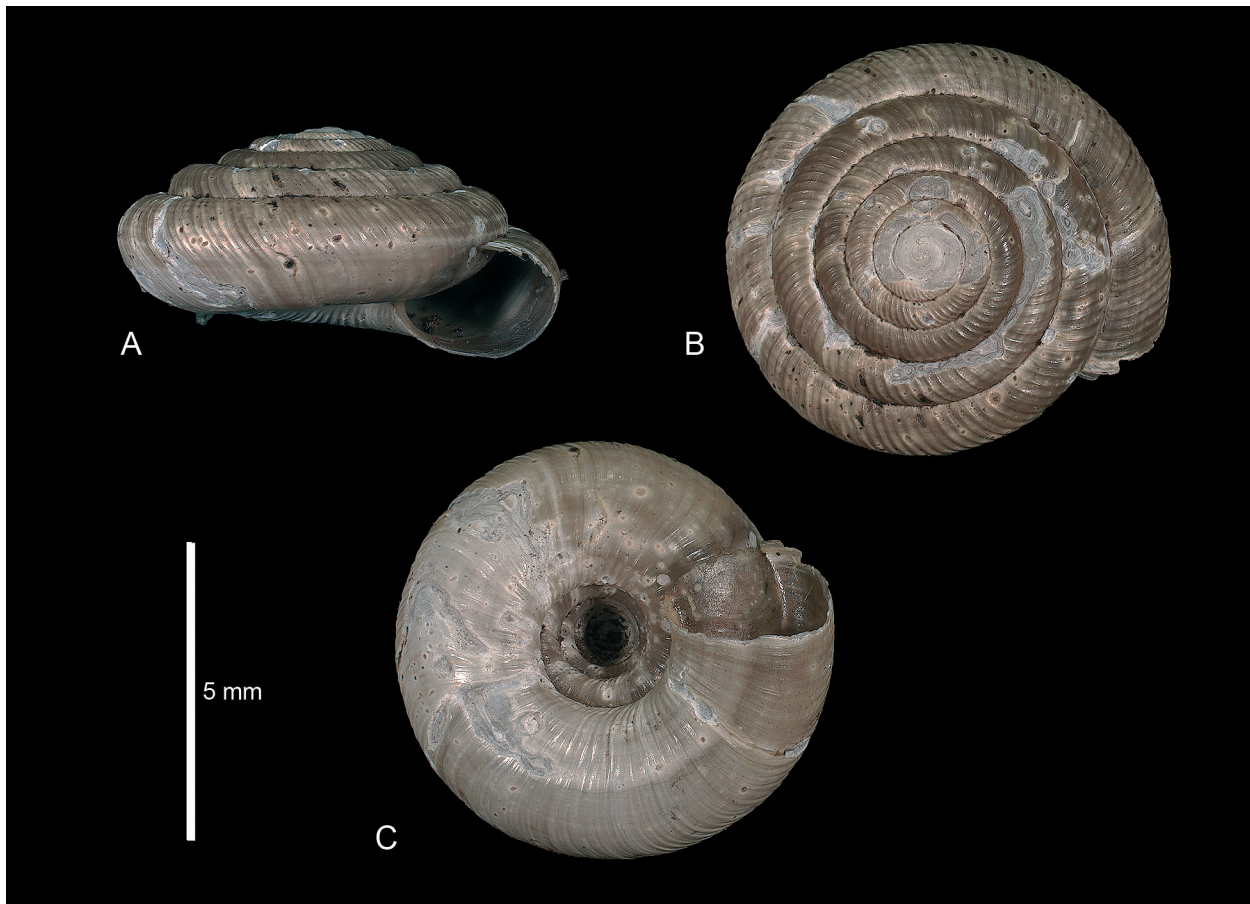
Figure 1. *Canaridiscus textilis* (Shuttleworth, 1852), fresh empty shell from La Palma, Cumbre Nueva (MNCN 15.05/94991), cloud forest on slope at 1400 m a.s.l. **A.** Apertural view. **B.** Apical view. **C.** Umbilical view.

C. textilis, apparently empty shells, was recently reported from Marcos y Cordero in the north-eastern part of La Palma (Yanes et al. 2011, Holyoak et al. 2011). A living specimen and some fresh empty shells were collected by the last author in Cumbre Nueva in 2013 (Fig. 1). This locality lies in the cloud forest zone of La Palma at 1400 m a.s.l., 25–30 km further south from the Marcos y Cordero locality. Despite the geographic distance, we confidently attribute this material to *C. textilis* in view of the similarity to the excellent photographs of a syntype by Neubert & Gosteli (2003: pl. 14, fig. 3) and the shell characters and photograph provided by Yanes et al.

Table 1. Species sequenced for the present study, with information on the GenBank accession numbers, locality where the specimens were collected, and registration number of the voucher specimens in the respective collections. The * indicates sequences already published in Salvador et al. (2020), obtained from the same voucher specimens.

Species	COI	16S	5.8S+ITS2+28S	Location	Voucher material
Anguispira alabama (Clapp, 1920)	—	ON749857	ON749850	USA, Alabama, Jackson	FMNH 303186
Anguispira kochi occidentalis (E. von Martens, 1882)	ON751968	ON749858	ON749851	Canada, British Columbia, Dodge Creek	RBCM 015-00443-001
Canaridiscus textilis (Shuttleworth, 1852)	ON720331	ON720565	ON720563	Spain, Canary Islands, La Palma, Cumbre Nueva	RMNH.MOL.342771
Discus catskillensis (Pilsbry, 1896)	ON751969	ON749859	MN782450*	Canada, New Brunswick, Spednic Lake Provincial Park	NMNZ M.328404
Discus marmorensis H.B. Baker, 1932	—	—	ON749853	USA, Idaho, Lucile	FMNH 384865
Discus whitneyi (Newcomb, 1864)	ON751970	ON749860	MN782456*	Canada, British Columbia, Elmer Creek	RBCM 016-00152-003
Oreohelix haydeni betheli Pilsbry & Cockerell, 1913	ON751971	ON749861	ON749855	USA, Colorado, Garfield	FMNH 374607
Oreohelix yavapai mariae Bartsch, 1916	ON751972	—	ON749856	USA, Montana, Boxeman	FMNH 386248

(2011) and HOLYOAK et al. (2011). The shell morphology of the other 2 species from La Palma attributed to *Canaridiscus* is rather different.

The species sequenced for the present study (Table 1) includes *C. textilis*, as mentioned above, as well as additional representatives of the Discoidea genera *Discus*, *Anguispira* Morse, 1864, and *Oreohelix* Pilsbry, 1904. The specimens (preserved in ethanol 70–98%) were obtained from the following natural history collections: Field Museum of Natural History (**FMNH**, Chicago, USA), Museum of New Zealand Te Papa Tongarewa (**NMNZ**, Wellington, New Zealand), and Royal British Columbia Museum (**RBCM**, Victoria, Canada). The sequenced specimen of *C. textilis* is deposited in the collection of the Naturalis Biodiversity Center (**RMNH**, Leiden, The Netherlands; specimen lot RMNH.MOL.342771); additional dry shell material is deposited in Naturalis (RMNH.MOL.342772–342774) and in the Museo Nacional de Ciencias Naturales (**MNCN**, Madrid, Spain; specimen lot MNCN 15.05/94991; Fig. 1).

DNA sequences of a further 25 representatives of the Discoidea were included from previously published studies (Table 2). Representatives of the Achatinidae and Streptaxidae were chosen as the outgroup (Table 2).

Table 2. Sequences extracted from GenBank, with information on the provenance of the sampled animals and reference to the original publications. The * indicates the species used as the outgroup.

Species	COI	16S	5.8S+ITS2+28S	Location	Reference
*Gulella caryatis (Melvill & Ponsonby, 1898)	HQ328133	HQ328323	GQ330510	Namibia	ROWSON et al. (2011)
*Subulina octona (Bruguière, 1789)	JX988066	JX988353	MF444887	Palau	PRÉVOT et al. (2013)
Anguispira alternata (Say, 1817)	MN792584	MN756711	MN782441	USA, Illinois, Sangamon	SALVADOR et al. (2020)
Anguispira alternata (Say, 1817)	MN792583	MN756710	MN782440	Canada, Ontario	SALVADOR et al. (2020)
Anguispira cumberlandiana (I. Lea, 1840)	MW543329	MW544210	—	USA, Tennessee, Battle Branch (N of Kimball)	CLUTTS (2008), RANKIN et al. (2021)
Anguispira fergusoni (Bland, 1862)	MW543321	MW544221	—	USA, Delaware, Blackbird State Forest	CLUTTS (2008), RANKIN et al. (2021)
Anguispira jessica Kutchka, 1938	MN792585	MN756712	MN782442	USA, North Carolina, Macon	SALVADOR et al. (2020)
Anguispira kochi occidentalis (E. von Martens, 1882)	MN792586	MN756713	MN782443	Canada, British Columbia, Bear Creek	SALVADOR et al. (2020)
Anguispira kochi kochi (L. Pfeiffer, 1846)	MN792587	MN756714	MN782444	USA, Illinois, Brown	SALVADOR et al. (2020)
Anguispira nimapuna H.B. Baker, 1932	MN792588	MN756715	MN782445	USA, Idaho, Lowell	SALVADOR et al. (2020)
Anguispira picta (G.H. Clapp, 1920)	MW543311	MW544248	—	USA, Tennessee, Buck Creek Cove	CLUTTS (2008), RANKIN et al. (2021)
Anguispira strongyloides (L. Pfeiffer, 1855)	—	MN756716	MN782446	USA, Florida	SALVADOR et al. (2020)
Discus marmorensis H.B. Baker, 1932	MW543387	MW544270	—	USA, Idaho, Slate Creek Road	RANKIN et al. (2021)
Discus nigrimontanus (Pilsbry, 1924)	MN792594	MN756721	MN782451	USA, Alabama, Jackson	SALVADOR et al. (2020)
Discus patulus (Deshayes, 1830)	MN792595	MN756722	MN782452	USA, North Carolina, Macon	SALVADOR et al. (2020)
Discus pauper (A. Gould, 1859)	*MW543400*	MW544266	—	Japan, Sendai	RANKIN et al. (2021)
Discus perspectivus (Megerle von Mühlfeld, 1816)	MN792596	MN756723	MN782453	Czech Republic, Litovelské Luhy Nature Reserve	SALVADOR et al. (2020)
Discus rotundatus (O.F. Müller, 1774)	FJ917285	FJ917265	FJ917240	Germany, Frankfurt am Main	DINAPOLI & KLUSSMANN-KOLB (2010)
Discus ruderatus (Hartmann, 1821)	MN792597	MN756724	MN782454	Italy, Trentino-Alto Adige	SALVADOR et al. (2020)
Discus shimekii (Pilsbry, 1890)	MN792598	MN756725	MN782455	Canada, British Columbia, Liard Plain	SALVADOR et al. (2020)
Oreohelix idahoensis (Hemphill, 1890)	MN792610	MN756734	MN782467	USA, Idaho, Lucile	SALVADOR et al. (2020)
Oreohelix cooperi (W.G. Binney, 1858)	MN695560	—	MN695818	Canada	DEMPSEY et al. (2020)
Oreohelix strigosa depressa Pilsbry, 1904	MN792611	MN756735	MN782468	USA, Colorado, Garfield	SALVADOR et al. (2020)
Oreohelix subrudis (Reeve, 1854)	MN792612	MN756736	MN782469	Canada, British Columbia, Flathead Service Road	SALVADOR et al. (2020)
Oreohelix variabilis Henderson, 1929	MF957140	MF957126	—	USA, Oregon, Wasco County	DEMPSEY et al. (2020)
Oreohelix vortex S.S. Berry, 1932	MN792613	MN756737	MN782470	USA, Idaho, White Bird	SALVADOR et al. (2020)
Radiodomus abietum H.B. Baker, 1930	MN792624	MN756750	MN782482	USA, Idaho, Seven Devils Mountains	SALVADOR et al. (2020)

A small tissue clip was obtained from each voucher specimen for DNA extraction, which followed the standard protocol of the QIAGEN DNEasy® Blood & Tissue Kit (adding a repetition of the final step to increase yield). The following molecular markers were targeted for this study: (1) the barcoding fragment, circa 650 bp long, of the mitochondrial COI gene (primers LCO/HCO; Folmer et al. 1994); (2) the circa 450-bp-long mitochondrial 16S rRNA gene (primers 16SarL/16SbrH; Simon et al. 1994); (3) a continuous fragment of nuclear DNA, circa 1,300 bp long, including the 3′ end of the 5.8S rRNA gene, the ITS2 region, and the 5′ end of the 28S rRNA gene (amplified in 2 fragments with primers LSU-1/LSU-3 and LSU-2/LSU-5; Wade & Mordan 2000, Wade et al. 2006).

The PCR amplification protocols were as follows: COI and 16S: initial denaturation at 96 °C (3 min); 35 cycles of denaturation at 95 °C (30 s), annealing at either 48 °C (COI) or 50 °C (16S) (1 min), and extension at 72 °C (2 min); final extension at 72 °C (5 min). 5.8S+ITS2+28S: initial denaturation at 95 °C (3 min); 40 cycles of denaturation at 95 °C (30 s), annealing at either 50 °C (ITS2 section) or 45 °C (28S section) (1 min), and extension at 72 °C (5 min for ITS2 section or 2 min for 28S section); final extension at 72 °C (4 min). Success of PCR was assessed visually via agarose gel electrophoresis; PCR products were cleaned with ExoSAP-IT™ (Affymetrix Inc.) according to the manufacturer's protocol; and samples were sent to Massey Genome Service (Massey University, Palmerston North, New Zealand) for Sanger sequencing.

Sequences were quality-checked and assembled in Geneious Prime (v. 2020.2.2, Biomatters Ltd). The consensus sequence was uploaded to GenBank (Table 1). Sequence alignment was done in Geneious Prime using the MUSCLE plugin (Edgar 2004) with default settings (i.e., optimized for accuracy). The resulting alignments were visually checked for inconsistencies and then run through Gblocks (Talavera & Castresana 2007) with the least restrictive settings to eliminate poorly aligned or data-deficient positions that could introduce noise into the analysis. The resulting post-Gblocks alignments were then concatenated for a single phylogenetic analysis. The sequences of *Discus marmorensis* H.B. Baker, 1932 stem from 2 voucher specimens, collected at localities that are about 12 km apart from one another (Tables 1, 2); they were concatenated as a single sequence representing this species for the analysis.

A Bayesian-inference phylogenetic analysis was performed using MrBayes (v. 3.2.7, Ronquist et al. 2012) via the CIPRES Science Gateway (v. 3.3, Miller et al. 2015). Two concurrent analyses were run, each with 4 Markov chains of 80 million generations (the first 20% discarded as "burn-in"), temperature parameter = 0.1, sampling every 1,000 generations, and with substitution model parameters unlinked across the markers (COI, 16S, and 5.8S+ITS+28S). Following Salvador et al. (2020), a generalized time reversible model, nst = 6, default priors, was used, with rates set to "invgamma". MCMC convergence was assessed by examining the standard deviation

of split frequencies (<0.001) and the potential scale reduction factor (PSRF = 1.0), as well as trace plots in Geneious (Ronquist et al. 2009).

A maximum-likelihood phylogenetic analysis was performed via the PhyML 3.0 online portal (Guindon et al. 2010). Smart model selection with Akaike information criterion (AIC) was used (Lefort et al. 2017), with 1,000 bootstrap replicates.

Results

The resulting 50% majority-rule consensus phylogenetic tree is shown in Figure 2. Both the Bayesian-inference and maximum-likelihood trees had the same topology. For clarity, we refer below only to Bayesian-inference posterior probability (PP) values, while the maximum-likelihood bootstrap support values can be seen in Figure 2.

Overall, the support of all clades was strong (PP ≥ 0.95) The sequences of each marker after Gblocks were 608 bp for COI, 387 bp for 16S, and 1,274 bp for 5.8S+ITS2+28S; a total of 2,269 bp. In the resulting tree, 31 terminal taxa of Discoidea are present, representing 29 species.

Oreohelicidae was recovered as the sister family to Discidae (PP = 1 for the former and 0.97 for the latter), supporting the previous results of Salvador et al. (2020). Supporting the previous results, the position of *Radiodomus* H.B. Baker, 1930 stemming from the most basal node of Discidae was recovered (Salvador et al. 2020).

The remaining Discidae form a well-supported clade (PP = 1). Branching out after the split of *Radiodomus*, there is a monophyletic group (PP = 1), sister to the remaining Discidae, formed by *Canaridiscus textilis* as sister taxon of a clade (PP = 1) composed of *D. rotundatus* and *D. perspectivus*. This group is far removed from the other *Discus* species on the tree, which form a clade (PP = 1) containing the European species *D. ruderatus*, the type species of the genus. As such, the genus *Discus* is polyphyletic as it stands, pending the exclusion of *D. rotundatus* and *D. perspectivus* (and possibly of *D. marmorensis*, see below). The non-monophyly of *Discus* had already been pointed out by Salvador et al. (2020).

In the "crown Discidae", the sister taxon of *Discus* sensu stricto is a clade (weakly-supported clade in the Bayesian tree, PP = 0.76, but more strongly supported in the maximum-likelihood analysis, 93%) formed by a well-supported *Anguispira* sensu stricto clade (PP = 0.99) and a virtually unsupported clade (PP = 0.66) containing *Anguispira nimapuna* H.B. Baker, 1932 and *Discus marmorensis*. That potentially (given the lower support of the branches) renders *Anguispira* paraphyletic, pending either the exclusion of *A. nimapuna* or the inclusion of *D. marmorensis*.

Discussion

Canaridiscus textilis clusters together with a clade formed by *Discus rotundatus* and *D. perspectivus*. The latter
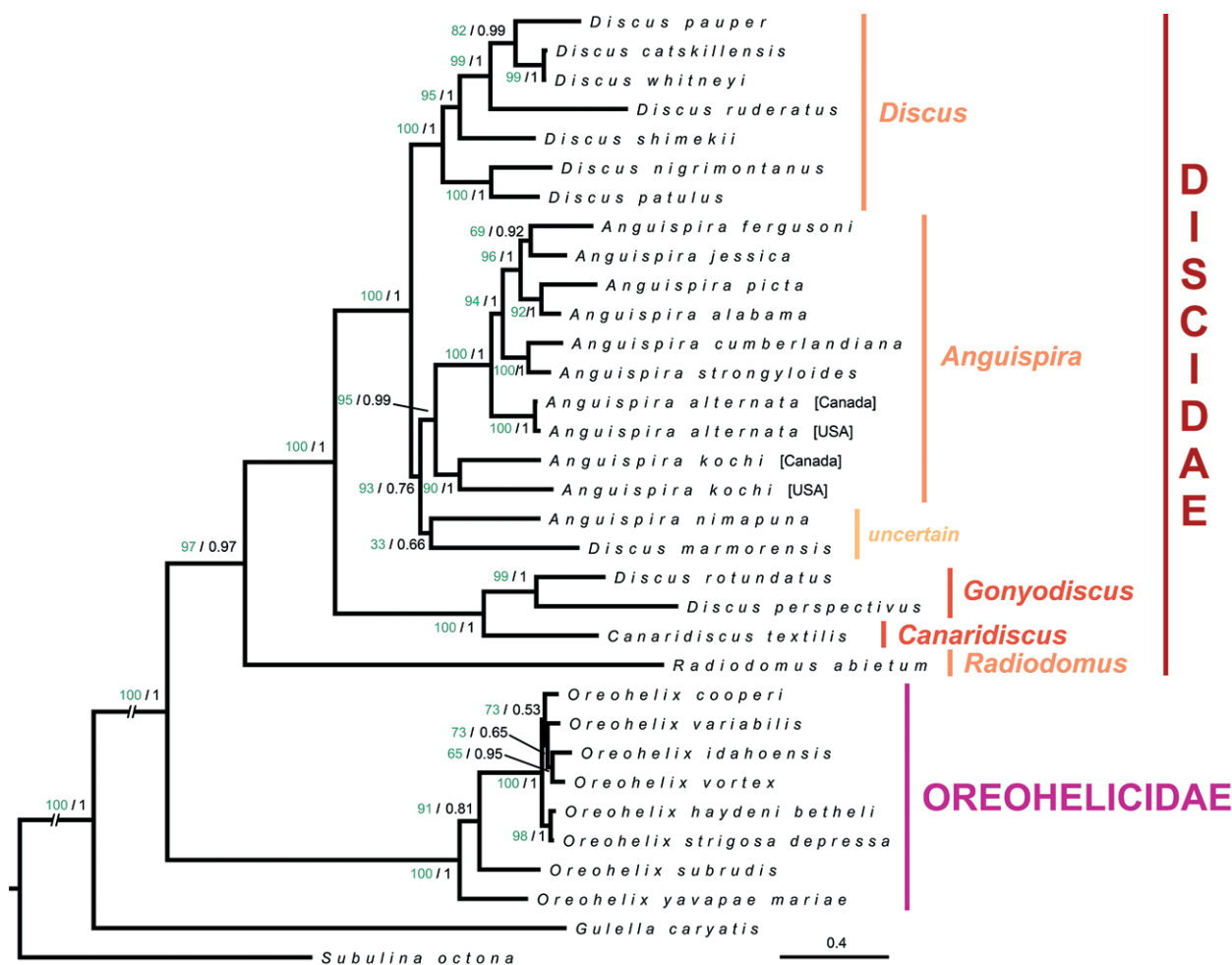
Figure 2. Bayesian-inference 50% majority-rule consensus tree of Discoidea based on CO1, 16S, and 5.8S+ITS2+28S. Numbers shown on nodes are maximum-likelihood bootstrap values (0–100%, in green) followed by Bayesian-inference posterior probabilities (0–1). Scale bar represents substitutions per site.

clade is far removed from the rest of the *Discus* species, which form a monophyletic group (see comments regarding *D. marmorensis* further below) that includes the type species *D. ruderatus* (Fig. 2). As this renders *Discus* paraphyletic, those 2 species need to be removed from the genus and reclassified, so that *Discus* becomes a monophyletic group. Luckily, there is already a name available for a clade with these 2 species. The oldest name available is *Gonyodiscus* Fitzinger, 1833, of which *Helix perspectiva* Megerle von Mühlfeld, 1816 is the type species.

Historically, *Gonyodiscus* has been considered a valid genus (mostly until the first half of the 20th century) or a subgenus of *Discus*, but commonly (and more recently) it has been treated as a synonym of the latter. Our results stemming from molecular data support the conclusions of Umiński (1962) based on comparative genital anatomy, who placed *Discus ruderatus* in *Discus* sensu stricto, while *D. rotundatus* and *D. perspectivus* were assigned to the subgenus *Gonyodiscus*. We thus propose the reinstatement of *Gonyodiscus* as an independent genus, containing 2 species reclassified in the combinations *Gonyodiscus perspectivus* (Megerle von Mühlfeld, 1816) and *G. rotundatus* (O.F. Müller, 1774).

A simple but general conchological diagnostic feature for the reestablished genus *Gonyodiscus* is the presence of a marked angulation on the mid-section of the body whorl, as seen in *G. perspectivus* and in the subspecies or form *G. r. omalisma* (Fagot, 1879) (the angulation is less prominent in other *G. rotundatus*). In comparison, the body whorl of *Discus* s.s. shells has a more rounded profile overall. Shells of *Gonyodiscus* species also have more whorls on average (5½–6) than *Discus* species (c. 4), though some species in the latter genus can be exceptions to this rule (e.g., *Discus macclintocki* (F.C. Baker, 1928)).

The same diagnostic characters of *Gonyodiscus* (greater number of whorls and the keel) are present in *Canaridiscus* (Holyoak et al. 2011, Yanes et al. 2011). In some species of *Canaridiscus* (including the type species), the keel is very strong (Holyoak et al. 2011), similar to, or more pronounced than, in *G. perspectivus*. Other species of *Canaridiscus* (like *C. textilis*, used in the present phylogeny) have a fainter angulation and the body whorl's profile is more rounded, being more similar to *G. rotundatus*, and a few lack the angulation altogether (Holyoak et al. 2011; Allgaier & Klemm 2012). Anatomically,

Canaridiscus appears to differ from *G. perspectivus* and *G. ruderatus* mainly by the possession of an extremely long, convoluted penis (HOLYOAK et al. 2011).

Unfortunately, we could not obtain specimens of the type species, *C. saproxylophagus* (Alonso, Holyoak & Yanes, 2011), or other congeners for sequencing. Attempts sequencing a specimen of *C. kompsus* (J. Mabille, 1883) from the isle of El Hierro in the Naturalis collection failed. The endemic species of the Canary Islands could represent a monophyletic lineage that differentiated from a single population that arrived on the islands, or it could represent a paraphyletic or polyphyletic assemblage resulting from multiple arrivals of European populations. Considering that *Canaridiscus* is an island endemic, mostly inhabiting a distinct biome, we treat *Canaridiscus* as a separate genus for the moment.

Considering the phylogenetic arrangement, the superfamily Discoidea and the family Discidae likely originated in North America. That is supported by the fossil record, as the oldest known fossils of both Oreohelicidae and Discidae date from the Late Cretaceous of Alberta, Canada, being classified in the modern genera *Oreohelix* Pilsbry, 1904, *Radiocentrum* Pilsbry, 1905, and *Discus* (HENDERSON 1935; TOZER 1956; ROTH 1986). Further fossils of those genera are known from the Paleocene and early Eocene of Canada and the USA (PILSBRY 1939, LA ROQUE 1960, ROTH 1986, SALVADOR et al. 2020). The European fossil record of Discidae begins in the late Paleocene/early Eocene with *Discus perelegans* (Deshayes, 1863) from the Paris Basin in France (WENZ 1923).

Thus, given its position close to the base of Discidae on the tree (Fig. 2), the branch formed by *Canaridiscus* plus *Gonyodiscus* is likely to be an old lineage that dispersed to Europe rather early in the family's history. In all likelihood, the Discidae fossils from the European Paleogene belong to this branch, such as the genera *Coxiola* Pfeffer, 1930 and *Calogoniodiscus* Pfeffer, 1930 from the early Eocene of the U.K., France and Spain (PFEFFER 1930, HARZHAUSER et al. 2020). Furthermore, there are numerous species from the Eocene and Oligocene of the U.K., France, and Germany currently assigned to *Discus* that likewise appear to belong to this lineage and potentially to one of the extinct genera listed above (e.g., EDWARDS 1852, NEWTON & HARRIS 1894, MILLER 1907, WENZ 1923, PFEFFER 1930, PREECE 1976, 1982, SALVADOR et al. 2016). Some of these fossils have a prominent keel (e.g., EDWARDS 1852), others apparently do not (e.g., NEWTON & HARRIS 1894, MILLER 1907, SALVADOR et al. 2016), and several have been at some point classified in *Gonyodiscus*. Finally, the fossil shells assigned to the genus *Manganellia* Harzhauser, Neubauer & Georgopoulou, 2014 from the Early to Middle Miocene of Europe also have a prominent keel (HARZHAUSER et al. 2014a, 2014b). In particular, *Manganellia schneideri* (Harzhauser & Neubauer, 2014), described from fragmentary specimens (HARZHAUSER et al. 2014a), resembles *G. perspectivus*. Considering the uncertainties surrounding the classification of the fossils, we opted for not using them

for dating the nodes on the tree until a taxonomic revision has been conducted.

At a certain point in the history of this "*Gonyodiscus* branch", 1 or more populations would have dispersed to the Canary Islands, potentially already during the Miocene, giving rise to *Canaridiscus*. The Canaries is a volcanic archipelago and its oldest islands surfaced during the Early to Middle Miocene: the oldest subaerial volcanisms on Fuerteventura, Lanzarote, and Gran Canaria date back to 20.6, 15.5, and 13.7 Ma, respectively (JEFFERY & GERTISSER 2018). The other islands surfaced during the Late Miocene, Pliocene, and Pleistocene (JEFFERY & GERTISSER 2018). Presently, species of *Canaridiscus* only inhabit the younger islands (HOLYOAK et al. 2011).

Considering the changes proposed above, the genus *Discus* now contains only 1 living European species, *D. ruderatus*. The remaining species inhabit North America, with the exception of *D. pauper* (A. Gould, 1859), from the Kuril Islands and northern Japan (Fig. 2). This implies at least 1 independent and more recent dispersion event of a *Discus* population into Europe (as well as another one into northeastern Asia via Alaska). There are also multiple Neogene fossils in Europe assigned to *Discus*, which could belong to either this genus or to the *Gonyodiscus* branch. All these fossils, as well as the older Paleogene ones mentioned above, are in need of revisionary work under the new phylogenetic framework proposed here.

Finally, *Anguispira* s.s. is a well-supported monophyletic group (Fig. 2), related to 2 species of uncertain position in the phylogeny: *Anguispira nimapuna* and *Discus marmorensis*. The latter 2 species form a virtually unsupported clade sister to *Anguispira* s.s. (Fig. 2). Both species are conchologically similar to one another and distinct from *Anguispira*, being more reminiscent of *Discus* and *Gonyodiscus*. The phylogenetic analysis of RANKIN et al. (2021) recovered *A. nimapuna* as sister to all other *Anguispira*, but with virtually no support. Likewise, those authors recovered *D. marmorensis* as sister to *Discus* plus *Anguispira*, but again, with virtually no support. As such, for now the phylogenetic position and the classification of these 2 species remains elusive. We suggest referring to them as "*Anguispira*" *nimapuna* and "*Discus*" *marmorensis* until more evidence becomes available.

Conclusion

Considering the present phylogenetic analysis, the studied taxa, and known fossil record, the following classification scheme is proposed here for the superfamily Discoidea. Genera exclusively known from fossils are indicated with a dagger (†).

Family Oreohelicidae
 Oreohelix Pilsbry, 1904
 Radiocentrum Pilsbry, 1905
Family Discidae
 Anguispira Morse, 1864
 † *Calogoniodiscus* Pfeffer, 1930

Canaridiscus M.R. Alonso & Ibáñez, 2011

†*Coxiola* Pfeffer, 1930

Discus Fitzinger, 1833 (= *Delomphalus* Charpentier, 1837; *Mexicodiscus* Pilsbry, 1926, *Antediscus* H.B. Baker, 1948, *Nematodiscus* Pilsbry, 1948)

Gonyodiscus Fitzinger, 1833 (= *Goniodiscus* [sic] Fitzinger, 1833; *Eyryomphala* H. Beck, 1837; *Patula* Held, 1838; *Euryomphala* [sic] Hermannsen, 1847; *Euromphala* [sic] Lowe, 1852; *Patularia* Clessin, 1876 [non Swainson, 1840])

†*Manganellia* Harzhauser, Neubauer & Georgopoulou, 2014

Radiodomus H.B. Baker, 1930

Acknowledgements

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