

Taxonomic revision of the genus *Hyperaulax* Pilsbry, 1897 (Gastropoda, Stylommatophora, Odontostomidae)

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Abstract

The genus *Hyperaulax* Pilsbry, 1897 comprises two living species endemic to the oceanic Fernando de Noronha Archipelago, off north-eastern Brazil. They are currently allocated in two subgenera, *Hyperaulax* s. str. and *Bonnanius* Jousseume, 1900, belonging to the family Odontostomidae. Herein we present a taxonomic revision of these species, assessing their familiar allocation within Orthalicoidea, offering updated diagnoses and descriptions, figuring the type materials and further relevant specimens, and providing barcoding DNA sequences. We conclude that *Bonnanius* is a junior synonym of *Hyperaulax*, which is classified in Odontostomidae. The genus contains two valid species, *H. ridleyi* and *H. ramagei*, both endemic to Fernando de Noronha.

Key Words

Bonnanius, endemic species, Fernando de Noronha, island speciation, Orthalicoidea, Pulmonata

Introduction

The genus *Hyperaulax* Pilsbry, 1897 had a unique composition. It comprised two living species endemic to the oceanic Fernando de Noronha Archipelago off Brazil, *H. ridleyi* (Smith, 1890) and *H. ramagei* (Smith, 1890), and eight species from Tampa Silex beds (Oligocene) of Florida, USA: *H. americanus* (Heilprin, 1887), *H. ballistae* (Dall, 1915), *H. floridanus* (Conrad, 1846), *H. heilprinianus* (Dall, 1890), *H. remolinus* (Dall, 1915), *H. stearnsii* (Dall, 1890), *H. tampae* (Dall, 1915), and *H. tortilla* (Dall, 1915). Suspecting this could not reflect an actual relationship, the fossil species previously assigned to *Hyperaulax* were revised by Auffenberg et al. (2015). Those authors concluded that the fossils bore only a superficial similarity to *Hyperaulax* and erected the new genus *Tocobaga* Auffenberg et al., 2015 to house the North American fossil species, which they classified in the Bulimulidae rather than in Odontostomidae. Auffenberg et al. (2015) considered most of the fossil forms to be synonymous and rec-

ognized only three valid species: *Tocobaga americanus*, *T. floridanus* and *T. wakullae* Mansfield, 1937 (previously considered a subspecies of *T. americanus*).

The two Recent species are also not without problems, as two names are currently considered synonymous with *H. ramagei*; moreover, this species is included in the subgenus *Bonnanius* Jousseume, 1900, which can sometimes be recognized as a valid genus (e.g., Simone 2006). The peculiar morphological features of *Hyperaulax* also present some challenges, as it is reminiscent of several lineages of Orthalicoidea. The genus is usually placed in Odontostomidae, but it also bears resemblance to insular Bulimulidae from the Galapagos; furthermore, *Hyperaulax* had also been assigned to the extinct family Grangerellidae by Henderson (1935), although this author suggested this based on Oligocene material from Florida (now in *Tocobaga*), not the Recent Brazilian species (for a full discussion see Auffenberg et al. 2015).

Therefore, herein we conducted a taxonomic review of the two Recent species of *Hyperaulax*, assessing their

familiar allocation within Orthalicoidea and the validity of the subgenus *Bonnanus* and of the two species synonymized with *H. ramagei*. Furthermore, an updated diagnosis and description, alongside images of the type and additional materials, is provided here for each species.

Methods

Fernando de Noronha is an archipelago located ca 350 km off northeastern Brazil ($3^{\circ}50'–3^{\circ}52'S$, $32^{\circ}24'–32^{\circ}28'W$) originating from extinct volcanic structures estimated to be 1.8–12.4 Ma old. It comprises the main island of Fernando de Noronha (17 km²) and over 20 smaller islands and rocks (Fig. 1). The local climate is dry tropical with a mean annual rainfall of 1,300 mm and a mean annual temperature of 25.4 °C. It has strong oceanic influence, with two well-defined seasons: dry from August to January and rainy from February to July (Fávaro et al. 2006; Marques et al. 2007). The vegetation on the islands has close affinities with the Atlantic Rainforest, though only 5% of the original cover remains (Claudino-Sales 2019). Even so, the islands are rich in endemic species of plants and animals but have a low overall diversity compared to the mainland, which is especially true for terrestrial snails, of which there are three known endemic species (Lopes and Alvarenga 1955). The entire area totals

112.7 km² including land and sea; it was designated as an environmental protection area by the Brazil in 1989 and became a World Heritage Site in 2001. Nevertheless, the islands are populated and suffer the negative impacts of overtourism and pollution (Claudino-Sales 2019).

All the type specimens were analyzed and the main museum collections worldwide that could contain material of *Hyperaulax* were visited or contacted for loans or photographs and information of their specimens. The type materials are illustrated herein, alongside additional specimens to thoroughly show conchological variation. Shell measurements were taken with a digital caliper. SEM images of the protoconchs were obtained at the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany).

The material studied in the present work is housed in the following collections: ANSP, Academy of Natural Sciences of Drexel University (Philadelphia, USA); MNHN, Muséum national d'Histoire naturelle (Paris, France); MNZ, Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand); MZSP, Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil); NHMUK, Natural History Museum (London, UK); USNM, Smithsonian Institution National Museum of Natural History (Washington, DC, USA); ZMB, Museum für Naturkunde, Leibniz Institute for Evolution and Bio-



Figure 1. Map showing the location of Fernando de Noronha, Brazil.

diversity Science (Berlin, Germany); ZSM, Zoologische Staatssammlung München (Munich, Germany).

The following abbreviations are used herein for shell dimensions: H, shell height (parallel to coiling axis); D, greatest shell width (perpendicular to H); h, aperture height (maximum length parallel to aperture plane); d, aperture width (maximum width parallel to aperture plane); W, number of whorls of shell (approximated to closest quarter); w = number of whorls of protoconch (approximated to closest quarter).

Two adult specimens of *H. ridleyi* from lot MZSP 89940 had a fraction of their foot clipped for molecular study. No specimen of *H. ramagei* with preserved soft parts is known. Given our suspected systematic affinity of *Hyperaulax*, we also sequenced a specimen of *Tomigerus corrugatus* Ihering, 1905 (lot MZSP 43077). DNA extraction was carried out with QIAGEN DNeasy Blood & Tissue Kit, standard protocol. We targeted the barcoding fragment of the mitochondrial COI gene (primers LCO and HCO of Folmer et al. 1994), with circa 650 bp. The PCR protocol was set as: (1) initial denaturation at 96 °C (2 minutes); (2) denaturation at 94 °C (30 seconds); (3) annealing at 48 °C (1 minute); (4) extension at 72 °C (2 minutes); (5) repeat steps (2) to (4) 34 times, for a total of 35 cycles; (6) final extension at 72 °C (5 minutes). PCR products were quantified via agarose gel electrophoresis, cleaned with ExoSAP-IT™ (Affymetrix Inc.), and Sanger sequenced. The sequences were assembled and quality-checked in Geneious Prime (version 2019.0.3, Biomatters Ltd), and uploaded to NCBI GenBank under the accession numbers [MN175954](#) and [MN175955](#) (*H. ridleyi*) and [MN175956](#) (*T. corrugatus*).

Additional orthalicoid COI sequences were obtained from GenBank, originating from the work of Breure and Romero (2012; see Appendix 1 for accession numbers). We excluded some species from those authors' dataset, namely those with uncertain identification, incomplete sequences, and the basal-most taxa (e.g., Bothriembryontidae, Megaspiridae), which could bring too much noise to the analysis. We used one Planorbidae as outgroup (sequence from GenBank, see Appendix 1). A total of 35 species were used from that work; sequences were 654 bp long, with the exception of the outgroup, with 669 bp due to an indel.

All sequences were aligned in Geneious Prime with the MUSCLE plugin (Edgar 2004; default settings, accuracy-optimized) and further proofed manually. A tree was built in Geneious Prime by Bayesian Inference (MrBayes plugin; Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003); settings: HKY85 substitution model, 200,000 burn-in length, 1,100,000 iterations.

Systematics

Superfamily Orthalicoidea

Family Odontostomidae Pilsbry & Vanatta, 1898

Genus *Hyperaulax* Pilsbry, 1897

Bulimulus (*Hyperaulax*) Pilsbry 1897a: 10; Pilsbry 1897b: 82.

Bonnanius Jousseaume 1900: 39; Schileyko 1999: 337.

Hyperaulax: Pilsbry 1901: 102; Wenz 1923: 729; Thiele 1931: 660; Henderson 1935: 145; Morretes 1949: 153; Oliveira et al. 1981: 350; Parkinson et al. 1987: 29; Schileyko 1999: 320; Salgado and Coelho 2003: 165; Simone 2006: 178; Salvador 2019: 87.

Hyperaulax (*Bonnanius*): Pilsbry 1901: 103; Thiele 1931: 661; Morretes 1949: 153; Zilch 1960: 505; Breure 1974: 52; Oliveira et al. 1981: 350.

Hyperaulax (*Hyperaulax*): Thiele 1931: 661; Morretes 1949: 153; Zilch 1960: 505; Breure 1974: 109.

Tomigerus (*Bonnanius*): Parodiz 1962: 453.

Bonnanius [sic]: Simone 2006: 178.

Type species. *Bulimus* (*Bulimulus*) *ridleyi* Smith, 1890, by original designation.

Included species. *Hyperaulax ridleyi* (Smith, 1890) and *H. ramagei* (Smith, 1890).

Diagnosis. Shell bulimoid. Protoconch sculptured by sinuous axial riblets, which can anastomose and fade on abapical region. Umbilicus surrounded by a periumbilical spiral angulation.

Description. Shell small to medium-sized, bulimoid, with ca 4–5 convex whorls; ground color cream, ochre or brown, with 1–4 lighter-colored spiral bands on lateral portion of whorls; periumbilical region completely or marginally discolored, whitish; apex (especially protoconch) usually of lighter color. Suture well-marked. Protoconch sculptured by numerous fine sinuous axial riblets, transition unclear. Teleoconch overall smooth except for axial growth lines. Aperture ovoid; peristome white, reflected, thickened, and continuous, with 0–4 apertural teeth. Umbilicus perforate, well marked.

Remarks. After Auffenberg et al. (2015) removed all fossil taxa from *Hyperaulax*, the genus was left only with two living species, *Hyperaulax ridleyi* (Fig. 2) and *H. ramagei* (Figs 3, 4), with the latter classified in the subgenus or full genus *Bonnanius*. Both species are known only from Fernando de Noronha Archipelago off north-eastern Brazil.

The genus *Bonnanius* is considered here synonymous with *Hyperaulax* as there are no diagnostic characters allowing its clear separation other than its larger shell size. The presence of teeth in the aperture of *H. ramagei* (previously classified in *Bonnanius*) could be used as a diagnostic genus-level character; however,

it is well known that odontostomid genera show great inter- and intraspecific variation in the presence and strength of apertural teeth. Moreover, some specimens of *H. ridleyi* do show a palatal tooth (Fig. 2A) similar in position and length to that of *H. ramagei*. Furthermore, for a genus with only two species, keeping them separated into two distinct subgenera is excessively zealous taxonomy. As for the other conchological characters, *Bonnanius* share all of them with *Hyperaulax*, as discussed below.

The protoconch sculpture has always been deemed a good character to define genera in Orthalicoidea and has more recently received large support from molecular studies (Breure and Romero 2012). The protoconchs of *Hyperaulax* and *Bonnanius* are very similar and indicate a close affinity between the two forms: same number of whorls (ca 1 $\frac{3}{4}$); same sculpture pattern (sinuous axial riblets, more clearly separate on adapical area of whorl, but anastomosing on abapical area and sometimes fading into scattered dots). There are also some differences on the protoconch, but nothing that would suggest two distinct genera (many genera of Orthalicoidea bear some minor differences in their protoconchs, which helps with species diagnosis; e.g., Salvador and Cavallari 2013; Salvador and Simone 2016). The main difference is that the protoconch of *H. ramagei* is more flattened and rounded, which makes the riblets a little more spaced; this can be attributed to its shell being larger and wider overall. Furthermore, the protoconch of *H. ridleyi* has a raised ridge on its middle region. Finally, the protoconch sculpture of museum specimens of *H. ramagei* is often faded or eroded, which has led to claims of a smooth protoconch in the literature (e.g., Parodiz 1962; Abbott 1989).

Other conchological characters are very similar in both *H. ridleyi* and *H. ramagei*: the roughly pentagonal shape of the aperture and its positioning in relation to the body whorl, the long palatal tooth (absent in most *H. ridleyi* specimens), the shape of the umbilicus and the periumbilical spiral angulation, the unsculptured teleoconch (except for growth striations), and the periostracum color (brown with at least one white spiral band).

The classification of *Hyperaulax* in Odontostomidae has been well supported in the literature, with just a few different classification schemes. For instance, Schileyko (1999) argued in favor of Bulimulidae because *H. ridleyi* has no teeth; however, not all odontostomids actually have teeth and some specimens of *H. ridleyi* do show a faint palatal tooth, as discussed above and already remarked by Pilsbry (1901). Moreover, *H. ridleyi* has the typical channel-like structure on the junction of the parietal and palatal regions of the peristome. Schileyko (1999), however, maintained *Bonnanius* (and hence *H. ramagei*) in Odontostomidae.

In any event, there are other conchological characters favoring an allocation within Odontostomidae, such as the elevated embryonic whorls (Auffenberg et al. 2015) and the protoconch sculpture (wavy riblets, similar to *Plagiodontes* Doering, 1876; Pizá and Cazzaniga 2016). The overall

shell shape of *Hyperaulax* is very similar to *Tomigerus* Spix, 1827 and *Biotocus* Salgado & Leme, 1990, but with a different position of the aperture in relation to the body whorl and a different structure of the umbilical region; also, the protoconch of *Tomigerus* is smooth. The periostracum color is also similar to what is seen in *Tomigerus* (e.g., *T. clausus* Spix, 1827, *T. matthewsi* Salgado & Leme, 1991, and *T. rochai* Ihering, 1905), but a striped pattern can also be found in species of *Moricandia* Pilsbry & Vanatta, 1898 and even *Anostoma* Waldheim, 1807. The dentition of *Hyperaulax* (mainly of *H. ramagei*) is similar to that of *Burringtonia* Parodiz, 1944 and also *Anctus angustomus* (Wagner, 1827). Finally, the channel-like structure on the junction of the parietal and palatal regions of the peristome is virtually identical to what is observed in some species of *Cyclodontina* Beck, 1837, *Spixia* Pilsbry & Vanatta, 1898, and *Anostoma* Waldheim, 1807.

Our analysis of interspecific affinities using the barcoding region of the COI marker has grouped *Hyperaulax* (*H. ridleyi* only) with *Tomigerus*, as expected by our morphological analysis, with a posterior probability of 0.997. However, these two species were grouped with *Simpulopsis* Beck, 1837 (family Simpulopsidae) in our Bayesian tree, instead of being grouped with other odontostomids. This is likely due to the fact that COI alone is not sufficient to solve family-level relationships among stylommatophoran snails (Breure and Romero 2012), despite being sufficient to capture the relationship of close species-level taxa. Based on morphological data, we retain *Hyperaulax* (and *Tomigerus*) in the family Odontostomidae.

It is curious that another orthalicoid lineage, from the other side of South America, evolved an uncannily similar shell shape to *Hyperaulax*: *Naesiotus wolffi* (Reibisch, 1892), from the Galapagos (lectotype ZMB 47.950, paralectotype NHMUK 1894.6.8.7). Furthermore, *N. wolffi* is within the size range of *Hyperaulax*, and has a similar color pattern to *H. ridleyi*, including the median white spiral band. The protoconch, naturally, is different (*Naesiotus* Albers, 1850 has very fine and well-defined axial striae), alongside other more general shell features: higher spire, different proportion of body whorl to spire, and a larger number of whorls (ca 6 $\frac{1}{2}$). In any event, this is a remarkable case of convergent evolution on islands and deserves further investigation.

Hyperaulax ridleyi (Smith, 1890)

Fig. 2

Bulimus (*Bulimulus*) *Ridleyi* E.A. Smith 1890: 501, pl. 30, fig. 9; Dall 1896: 415.

Bulimulus (*Hyperaulax*) *ridleyi*: Pilsbry 1897a: 10; Pilsbry 1897b: 82, pl. 14, figs 11–13.

Buliminus ridleyi: Möllendorff 1901: 126.

Hyperaulax ridleyi: Pilsbry 1901: 103; Ihering 1923: 191; Wenz, 1923: 729; Schileyko 1999: 321, fig. 396; Salgado and Coelho 2003: 165; Simone 2006: 178, fig. 637; Breure and Ablett 2012: 36, figs 20C, D, 20ii; Salvador 2019: 87.

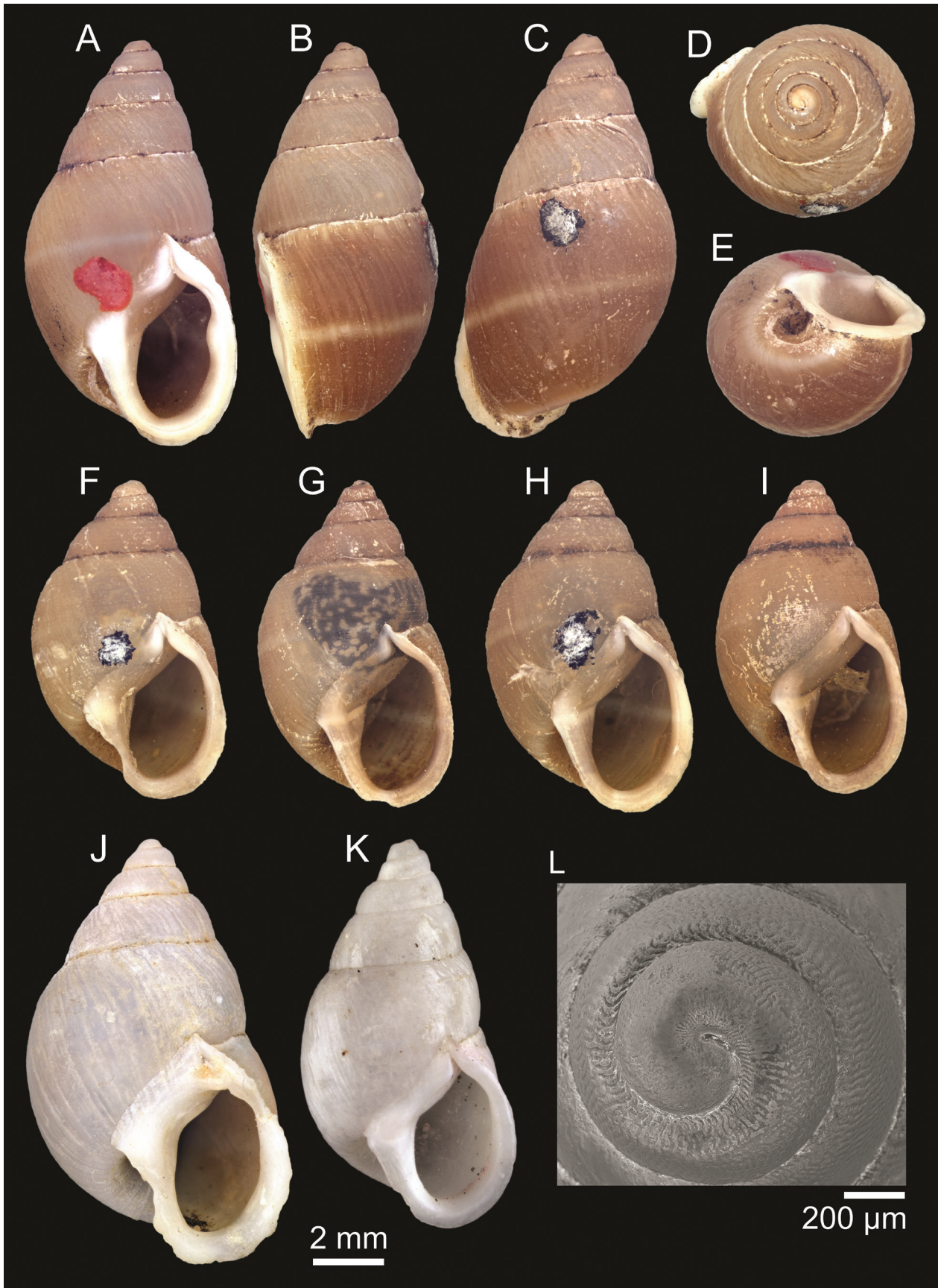


Figure 2. *Hyperaulax ridleyi*. A–E. Lectotype, NHMUK 1888.6.27.106. F–I. Paralectotypes #1 to #4 (in order), NHMUK 1888.6.27.107–110. J. Extreme form, large and with thick callus, NHMUK 1888.6.27.88–94. K. Weathered specimen, ZMS unnumbered (ex Heimburg colln.). L. Protoconch detail (same specimen from K).

Hyperaulax (*Hyperaulax*) *ridleyi*: Thiele 1931: 661; Morretes 1949: 153; Zilch 1960: 505, fig. 1771; Breure 1974: 51; Breure and Schouten 1985: 4.

Hyperaulax (s. str.) *ridleyi*: Lopes and Alvarenga 1955: 181.

Bulimus (*Bulimulus*) *ridleyi*: Oliveira and Oliveira 1984: 19.

Type locality. Fernando de Noronha Archipelago, Fernando de Noronha Island and Rata Island. Original (Smith 1890: 501): "Living under bark of Mango-trees in the garden and on north side of island; also at base of the Peak, north side, under stones, and on Rat Island."

Distribution. Known only from Fernando de Noronha Archipelago.

Type material. Lectotype NHMUK 1888.6.27.106 (designation by Breure and Ablett 2012). Paralectotypes: NHMUK 1888.6.27.107-110, 4 shells.

Material examined. Types. **BRAZIL:** Fernando de Noronha: ANSP 71271, 7 shells, H.H. Smith leg., 1896; MNZ 205835, 4 shells, ex Suter coll. 5637; ANSP 81426, 1 shell; ANSP 100530, 4 shells, H.v. Ihering leg., 1910; ANSP 220399, 2 shells, ex B.R. Bales coll., J.S. Schwengel leg., 1958; MNZ 205835, 4 shells, ex Suter coll. 5637; MZSP 501, 14 shells, 1900; MZSP 7752, 20 shells. MZSP 30134, 10 shells, dunes of Praia das Caieiras, E.F. Nonato leg., 25/vii/1955; MZSP 30135, 8 shells, de Fiore leg., 1983; MZSP 31064, 1 shell, Praia do Meio, L.R.L. Simone & Souza leg., 22/vii/1999; MZSP 31305, 30 specimens, between Baía dos Porcos and Baía do Sancho, L.R.L. Simone leg., 21/vii/1999; MZSP 31676, 14 shells, Praia das Caieiras, L.R.L. Simone et al. leg., 23/vii/1999; MZSP 31681, 15 specimens, mangrove on Praia do Sudeste, C.M. Martins leg., 20/vii/1999; MZSP 31686, 50 specimens, Praia do Meio, C.M. Martins leg., 17-23/vii/1999; MZSP 48824, 1 shell, Praia do Porto, 3°50'05"S, 32°24'04"W, L.R.L. Simone leg., 30/iv/2005; MZSP 48990, 9 shells, Praia das Caieiras, 3°50'19"S, 32°24'00"W, L.R.L. Simone leg., 3/v/2006; MZSP 49001, 11 shells, mangrove on Praia do Sudeste, 3°51'58"S, 32°25'35"W, L.R.L. Simone leg., 4/v/1005; MZSP 49089, 39 shells, in front of Morro Dois Irmãos and Cacimba do Padre, L.R.L. Simone leg., 3/v/2005; MZSP 86542, 13 shells; Praia do Porto, 3°50'11"S, 32°24'04"W, L.R.L. Simone et al. leg., 28/x/2007; MZSP 89929, >50 shells, 3°50'00"S, 32°24'05"W, L.R.L. Simone & C.M. Cunha leg., iii/2009; MZSP 89933, 17 shells, L.R.L. Simone & C.M. Cunha leg., 11/iii/2009; MZSP 89939, 2 specimens; 3°50'21"S, 32°24'10"W, L.R.L. Simone & C.M. Cunha leg., 12/iii/2009; MZSP 89940, 5 specimens, Mirante, L.R.L. Simone & C.M. Cunha leg., 11/iii/2009; MZSP 89993, 1 shell, Praia do Sudeste, 3°52'06"S, 32°25'32"W, L.R.L. Simone & C.M. Cunha leg., 9/iii/2009; MZSP 97854, 3 shells, ex J. Vaz coll., A. Nüssenbaum leg., viii/1973; MZSP 97878, 3 shells, ex J. Vaz coll., Praia das Caieiras, C. Bardelli leg., vi/1994; MZSP 119089, 23 shells, Cacimba do Pa-

dre, 3°50'36"S, 32°25'14"W, L.R.L. Simone et al. leg., 8/v/2013; MZSP 119090, 29 shells, Cacimba do Padre, 3°50'36"S, 32°25'14"W, L.R.L. Simone et al. leg., 7/v/2013; NHMUK 1888.6.27.88-94, 7 shells; NHMUK 1888.6.27.95-100, 6 shells, Rata Island; NHMUK 1888.6.27.101-105, 5 shells; NHMUK 20170270, 4 shells, H.E.J. Biggs coll., H. Fiedrick leg.; USNM 134849, 1 shell, H.A. Pilsbry leg.; USNM 214401, 1 shell, H.A. Pilsbry leg.; USNM 307580, 2 shells, Henderson coll., H. Clapp leg.; USNM 518214, 3 shells, W. Williamson leg.; ZSM no nr., 2 shells, Blume coll. 4003; ZSM no nr., 4 shells, H.H. Smith coll.

Diagnosis. The shell is smaller overall and has a more elongated and slender profile. The protoconch has a more raised ridge and its sculpture consists largely of more anastomosed riblets. Typically, there is no apertural dentition.

Description. Shell small, bulimoid, slender; spire tall; $W \sim 4\frac{3}{4}$ -5. Shell color ochre to brown; body whorl sometimes darker than rest; fine white spiral band on middle portion of whorl; periumbilical spiral angulation discolored, whitish; peristome white. Protoconch ($w \sim 1\frac{3}{4}$) rounded, with raised ridge that becomes a faint sub-sutural ridge on teleoconch; sculptured by fine sinuous axial riblets, which sometimes anastomose (especially on abapical area of whorl); transition to teleoconch unclear. Teleoconch smooth (except for growth lines). Suture well marked, but not deep. Aperture ovoid, elongated. Peristome reflected and slightly thickened; presence of small channel-like structure on division between parietal and palatal regions of aperture; parietal callus might be present in older specimens. Apertural teeth usually absent, but faint elongated tooth on middle portion of palatal region may be present (Fig. 2A). Umbilicus narrow, deep, surrounded by a periumbilical spiral angulation.

Dimensions. Lectotype: H = 11.4 mm, D = 5.9 mm, h = 4.8 mm, d = 3.0, W = $5\frac{1}{4}$, w = $1\frac{3}{4}$. Paralectotype #1: H = 9.5 mm, D = 5.3 mm, h = 4.4 mm, d = 3.0 mm, W = $4\frac{1}{2}$, w = $1\frac{1}{2}$. Paralectotype #2: H = 9.1 mm, D = 5.3 mm, h = 4.3 mm, d = 2.9 mm, W = $4\frac{1}{2}$, w = $1\frac{3}{4}$. Paralectotype #3: H = 8.9 mm, D = 5.2 mm, h = 4.3 mm, d = 2.9 mm, W = $4\frac{1}{2}$, w = $1\frac{3}{4}$. Paralectotype #4: H = 8.9 mm, D = 5.2 mm, h = 4.2 mm, d = 2.8 mm, W = $4\frac{1}{2}$, w = $1\frac{3}{4}$. Average ($n = 63$, except for w, where $n = 10$): H = 10.2 ± 1.00 mm (min = 7.8 mm, max = 12.7 mm), D = 5.7 ± 0.51 mm, h = 4.9 ± 0.45 mm, d = 3.5 ± 0.34 mm, W = $4\frac{3}{4}$ to 5 (min = $4\frac{1}{4}$, max = $5\frac{1}{2}$), w = $1\frac{3}{4}$ (occasionally $1\frac{1}{2}$).

Remarks. Other than showing a reasonable variation in shell size, the species displays little conchological variation (Fig. 2). Rare specimens, however, do deviate from the typical form, for instance by having broader shells with shorter spires (Fig. 2F-I) or by having a palatal tooth (Fig. 2A, lectotype). The color might vary from more ochre tones to more reddish-brown ones, but the single white spiral band on the mid-section of the whorl is always pres-

ent. *Hyperaulax ridleyi* can be easily distinguished from its only congener, *H. ramagei*, by its smaller shell (with a single spiral white band) and more elongated and slender shell profile. Moreover, its protoconch has a more raised ridge and the riblets of its sculpture are much more anastomosed. Finally, *H. ridleyi* typically bears no apertural dentition (although a weak palatal tooth might be present; Fig. 2A).

Unfortunately, not much can be found in the literature about this species' habitat or habits, but the museum labels point to a variety of collection locales, albeit more usually referring to dead shells only. In any event, this species has been reported alive from forested areas, mangrove, beaches, dunes, and gardens.

Hyperaulax ramagei (Smith, 1890)

Figs 3, 4

“Turbine, in cui la prima voluta è (...)” Buonanni 1681: 185, fig. Turbine #44.

Bulimus (Tomigerus) Ramagei E.A. Smith 1890: 500, pl. 30, fig. 8.

Bulimus (Tomigerus?) Ramagei: Dall 1896: 415.

Bonnanius bouvieri Jousseaume 1900: 39, pl. 1, fig. 19.

Bonnanius bonnanius Jousseaume 1900: 41.

Hyperaulax (Bonnanius) ramagei: Pilsbry 1901: 103, pl. 11, figs 60–62;

Thiele 1931: 611; Morretes 1949: 153; Lopes and Alvarenga 1955: 181; Zilch 1960: 505, fig. 1772; Breure 1974: 52; Breure 1975: 1158; Oliveira et al. 1981: 350; Parkinson et al. 1987: 29; Abbott 1989: 106, text fig.

Tomigerus (Bonnanius) ramagei: Parodiz 1962: 453.

Bulimus (Tomigerus) ramagei: Oliveira and Oliveira 1984: 19.

Bonnanius ramagei: Schileyko 1999: 339, fig. 419; Breure and Ablett 2012: 34, figs 20A, B, 20i.

Hyperaulax ramagei: Salgado and Coelho 2003: 165; Salvador 2019: 87.

Bonnanius [sic] *ramagei*: Simone 2006: 178, fig. 638.

Type locality. Fernando de Noronha Archipelago, Fernando de Noronha Island, Ponta do Tabaco. Original (Smith 1890: 500): “imbedded in sandy mud on a raised reef at Tobacco Point (G.A. Ramage leg.)”.

Distribution. Known only from Fernando de Noronha Archipelago.

Type material. Lectotype NHMUK 1888.6.27.163 (designation by Breure and Ablett 2012). Paralectotypes: NHMUK 1888.6.27.164–170, 7 shells.

Material examined. Types. **BRAZIL:** Fernando de Noronha: ANSP 100531, 4 shells, H.v. Ihering leg., 1910; MNZ 205835, 4 shells, ex Suter coll. 5637; MNHN-IM-2000-28020 syntype of *Bonnanius bouvieri*, Jousseaume coll.; MNZ 205822, 5 shells, ex Suter coll. 5639; MZSP 7738, 14 shells; MZSP 97933, 3 shells, ex J. Vaz coll., A. Nüssenbaum leg., viii/1973; NHMUK 1902.10.16.4, 1 shell; MZSP 131996, 3 shells, Ponta das Caracas, 3°52'28"S, 32°25'24"W, F. Schunck leg., 27/ix/2013; NHMUK 20170271, 13 shells, from sand

on north end of island, 16/vi/1887; USNM 518215, >30 shells, W. Williamson leg.; USNM 709805, >30 shells, dunes in Porto Santo Antônio, L. Storrs et al. leg., vii–viii/1973; USNM 709806, >30 shells, Porto Santo Antônio, L. Storrs et al. leg.; ZSM 7861, 1 shell, 1940; ZSM no nr., 3 shells.

Diagnosis. The shell is larger overall and has a broader profile. The riblets on the second part of the protoconch are more defined. The peristome is strongly thickened and displays marked apertural teeth.

Description. Shell medium-sized, bulimoid, rounded; $W \sim 4\frac{1}{2}$. Shell color chestnut brown; spire apex light brown to cream-colored; up to four equidistant white spiral bands might be present on lateral portion of whorls (but entirely brown morphs also occur); periumbilical region usually discolored, whitish; peristome and apertural teeth white. Protoconch ($w \sim 1\frac{3}{4}$) rounded; first $\frac{1}{2}$ whorl presenting undefined anastomosing sculpture; remainder sculptured by fine sinuous axial usually well-defined riblets (but sometimes anastomosed in some areas) that become less pronounced towards teleoconch; transition to teleoconch unclear (but sometimes with thickening of the last riblet). Teleoconch smooth (except for growth lines, which become more marked towards aperture). Suture well-marked, but not deep. Aperture roughly ovoid, but angulate. Peristome reflected and strongly thickened; some older specimens show continuous thickening of the peristome; parietal callus might be present in older specimens. Apertural teeth present: two knob-like parietal teeth positioned slightly towards the interior of shell (not always present); long palatal tooth in the middle portion of palatal region (its surface goes from smooth to serrated, with up to three distinct points); columellar tooth elongated, with smooth surface. Both columellar and palatal tooth produce a marked depression on outer wall of shell. Umbilicus slit-like.

Dimensions. Lectotype: $H = 17.3$ mm, $D = 12.3$ mm, $h = 8.8$ mm, $d = 6.6$, $W = 4$, $w = 2$. Paralectotype #1: $H = 22.3$, $D = 15.6$ mm, $h = 10.9$ mm, $d = 7.7$ mm, $W = 4\frac{3}{4}$. Paralectotype #2: $H = 23.5$ mm, $D = 16.0$ mm, $h = 11.2$ mm, $d = 8.7$ mm, $W = 5$. Paralectotype #3: $H = 19.5$ mm, $D = 14.6$ mm, $h = 10$ mm, $d = 7.2$ mm, $W = 4\frac{1}{2}$, $w = 1\frac{3}{4}$. Paralectotype #4: $H = 19.6$ mm, $D = 13.7$ mm, $h = 8.8$ mm, $d = 6.7$ mm, $W = 4\frac{1}{2}$. Paralectotype #5: $H = 20.3$ mm, $D = 13.2$ mm, $h = 9.8$ mm, $d = 7.4$ mm, $W = 4\frac{3}{4}$, $w = 1\frac{3}{4}$. Syntype of *Bonnanius bouvieri*: $H = 22.5$ mm, $D = 15.4$ mm (Breure, 1975). Average ($n = 34$, except for w , where $n = 10$): $H = 17.9 \pm 1.56$ mm (min = 16.1 mm, max = 22.0 mm), $D = 12.9 \pm 0.96$ mm, $h = 9.7 \pm 0.71$ mm, $d = 7.6 \pm 0.63$ mm, $W = 4\frac{1}{2}$ (min = $4\frac{1}{4}$, max = 5), $w = 1\frac{3}{4}$ (occasionally 2).

Remarks. The names *H. bouvieri* and *H. bonnanius* were synonymized with *H. ramagei* by Pilsbry (1901); this decision is followed here. The syntype of *H. bouvieri* (Fig.

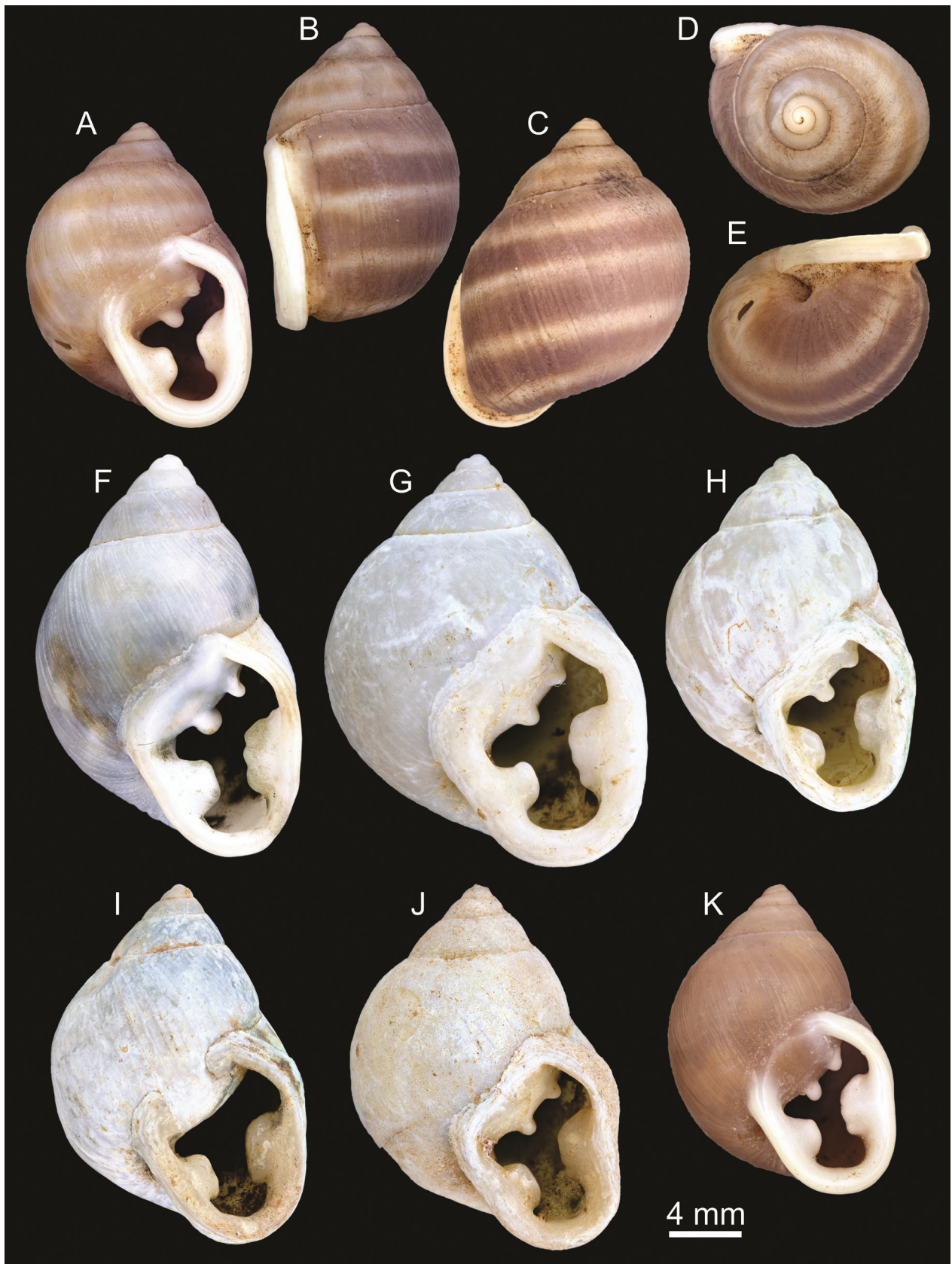


Figure 3. *Hyperaulax ramagei*. A–E. Lectotype, NHMUK 1988.6.24.163. F–J. Paralectotypes #1 to #5 (in order), including large forms in apparent sub-fossil state, NHMUK 1988.6.24.164-170. K. Specimen without the white spiral bands, NHMUK 1902.10.16.4.

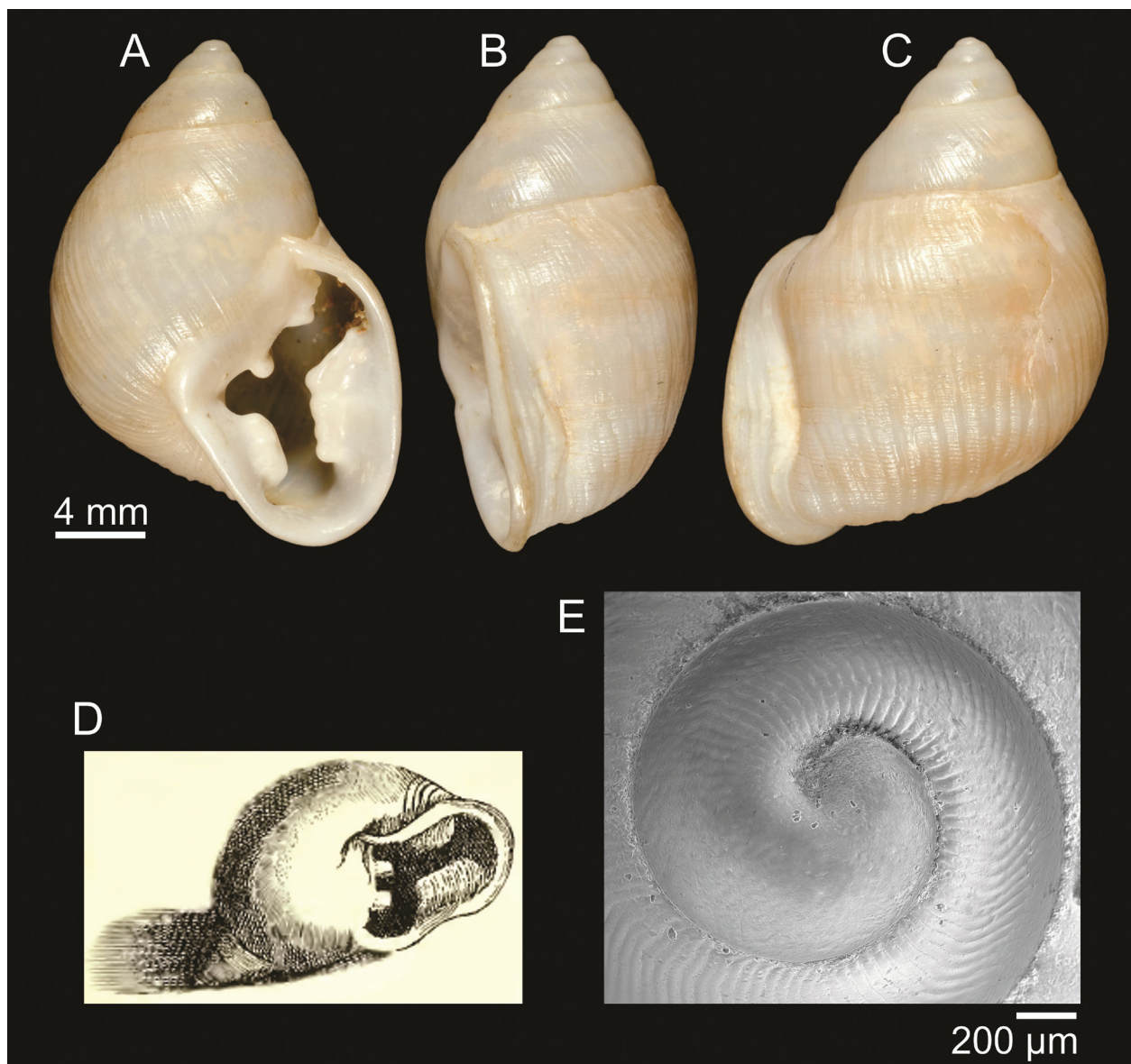


Figure 4. *Hyperaulax ramagei*. **A–C.** Syntype of *Bonnanus bouvieri*, MNHN-IM-2000-28020 (MNHN). **D.** Reproduction of “Turbine #44” of Buonanni (1861), the holotype of *Bonnanus bonnanius*. **E.** Protoconch detail, NHMUK 1902.10.16.4.

4A–C) is indistinguishable from *H. ramagei*, but the discussion regarding *H. bonnanius* is slightly more colorful and it is worthwhile to recapitulate it here. Its original description (Jousseume 1900) was based upon the work of the Jesuit scholar Filippo Buonanni (1638–1723), who compiled the first conchology manual (Buonanni 1681) and is thus considered the Father of Conchology (Leonhard 2007). As Pilsbry (1901) argued, Buonanni’s (1681) description of his Turbine #44 and its illustration (allowing for some distortion in the drawing) are vastly consistent with *H. ramagei*. Despite later authors such as Linnaeus having relied on Buonanni’s work, this particular species was overlooked until Jousseume (1900) published it as *Bonnanus Bonnanius*, misspelling the Jesuit’s name and likely without knowing the work of Smith (1890).

The shell features of *H. ramagei* display some morphological variation: (1) shell size, from some rather

small specimens to very large ones ($H_{\min} = 16$ mm and $H_{\max} = 22$ mm); (2) shell color can go from entirely brown to marked with four white spiral bands; (3) aperture size, relative to remainder of the shell; (4) shell shape, with some specimens having a much shorter spire (Fig. 3A–C, lectotype); (5) two parietal teeth might be absent (Fig. 3I); (6) the surface of the palatal tooth goes from nearly smooth (Fig. 3I, J) to serrated (Fig. 3F, G), with up to three distinct points (Fig. 3A), reminiscent of the carnassial tooth of Carnivora (apparently this is not related to the age of the individual or to the freshness of the specimen when collected). The syntype of *H. bouvieri* show a four-pronged palatal tooth, which is also unusually large, and a three-pronged parietal tooth (Fig. 4A–C); this could be seen as morphological variation, but, as this specimen bears a mark of breakage near the aperture and further growth (Fig. 4C), it could be simply post-trauma anom-

alous growth. For a comparison with its single congener, *H. ridleyi*, see the Discussion section of that species.

Some of the specimens available (including some paratypes) appear to be of a sub-fossil state, as already noted by Smith (1890). These appear to be larger than the fresh specimens, but this could be due to collection bias towards larger specimens; at present, there is not enough sub-fossil material for a statistically meaningful assessment.

Conclusions

Hyperaulax is here classified in the Odontostomidae and presently contains two species, *H. ridleyi* and *H. ramagei*, both endemic to Fernando de Noronha Archipelago. This genus seems to be more closely related to *Tomigerus* than to other odontostomids.

According to recent collection events on Fernando de Noronha, *H. ramagei* cannot be found alive in spite of meaningful search efforts (L.R.L. Simone personal communication). In fact, museum specimens of *H. ramagei* still bearing the periostracum typically date back to the first half of the 20th century. It is a troubling possibility that presently this species has a much-reduced range or is altogether extinct. Future collection efforts should focus on this species to properly define its status according to current guidelines for conservation (IUCN 2012).

Finally, another curious aspect of the fauna of Fernando de Noronha deserving further study is *Amphisbaena ridleyi* Boulenger, 1890, an amphisbaenid (worm lizard) endemic to the archipelago that possesses adaptations for a durophagous diet including a large proportion of land snails (Pregill 1984). In the original report, the author could not indicate which species of terrestrial gastropods were part of the lizard's diet and a study involving this species and possible defensive adaptations of the snails would be very welcome.

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Appendix 1

Below are listed the COI sequences of other Orthalicoidea species, obtained from the work of Breure and Romero (2012), used to ascertain the classification of the species studied herein. The list is organized by family and species (in alphabetical order), followed by the respective GenBank accession number. Bulimulidae: *Bostryx agueroi* JF514623; *Bostryx bilineatus* JF514637; *Bostryx edmundi* JF514622; *Bostryx longispira* JF514624; *Bostryx strobili* JF514636; *Bostryx superbus* JF514621; *Bulimulus diaphanus* JF514633; *Bulimulus guadalupensis* JF514630; *Bulimulus hummelincki* JF514629; *Bulimulus sporadicus* JF514632; *Bulimulus tenuissimus* JF514631; *Drymaeus inusitatus* JF514648; *Drymaeus laticinctus* JF514646; *Drymaeus multifasciatus* JF514647; *Drymaeus serratus* JF514649; *Drymaeus vexillum* JF514625; *Naesiotus quitensis* JF514635; *Naesiotus stenogyroides* JF514650; *Neopetraeus tessellatus* JF514627; *Rabdotus alternatus* JF514638; *Scutalus chiletensis* JF514628. Odontostomidae: *Clessinia cordovana cordovana* JF514618; *Clessinia cordovana stelzneri* JF514617; *Clessinia pagoda* JF514613; *Cyclodontina guarani* JF514619; *Plagiodontes multiplicatus* JF514620; *Spixia pervarians* JF514614; *Spixia philippii* JF514612; *Spixia popana* JF514616; *Spixia tucumanensis* JF514615. Simpulopsidae: *Leiostracus perlucidus* JF514640; *Simpulopsis decussata* JF514639.

The sequence of the outgroup taxon was obtained from GenBank: *Planorbis planorbis* EF012175 (Planorbidae).