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Phylogenetic position of the genus Ridleyconcha (Gastropoda, Stylommatophora)

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Abstract: The Fernando de Noronha Archipelago off NE Brazil harbors a few unique terrestrial gastropod species. One of them, the monotypic genus Ridleyconcha Christensen, 2020, presents such an idiosyncratic shell morphology that, in the 130 years since its description, it has been variously allocated in unrelated families: Streptaxidae, Endodontidae, Charopidae, Camaenidae, and Scolodontidae. Herein, R. quinquelirata is included into a molecular phylogenetic framework of stylommatophoran land snails to clarify its taxonomic position. The analysis supports the latest morphological revision classifying Ridleyconcha in Scolodontidae. Considering the present sampling, Ridleyconcha appears to be the sister taxa of Entodina Ancey, 1887.

Key words: Brazil, Fernando de Noronha, insular fauna, land snails, Scolodontidae.

Brazil is a megadiverse country for most animal taxa, in particular invertebrates (Lewinsohn et al. 2005). The study of the country’s terrestrial gastropods, though, remains incipient in many fronts. Salvador (2019a) identified five study areas of particular interest in need of attention in Brazil, among which were (1) investigating phylogenetic relationships of taxa above the species level, and (2) studying poorly-sampled regions and habitats, such as islands.

The insular snail fauna in Brazil has been receiving a little extra attention lately, from both continental islands (Simone and Amaral 2018, Simone et al. 2020) and oceanic ones, such as the archipelagoes of Trindade and Martin Vaz (Salvador et al. 2013, 2014, Cunha et al. 2015) and Fernando de Noronha (Freitas et al. 2019, Salvador and Cavallari 2019).

Fernando de Noronha is situated circa 350 km off the northeastern Brazilian coast (Fig. 1), with 21 islands and islets, all of volcanic origin. The eponymous main island was an important midway site for the exploitation of Brazilian resources during the 16th and 17th centuries and was briefly occupied by the British and the French, and, for over two decades, the Dutch, with Portugal finally starting to fortify the island in the 18th century (Lins e Silva 2013, Pessoa 2014). Fernando de Noronha also served as a prison until the mid-20th century (Pessoa 2014). The island still had its natural cover when Darwin visited it in 1832 (Darwin 1839), but much of its vegetation had already been cut down by the end of the 19th century (Ridley 1890). Today, most of Fernando de Noronha’s area is a national marine reserve and the archipelago is a UNESCO World Heritage Site.

As expected of oceanic islands, Fernando de Noronha has its share of endemic species, from the songbirds Elaenia ridleyana Sharpe, 1888 and Vireo gracilirostris Sharpe, 1890 to invertebrates. Among the latter, there are three unique land snails: two species of Hyperaulax Pilsbry, 1897 belonging to family Odontostomidae, one of which is likely extinct (Salvador and Cavallari 2019); and Ridleyconcha quinquelirata (E.A. Smith, 1890), whose shell morphology seems like a potpourri of features from several land snail families (Fig. 2A–H).

Consequently, ever since its description R. quinquelirata has been variously allocated in unrelated families: Streptaxidae, Endodontidae, Charopidae, Camaenidae and Scolodontidae (Ancey 1901, Salvador 2019b). Salvador (2019b) remarked that live-collected specimens would be necessary to settle the matter, but only dry shells were known so far, some of which apparently sub-fossil (Fig. 2F–H). Smith (1890) had mentioned live specimens in the species’ original description, but none have been collected until very recently: Freitas et al. (2019) reported live specimens of R. quinquelirata in their recent survey on Fernando de Noronha; and previous material (from 1999 and 2009) has since been found in the collection of the Museu de Zoologia da Universidade de São Paulo (MZSP; São Paulo, Brazil).

Herein, the newly found material from the MZSP collection is used to place R. quinquelirata into a molecular phylogenetic framework of stylommatophoran land snails to clarify its taxonomic position. A detailed history of the taxonomy of Ridleyconcha is also presented and its distribution in Fernando de Noronha reassessed.

MATERIAL AND METHODS

Two specimens of R. quinquelirata (registration number MZSP 89945) had a small section of tissue clipped for DNA extraction (standard protocol, QIAGEN DNEasy® Blood & Tissue Kit). Dry specimens from museum collections (including the type series) were used (after having their identity confirmed) to assess the distribution of...
R. quinquelirata within the Fernando de Noronha Archipelago. A full list of the analyzed material is presented in the Appendix. They are housed in the collections of the MZSP, NHMUK (Natural History Museum, London, UK), and NMNZ (Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand).

For the phylogenetic analysis, the following markers were targeted for amplification: (1) the barcoding fragment of the mitochondrial COI gene (primers LCO/HCO; Folmer et al. 1994); and (2) a continuous fragment of nuclear DNA containing the 3′ end of the 5.8S rRNA gene, the ITS2 region, and the 5′ end of the 28S rRNA gene (amplified in two fragments with primers LSU-1/LSU-3 and LSU-2/LSU-5; Wade and Mordan 2000; Wade et al. 2006). PCR amplification for COI consisted of: initial denaturation at 96°C (3 min); 35 cycles of denaturation at 95°C (30 s), annealing at 48°C (1 min), and extension at 72°C (2 min); final extension at 72°C (4 min). PCR products were checked via agarose gel electrophoresis, cleaned with ExoSAP-IT™ (Affymetrix Inc.), and Sanger sequenced at Massey Genome Service (Massey University, Palmerston North, New Zealand). Sequences were assembled in Geneious Prime (v. 2020.2.2, Biomatters Ltd.), quality-proofed, and uploaded to GenBank.

A phylogenetic analysis was conducted to determine the position of R. quinquelirata within the Stylommatophora. To that end, genetic sequences of 52 species (ITS2+28S marker) were extracted from GenBank as suitable representatives of Stylommatophora diversity. Emphasis was given to the families into which R. quinquelirata has been previously classified: Scolodontidae, Streptaxidae, Endodontidae, Charopidae, and Camaenidae. One species of Hygrophila (Planorbidae) and one of Veronicaellidae were chosen as outgroups. Refer to the Appendix for the full list of species and their sequences’ registration numbers.

Sequence alignment was conducted in Geneious Prime using the MUSCLE plugin (Edgar 2004) with default settings.
The phylogenetic analysis (Bayesian inference) was performed with MrBayes (v.3.2.7: Ronquist et al. 2012) via the CIPRES Science Gateway (v. 3.3: Miller et al. 2015). Two analyses were run, each with 4 Markov chains of 20 million generations (the first 20% discarded as ‘burn-in’), the default priors, nst = 6, rates = invgamma, temperature parameter = 0.1, sampling every 1,000 generations. Markov chain Monte Carlo (MCMC) convergence was assessed by examining the standard deviation of split frequencies (<0.01) in the MrBayes report and by visually examining trace plots in Geneious (Rambaut et al. 2018).

RESULTS

Taxonomic background

*Ridleyconcha quinquelirata* was originally described as *Helix (Ophiogyra?) quinquelirata* E. A. Smith, 1890 (p. 500, pl. 30, figs. 7–7c). The genus *Ridleya* Ancey, 1901 was subsequently established to house this unique species. However, Christensen (2020) noted that the name *Ridleya* was preoccupied by the sponge genus *Ridleya* Delage & Hérouard, 1899 (in turn an unjustified emendation of *Ridleia* Dendy, 1888). As such, the new name *Ridleyconcha* Christensen, 2020 was proposed.

*Ridleyconcha quinquelirata* has a history of complicated classification, having been allocated to very distinct families. As mentioned above, Smith (1890) originally (and tentatively) classified his new species in the subgenus *Ophiogyra* Albers, 1850, which is a junior synonym of *Polygyra* Gray, 1847. The monotypic genus *Polygyra* has been placed in several different helicoid families throughout the decades, but it is now classified in family Scolodontidae (Salvador and Cavalieri 2020). Fittingly, Smith (1890) remarked that his new species seemed to be closely related to *Systrophia entodonta* L. Pfeiffer, 1859 from Ecuador, also a member of Scolodontidae (MolluscaBase 2021).

Ancey (1901), when proposing the new genus *Ridleya*, commented on the similarities of *R. quinquelirata* to the chararopid genus *Helenoconcha* Pilsbry, 1892 from Saint Helena,
 Ridleyconcha was recovered as the sister taxa of Entodina jekylli Baker, 1914 with good support (Fig. 3; PP=0.96). Entodina Ancy, 1887 is widely considered a synnym or subgenus of Systrophia L. Pfeiffer, 1855, but the two Systrophia spp. used in the present analysis grouped (with low support) with Scolodonta spp. and Tamayoa decolorata (Droué, 1859) (Fig.3). It is thus possible that Entodina should be raised to genus level, though an analysis including the type species of each genus is necessary.

**DISCUSSION**

**Systematics**

Given the strong support of family Scolodontidae recovered herein (PP=1), and the position of R. quinquelirata within this group (Fig. 3), the classification of previous authors (Smith 1890, Salvador 2019b) based on conchological characters is thus supported by molecular data.

As remarked by Salvador (2019b), the following conchological features of R. quinquelirata (Fig. 2A–H) are in line with Scolodontidae, particularly with Systrophia/Entodina: smooth protoconch; large number of tightly-coiled whorls; whorl profile with slight angulations; wide-open umbilicus; aperture shape with lightly bent palatal region; reflexed peristome. The apertural lamellae of R. quinquelirata (Fig. 2A, D–F) are an unusual feature in the family, though known from some Entodina spp. and from the monotypic genus Patagocharopa Miqel and Rodriguez, 2015 from the Miocene of Argentina. The latter is presently classified in Charopidae (Salvador et al. 2020), though Salvador and Cavallari (2020) have pointed out that it is possibly a Scolodontidae.

The two parietal lamellae of R. quinquelirata are continuous, running from the first whorls until the aperture, and there are two other short basal/palatal lamellae that are more internally positioned from the aperture (Fig. 2E). The only other member of the Scolodontidae presenting internal lamellae is Polygyrata polygyrata (Born, 1778), which is reminiscent of those present in R. quinquelirata, as already pointed out by Salvador and Cavallari (2020). Those authors could not successfully extract good quality DNA from the specimens of P. polygyrata available to them, so the exact relationship of that species with R. quinquelirata remains unknown.

**Geographic distribution**

All literature sources that analyzed physical specimens refer only to the northern part of the eponymous Fernando de Noronha Island (Fig. 1) as the area inhabited by R. quinquelirata (Smith 1890, Freitas et al. 2019, Salvador 2019b). Smith (1890) also mentioned a “Platform Island”, a locality a British Island in the South Atlantic, but suggested a placement in Streptaxidae instead. Ancy (1901) also remarked on the similarities with the North and Central American genera Thysanophora Strebel & Pfeffer, 1879 (Thysanophoridae) and Sagda H. Beck, 1837 (Sagdidae).

Thiele (1931) not only placed Ridleyconcha in Endodontidae, but also considered it a junior synonym of Ptychodon Ancy, 1888, a genus endemic to New Zealand (and currently classified in Charopidae; MolluscaBase 2021). Further authors followed this placement (Morretes 1949, Lopes and Alvarenga 1955, Zilch 1959, Miquel and Cádiz Lorca 2008), but treated Ridleyconcha either as a subgenus of Ptychodon (Zilch 1959) or as a distinct genus (Morretes 1949; Lopes and Alvarenga 1955; Miquel and Cádiz Lorca 2008). It is, however, a very unlikely classification given that the Endodontidae are restricted to the Pacific Islands (Solem 1976, Christensen 2020, Salvador et al. 2020). It has been common practice in later publications to move the supposed South American “endodontids” to its related and native family Charopidae (Salvador and Simone 2013). As such, more recent classifications of Ridleyconcha reflected this (Schileyko 2001, Salgado and Coelho 2003). More specifically, Schileyko (2001) placed the genus in the subfamily Rotadiscinae, remarking that it was subfossil (and thus, extinct).

Curiously, in his catalog of Brazilian land and freshwater gastropods, Simone (2006) placed Ridleyconcha in Camaenidae, a family now restricted to Asia and Oceania (Sei et al. 2017, Calcutt et al. 2020), without providing an explanation for such a choice. Later on, Salvador (2019b) agreed with the assessment of Smith (1890) and “returned” Ridleyconcha to Scolodontidae based on shell morphology. Subsequent authors have adopted that classification (Freitas et al. 2019, Christensen 2020, MolluscaBase 2021).

**Phylogenetic analysis**

The ITS2+28S fragment (ca. 1200 bp) of both specimens of R. quinquelirata was successfully sequenced (GenBank registration numbers MZ130665 and MZ130666). The COI fragment, however, had poor results after several attempts (including variations in the PCR protocol); the sequences were ambiguous and were thus discarded.

The ITS2+28S sequences of R. quinquelirata were put into a phylogenetic framework spanning all Stylommatophoran superfamily-level clades, as well as for the Limacoidea infraorder. The phylogenetic analysis supports the inclusion of Ridleyconcha quinquelirata in the Scolodontidae with maximum support (Fig. 3; posterior probability PP=1). Ridleyconcha was recovered as the sister taxa of Entodina jekylli Baker, 1914 with good support (Fig. 3; PP=0.96). Entodina Ancy, 1887 is widely considered a synonym or subgenus of Systrophia L. Pfeiffer, 1855, but the two Systrophia spp. used in the present analysis grouped (with low support) with Scolodonta spp. and Tamayoa decolorata (Droué, 1859) (Fig.3). It is thus possible that Entodina should be raised to genus level, though an analysis including the type species of each genus is necessary.
Figure 3. Bayesian Inference tree showing the position of *Ridleyconcha quinquelirata* among the stylommatophoran gastropods. The families into which *R. quinquelirata* has been historically classified are highlighted for convenience (note that Charopidae is paraphyletic, as previously reported by Salvador *et al.* 2020). The nodes show the posterior probabilities (0 to 1). Scale bar is substitutions per site.
that was repeated in the catalogues of Morretes (1949) and Simone (2006). Ridley (1890), in his introduction to the zoology of Fernando de Noronha, likewise mentioned that many terrestrial gastropods were found on “Platform Island”. However, there is no such island in the records of the archipelago (Pessoa 2014, Assis et al. 2018). The scientific literature in English and French mentions this island repeatedly (e.g., Renard 1882, Lea 1888, Ridley 1890, Smith 1890), so the name “Platform” is likely a misinterpretation (or mistranslation from Portuguese) of the name of one of the small islands or islets in Fernando de Noronha. By the geological description of “Platform Island” given by Renard (1882), and his comparison with Rata Island, it is possible that “Platform Island” refers to one of the islets between Fernando de Noronha and Rata Islands (Fig. 1), although it is presently not possible to confirm this.

The examination of the present material (see the Appendix) contradicts the assertion that the population of R. quinquelirata is restricted to the northern portion of Fernando de Noronha Island. While most specimens have been collected on the north, a few specimens collected in 1999–2009 come from southern localities (e.g., Mangue do Sueste), thus expanding the known range of the species on the island. Furthermore, new records are here reported from Rata Island, located to the northeast of Fernando de Noronha Island (Fig. 1).

Habitat

Until the observations of Freitas et al. (2019), nothing was known about the habits of R. quinquelirata other than the fact that most specimens had been recovered from littoral areas. Those authors observed live individuals alone or in small groups (up to 6) sheltered under fallen bark or under wood debris and rocks on the ground. Some of the present specimens (dry shells only, but in good condition) were collected on dunes (see the Appendix), so it is likely individuals of R. quinquelirata also live on the ground amid the dunes’ vegetation.

The placement of R. quinquelirata in Scolodontidae might also have some ecological implications. Members of this family are generally carnivorous, feeding on snails and earthworms (Barker and Efford 2004, Hausdorf 2006, Ramirez et al. 2012, Miquel and Bungartz 2017, Miquel 2020). Thus, in principle, it is expected that R. quinquelirata is also a predatory species.

CONCLUSION

The results of the molecular phylogeny place Ridleyconcha confidently within the Scolodontidae, supporting the latest revision based on conchological characters (Salvador 2019b). Considering the present sampling, Ridleyconcha appears to be the sister taxa of Entodina. Ridleyconcha quinquelirata can still be found alive in Fernando de Noronha archipelago and, while still uncommon, has a broader distribution than previously reported.

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LITERATURE CITED


Talavera, G. and J. Castresana. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks...


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APPENDIX

Material analyzed

Below is listed all the material analyzed for the present work. Species identification was confirmed by the author.

Abbreviations: col. = collector(s); colln. = collection; sh = dry shell; spm = ethanol-preserved specimen; MZSP = Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil); NHMUK = Natural History Museum (London, UK); NNMZ = Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand).

Syntypes: NHMUK 1988.6.27.135–140 (6 sh; Fernando de Noronha, north end of island; col. G.A. Ramage, viii–ix/1887; presented by the Royal Society of London). Further specimens: MZSP 593 (>50 sh; Fernando de Noronha); MZSP 17052 (22 sh; Fernando de Noronha; ex F.L. Morretes colln.); MZSP 31306 (2 spm; Fernando de Noronha, trail between Baía dos Porcos and Praia do Sancho; col. L.R.L. Simone, 21/vii/1999); MZSP 31677 (>50 sh; Fernando de Noronha, Enseada da Caieira; col. C.M. Martins, 23/vii/1999); MZSP 31683 (4 spm; Fernando de Noronha, Praia do Sueste; col. C.M. Martins, 20/vii/1999); MZSP 31689 (4 spm; Fernando de Noronha, Praia do Meio; col. C.M. Martins, 17–23/vii/1999); MZSP 47598 (4 sh; Fernando de Noronha; ex F.L. Morretes colln.); MZSP 48142 (>50 sh; Fernando de Noronha, Enseada da Caieira, on dunes; col. E.F. Nonato, 25/vii/1955); MZSP 48146 (22 sh; Fernando de Noronha, Enseada da Caieira, on dunes; col. E.F. Nonato, 25/vii/1955); MZSP 48989 (12 sh; Fernando de Noronha, Enseada da Caieira, 3°50'19"S 32°24'40"W; col. L.R.L. Simone, 03/v/2005); MZSP 49088 (>50 sh; Fernando de Noronha, in front of Morro Dois Irmãos and Cacimba do Padre; col. L.R.L. Simone, 03/v/2005); MZSP 49091 (14 sh; Fernando de Noronha, in front of Morro Dois Irmãos and Cacimba do Padre; col. L.R.L. Simone, 03/v/2008); MZSP 52288 (>50 sh; Fernando de Noronha); MZSP 86543 (8 sh; Fernando de Noronha, Praia do Porto, 3°50’11”S 32°24’40”W; col. L.R.L. Simone, C.M. Cunha & E.P. Gonçalves, 28/x/2007); MZSP 89930 (>100 sh; Fernando de Noronha, 3°50’15”S 32°24’05”W; col. L.R.L. Simone & C.M. Cunha, iii/2009); MZSP 89941 (1 spm; Fernando de Noronha, Mirante, 3°50’21”S 32°24’10”W; col. L.R.L. Simone & C.M. Cunha, 12/iii/2009); MZSP 89945 (7 spm; Fernando de Noronha, Mirante, 3°50’21”S 32°24’10”W; col. L.R.L. Simone & C.M. Cunha, 12/iii/2009); MZSP 89994 (1 sh; Fernando de Noronha, Praia do Sueste, 3°52’03”S 32°25’32”W; col. L.R.L. Simone & C.M. Cunha, 09/iii/2009); MZSP 112946 (1 sh; Fernando de Noronha, Ilha da Rata, 3°48’49”S 32°23’27”W; col. L.R.L. Simone, 07/v/2013); MZSP 113488 (12 sh; Fernando de Noronha, Enseada da Caieira; col. C. Bardelli, vi/1994; ex J. Vaz colln.); MZSP 114195 (1 sh; Fernando de Noronha; col. A. Nüssenbaum; ex J. Vaz colln.); MZSP 119097 (>50 sh; Fernando de Noronha, Enseada da Caieira, on dunes, 3°50’12”S 32°24’04”W; col. L.R.L. Simone, 06/v/2013); NNMZ M.205844 (19 sh; Fernando de Noronha; ex H.A. Suter colln. 5635).

Sequence data

Below are listed the species used in the phylogenetic analysis, with the GenBank registration number of their ITS2+28S sequences. The species are presented in alphabetical order for ease of use. Note that some specimens may not have sections of the ITS2 or the 28S markers.