



# One for each ocean: revision of the *Bursa granularis* (Röding, 1798) species complex (Gastropoda: Tonnoidea: Bursidae)

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**One for each ocean: revision of the *Bursa granularis* (Röding, 1798) species complex  
(Gastropoda: Tonnoidea: Bursidae)**

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Running title: *BURSA GRANULARIS* COMPLEX

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**ABSTRACT**

*Bursa granularis* (Röding, 1798) is a tonnoidean gastropod viewed as broadly distributed throughout the Indo-Pacific and tropical western Atlantic. Because of its variable shell it received no less than thirteen names, now all synonymized under the name *B. granularis*. We sequenced a fragment of the *cox1* gene for 82 specimens covering a large part of its distribution and most type localities. Two delimitation methods were applied, one based on genetic distance (ABGD) and one based on phylogenetic trees (GMYC). All analyses suggest that specimens identified as *B. granularis* comprise four distinct species: one limited to the tropical western Atlantic; another to southwestern Western Australia; and two in the Indo-Pacific, from the Red Sea to the open Pacific, partly sympatric - but not syntopic - in Japan, the Philippines, Vanuatu and New Caledonia. Based on shells characters, we applied available names to each of the four species, respectively *B. cubaniana* (d'Orbigny, 1841), *B. elisabettae* Nappo, Pellegrini & Bonomolo, 2014, *B. granularis* s.s., and *B. affinis* Broderip, 1833, and we provide new standardized conchological descriptions for all of them. Our results demonstrate that a long planktotrophic larval stage, common among Tonnoidea, does not necessarily ensure a circum-tropical species distribution.

**INTRODUCTION**

Tonnoideans are a rather small superfamily of Caenogastropoda (~357 species, WoRMS 2017) related to the neogastropods, either as its sister group (Zou *et al.* 2011) or belonging in Neogastropoda (Colgan *et al.*, 2007; Cunha *et al.*, 2009; Hayashi, 2005; Williams *et al.*, 2014, Osca *et al.*, 2015). Notwithstanding the non-planktotrophic development of a few Australian species, one of the characteristic features of tonnoidean gastropods is their long to extremely long planktonic larval stages, named teleplanic larvae [based on the Greek *tele*, distant, and *planos*, wandering; Scheltema (1971)]. The record has been observed for a larva of *Fusitriton oregonensis* Redfield, 1846 (Ranellidae), which lived in an aquarium for 4.5 years without metamorphosing (Strathmann & Strathmann, 2007). An indirect estimation of the duration of larval life was also proposed by Scheltema (1972) who, based on the extent of the distribution area and the speed of ocean currents, inferred the time it would take for the larvae to cross ocean basins — generally several months. Conversely, and in quite circular reasoning, the duration of this larval time led to the hypothesis that some species may have trans-oceanic dispersal capabilities (e.g., Scheltema, 1966, 1968, 1971, 1972, 1986a, 1986b, 1988; Laursen, 1981; Pechenik *et al.*, 1984), resulting in a cosmopolitan distribution. Scheltema (1971, table 1) also kept larvae alive in an aquarium that had been collected in the plankton, and found that some taxa lived as planktonic veliger larvae for several months [e.g., *Monoplex nicobaricus* (Röding, 1798) lived for 390 days in captivity].

As in most other marine gastropods, tonnoidean species were described based on features of the teleoconch, using a limited number of specimens and characters. The available material of many species of Bursidae described before 1960 rarely exceeded three specimens. Because of this limited evaluation of the intraspecific variability, numerous new species were described for every newly recognized morphological form. When additional material became available, malacologists realized that they may have greatly underestimated the intraspecific shell variability, since supposedly geographically restricted species were actually morphologically highly similar to other nominal species from other localities, moreover sharing identical protoconchs. This was the first step towards an important synonymization trend in tonnoidean systematics. Also, taking into account the expected great dispersal abilities, modern authors (e.g., Beu, 1998, Nappo *et al.*, 2014) followed the path led by Scheltema to the point where some very well-defined morphs were ranked as no more than subspecies. They thus recognized a smaller number of species, but with trans-oceanic distributions.

Among the Tonnoidea, the family Bursidae includes 54 Recent species (WoRMS 2017), among which several are potentially species complexes, i.e., species for which

alternative hypotheses of delimitation have been proposed in the literature. In particular, the *Bursa granularis* complex, already identified as such by Castelin *et al.* (2012), is typically recognized as a single species by modern authors (Beu, 1998, 2005, 2010), although sometimes with subspecies (Nappo *et al.*, 2014). According to both the literature and the GBIF database (2016) (Fig. 1), *B. granularis* has a subtropical and tropical distribution throughout the Indo-West Pacific, the eastern Pacific, and the tropical western Atlantic. [In the eastern Atlantic, it has only been recorded from the Cape Verde Islands (Garcia-Talavera, 1983, cited by Beu 1998), but this record is unconfirmed by Rolán (2005).] This distribution would make it one of the most cosmopolitan species among the Tonnoidea. However, this apparently cosmopolitan species has received no fewer than ten names (Beu, 1998). WoRMS (2017) lists 13 synonyms of *Tritonium granulare* Roding, 1798: *Tritonium jabick* Roding, 1798, *Biplex rubicola* Perry, 1811, *Ranella granifera* Lamarck, 1816, *Ranella affinis* Broderip, 1833, *Ranella cubaniana* d'Orbigny, 1841, *Ranella livida* Reeve, 1844, *Bursa cumingiana* Dunker, 1862, *Bursa alfredensis* Turton, 1932, *Bursa kowiensis* Turton, 1932, *B. cubaniana intermedia* Nowell-Usticke, 1959, *Bursa corrugata lineata* Nowell-Usticke, 1959 and *Bursa granularis elisabettae* Nappo, Pellegrini & Bonomolo, 2014. The numerous alternative species hypotheses led to various usages of these names in the literature; whereas 19th century authors (e.g. Reeve, 1844b) recognized up to four different species, the last revision proposed to group them all under the name *Bursa granularis* (Beu, 1998). Two of these, however — *B. granularis cubaniana* (d'Orbigny, 1841) and *Bursa granularis elisabettae* Nappo, Pellegrini & Bonomolo, 2014 — are accepted by Nappo *et al.* (2014) at the rank of subspecies besides the nominate subspecies *Bursa granularis granularis* (Röding, 1798).

Using several molecular markers, Castelin *et al.* (2012) identified two morphologically distinct clades within the *Bursa granularis* complex. Interestingly, these two clades were found in sympatry in Vanuatu, at similar depths, and the authors suggested that additional sampling would be needed to clarify species delimitations within the group. We increased the size of the dataset, including both additional species from the same geographical region sampled by Castelin *et al.* (2012) and samples from other localities, with a particular focus on type localities, covering a large part of the global distribution of the *Bursa granularis* complex. Our goal is to clarify the species delimitation within the *Bursa granularis* complex and to test the hypothesis that this species has a world-wide geographical distribution. The specimens were first separated tentatively into morphospecies based on shell characters. In a second step, all the specimens were sequenced (cox1 gene) to test whether the recognized

morphogroups correspond to distinct molecular clusters. Finally, we attributed the different genetic and morphological groups identified within the complex to names available in the literature and discuss the implication in term of their geographical distribution. .

## MATERIAL AND METHODS

### *Sampling*

The material for this study was collected from various localities during a series of shallow-water and deep-sea expeditions to Saudi Arabia (UF 2013), Viet Nam (NT 2014), Vanuatu (UF 2005, Santo Marine biodiversity survey 2006), Mozambique (MAINBAZA 2009, INHACA 2011), Madagascar (UF 2008), the Philippines (PANGLAO 2004, UF 2015), Mariana Island (UF 2008), Micronesia (UF 2008), Okinawa Japan (UF 2010), Guam (UF 2010), Marquesas Islands (Pakaihi I Te Moana 2012), Papua New Guinea (PAPUA NIUGINI 2012), Marshall Islands (UF 2008), New Caledonia (TERRASSES 2008, UF 2013), Taiwan (UF 2005), Florida, USA (UF 2010), Guadeloupe (KARUBENTHOS 2012), and Western Australia (UF 2009, WESTERN AUSTRALIA 2011). MNHN specimens collected before 2012 were anaesthetized with an isotonic solution of  $MgCl_2$  and fixed in 96% ethanol. Specimens collected after 2012 were processed with a microwave oven (Galindo *et al.* 2014); the living molluscs in small volumes of sea water were exposed to microwaves for ca. 30 seconds. Bodies were immediately removed from shells and dropped into 96% ethanol. UF specimens were directly put alive into 75 or 95% ethanol. The analysed material includes 82 specimens, 42 registered in the MNHN and 40 in the UF collections (Supplementary Material Table 1). The specimens and the corresponding sequences are also registered in the Barcode of Life Datasystem (project BURSA) and GenBank. Maps with the sampling locality of all the specimens were generated using Qgis 2.16.3 (Fig. 1).

### *DNA sequencing*

DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturers' recommendations. A fragment of the cytochrome oxidase subunit I (cox1) gene was amplified using the universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994). PCR reactions were performed in volumes of 20  $\mu$ l, containing 3 ng DNA, 1X reaction buffer, 2.5 mM  $MgCl_2$ , 0.26 mM dNTP, 0.3 mM of each primer, 5% DMSO and 1.5 units of Qbiogene Q-Bio Taq. The amplification consisted of an initial denaturation step at 94°C for 5 min, followed by 40 cycles of denaturation at 94°C for 30 s, annealing at 47°C for 30 s,

followed by extension at 72°C for 1 min. The final extension was at 72°C for 5 min. PCR products were purified and sequenced (both strands) by the Eurofins sequencing facility.

### *Species delimitation*

All specimens were first separated into morphogroups, using characters of the teleoconch and in particular the outer lip. In a second step, the *cox1* sequences were analysed. Alignment was done by eye. Pairwise genetic distances were calculated using MEGA v. 6 (Tamura *et al.*, 2013). Phylogenetic trees were reconstructed using maximum likelihood (ML) and Bayesian inference approaches (BI), with MEGA v. 7 (with Bootstraps 100 replications and default parameters for tree inference options) for ML analysis, and with MrBayes (Huelsenbeck, Ronquist & Hall, 2001) (six Markov chains and 10,000,000 generations, five chains, three swaps at each generation, a sampling frequency of one tree each 1,000 generations, chain temperature set at 0.02) and BEAST v1.8.3 (Drummond *et al.*, 2012) (with uncorrelated relaxed clock, and 10,000,000 generations) for the BI analysis. In all analyses the three codon positions of the *cox1* gene were treated as independent partitions and the substitution model was set to GTR+G and GTR+I+G for the ML and BI analyses, respectively. Convergence for both BI analysis was evaluated using Tracer v. 1.4.1 (Rambaut *et al.*, 2014) to check that all effective sample size values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. Nodal support was assessed as posterior probability (PP) in the BI analyses and as bootstraps (BS) for the ML analysis. Closely related bursid species were used as outgroups: *Bursa latitudo* Garrard, 1961, *Bursina ignobilis* (Beu, 1987) and *Tutufa bufo* (Röding, 1798), following Castelin *et al.* (2012).

Species delimitations were performed using the online versions of the Automatic Barcode Gap Discovery (ABGD; Puillandre *et al.*, 2012a) using a simple distance (p-distance) model and default parameters. ABGD automatically detects the barcode gap in the pairwise distribution of genetic distances between low and high genetic distances, hypothesized to correspond to intra- and inter-specific genetic distances, respectively. The General Mixed Yule Coalescent (GMYC) method (Pons *et al.*, 2006; Monaghan *et al.*, 2009) was also used, with default parameters (both single and multiple methods). GMYC defines the transition (unique in the single version, but variable between lineages in the multiple version) between speciation and coalescent events in the ultrametric tree obtained with BEAST, inferred from the rate of splits in the tree.

### *Shell description*

Fig. 2

Once the species were delimited based on molecular data, shells were described using the methods developed by Merle (2001, 2005) for primary homologies definition. Primary cords are spiral ornamentations present from the first teleoconch whorl. Secondary cords (S) are spiral ornamentations appearing later during shell ontogeny. The shoulder cord is designated as P1. Cords of the convex part of the whorl are added from adapical to abapical (P2 to P6, Fig. 2A). The primary cord of the infrasutural ramp is designated IP and the secondary cord IS. Secondary cords on the convex part of the whorl are designated S1 to S6. Cords of the siphonal canal were not considered. Denticles inside the outer lip are named D1 to D6, starting under the shoulder cord and added from adapical to abapical; denticles above the shoulder are designed as ID1 and ID2 added from abapical to adapical (ID2 is not shown in Fig. 2). Denticles are bifid on most specimens but can merge or further bifurcate. In order to describe the outer lip we introduce here the outer lip denticles formula (OLDF). It is a four-digit sequence representing the number of visible denticles (D) between a notch and the preponderant primary cord (P1, P3 and P5) or between two preponderant primary cords, starting from the anal notch towards the siphonal one. For example, in the specimen of *B. granularis* figured in Fig. 2, the OLDF should be read as AN, 2, P1, 4, P3, 4, P5, 4, SC or 2, 4, 4, 4 for short.

## ABBREVIATIONS

### *Depositaries*

MAC. ML Museo di Storia Naturale Aquilegia, Cagliari

MHNG Muséum d'Histoire naturelle, Geneva, Switzerland

MNHN Muséum National d'Histoire Naturelle, Paris, France

NHMUK Natural History Museum, London, United Kingdom

RASM Russian Academy of Science, Moscow

UF Florida Natural History Museum, University of Florida, Gainesville, United States

### *Shell characters*

AN anal notch

SC siphonal canal

H height

P Primary cord

IP: infrasutural primary cord

204 P1 Shoulder cord  
 205 P2-6 primary cords of the convex part of the whorl  
 206 S secondary cord  
 207 IS infrasutural secondary cord  
 208 S1-6 secondary cords of the convex part of the whorl  
 209 D denticle of the outer lip  
 210 ID1-2 denticle of the infrasutural ramp  
 211 D1-6 denticles of the convex part of the whorl  
 212 OLDF outer lip denticles formula

213  
 214  
 215  
 216

## 217 RESULTS

218 Among the 82 specimens, excluding outgroups, three morphogroups were initially  
 219 recognized. The ABGD (both initial and recursive partitions) and GMYC (single) methods  
 220 consistently found 4 clusters. The only exception is the multiple method of GMYC: five  
 221 clusters are proposed, one specimen (IM-2013-19496) from the Caribbean cluster (see below)  
 222 being considered different. Given that this specimen is very close in molecular sequences to  
 223 other Caribbean specimens, we conclude this to be an artefact of the multiple method of  
 224 GMYC, which is known to oversplit (Fujisawa and Barraclough, 2013; Kekkonen and Hebert,  
 225 2014). Among the four clusters recognized with the *cox1* gene, two correspond to two  
 226 morphogroups. One morphogroup is thus divided into two genetic clusters, corresponding to  
 227 the two clades revealed by Castelin *et al.* (2012). *A posteriori* re-examination of the shells  
 228 revealed stable teleoconch characters distinguishing the two genetic clusters. The  
 229 morphological characters used to recognize first the three morphogroups, and, after the  
 230 molecular analyses, the final four morphogroups, are described in the SYSTEMATICS  
 231 section. The four genetic clusters also correspond to highly supported clades in both BI and  
 232 ML analyses (PP > 0.99 and BS > 80) (Fig. 3). Pairwise genetic distances between clades  
 233 were never less than 6.4%, while within cluster genetic distances never exceeded 1.8%, even  
 234 between geographically distant localities such as Saudi Arabia and Western Australia.  
 235 Remarkably, all clades are structured geographically: Clade 1 ranges from Mozambique to the  
 236 Red Sea, Vietnam, Japan, the Philippines, Western Australia, Vanuatu and New Caledonia,  
 237 suggesting an occurrence throughout the whole Indian Ocean and western Pacific; Clade 2 is



Fig. 3

found in sympatry with Clade 1 in Okinawa, the Philippines, Vanuatu and New Caledonia, but is also present in Taiwan and Papua New Guinea and extends further east to Guam and French Polynesia; although Clades 1 and 2 can be found in sympatry they never occur in syntopy. Clade 3 is circumscribed to the Caribbean; and Clade 4 is limited to southernmost Western Australia.

Based on the original descriptions and type localities, we have attributed the name *Bursa granularis* to Clade 1; *Bursa affinis* to Clade 2; *Bursa cubaniana* to Clade 3; and *Bursa elisabettae* to Clade 4.

## SYSTEMATIC DESCRIPTIONS

### Superfamily TONNOIDEA Suter, 1913 (1825)

#### Family BURSIDAE Thiele, 1925

*Bursa* Röding, 1798

Type species: *Bursa monitata* Röding, 1798, by subsequent designation (Jousseaume, 1881: 174) (junior synonym of *Murex bufonius* Gmelin, 1791, by First Reviser's action of Winckworth, 1945: 137).

*Bursa granularis* (Röding, 1798)

(Fig. 4 A-D, J)

*Tritonium granulare* Röding, 1798: 127. (Red Sea, in accordance with ICZN Art. 76.3; original types lost. Neotype MHNG 1098/85/1, designated by Beu, 1998: 150).

*Bursa granularis* — H. & A. Adams, 1852: 106; Barnard, 1963: 17; Hinton, 1972: 12, pl. 6, fig. 22; Hinton, 1978: 32, fig. 8; Kilburn & Rippey, 1982: 73, pl. 16, fig. 14, Drivas & Jay, 1988: 62, pl. 16, fig. 4; Wilson, 1993: 226, pl. 43, figs 11a-b, 12; Kubo *in* Kubo & Kurozumi, 1995: 74, 78, fig. 7; Beu, 1998: 150, figs 48a-e, 58d; Beu, 1999: 44, fig. 85; Beu, 2005: 19, figs 27-28; Lee & Chao, 2003: 40, pl. 4, fig. 93; Castelin *et al.*, 2012: 4843, fig. 4; Dolorosa *et al.*, 2013: 8, fig. 3D.

*Colubrellina granularis* — Habe, 1961: 47, pl. 24, fig. 5; Okutani, 1986: 116-117, top left fig. *Colubrellina (Dulcerana) granularis* — Habe, 1964: 76, pl. 24, fig. 5; Wilson & Gillett, 1971: 80, pl. 54, figs 7-7b.

*Bursa (Colubrellina) granularis granularis*. — Beu, 1985: 64; Cossignani, 1994: 75-77; Nappo *et al.*, 2014: pl. 3, figs 1-3, pl. 4, figs 1-4, pl. 5, fig. 1, pl. 7, fig. 1.

*Bursa (Bufonariella) granularis* — Bosch *et al.*, 1995: 102, fig. 737.

Fig. 4

272 *Bursa (Colubrellina) granularis* — Okutani, 2000: 269, pl. 133, fig. 1; Zhang & Ma, 2004:  
 273 182, text-figs 113a-c, pl. 5, figs 1-3.  
 274 *Tritonium jabick* Röding, 1798: 127 (Red Sea, in accordance with ICZN Art. 76.3; original  
 275 types lost. Neotype MHNG 1098/85/1, designated by Beu, 1998: 150).  
 276 *Dulcerana jabick* — Iredale, 1931: 213.  
 277 *Colubrellina jabick* — Oyama & Takemura, 1960: *Colubrellina* pl., figs 3-4.  
 278 *Biplex rubicola* Perry, 1811: pl. 5, fig. 4 (Red Sea, in accordance with ICZN Art. 76.3;  
 279 original types lost. Neotype MHNG 1098/85/1, designated by Beu, 1998: 150).  
 280 *Ranella granifera* Lamarck, 1816: pl. 414, fig. 4, “Liste des objets”: 4; 1822: 153 (Red Sea,  
 281 designated by Beu 1998:150; Lectotype MHNG 1098/85/1, designated by Beu, 1998:150);  
 282 Kiener, 1841: 16, pl. 11, fig. 1; Deshayes, 1843: 548; Reeve, 1844a: pl. 6, fig. 30; Küster,  
 283 1871 [in Küster & Köbelt, 1870-1878]: 143, pl. 39, fig.1.  
 284 *Bursa cumingiana* Dunker, 1862: 238; New Caledonia; Lectotype NHMUK 1968530  
 285 designated by Beu 1998:150 — Dunker, 1863: 59, pl. 19, figs 7-8.  
 286 *Ranella (Lampas) granifera* — Tryon, 1880: 41, pl. 22, figs 35-40.  
 287 *Ranella semigranosa* — Reeve, 1844b: pl. 6, fig. 25; Krauss, 1848: 113 (not of Lamarck,  
 288 1822).  
 289  
 290 *Material examined:* See Supplementary material table 1.  
 291 *Diagnosis:* Shell biconic, varices strictly aligned, numerous nodules on all primary, secondary  
 292 and tertiary cords, OLDF: 2.4.4.4, or 2.4.4.3 in large specimens  
 293 *Description:* Protoconch of 3.75 whorls (following the counting method of Bouchet &  
 294 Kantor, 2004), rather tall with weakly impressed suture, with finely reticulate protoconch I of  
 295 0.5 whorls, reticulate sculpture on first whorl of protoconch II, fading out before end of last  
 296 protoconch whorl. Teleoconch: tall and relatively narrow with 4-5 whorls (up to 6 in very  
 297 large specimens) Height (H) around 40mm, up to 60mm. Spire angle 50°. proportion of  
 298 aperture 53. % of the shell width. Proportion of the last whorl 54%.of the height. Varices  
 299 strictly aligned for most of spire height, becoming slightly displaced only on last whorl or two  
 300 of large specimens. Abapertural face of each varix slightly excavated, buttressed by spiral  
 301 cords. Spiral ornamentation of 7 primary cords, one on infrasutural ramp (IP) and 6 on convex  
 302 part of whorl (P1-6). After whorl 2.5 (varix 5) IP becoming very reduced, noticeable only  
 303 where it intersects varices. Secondary cords in interspaces between primary cords. Primary  
 304 cord above IP remaining reduced throughout shell ontogeny whereas others growing in  
 305 similar fashion to primary cords. On last whorl, spiral ornamentation composed of 9 nodules

Fig. 5

per primary cord between two varices (and secondary cords of infrasutural ramp) and double this number for secondary ones. Apertural lip well flared, bearing numerous prominent, narrow, transverse denticles. Outer lip bearing numerous denticles; ID1 bifid, ID2 absent, D1-4 bifid, D5 bifid but merged in large specimens, D6 bifid (Fig. 5).

Fig. 6

*Distribution and habitat:* *Bursa granularis* has a tropical distribution throughout the Indo-West Pacific province (Fig.1), from the Mozambique Channel throughout East Africa and the Red Sea to the northern Indian Ocean, in the western Pacific from Kii Peninsula and Yamaguchi Prefecture, Honshu, Japan (Beu, 1999), south to Rottneest Island in Western Australia (Wilson, 1993). Its eastward distribution in the Pacific extends from Japan to Australia through the Philippines, Vanuatu and New Caledonia. *Bursa granularis* is commonly found in very shallow water but some specimens were found alive around 100m deep.

*Remarks:* The nomenclatural history of *Bursa granularis* is a particularly complex one. The types of *Tritonium granulare*, *T. jabick* and *Biplex rubicola* are lost. Beu (1998) designated the lectotype of *Ranella granifera* as neotype of the three other names. As a consequence these formerly subjective synonyms became objective synonyms and following ICZN Art. 76.3 they also all share the same type locality, the Red Sea. There is only one species belonging to the complex in this locality, to which the name *B. granularis* can thus unambiguously be attributed. Furthermore the type specimen of *Ranella granifera* displays characters congruent with the description above (Fig. 4,A).

*Bursa cumingiana* (type locality New Caledonia) is another available name in the *B. granularis* complex. There are two (and only two) Molecular Operational Taxonomic Unit (MOTU) living sympatrically in this region and the lectotype of *Ranella cumingiana* (NHMUK 1968530) is a well-preserved adult specimen, which distinctively displays four denticles between P5 and the anterior canal, identifying it as *Bursa granularis*. The color pattern of the teleoconch of *B. granularis* is highly variable, from off-white, pale brown or pale orange to deep reddish brown. Some specimens bear the same striped color pattern as *B. cubaniana*. A few young specimens display the angular profile of *B. affinis*, especially in the Mozambique Channel, but it never occurs in fully grown specimens.

*Bursa affinis* (Broderip, 1833)

(Fig. 4 E-I,K)

*Ranella affinis* Broderip, 1833: 179 (“Anaa,” Tuamotu Islands, Lectotype NHMUK

1950.11.28.4, designated by Beu, 1998:150); G. B. Sowerby II, 1835: pl. 89, fig. 12; Reeve, 1844b: pl. 4, fig. 19; Küster, 1871 [in Küster & Köbelt, 1870-1878]: 142, pl. 38a, fig. 5.

*Bursa granularis affinis* — Hertlein & Allison, 1960: 15.

*Ranella livida* Reeve, 1844a: pl. 6, fig. 28; (“Anaa,” Tuamotu Islands, Lectotype NHMUK 1967657\_1, designated by Beu, 1998:150); 1844b: 138; Krauss, 1848: 113.

*Dulcerana granularis* — Iredale, 1931: 213; Ripplingale & McMichael, 1961: 69, pl. 7, fig. 19 (not of Röding, 1798).

*Bursa granularis* — Hertlein & Allison, 1960: 15; Salvat & Rives, 1975: 307, fig. 179; Kay, 1979: 227, fig. 80A; Severns 2011: 150, pl. 59, fig. 6; Beu *et al.*, 2012: 67, fig. E2 (not of Röding, 1798).

*Bursa (Colubrellina) granularis* — Kaiser, 2007: 39, pl. 26, figs 7a-b (not of Röding, 1798).

*Material examined:* See Supplementary material table 1.

*Diagnosis:* Shell biconic, varices strictly aligned, numerous nodules on all primary, secondary and tertiary cords, shoulder angular prominent, OLDF: 2,3,4,3 or 3,4,4,3 in particularly large specimens.

*Description:* Protoconch as in *B. granularis*. Teleoconch tall and relatively narrow with 4–5 whorls (up to 6 on large specimens). H 40 to 50 mm, up to 80 mm. Spire angle 55°.

Proportion of aperture, 50% of the shell width. Proportion of last whorl 52% of the height.

Varices strictly aligned for most of spire height, becoming a little displaced only on last whorl or two of large specimens. Abapertural face of each varix deeply excavated, buttressed by

spiral cords. Spiral ornamentation as in *B. granularis*. After whorl 2 (varix 4) IP grows in

importance to equal other cords, only to reduce again after varix 6, leaving room for

development of secondary cord above it. Every primary cord surrounded by secondary cords,

growing in importance similarly to primary cords. Spiral ornamentation composed, on last

whorl, of 9 nodules per primary cord between two varices with the exception of P1, which

bears much bigger nodules, pointing slightly upwards, and decreasing in number with

ontogeny, from 9 to 5. Secondary cords bear same number of small nodules as *B. granularis*.

Nodules on varices where they meet P1 angulating the shoulder. Apertural lips well flared,

bearing numerous prominent, narrow, internal transverse denticles. ID2 present in large

specimens, ID1 bifid, D1 bifid, D2 single but bifid in large specimens, D3-4 bifid, D5 single, D6 bifid (Fig. 5).

*Distribution and habitat:* *Bursa affinis* has a tropical distribution throughout the Pacific Ocean (Fig. 1), from Okinawa, Japan to Sydney Harbour, New South Wales, Australia, and throughout Polynesia to Hawaii (Beu, 1998). In the eastern Pacific, particularly large specimens are common at Clipperton Island (Hertlein & Allison, 1960; Kaiser, 2007) and specimens were recorded by Emerson (1991) from the Revillagigedo Islands, Cocos Island, and the mainland coast at Bahia Chamela, Jalisco, western Mexico (Beu, 2010). Its westward distribution in the Pacific extends from Japan to Australia through the Philippines, Papua New Guinea, Vanuatu and New Caledonia. *Bursa affinis* is commonly found in very shallow water but specimens are occasionally found alive in around 40 m deep.

*Remarks:* *Bursa affinis* and *Bursa livida* have the same type locality; “Anaa,” [now Anaa] Tuamotu Islands. The type specimens (Fig. 4 E,G) of both have the same OLDF, and we consider the latter to be a junior synonym of the former. Considering that there is only one MOTU occurring in Outer Oceania in general (Fig. 1), and French Polynesia in particular, we attribute to it the name *affinis*.

301

Fig.6

*Bursa cubaniana* (d’Orbigny, 1841)

(Fig. 6 A-D,L)

*Ranella cubaniana* d’Orbigny, 1841: 165, pl. 23, fig. 24 (Ste Lucie, West Indies, Holotype NHMUK 1854.10.4.412); Mörch, 1877: 24.

*Gyrineum affine* var. *cubanianum* — Dall, 1889: 224.

*Gyrineum affine* (sic) *cubanianum* — Morretes, 1949: 92.

*Bursa (Colubrellina) cubaniana* — Abbott, 1958: 57, text-fig. 2, pl. 1, fig. k. Warmke & Abbott, 1961: 103, pl. 18, fig. i; Rios, 1970: 70; Coelho & Matthews, 1971: 52, figs 11-12; Humfrey, 1975: 126, pl. 14, figs 4, 4a; H. & E. Vokes, 1983: 23, pl. 11, fig. 14.

*Bursa cubaniana* — Nowell-Usticke, 1959: 61. Work, 1969: 663; Kaufmann & Gotting, 1970: 372, fig. 87; Matthews & Kempf, 1970: 28; de Jong & Coomans, 1988: 214, pl. 16, fig. 382.

*Bursa cubaniana* var. *intermedia* Nowell-Usticke 1959: 61-62, pl. 3, fig. 13 (North of Fredericksted, St. Croix, Virgin Islands).— Boyko & Cordeiro, 2001: 24.

- 407 *Bursa corrugata* var. *lineata* Nowell-Usticke 1959: 61-62, pl. 3, fig. 12 (North of  
 408 Fredericksted, St. Croix, Virgin Islands).— Boyko & Cordeiro, 2001:24 .
- 409 *Bursa granularis cubaniana* — Abbott, 1974: 167, pl. 7, fig. 1781 (as *B. granularis* in pl.  
 410 caption). Rios, 1975: 81, pl. 23, fig. 331; Finlay, 1978: 149; Bandel, 1984: 102, pl. 10, figs 3,  
 411 8; Diaz & Gotting, 1988: 156; Diaz, 1990: 19; Diaz & Puyana, 1994: 174, fig. 650; Redfern,  
 412 2001: 58, pl. 29, figs 247A-B. Nappo *et al.*, 2014: pl. 5, figs. 2-3, pl. 6, figs. 1-3, pl. 7, fig. 2
- 413 *Bursa (Colubrellina) granularis cubaniana* — Rios, 1975: 81, pl. 23, fig. 331; Beu, 1985: 64;  
 414 Cossignani, 1994: 78.
- 415 *Bursa (Colubrellina) granularia (sic) cubaniana* — Rios, 1994: 92, pl. 31, fig. 365.
- 416 *Bursa granularis* — Leal, 1991: 111, pl. 16, figs C-D; Lipe & Abbott, 1991: 14-15, illus ; Beu  
 417 2010: 48, pl. 3, figs 1, 3; Redfern, 2013: 83, figs 241 (not Röding, 1798).
- 418 *Bursa (Colubrellina) granularia (sic)* — Rios, 1985: 79, pl. 28, fig. 347 (not of Röding,  
 419 1798).
- 420 *Gyrineum affine* — Dall, 1903: 132 (not of Broderip, 1833).
- 421 *Ranella (Bursa) affinis* — Trechmann, 1933: 39 (not of Broderip, 1833).
- 422
- 423 *Material examined:* See Supplementary Material table 1.
- 424 *Diagnosis:* Shell biconic, varices strictly aligned, varices abaperturally deeply excavated,  
 425 relatively numerous nodules on all primary cords, particularly large one on P1, beige stripes  
 426 following primary cords, OLDF: 3,5,4,3 or 3,5,5,4 in particularly large specimens.
- 427 *Description:* Protoconch similar to other species in the complex (see above). Teleoconch tall  
 428 and relatively narrow with 4-5 whorls (up to six for larger specimens). H around 50 mm, up to  
 429 60 mm. Spire angle 55°; proportion of aperture, 50% of the shell width; proportion of last  
 430 whorl 47% of the height. Varices strictly aligned for most of spire height, becoming a little  
 431 displaced only on last whorl or two in large specimens. Abapertural face of each varix deeply  
 432 excavated, buttressed by spiral cords. Spiral ornamentation much reduced compared to *Bursa*  
 433 *granularis* and *B. affinis*. P1, 3 and 5 much more pronounced than others. Primary cords (IP  
 434 included) bearing 4 rather large nodules, with small nodules overlying large ones on large  
 435 specimens. Secondary cords not visible on shell after whorl 1, except slightly visible where  
 436 intersecting varices. Nodules on varices where they meet P1, angulating shoulder, not as sharp  
 437 as on *B. affinis*. Apertural lips well flared, bearing numerous prominent, narrow transverse  
 438 internal denticles;s ID2 single, ID1 bifid, trifurcated in large specimens, D1 bifid, trifurcated  
 439 in large specimens, D2 bifid, D3 bifid, trifurcated in large specimens, D4 bifid, D5 single,

bifid in large specimens, D6 bifid (Fig. 5). Shells distinctively bearing beige-cream stripes following the spiral cords.

*Distribution and habitat:* *Bursa cubaniana* occurs in the western Atlantic (Fig. 1; Rosenberg 2009), where it is recorded from southeastern Florida (Abbott, 1974; this study), Texas and Louisiana (Garcia, 1999) westwards to Mexico, Costa Rica, Panama and Colombia (Massemin *et al.* 2009), the Bahamas (Redfern 2013), Guadeloupe (this study), Jamaica, Cuba and St Lucia (d'Orbigny, 1841) south to French Guiana (Massemin *et al.* 2009), Bahia and Pernambuco, Brazil (Matthews, 1968; Rios, 1985, 1994, Mello & Perrier 1986). In the eastern Atlantic, it has been recorded only from the Cape Verde Islands, but this record in unconfirmed (Rolán, 2005).

*Remarks:* The type locality of *Bursa cubaniana* is Cuba and there is only one MOTU in the Caribbean region (Fig. 1). So the name *Bursa cubaniana* is unambiguously attributed to this MOTU.

*Bursa elisabettae* Nappo, Pellegrini & Bonomolo, 2014  
(Fig. 6 E-G,M)

*Bursa granularis elisabettae* Nappo, Pellegrini & Bonomolo, 2014: 5, pl. 1, figs 1- 3; pl. 2, figs 1-3; pl. 3, figs 1-3 (Flinders Bay, Cape Leeuwin, southern Western Australia, 12 m, MAC.ML 1536)

*Bursa cf. nodosa* — Bozzetti, 1991:1, fig.1 (not of Borson, 1823)

*Bursa granularis "affinis"* form — Wilson, 1993: pl. 43, fig. 12 (not of Röding, 1798).

*Material examined:* See Supplementary Material table 1.

*Diagnosis:* Shell biconic, varices strictly aligned, varices abaperturally rather excavated, nodules weak on the first primary cords, brown stripes following primary cords, outer lip denticles small, OLDF:4,3,3,3 or 4,3,2,3 in large specimens.

*Description:* Protoconch similar to that of other species in the complex (see above).

Teleoconch tall, relatively narrow with 4-5 whorls, H around 50 mm. Spire angle 45°; % of aperture, 52% of the shell width; % of last whorl 52% of the height. Varices strictly aligned, although low and hardly visible in some specimens. Spiral ornamentation very reduced to absent from some specimens. Primary cords P1, 3 and 5 are the only ones visible; each bears 4 nodules between two varices, especially visible on P1. No secondary cords present. Nodules on varices where they meet P1 angulate shoulder, although not as sharply as in *B. affinis*.

Apertural lips well flared, bearing numerous prominent, narrow transverse internal denticles; ID2-1 bifid, D1 single, D2 bifid, D3 single, D4 bifid, merged in large specimens, D5 single, D6 bifid (Fig. 5).

*Distribution and habitat:* The known distribution of *Bursa elisabettae* is restricted to southwestern Western Australia, in shallow water.

*Remarks:* *Bursa elisabettae* is the last species described in the complex. There is only MOTU occurring around Cape Leeuwin, southwestern Australia (type locality) to which we attribute the name *B. elisabettae*. The possible occurrence of *B. elisabettae* in South Africa is discussed below.

## DISCUSSION

*Bursa granularis* is considered to be easy to identify, although it is most variable, hence the thirteen names it received through history and the innumerable subsequent references in the literature. Previous works failed to provide a comprehensive characterization of such variability, leading to the aggregation of the whole morphological spectrum under a single name, *Bursa granularis* (Beu, 1998, 2005, 2010). An integrated taxonomic approach based on extensive sampling (geographical, bathymetrical, and type locality of many nominal taxa), coupled with a detailed analysis of the shell variability and the sequencing of the *cox1* gene, analysed with two methods (ABGD and GMYC), revealed four groups within the *Bursa granularis* complex, here considered to be distinct species. However, our species hypotheses are supported by one gene and morphological data only; an independent genetic marker would help to determine whether the partition obtained with the Cox-1 gene corresponds to the species limits.

Among the four delimited species, one pair, *Bursa granularis* and *B. affinis*, is barely distinguishable morphologically, and without molecular evidence they would hardly be suspected to be separate species. Furthermore, the intraspecific morphological variability sometimes exceeds the interspecific disparity, particularly in shell coloration; the pinkish coloration of the first whorls, formerly used to discriminate *B. affinis* (see Reeve, 1844) can be found in specimens of both species, and some specimens present the striped pattern usually attributed to *B. cubaniana* (for which this pattern is stable). We were able to discriminate species on morphology only through the detailed observation of the spiral ornamentation of the shells. The importance of such ornamentation for systematics was previously recognized



in, e. g., Muricidae (Merle & Houart, 2003; Merle, 2005; Merle *et al.*, 2001), Mathildidae (Bieler, 1995) and Calliostomatidae (Marshall, 1995). Although Muricidae and Bursidae are not closely related, they have a similar morphological organization of the sculptural elements and the methodology applies as well to Bursidae as to Muricidae. Other morphological characters, e.g. apertural color, spire height, and sculptural prominence (considering one cord at a time), are of very little value.

Other anatomical characters and radulae were not considered in the present study but may perhaps provide useful information. Abbott (1958) pointed out differences between *B. cubaniana* and *B. granularis* in denticle size and number on the central teeth (Abbott, 1958: figs 1d, 2c), but radular studies are often based on too small a sample size and their results may not be significant. For good pictures of the radula of *B. granularis*, see Barbakova *et al.* (2016) and for insight on the general anatomy of *B. cubaniana* see Simone (2011).

The integrated taxonomic approach followed here was thus efficient to propose robust species hypotheses. It is an additional example of the value of molecular characters when species cannot readily be distinguished morphologically, a common pattern in gastropods (e. g. Puillandre *et al.*, 2012b, Duda *et al.*, 2008). However, if proposing putative species using DNA sequences is now a common practice, linking the species hypotheses to available names attached to non-sequenced name-bearing types remains daunting. Indeed all the species in the *Bursa granularis* complex were described based on shell characters only, including *B. elisabettae*, described as recently as 2014. More generally, most species of molluscs were described before the molecular era, and the application of historical names remain based on non-sequenced, sometimes problematical, dry material (Bouchet & Strong, 2010).

Because we did not sample the entire distribution area of the complex, additional species possibly may be recognized in the future. *Bursa alfredensis* and *B. kowiensis* (Fig 6 I-K, N) were both described from Port Alfred, South Africa and are the only two names that we have refrained from associating with one of the MOTU of this study. The types of both are specimens displaying a loss of the fine sculpture early in ontogenesis. The adult South African specimen in Fig. 6 I (for which we have no molecular data) certainly corresponds to the nominal species described as *B. kowiensis* by Turton (1932). This loss of ornamentation resembles the one displayed by *B. cubaniana*, but even more by *B. elisabettae*. If *B. elisabettae*, *B. alfredensis* and *B. kowiensis* were found to be a single species, then *B. kowiensis* or *B. alfredensis*, both names established in 1932, would be the valid name. Such a scenario would be congruent with the hypothesis of a Pleistocene colonization of the Caribbean (which happens to be the stratigraphic distribution of *B. cubaniana* in the region;

Beu, 2010) from the Indian Ocean, around South Africa. This hypothesis was discussed by Vermeij & Rosenberg (1993) for 17 Indo-West-Pacific species.

South African collectors (R. Aiken, pers. com.) have also drawn our attention to a small form of *Bursa granularis* that is dredged in "deep water" (Fig.6 H). We have not seen this variation from anywhere else, and the deep water (100 meters?) habitat is very unusual from *B. granularis* s.s., which has been exceptionnally dredged alive in 87-90 m (specimen MNHN IM-2009-5148, sequenced). The status of this small, South African, deep-water form will have to be evaluated by sequencing.

Recent work (Nappo *et al.*, 2014) suggested that *Bursa granularis*, *B. cubaniana*, and *B. elisabettae* were subspecies of *B. granularis*. We rank them here as full species. Firstly, as we showed above, the two pairs *B. granularis-affinis* and *B. cubaniana-elisabettae* seem to have very distinct biogeographical histories. Secondly, Castelin *et al.* (2012, fig. 7) showed that the pair *B. granularis-affinis* diverged from each other over 11 MYA (the distance between *B. cubaniana* and *B. elisabettae* would suggest a comparable time of divergence, although it was not tested). The divergence between the two pairs is necessarily older. The estimated divergence time (11 MYA; Castelin *et al.*, 2012) between *Bursa granularis* and *B. affinis* corresponds to the Seravallian/Tortonian stages, a period with a particularly low sea level (around 100 m lower than today; Scotese, 2014). Australia, Papua New Guinea, Indonesia, Japan and the Philippines were all connected to Eurasia by a series of land bridges or very shallow seas, reducing to nearly zero all marine connectivity between the Pacific and Indian Oceans. Given the sympatric distribution of *B. granularis* and *B. affinis* in an area extending from Japan to eastern Australia through the Philippines, Papua New Guinea and New Caledonia, this speciation event would represent an example of allopatric speciation with secondary contact subsequent to recolonisation events. However, because our results are based only on mitochondrial data, we cannot rule out an alternative scenario in which both groups are actually still genetically connected. In this scenario, the pattern observed with the *cox1* gene would only be the result of an ancient allopatric divergence, the secondary contact being too recent to homogenize both mitochondrial gene pools. Although the number of sequenced specimens and the high genetic divergence between *B. affinis* and *B. granularis* do not support this hypothesis, nuclear data would help support one or the other of these scenarios. In a forthcoming molecular phylogeny of the Tonnoidea (Strong *et al.*, in prep.), nuclear gene sequences are available for a limited number of specimens in the *Bursa granularis* complex but they do provide confirmation of the present *cox-1* based species delimitations.

One of the main consequences of the partition into four species proposed here is that larval duration alone does not explain geographical distributions. Other factors, such as availability of suitable habitats, may limit distribution areas, in spite of a species' large dispersal abilities. A striking example is *Fusitriton oregonensis*; it is the only species for which the larval duration has been directly measured (although under laboratory conditions), with an estimated larval stage of 5 years (Strathmann & Strathmann, 2007), but its distribution area is limited to the North Pacific from central Japan to California, extending south to off Panama in deep water (Smith, 1970).

While the distribution area of *Bursa granularis* remains large, we have shown that it was greatly overestimated in the classic taxonomic extension of the species. It is not unlikely that the same pattern – one very variable species with an extremely large distribution being in fact several species with smaller distributions – could be found in other tonnoideans. For Bursidae only, *Bursa corrugata* (Perry, 1811) (8 subjective synonyms and recorded from East Pacific, Eastern Atlantic Ocean and the Caribbean), *Bursa ranelloides* (Reeve, 1844) (7 subjective synonyms, recorded from the Indian and Atlantic Oceans, and Japan and Hawaii in the Pacific) and *Bursa rhodostoma* (G. B. Sowerby II, 1835) (6 subjective synonyms, recorded from the whole Indo-Pacific and the Caribbean) are good candidates for an integrative taxonomy-based revision. However, achieving a representative sampling for molecular taxonomy becomes increasingly difficult, considering the multiplicity of permits necessitated by sampling distribution areas that span numerous countries. The future will tell whether Article 8a of the Nagoya Protocol to the Convention of Biological Diversity (encouraging the Parties to the protocol to “create conditions to promote and encourage research [...] through simplified measures on access for noncommercial research purposes”) will reverse the ebb of the tide (Bouchet *et al.*, 2016). For the time being, complying with regulations on “Access and Benefit Sharing” and “Prior Informed Consent” is a formidable obstacle on the road of academic researchers investigating species limits and their names.

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## REFERENCES

- ABBOTT, R. T. 1958. The marine mollusks of Grand Cayman Island, British West Indies. *Monographs of the Academy of Natural Sciences of Philadelphia*, **11**: 1-138
- ABBOTT, R. T. 1974. *American Seashells*, [2nd ed]. *The Marine Mollusca of the Atlantic and Pacific Coasts of North America*. Van Nostrand Reinhold, New York.
- ADAMS, H., & A. ADAMS. 1853-1858. *The Genera of Recent Mollusca, Arranged According to their Organisation*. J. van Voorst, London.

- 643 BANDEL, K. 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda.  
644 *Zoologische Verhandlungen*, **214**: 1-88.
- 645 BARKALOVA, V. O., FEDOSOV, A. E., & KANTOR, Y. I. 2016. Morphology of the  
646 anterior digestive system of tonnoideans (Gastropoda: Caenogastropoda) with an emphasis on  
647 the foregut glands. *Molluscan Research*, **36**(1): 54-73.
- 648 BARNARD, K. H. 1963. Contributions to the knowledge of South African marine Mollusca.  
649 Part III. Gastropoda: Prosobranchiata: Taenioglossa. *Annals of the South African Museum*, **47**:  
650 1-199.
- 651 BEU, A. G. 1985. A classification and catalogue of living world Ranellidae (= Cymatiidae)  
652 and Bursidae. *Conchologists of America Bulletin*, **13**: 55-66.
- 653 BEU, A. G. 1987. Taxonomy of gastropods of the families Ranellidae (= Cymatiidae) and  
654 Bursidae. Part 2. Descriptions of 14 new modern Indo-West Pacific species and subspecies,  
655 with revisions of related taxa. *New Zealand Journal of Zoology*, **13**: 273-355 ["1986", issued  
656 January 1987].
- 657 BEU, A. G. 1998. Indo-West Pacific Ranellidae, Bursidae and Personidae. A monograph of  
658 the New Caledonian fauna and revisions of related taxa. Résultats du Campagnes Musorstom,  
659 vol. 19. *Mémoires du Muséum National d'Histoire Naturelle*, **178**.
- 660 BEU, A. G. 1999. Ranellidae, Bursidae and Personidae (Gastropoda: Tonnoidea) of  
661 Yamaguchi Prefecture, western Honshu, Japan. The Yuriyagai, *Journal of the*  
662 *Malacozoological Association of Yamaguchi*, **7**: 1-91.
- 663 BEU, A. G. 2005. Neogene fossil tonnoidean gastropods of Indonesia. *Scripta Geologica*,  
664 **130**: 1-186.
- 665 BEU, A. G. 2010. Neogene tonnoidean gastropods of tropical and South America; a  
666 contribution to the Dominican Republic and Panama Paleontology projects and uplift of the  
667 Central American Isthmus. *Bulletins of American Paleontology* **377–378**: 1–550.
- 668 BEU, A. G., BOUCHET, P., & TRÖNDLE, J. 2012. Tonnoidean gastropods of French  
669 Polynesia. *Molluscan Research*, **32**(2): 61-120.
- 670 BIELER, R. 1995. Mathildidae from New Caledonia and the Loyalty Islands (Gastropoda:  
671 Heterobranchia).. *Mémoires du Muséum National d'Histoire Naturelle*, **167** (Résultats des  
672 Campagnes MUSORSTOM, 14): 595-641.
- 673 BOSCH, D. T., DANCE, S. P., MOOLENBEEK, R. G., & OLIVER, P. G. 1995. *Seashells of*  
674 *Eastern Arabia*. Motivate Publishers, Dubai & London.

- BOUCHET, P. & KANTOR, Y. I. 2003. New Caledonia: the major centre of biodiversity for volutomitrid molluscs (Mollusca: Neogastropoda: Volutomitridae). *Systematics and Biodiversity*, **1**(4), 467-502.
- BOUCHET, P., & STRONG, E. 2010 Historical name-bearing types in marine molluscs: an impediment to biodiversity studies? In Polaszek, A., *Systema Naturae 250*, CRC Press, London: 63-74.
- BOUCHET, P., BARY, S., HEROS, V., & MARIANI, G. 2016. How many species of molluscs are there in the world's oceans, and who is going to describe them? *Mémoires du Muséum national d'Histoire naturelle*, **208** (Tropical Deep-Sea Benthos. Vol. 29): 9-24.
- BOYKO, C. B. & CORDEIRO, J. R.. 2001. Catalog of Recent type specimens in the division of invertebrate zoology, American Museum of Natural History. V. Mollusca, Part 2. *Bulletin of the American Museum of Natural History*, **262**: 1-170.
- BOZZETTI, L., 1991. *Bursa nodosa* (Borson, 1823) survives in Australia? *La Conchiglia*, **22**(260): 2-4.
- BRODERIP, W. J. 1833. Characters of new species of Mollusca and Conchifera, collected by Mr. Cuming. *Proceedings of the Committee of Science and Correspondence of the Zoological Society of London*, **2**: 173-179 [January]; 194-202 [March]; **3**: 4-8 [May].
- CASTELIN, M., LORION, J., BRISSET, J., CRUAUD, C., MAESTRATI, P., UTGE, J., & SAMADI, S. 2012. Speciation patterns in gastropods with long-lived larvae from deep-sea seamounts. *Molecular ecology*, **21**(19), 4828-4853.
- COELHO, A. C. DOS SANTOS, & MATTHEWS, H. R. 1971. Superfamilia Tonnacea do Brasil. III - Familia Bursidae (Mollusca: Gastropoda). *Arquivos do Ciencias do Mar*, **11**: 45-58.
- COLGAN, D.J., PONDER, W.F., BEACHAM, E. & MACARANAS, J. 2007. Molecular phylogenetics of Caenogastropoda (Gastropoda: Mollusca). *Molecular Phylogenetics and Evolution*, **42**: 717-737.
- COSSIGNANI, T. 1994. *Bursidae of the World*. L'Informatore Piceno, Ancona.
- CUNHA, R.L., GRANDE, C. & ZARDOYA, R. 2009. Neogastropod phylogenetic relationships based on entire mitochondrial genomes. *BMC Evolutionary Biology*, **9**: 210.
- DALL, W. H. (1903). *A Preliminary Catalogue of the Shell-bearing Marine Mollusks and Brachiopods of the Southeastern Coast of the United States, with Illustrations of Many of the Species*. Reprint, to which are added Twenty-one Plates not in the Edition of 1889. Government Printing Office, Washington, D.C.,

- 708 DALL, W. H. 1889. Reports on the results of dredging, under the supervision of Alexander  
709 Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80), by the ...  
710 “Blake” ... Report on the Mollusca. Part II. - Gastropoda and Scaphopoda. Bulletin of the  
711 Museum of Comparative Zoology at Harvard College, **18**: 1-492.
- 712 DESHAYES, G. P. 1843. *Histoire Naturelle des Animaux sans Vertèbres, Présentant les*  
713 *Caractères Généraux et Particuliers ... par J. B .P. A. de Lamarck. Deuxième édition. Revue*  
714 *et Augmentée de Notes Présentants les Faits Nouveaux Dont la Science s’est Enrichie Jusqu’a*  
715 *ce Jour. Tome 9. Histoire des Mollusques.* J. B. Baillière, Paris.
- 716 DIAZ, J. M. 1990. Malacofauna subfossil y reciente de la Bahía de Portete, Caribe  
717 Colombiano, con notas sobre algunas fósiles del Terciario. *Boletín Ecotópica*, **23**: 1-22.
- 718 DIAZ, J. M., & K. J. GÖTTING. 1988. The mollusks of the Bahía de Nenguange (Caribbean  
719 Sea, Colombia) and their zoogeographical relationships. *Zoologische Jahrbücher, Abteilung*  
720 *für Systematik*, **115**: 145-170
- 721 DIAZ, J. M., & PUYANA, M. 1994. *Moluscos del Caribe Colombiano. Un Catálogo*  
722 *Ilustrado.* Colciencias y Fundación Natura Colombia, Santa Fe de Bogotá.
- 723 DOLOROSA, R. G., CONALES, S. F., & BUNDAL, N. A. 2013. Status of Horned Helmet  
724 *Cassis cornuta* in Tubbataha Reefs Natural Park, and its trade in Puerto Princessa City,  
725 Philippines. *Atoll Research Bulletin*, **595**, 1-17.
- 726 DRIVAS, J., & JAY, M. 1988. *Coquillages de la Réunion et de l’Île Maurice.* Delachaux &  
727 Niestlé, Neuchâtel & Paris.
- 728 DRUMMOND, A.J., SUCHARD, M.A., XIE, D. & RAMBAUT, A. 2012. Bayesian  
729 phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969–  
730 1973.
- 731 DUDA, T. F., JR., M. B. BOLIN, C. MEYER, ET A. J. KOHN. 2008. Hidden diversity in a  
732 hyperdiverse gastropod genus: discovery of previously unidentified members of a *Conus*  
733 species complex. *Molecular Phylogenetics and Evolution*, **49**: 867-76.
- 734 DUNKER, W. 1862. Species nonnullae Bursarum vel Ranellarum collectionis Cumingianae.  
735 *Proceedings of the Zoological Society of London*, **1862**: 238-240.
- 736 EMERSON, W. K. 1991. First records for *Cymatium mundum* (Gould) in the eastern Pacific  
737 Ocean, with comments on the zoogeography of the tropical trans-Pacific tonnacene and non-  
738 tonnacene prosobranch gastropods with Indo-Pacific faunal affinities in West American  
739 waters. *The Nautilus*, **105**: 62-80.
- 740 FINLAY, C. J. 1978. Review of the genus *Bursa* in the western Atlantic. *The Nautilus*, **92**:  
741 147-150.

- 742 FOLMER, O., BLACK, M., HOEH, W., LUTZ, R. & VRIJENHOEK, R. 1994. DNA primers  
743 for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan  
744 invertebrates. *Molecular Marine Biology and Biotechnology*, **3**: 294–299.
- 745 FUJISAWA, T., BARRACLOUGH, T.G., 2013. Delimiting species using single-locus data  
746 and the generalized mixed yule coalescent (GMYC) approach: a revised method and  
747 evaluation of? simulated datasets. *Systematic Biology*. **62**(5): 707-724.
- 748 GALINDO, L.A., PULLANDRE, P., STRONG, E.E. & BOUCHET, P. 2014. Using  
749 microwaves to prepare gastropods for DNA barcoding. *Molecular Ecology Resources*, **14**:  
750 700–705.
- 751 GARCIA, E., F. 1999. New molluscan records for the northwestern Gulf of Mexico.  
752 *American Conchologist*. **27**(2):27.
- 753 GARCIA-TALavera, F. 1983. *Los Moluscos Gasteropodos Anfiatlanticos, Estudio Paleo y*  
754 *Biogeografico de las Especies Bentonicas Litorales*. Secretariado de Publicaciones de  
755 laUniversidad de La Laguna [Tenerife, Canary Islands], Colección Monografías, 10.
- 756 GARRARD, T. 1961. Mollusca collected by MV “Challenge” off the east coast of Australia.  
757 *Journal of the Malacological Society of Australia*, **1**(5): 2-37.
- 758 GBIF. 2016. GBIF.org (11th November 2016) GBIF Occurrence  
759 Download <http://doi.org/10.15468/dl.ma8dle> .
- 760 GMELIN, J. F. 1791. *Caroli a Linné, Systema Naturae per Regna Tria Naturae ... Editio*  
761 *Decima Tertia, Aucta, Reformata, cura J. F. Gmelin. Tomus I, Pars VI, Vermes*. G. E. Beer,  
762 Lipsiae.
- 763 HABE, T. 1961. [*Colored Illustrations of the Shells of Japan, Vol. 2*] (in Japanese). Hoikusha  
764 Publishing Company, Osaka, Japan.
- 765 HABE, T. 1964. *Shells of the Western Pacific in Color, Vol. 2*. Hoikusha Publishing  
766 Company, Osaka, Japan.
- 767 HAYASHI, S. 2005. The molecular phylogeny of the Buccinidae (Caenogastropoda:  
768 Neogastropoda) as inferred from the complete mitochondrial 16S rRNA gene sequences of  
769 selected representatives. *Molluscan Research*. **25** (2): 85–98.
- 770 HERTLEIN, L. G., & E. C. ALLISON. 1960. Gastropods from Clipperton Island. *The*  
771 *Veliger*, **3**: 13-16.
- 772 HINTON, A. G. 1972. *Shells of New Guinea and the Central Indo-Pacific*. Robert Brown &  
773 Associates, Port Moresby and Jacaranda Press, Brisbane, Australia.
- 774 HINTON, A. G. 1978. *Guide to Australian Shells*. Robert Brown & Associates, Port Moresby,  
775 New Guinea.



- 776 HUELSENBECK, J.P., RONQUIST, F. & HALL, B. 2001. MrBayes: Bayesian inference of  
777 phylogeny. *Bioinformatics*, **17**: 754–755.
- 778 HUMFREY, M. 1975. *Sea Shells of the West Indies*. Taplinger Publishing Company, New  
779 York.
- 780 IREDALE, T. 1931. Australian molluscan notes. No. 1. *Records of the Australian Museum*,  
781 **18**: 201-235.
- 782 JONG, K. M. DE, & COOMANS, H. E. 1988. *Marine Gastropods from Curaçao, Aruba and*  
783 *Bonaire*. E. J. Brill, Leiden.
- 784 JOUSSEAUME, F. 1881. Description de nouvelles coquilles. *Bulletin de la Société*  
785 *Zoologique de France*, **6**, 172-188.
- 786 KAISER, K. L. 2007 The Recent molluscan fauna of Île Clipperton (tropical eastern Pacific).  
787 *The Festivus*, **39** (suppl.): 1-162.
- 788 KAUFMANN, R., & GÖTTING, K. J. 1970. Prosobranchia aus dem Litoral der karabischen  
789 Küste Kolumbiens. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **21**: 333-398.
- 790 KAY, E. A. 1979. *Hawaiian Marine Shells. Reef and Shore Fauna of Hawaii, Section 4:*  
791 *Mollusca*. B. P. Bishop Museum Special Publication **64**, part 4.
- 792 KEKKONEN, M. & HEBERT, P.D.N., 2014. DNA barcode-based delineation of putative  
793 species: efficient start for taxonomic workflows. *Molecular Ecology Resources*, **14**: 706–715.
- 794 KIENER, L. C. 1841. *Spécies Général et Iconographie des Coquilles Vivantes, Comprenant*  
795 *la Collection du Muséum d'Histoire Naturelle de Paris, la Collection Lamarck, Celle du*  
796 *Prince Masséna, (Appartenant Maintenant à M. le Baron Benjamin Delessert), et les*  
797 *Découvertes Récentes des Voyageurs. Famille des Purpurifères. Première Partie. Volume 7.*  
798 *Famille des canalifères. Troisième partie. Genre ranelle (Ranella, Lam.).* Rousseau, and J. B.  
799 Baillièrre, Paris.
- 800 KILBURN, R. N., & RIPPEY, E. 1982. *Seashells of Southern Africa*. Macmillan South  
801 Africa, Johannesburg, South Africa.
- 802 KRAUSS, F. 1848. *Die Südafrikanischen Mollusken. Ein Beitrag zur Kenntniss der*  
803 *Mollusken des Kap- und Natallandes und zur Geographischen Verbreitung Derselben, mit*  
804 *Beschreibung und Abbildung der Neuen Arten*. Ebner & Seubert, Stuttgart, Germany.
- 805 KUBO, H. 1995. Marine and freshwater mollusks. Pp. 15-210, in: [*Mollusks of Okinawa*] (in  
806 Japanese), H. KUBO & T. KUROSUMI, Okinawa Suppan Company Ltd., Urasoe City,  
807 Okinawa.
- 808 KÜSTER, H.C. & KOBELT, W. 1870-1878. *Ranella* und *Triton*. In: Die geschwänzten und  
809 bewehrten Purpurschnecken (*Murex*, *Ranella*, *Tritonium*, *Trophon*, *Hindsia*). Begonnen van

- 810 Dr. H.C. Küster [1839-1856], fortgesetzt und beendet von Dr. W. Kobelt [1868-1878].  
 811 *Systematisches Conchylien-Cabinet von Martini und Chemnitz*, ed. 2, 3(2): 119-336, pls 36-  
 812 77. Bauer & Raspe, Nürnberg.
- 813 LAMARCK, J. B. P. A. de M. de. 1816. *Tableau Encyclopédique et Méthodique des Trois*  
 814 *Règnes de la Nature ... Vingt-troisième Partie. Mollusques et Polypes Divers. Liste des Objets*  
 815 *Représentés dans les Planches de Cette Livraison*, Mme Veuve Agasse, Paris.
- 816 LAURSEN, D. 1981. *Taxonomy and distribution of teleplanic prosobranch larvae in the*  
 817 *North Atlantic. Dana Reports*, **89**: 1–43.
- 818 LEAL, J. H. 1991. *Marine Prosobranch Gastropods from Oceanic Islands off Brazil. Species*  
 819 *Composition and Biogeography*. Universal Book Services/Dr. W. Backhuys, Oegstgeest, The  
 820 Netherlands.
- 821 LEE, S. C., & CHAO, S. M. 2003. Shallow-water marine shells from northwestern Taiwan.  
 822 *Collection and Research [National Museum of Natural Science, Taichung, Taiwan]*, **16**: 29-  
 823 59.
- 824 LIPE, R. E., & ABBOTT, R. T. 1991. *Living Shells of the Caribbean and Florida Keys*.  
 825 American Malacologists, Melbourne, Florida.
- 826 MARSHALL, B.A., 1995. Calliostomatidae (Mollusca: Gastropoda: Trochoidea) from New  
 827 Caledonia, the Loyalty Islands, and the northern Lord Howe Rise. *Mémoires de la Muséum*  
 828 *National d'Histoire Naturelle*, **167** (Résultats des Campagnes Musorstom 14): 381-458.
- 829 MASSEMIN, D., LAMY, D., POINTIER, J. P. & GARGOMINY, O. 2009. *Coquillages et*  
 830 *escargots de Guyane*. Biotope, Collection Parthénope, Mèze.
- 831 MATTHEWS, H. R. 1968. Mollusks found in the digestive tract of the fish *Amphichthys*  
 832 *cryptocentrus* (Valenciennes, 1837). *Proceedings of the Malacological Society of London*, **38**:  
 833 247-250.
- 834 MATTHEWS, H. R., & KEMPF, M. 1970. Moluscos marinhos do norte e nordeste do Brasil.  
 835 II – Moluscos do Arquipelago de Fernando de Noronha (com algumas referências ao Atol das  
 836 Rocas). *Arquivos do Ciências do Mar*, **10**: 1-53.
- 837 Mello, R. L. S. & Perrier, L. L. 1986. Polyplacophora e Gastropoda do litoral sul de  
 838 Pernambuco, Brasil. *Caderno Ômega da Universidade Federal Ruaral de Pernambuco, Série*  
 839 *Ciências Aquáticas –Recife*, **2**: 107-144
- 840 MERLE, D. 2001. The spiral cords and the internal denticles of the outer lip in the Muricidae:  
 841 terminology and methodological comments. *Novapex*, **2**(3): 69-91.

- 842 MERLE, D. 2005. The spiral cords of the Muricidae (Gastropoda, Neogastropoda):  
 843 importance of ontogenetic and topological correspondences for delineating structural  
 844 homologies. *Lethaia*, **38**(4): 367-379.
- 845 MERLE D., GARRIGUES B. & POINTIER J.P., 2001. An analysis of the sculptural pattern  
 846 of the shell in Caribbean members of the genus *Chicoreus* (*Siratus*) Jousseaume, 1880  
 847 (Gastropoda : Muricidae), with description of a new species. *Zoosystema*, **23** (3): 417-431.
- 848 MERLE, D., & HOUART, R. 2003. Ontogenetic changes of the spiral cords as keys  
 849 innovation of the muricid sculptural patterns: the example of the *Muricopsis*–*Murexsul*  
 850 lineages (Gastropoda: Muricidae: Muricopsinae). *Comptes Rendus Paleovol*, **2**(6-7): 547-561.
- 851 MONAGHAN, M.T., WILD, R., ELLIOT, FUJISAWA, T., BALKE, M., INWARD, D.J.G.,  
 852 LEES, D.C., RANAIVOSOLO, R., EGGLETON, P., BARRACLOUGH, T. & VOGLER AP.  
 853 2009. Accelerated species inventory on Madagascar using coalescent-based models of species  
 854 delineation. *Systematic Biology* **58**: 298–311.
- 855 MORRETES, F. L. de. 1949. Ensaio de catálogo dos moluscos do Brasil. *Arquivos do Museu*  
 856 *Paranaense, Curitiba*, **7**: 5-216.
- 857 NAPPO A., PELLEGRINI D. & BONOMOLO G. 2014. *Bursa granularis elisabettae* una  
 858 nuova sottospecie dall'Australia Sud-Occidentale (Gastropoda: Bursidae). *Il Notiziario di*  
 859 *Malachia*. 3: 4-23.
- 860 NOWELL-USTICKE, G. W. 1959. *A Check List of the Marine Shells of St. Croix, U. S.*  
 861 *Virgin Islands, with Random Annotations*. G. W. Nowell-Usticke, Christiansted, St. Croix,  
 862 Virgin Islands.
- 863 OKUTANI, T. (ed). 1986. [*Shells [Mollusca]. The Definitive Edition; the Big Book of Life*]  
 864 (in Japanese). Sekaibunka-sha.
- 865 OKUTANI, T. (ed.). 2000. [*Marine Mollusks in Japan*] (in Japanese). Tokai University Press,  
 866 Tokyo.
- 867 ORBIGNY, A. d'. 1841 [in 1841-1853]. Mollusques. 1(1-14): 1-208 (1841); 1(15-17): 209-  
 868 264 (1842); 2(1-7): 1-112 (1846); 2(8- 24): 113-380 (1853), in: *Histoire Physique, Politique*  
 869 *et Naturelle de l'Ile de Cuba*, R. de la Sagra (ed.), Arthus Bertrand, Paris.
- 870 OSCA, D., TEMPLADO, J. & ZARDOYA, R. 2015. Caenogastropod mitogenomics.  
 871 *Molecular Phylogenetics and Evolution*, **93**: 118–128.
- 872 OYAMA, K., & TAKEMURA Y. 1960. *The Molluscan Shells, IV. Resources Exploitation*  
 873 Institute, Tokyo.

- 874 PECHENIK, J.A., SCHELTEMA, R.S., & EYSTER, L.S. 1984. Growth stasis and limited  
875 shell calcification in larvae of *Cymatium parthenopeum* during trans-Atlantic transport.  
876 *Science*. **224**: 1097-1099.
- 877 PERRY, G. 1811. *Conchology, or the Natural History of Shells: Containing a New*  
878 *Arrangement of the Genera and Species, Illustrated by coloured Engravings Executed from*  
879 *the Natural Specimens, and Including the Latest Discoveries*. William Miller, London.
- 880 PONS, J., BARRACLOUGH, T.G., GOMEZ-ZURITA, J., CARDOSO, A., DURAN, D.P.,  
881 HAZELL, S., KAMOUN, S., SUMLIN, W.D. & VOGLER, A.P. 2006. Sequence-based  
882 species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology* **55**:  
883 595–609.
- 884 PUILLANDRE, N., LAMBERT, A., BROUILLET, S. & ACHAZ, G. 2012. ABGD,  
885 Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* **21**:  
886 1864–1877.
- 887 PUILLANDRE, N., M. V. MODICA, Y. ZHANG, L. SIROVITCH, M.-C. BOISSELIER, C.  
888 CRUAUD, M. HOLFORD, ET S. SAMADI. 2012b. Large scale species delimitation method  
889 for hyperdiverse groups. *Molecular Ecology*, **21**: 2671–91.
- 890 RAMBAUT, A., SUCHARD, M.A., XIE, D. & DRUMMOND, A.J. 2014. Tracer v1.4. In.  
891 <http://beast.bio.ed.ac.uk/Tracer>.
- 892 RAY, H. C. 1949. On a collection of Mollusca from the Coromandel Coast of India. *Records*  
893 *of the Indian Museum*, **46**: 87-122.
- 894 REDFERN, C. 2001. *Bahamian Seashells. A Thousand Species from Abaco, Bahamas*.  
895 Bahamianseashells.com, Boca Raton, Florida.
- 896 REDFERN, C. 2013. *Bahamian Seashells: 1161 Species from Abaco, Bahamas*.  
897 Bahamianseashells.com, Boca Raton, Florida.
- 898 REEVE, L. A. 1844a. Monograph of the genus *Ranella*. *Conchologia Iconica, or illustrations*  
899 *of the shells of molluscous animals*, **2**. L.A. Reeve, London.
- 900 REEVE, L. A. 1844b. Descriptions of new species of *Ranella*. *Proceedings of the Zoological*  
901 *Society of London*, **12**: 136-140
- 902 RIOS, E. C. 1970. *Coastal Brazilian Seashells*. Fundação Cidade do Rio Grande, Rio Grande,  
903 Brazil.
- 904 RIOS, E. C. 1975. *Brazilian Marine Mollusks Iconography*. Museu Oceanográfico do  
905 Fundação Universidade do Rio Grande, Rio Grande RS, Brazil.
- 906 RIOS, E. C. 1985. *Seashells of Brazil*. Museu Oceanográfico, Fundação Universidade do Rio  
907 Grande, Rio Grande RS, Brazil.

- 908 RIOS, E. C. 1994. *Seashells of Brazil, 2nd ed.* Collaborators: M. Haimovici, J. A. Peros, & R.  
 909 A. dos Santos. Museu Oceanográfico Prof. E. C. Rios, Editora da Fundação Universidade do  
 910 Rio Grande, Rio Grande RS, Brazil.
- 911 RIPPINGALE, O. H., & MCMICHAEL, D. F. 1961. *Queensland and Great Barrier Reef*  
 912 *Shells*. Jacaranda Press, Brisbane, Australia.
- 913 RÖDING, P.F. 1798. *Museum Boltenianum sive Catalogus cimeliorum e tribus regnis*  
 914 *naturae quae olim collegerat Joa. Fried. Bolten M. D. p. d. Pars secunda continens*  
 915 *Conchylia sive Testacea univalvia, bivalvia et multivalvia*. Hamburg.
- 916 ROLÁN, E. 2005. *Malacological fauna from the Cape Verde archipelago*. ConchBooks,  
 917 Hackenheim,
- 918 ROSENBERG, G. 2009. *Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca*.  
 919 [WWW database (version 4.1.1)] URL <http://www.malacolog.org/>.
- 920 SALVAT, B., & C. RIVES. 1975. *Coquillages de Polynésie*. Editions du Pacifique, Papeete,  
 921 Tahiti.
- 922 SCHELTEMA, R. 1966. Evidence for trans-Atlantic transport of gastropod larvae belonging  
 923 to the genus *Cymatium*. *Deep Sea Research and Oceanographic Abstracts*, **13**(1): 83-95.
- 924 SCHELTEMA, R. 1968. Dispersal of Larvae by Equatorial Ocean Currents and its  
 925 Importance to the Zoogeography of Shoal-water Tropical Species. *Nature*, **217**(5134): 1159-  
 926 1162.
- 927 SCHELTEMA, R. 1971. Larval dispersal a means of genetic exchange between  
 928 geographically separated populations of shallow-water benthic marine gastropods. *The*  
 929 *Biological Bulletin*, **140**: 284-322.
- 930 SCHELTEMA, R. 1972. Eastward and Westward Dispersal across the Tropical Atlantic  
 931 Ocean of Larvae Belonging to the Genus *Bursa* (Prosobranchia, Mesogastropoda, Bursidae).  
 932 *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, **57**(6): 863-873.
- 933 SCHELTEMA, R. 1986a. Long-distance dispersal by planktonic larvae of shoal-water benthic  
 934 invertebrates among central pacific islands. *Bulletin of marine science*, **39**(2): 241-256.
- 935 SCHELTEMA, R. 1986b. On dispersal and planktonic larvae of benthic invertebrates: an  
 936 eclectic overview and summary of problems. *Bulletin of marine science*, **39**(2): 290-322.
- 937 SCHELTEMA, R. 1988. Initial Evidence for the transport of teleplanic larvae of benthic  
 938 invertebrates Across the East Pacific Barrier. *The biological bulletin*, **174**: 145-152.
- 939 SCOTese, C.R., 2014, *The PALEOMAP Project PaleoAtlas for ArcGIS, version 2, Volume*  
 940 *1, Cenozoic Plate Tectonic, Paleogeographic, and Paleoclimatic Reconstructions, Maps 1-15*,  
 941 PALEOMAP Project, Evanston, IL.

- 942 SIMONE, L. R. L. 2011 Phylogeny of the Caenogastropoda (Mollusca), based on  
 943 comparative morphology. *Arquivos de Zoologia*, , **42**(4): 161-323.
- 944 SEVERNS, M. 2011. *Shells of the Hawaiian Islands: the sea shells. The verifiable species*  
 945 *and their described variants illustrated by 2828 images on 225 plates*. ConchBooks,  
 946 Hachenheim, Germany.
- 947 SMITH, J. T. 1970. Taxonomy, distribution and phylogeny of the cymatiid gastropods  
 948 *Argobuccinum*, *Fusitriton*, *Mediargo* and *Priene*. *Bulletins of American Paleontology*  
 949 **56**(254): 443–573.
- 950 SOWERBY, G. B. [II]. 1832-1841. *The Conchological Illustrations, or Colored Illustrations*  
 951 *of All the Hitherto Unfigured Recent Shells*. G. B. Sowerby, London.
- 952 STRATHMAN RR. & STRATHMANN M. 2007. An extraordinarily long larval duration of  
 953 4.5 years from hatching to metamorphosis for teleplanic veligers of *Fusitriton oregonensis*.  
 954 *The Biological Bulletin* , **213**:152–9.
- 955 SUTER, H. 1913. *Manual of the New Zealand Mollusca: With an atlas of quarto plates*. J.  
 956 Mackay, Government Printer.
- 957 TAMURA, K., STECHER, G., PETERSON, D., FILIPSKI, A. & KUMAR, S. 2013. MEGA6:  
 958 Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, **30**:  
 959 2725–2729.
- 960 THIELE, J. 1925. Solenogastres. Mollusca. In: *Handbuch der Zoologie. Eine Naturgeschichte*  
 961 *der Stämme des Tierreiches*, W. Kükenenthal & T. Krumbach (eds), W. de Gruyter &  
 962 Company, Berlin & Leipzig.
- 963 TRECHMANN, C. T. 1933. The uplift of Barbados. *The Geological Magazine*, **52**: 19-47.
- 964 TRÖNDLÉ, J. & BOUTET, M. 2009. Inventory of marine molluscs of French Polynesia.  
 965 *Atoll Research Bulletin*, **570**: 1–87.
- 966 TRÖNDLE, J. & COSEL, R. VON 2005. Inventaire bibliographique des mollusques marins  
 967 de l'Archipel des Marquises (Polynésie Française). *Atoll Research Bulletin*, **542**: 265–340.
- 968 TRYON, G. W. 1880-1881. *A Manual of Conchology, Structural and Systematic: with*  
 969 *Illustrations of the Species. Ser. 1, Vol. 3. Tritonidae, Fusidae, Buccinidae*. G. W. Tryon,  
 970 Philadelphia, Pennsylvania.
- 971 TURTON, W. H. 1932. *The Marine Shells of Port Alfred, S. Africa*. Oxford University Press,  
 972 Oxford, U.K., and Humphrey Milord, London.

- 973 VERMEIJ, G. J., & ROSENBERG, G. 1993. Giving and receiving: the tropical Atlantic as  
 974 donor and recipient region for invading species. *American Malacological Bulletin*, **10**: 181-  
 975 194.
- 976 VOKES, H. E., & VOKES, E. H. 1983. Distribution of shallow-water marine Mollusca,  
 977 Yucatan Peninsula, Mexico. *Mesoamerican Ecology Institute, Tulane University, New*  
 978 *Orleans, Monograph*, **1**(viii).
- 979 WARMKE, L. G., & ABBOTT, R. T. 1962. *Caribbean Seashells. A Guide to the Marine*  
 980 *Mollusks of Puerto Rico and Other West Indian Islands, Bermuda and the Lower Florida*  
 981 *Keys*. Livingston Publishing Company, Narberth, Pennsylvania.
- 982 WILLIAMS, S.T., FOSTER, P.G. & LITTLEWOOD, D.T.J. 2014. The complete  
 983 mitochondrial genome of a turbinid vetigastropod from MiSeq Illumina sequencing of  
 984 genomic DNA and steps towards a resolved gastropod phylogeny. *Gene*, **533**: 38–47.
- 985 WILSON, B. R. & GILLET, K., 1971. *Australian shells*. A. H. & A. W. Reed, Sydney.
- 986 WILSON, B. R. 1993. *Australian Marine Shells. I. Prosobranch Gastropods. Part 1*. Odyssey  
 987 Publishing, Perth, Western Australia.
- 988 WINCKWORTH, M. A. 1945. The types of the Boltenian genera. *Proceedings of the*  
 989 *Malacological Society of London*, **26**, 136-148.
- 990 WoRMS, World Register of Marine Species. 2017. [http://www. marinespecies.org/index.php](http://www.marinespecies.org/index.php)  
 991 (accessed on the 2<sup>nd</sup> of January 2017).
- 992 ZHANG, S.P., & MA, X.T. 2004. [*Fauna Sinica. Invertebrata vol. 34. Mollusca, Gastropoda,*  
 993 *Tonnacea*] (*in Mandarin*). Science Press, Beijing.
- 994 ZOU, S., LI, Q. & KONG, L., 2011. Additional gene data and increased sampling give new  
 995 insights into the phylogenetic relationships of Neogastropoda, within the caenogastropod  
 996 phylogenetic framework. *Molecular Phylogenetics and Evolution*, **61**: 425–435.

## 998 CAPTIONS

999 **Figure 1.** Distribution of the *Bursa granularis* complex recorded by the Global Biodiversity  
 1000 Information Facility (GBIF 2016). Records from Senegal were removed after being re-identified as  
 1001 *Bursa scrobilator* (Linnaeus, 1758). Type localities of corresponding species are marked by arrows.

1002 **Figure 2.** Shell characters of *Bursa granularis*: **A.** global apertural view. **B.** outer lip.  
 1003 (Specimen figured: UF-423792, UF cruise 2008 (Madagascar), Nosy Komba, NW side). IP:  
 1004 infrasutural ramp primary cord, IS: infrasutural ramp secondary cord, P1-6: primary cords, S1-6:  
 1005 secondary cords, AN: anal notch, SC: syphonal canal. ID1: infrasutural denticle; , D1-6 Denticles of  
 1006 the convex part of the whorl.

**Figure 3.** Molecular tree for the *cox1* gene. *Bursa granularis* (Röding, 1798) is represented by the shell of UF-423792 (marked by a black square on the tree); *Bursa affinis* (Broderip, 1833) is represented by the shell of IM-2007-43056 (marked by a white square on the tree); *Bursa cubaniana* (d'Orbigny, 1841) is represented by the shell of IM-2009-23406 (marked by a black hexagon) and *Bursa elisabettae* Nappo, Pellegrini & Bonomolo, 2014 is represented by the shell of IM-2009-23322 (marked by a black star). Support for nodes is given as PP/BS, where these exceed 0.95 and 95, respectively. PNG: Papua New Guinea.

**Figure 4.** Shells of the *Bursa granularis* complex. **A-D.** *Bursa granularis* (Röding, 1798): **A.** MHNG 1098/85/1, Lectotype of *Ranella granifera* Röding, 1798, Neotype of *Tritonium granulare* Röding, 1798, of *T. jabick* Röding, 1798, and of *Biplex rubicola* Perry, 1811, from the Red Sea H: 64 mm. **B.** IM-2009-5148, MAINBAZA 2009 (Mozambique Channel), stn DW3168, H: 26 mm. **C.** UF-423792, UF 2008 (Madagascar), Nosy Komba, NW side. H: 40 mm. **D.** IM-2007-43071, Santo Marine Biodiversity Survey 2006 (Vanuatu), stn VM62, H: 25 mm. **E-I.** *Bursa affinis* (Broderip, 1833): **E.** MNHUK 1950.11.28.4, Lectotype of *Ranella affinis* Broderip, 1833, supposedly from “Anaa,” Tuamotu Islands, H: 62.5 mm **F.** IM-2007-43056, Santo Marine Biodiversity Survey 2006 (Vanuatu), stn VM02, H: 37 mm. **G.** NHMUK 1967657 Lectotype of *Ranella livida* Reeve, 1844, supposedly from “Anaa,” Tuamotu Islands, H: 56.8 mm **H.** UF-422918, UF 2008 (Federated States of Micronesia), Kosrae Letu, in front of Nautilus Hotel, H: 25 mm. **I.** IM-2007-43039, PANGLAO 2004 (Philippines), stn R24, H: 41mm. **J.** IM-2009-5148 *Bursa granularis* protoconch close-up. **K.** IM-2007-43056 *Bursa affinis* protoconch close-up. P1, P3, P5 preponderant primary cords; numbers indicates the number of denticles

**Figure 5.** Synthetic diagrams showing the sequences of appearance of the primary and secondary cords in the four species of the *Bursa granularis* complex. In all ontogenies, the primary cords (black lines) are numbered following an adapical to abapical order.

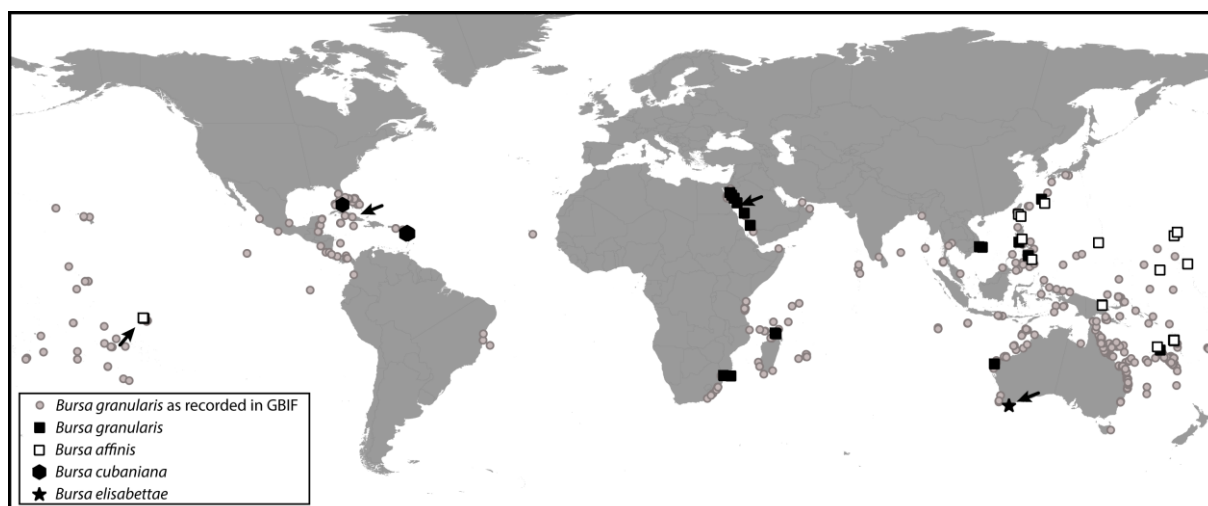
**Figure 6.** Shells of the *Bursa granularis* complex. **A-D.** *Bursa cubaniana* (d'Orbigny, 1841): **A.** NHMUK 1854.10.4.412, Holotype of *Ranella cubaniana* d'Orbigny, 1841, St. Lucie, West Indies, H: 51.7 mm **B.** IM-2009-23406, Port Louis, Pointe Antisu, Guadeloupe, H: 41mm. **C.** IM-2013-20184, KARUBENTHOS 2012 (Guadeloupe), stn GM09, H: 51mm. **D.** UF 437626, UF 2010 (Florida, USA), Florida, Monroe County, Florida Keys, Tennessee Reef, H: 3.5 cm. **E-G.** *Bursa elisabettae* Nappo, Pellegrini & Bonomolo, 2014 **E.** MAC.ML 1536 Holotype of *Bursa granularis elisabettae* Nappo, Pellegrini & Bonomolo, 2014, Flinders Bay, Cape Leeuwin, South West Australia, H: 35 mm. **F.** IM-2009-23319, WESTERN AUSTRALIA 2011, stn WA17, H: 31mm. **G.** IM-2009-23313, WESTERN AUSTRALIA 2011, stn WB28, H: 28 mm. **H** “deep sea” form of south African *Bursa granularis* MNHN ex coll. Aiken, off Richard bay, South Africa, dredge H: 24.8mm-**I** *Bursa aff.kowiensis* MNHN ex coll. Aiken, Coffee Bay, South Africa H: 40 mm. dived **J.** Holotype of *Bursa kowiensis*



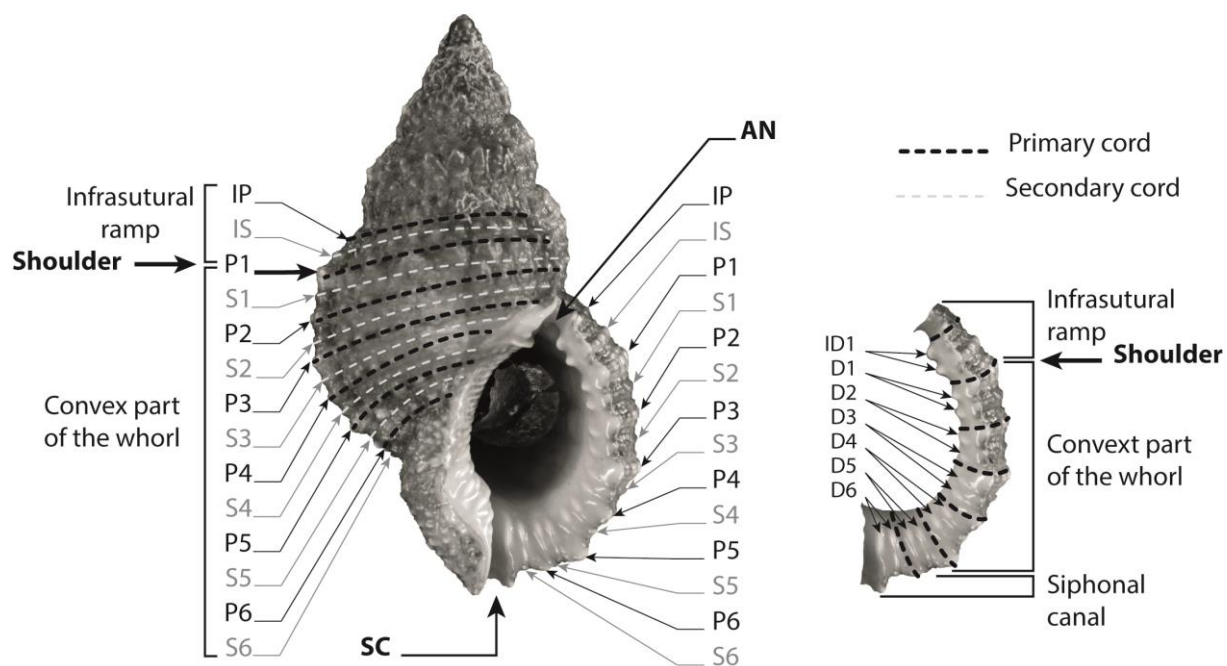
1044 Turton, 1932 H: 35 mm **K.** holotype of *Bursa alfredensis* Turton, 1932 H: 15 mm, **L.** IM-2013-20247,  
 1045 *Bursa cubaniana* protoconch close up. **M.** IM-2009-23313, *Bursa elisabettae* protoconch close-up. **N.**  
 1046 MNHN ex coll. Aiken, *Bursa* aff. *kowiensis* protoconch close-up. P1, P3, P5 preponderant primary  
 1047 cords; numbers indicates the number of denticles

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