



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

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ABSTRACT

Bursa granularis (Röding, 1798) is a tonnoidean gastropod that is regarded as broadly distributed throughout the Indo-Pacific and tropical western Atlantic. Because of its variable shell it has 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) that are partly sympatric—but not syntopic—in Japan, the Philippines, Vanuatu and New Caledonia. Based on comparison of shell characters, we applied the following available names to the four species, respectively: *B. cubaniana* (d'Orbigny, 1841), *B. elisabettae* Nappo, Pellegrini & Bonomolo, 2014, *B. granularis* s. s. and *B. affinis* Broderip, 1833. We provide new standardized conchological descriptions for each of them. Our results demonstrate that a long planktotrophic larval stage, common among Tonnoidea, does not necessarily ensure a circumtropical species distribution.

INTRODUCTION

Tonnoideans are a rather small superfamily of Caenogastropoda (about 357 species, WoRMS, 2017) related to the neogastropods, either as its sister group (Zou, Li & Kong, 2011) or belonging within Neogastropoda (Hayashi, 2005; Colgan *et al.*, 2007; Cunha, Grande & Zardoya, 2009; Williams, Foster & Littlewood, 2014; Osca, Templado & Zardoya, 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, termed teleplanic larvae (derived from the Greek *tele*, distant and *planos*, wandering; Scheltema, 1971). The record has been observed for a larva of *Fusitriton oregonensis* (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, b, 1988; Laursen, 1981; Pechenik,

Scheltema & Eyster, 1984), resulting in a cosmopolitan distribution. Scheltema (1971) also kept larvae that had been collected in the plankton alive in an aquarium, and found that some taxa lived as planktonic veliger larvae for several months or more (e.g. *Monoplex nicobaricus* lived for 390 d in captivity).

As in most other marine gastropods, tonnoidean species were first 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 might have greatly underestimated the intraspecific shell variability, since supposedly geographically restricted species were actually morphologically highly similar to other nominal species from other localities, to the extent that they shared 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, Pellegrini & Bonomolo, 2014) followed the lead of 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 (2016) database (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 (García-Talavera, 1983, cited by Beu, 1998), but this record was not confirmed by Rolán (2005).] This distribution would make it one of the most widespread 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* Röding, 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 koviensis* Turton, 1932, *Bursa cubaniana intermedia* Nowell-Usticke, 1959, *Bursa corrugata lineata* Nowell-Usticke, 1959 and *Bursa granularis elisabetae* Nappo *et al.* 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 latest revision proposed to group them all under the name *B. granularis* (Röding, 1798) (Beu, 1998). Two of these names, however have been accepted by Nappo *et al.* (2014) at the rank of subspecies—*B. granularis cubaniana* and *B. granularis elisabetae*—in addition to the nominotypical subspecies *B. granularis granularis*.

Using several molecular markers, Castelin *et al.* (2012) identified two morphologically distinct clades within the *B. 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 boundaries within the group. We increased the size of the dataset, including samples from the geographical region sampled by Castelin *et al.* (2012) as well as from other localities, with a particular focus on type localities, and covering a large part of the global distribution

of the *B. granularis* complex. Our goal was to clarify species delimitation within the *B. granularis* complex and to test the hypothesis that this supposed 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 (cytochrome *c* oxidase subunit I gene) to test whether the recognized morphogroups corresponded to distinct molecular clusters. Finally, we assigned available names to the different genetic and morphological groups identified within the complex and considered the implication in terms of their geographical distributions.

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 (University of Florida UF 2013), Vietnam (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 Islands (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 MgCl₂ 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 *c.* 30 s. 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 included 82 specimens, 42 deposited in the Muséum national d'Histoire naturelle, Paris (MNHN) and 40 in the Florida Natural History Museum (UF) collections (Supplementary Material Table S1). The specimens and corresponding sequences are also registered in the Barcode of Life Data System (project BURSA)

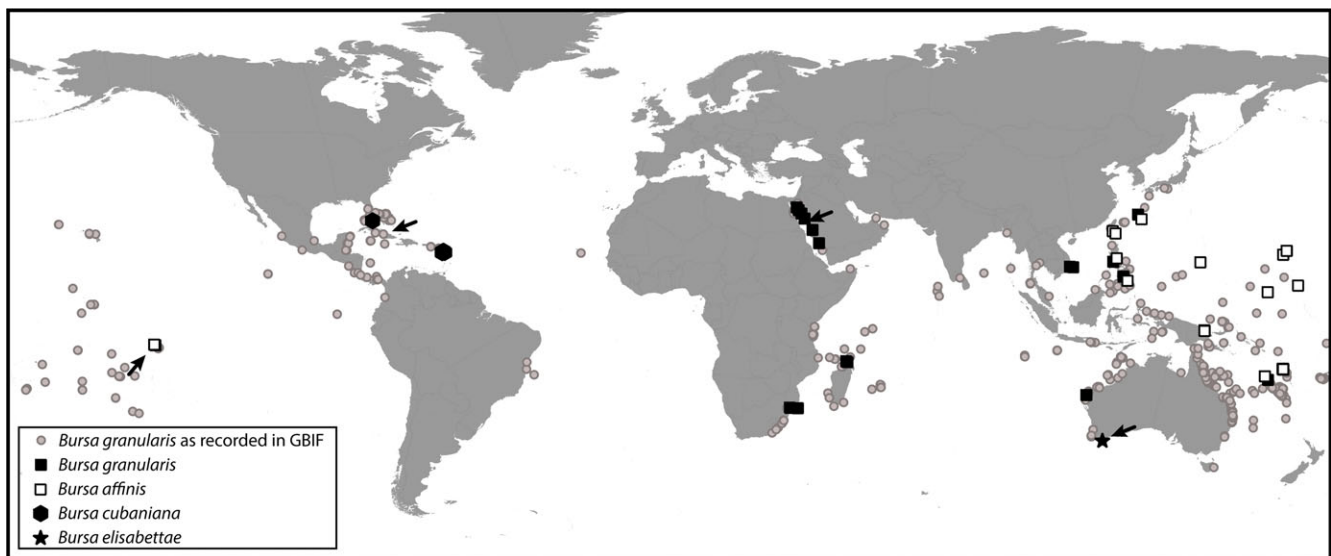


Figure 1. Distribution of the *Bursa granularis* complex recorded by the Global Biodiversity Information Facility (GBIF, 2016). Records from Senegal were removed after being reidentified as *Bursa scrobilator* (Linnaeus, 1758). Type localities of corresponding species are marked by arrows.

and GenBank. Maps showing the sampling localities of all the specimens were generated using Qgis v. 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 *c* 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 μ l, containing 3 ng DNA, 1 \times reaction buffer, 2.5 mM MgCl₂, 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 in both directions by the Eurofins sequencing facility.

Species delimitation

All specimens were first separated into morphogroups, using characters of the teleoconch and in particular of 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 (BI) approaches, with MEGA v. 7 (with Bootstraps 100 replications and default parameters for tree inference options) for ML analysis and, for the BI analyses, 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 v. 1.8.3 (Drummond *et al.*, 2012) (with uncorrelated relaxed clock, and 10,000,000 generations). 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 analyses 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) method 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 interspecific 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

Once the species were delimited based on molecular data, shells were described using the methods developed by Merle (2001, 2005) for primary homology definition. Primary cords (P) 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

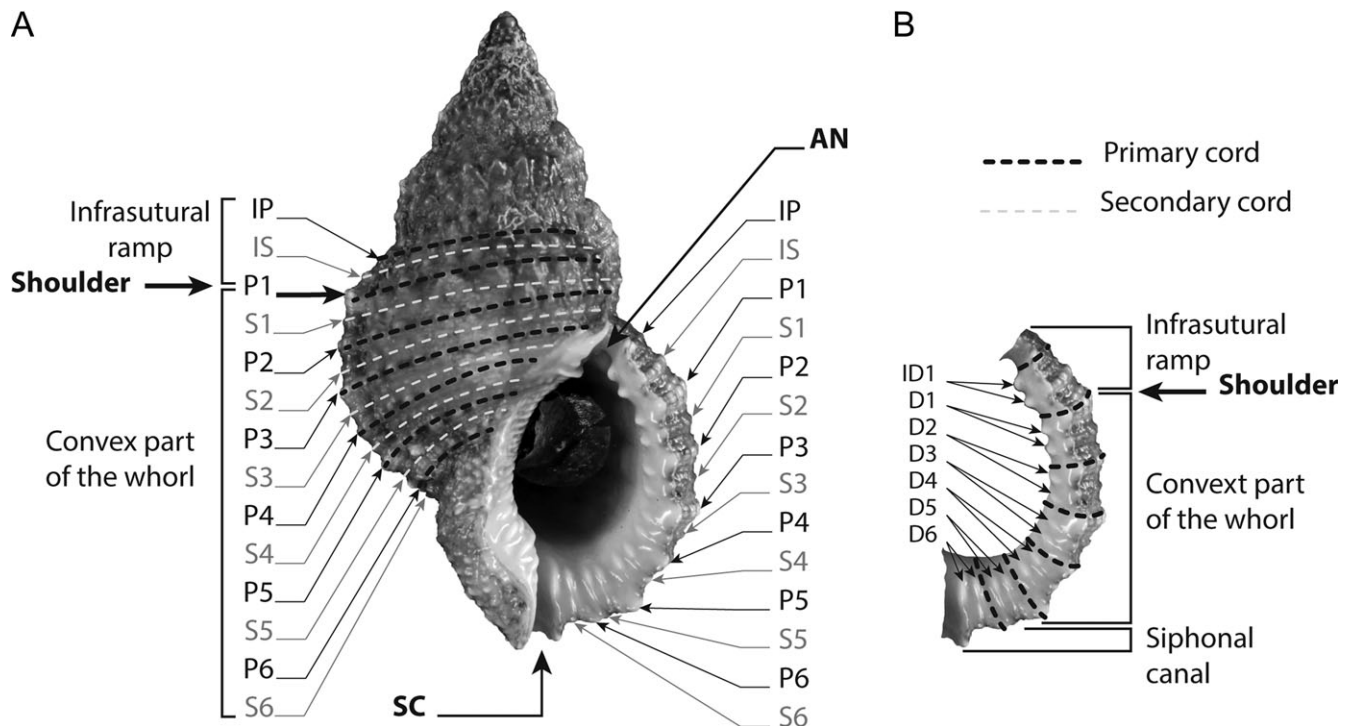


Figure 2. Shell characters of *Bursa granularis* complex. **A.** Apertural view. **B.** Outer lip. Specimen figured: UF-423792, UF cruise 2008 (Madagascar), Nosy Komba, NW side. Abbreviations: IP, infrasutural ramp primary cord; IS, infrasutural ramp secondary cord; P1-6, primary cords; S1-6, secondary cords; AN, anal notch; SC, siphonal canal; ID1, infrasutural denticle; D1-6, denticles of convex part of whorl.

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 apical to abapical; denticles above the shoulder are designed as ID1 and ID2 added from abapical to apical (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 denticle formula (OLDF). This 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 in the direction of the siphonal notch. For example, in the specimen of *B. granularis* figured in Figure 2, the OLDF should be read as AN, 2, P1, 4, P3, 4, P5, 4, SC or 2,4,4,4 for short.

Abbreviations

Specimen repositories:

MAC.ML	Museo di Storia Naturale Aquilegia, Cagliari, Sardinia
MHNG	Muséum d'Histoire naturelle, Geneva
MNHN	Muséum national d'Histoire naturelle, Paris
NHMUK	Natural History Museum, London
RASM	Russian Academy of Science, Moscow
UF	Florida Natural History Museum, University of Florida, Gainesville, FL

Shell characters:

AN	anal notch
D	denticles of the outer lip
D1-6	denticles of the convex part of the whorl
H	height
ID1-2	denticles of the infrasutural ramp
IP	infrasutural primary cord
IS	infrasutural secondary cord
OLDF	outer lip denticle formula
P	primary cord
P1	shoulder cord
P2-6	primary cords of the convex part of the whorl
S	secondary cord
S1-6	secondary cords of the convex part of the whorl
SC	siphonal canal
W	width

RESULTS

Among the 82 specimens, excluding outgroups, three morphogroups were initially recognized. The ABGD (both initial and recursive partitions) and GMYC (single threshold) methods consistently found four clusters. The only exception is the multiple-threshold approach of GMYC: five clusters were supported, one specimen (IM-2013-19496) from the Caribbean cluster (see below) being considered different. Given that this specimen is very close in molecular sequences to other Caribbean specimens, we conclude this to be an artefact of the multiple-threshold method of GMYC, which is known to oversplit (Fujisawa & Barraclough, 2013; Kekkonen & Hebert, 2014). Among the four clusters recognized with the *cox1* gene, two correspond to two morphogroups. One morphogroup is thus divided into two genetic clusters, corresponding to the two clades revealed by Castelin *et al.* (2012). A *posteriori* re-examination of the shells revealed stable teleoconch

characters distinguishing these two genetic clusters. The morphological characters used to recognize first the three morphogroups and, after the molecular analyses, the final four morphogroups, are described in the systematic section (below). The four genetic clusters also correspond to highly supported clades in both BI and ML analyses (PP > 0.99 and BS > 80) (Fig. 3). Pairwise genetic distances between clades were never less than 6.4%, while within cluster genetic distances never exceeded 1.8%, even between geographically distant localities such as Saudi Arabia and Western Australia. All clades correspond to geographically defined areas: Clade 1 ranges from Mozambique to the Red Sea, Vietnam, Japan, the Philippines, Western Australia, Vanuatu and New Caledonia, suggesting an occurrence throughout the Indian Ocean and western Pacific; Clade 2 is 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 restricted to the Caribbean; and Clade 4 is limited to southernmost Western Australia.

Based on the original descriptions and type localities, we have attributed available names as follows: *B. granularis* to Clade 1, *B. affinis* to Clade 2, *B. cubaniana* to Clade 3 and *B. 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 (Jousseume, 1881: 174) (junior synonym of *Murex bufonius* Gmelin, 1791, by First Reviser's action of Winckworth, 1945: 137).

Bursa granularis (Röding, 1798)

(Fig. 4A–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, 1853: 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, Conales & Bundal, 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, fig. 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.

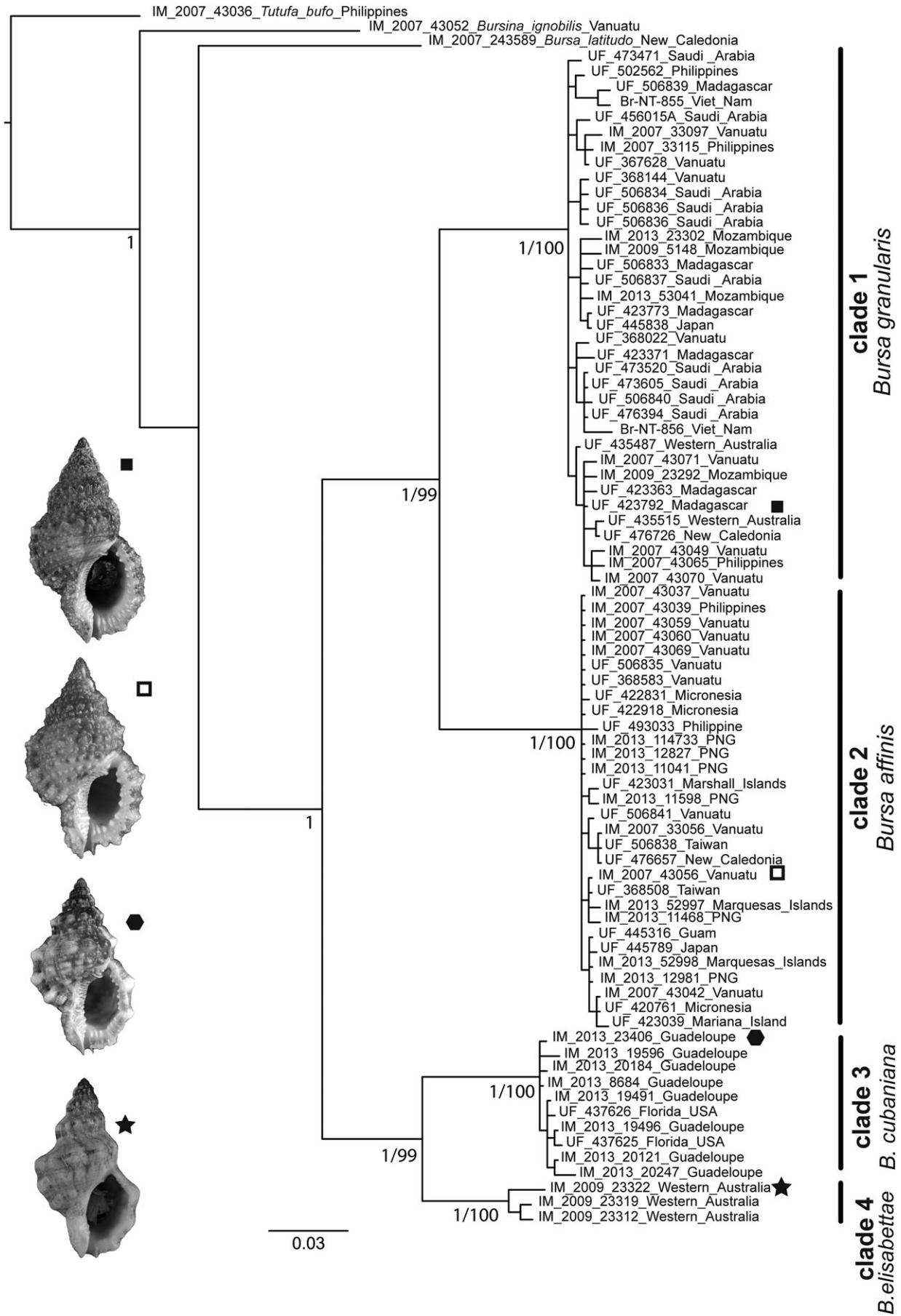
Bursa (Bufonariella) granularis—Bosch *et al.*, 1995: 102, fig. 737.

Bursa (Colubrellina) granularis—Okutani, 2000: 269, pl. 133, fig. 1; Zhang & Ma, 2004: 182, text-figs 113a–c, pl. 5, figs 1–3.

Tritonium jabick 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).

Dulcerana jabick—Iredale, 1931: 213.

Colubrellina jabick—Oyama & Takemura, 1960: *Colubrellina* pl., figs 3, 4.



Biplex rubicola Perry, 1811: pl. 5, fig. 4 (Red Sea, in accordance with ICZN Art. 76.3; original types lost; neotype MHNG 1098/85/1, designated by Beu, 1998: 150).

Ranella granifera Lamarck, 1816: pl. 414, fig. 4, 'Liste des objets': 4; 1822: 153 (Red Sea, designated by Beu 1998: 150; lectotype MHNG 1098/85/1, designated by Beu, 1998: 150); Kiener, 1841: 16, pl. 11, fig. 1; Deshayes, 1843: 548; Reeve, 1844a: pl. 6, fig. 30; Küster, 1871 [in Küster & Köbelt, 1870–1878]: 143, pl. 39, fig. 1.

Bursa cumingiana Dunker, 1862: 238; New Caledonia; lectotype NHMUK 1968530 designated by Beu 1998: 150; Dunker, 1863: 59, pl. 19, figs 7, 8.

Ranella (Lampas) granifera—Tryon, 1880 [in 1880–1881]: 41, pl. 22, figs 35–40.

Ranella semigranosa—Reeve, 1844b: pl. 6, fig. 25; Krauss, 1848: 113 (not Lamarck, 1822).

Material examined: Supplementary Material Table S1.

Diagnosis: Shell biconic, varices strictly aligned, numerous nodules on all primary, secondary and tertiary cords, OLF: 2,4,4,4, or 2,4,4,3 in large specimens.

Description: Protoconch of 3.75 whorls (following counting method of Bouchet & Kantor, 2003), rather tall with weakly impressed sutures, with finely reticulate protoconch I of 0.5 whorls, reticulate sculpture on first whorl of protoconch II, becoming obsolete before end of last protoconch whorl. Teleoconch: tall, relatively narrow, 4–5 whorls (up to 6 in very large specimens). H about 40 mm, up to 60 mm. Spire angle 50°. Aperture 53% of W. Last whorl 54% of H. Varices strictly aligned for most of spire height, becoming slightly displaced only on last 1 or 2 whorls of large specimens. Abapertural face of each varix slightly excavated, buttressed by spiral cords. Spiral ornamentation of 7 primary cords, 1 on infrasutural ramp (IP) and 6 on convex part of whorl (P1–6). After whorl 2.5 (varix 5) IP becoming very reduced, noticeable only where it intersects varices. Secondary cords in interspaces between primary cords. Primary cord above IP remaining reduced throughout shell ontogeny whereas others growing in similar fashion to primary cords. On last whorl, spiral ornamentation composed of 9 nodules per primary cord between two varices (and secondary cords of infrasutural ramp) and double this number for secondary cords. 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).

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 in about 100 m depth.

Remarks: The nomenclatural history of *B. granularis* is a particularly complex one. The types of *Tritonium granulare*, *T. jabick* and *Biplex rubicola* are lost. Beu (1998) designated the lectotype of *R. 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 *R. granifera* displays characters congruent with the description above (Fig. 4A).

Bursa cumingiana (type locality New Caledonia) is another available name in the *B. granularis* complex. There are two (and only two) molecular operational taxonomic units (MOTU) living sympatrically in this region and the lectotype of *Ranella cumingiana* (NHMUK 1968530) is a well-preserved adult specimen, which displays four distinctive denticles between P5 and the anterior canal, identifying it as *B. granularis*. The colour 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 colour 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. 4E–I, K)

Ranella affinis Broderip, 1833: 179 ('Anmaa,' Tuamotu Islands, lectotype NHMUK 1950.11.28.4, designated by Beu, 1998: 150); G.B. Sowerby II, 1835 [in 1832–1841]: 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; ('Anmaa,' Tuamotu Islands, lectotype NHMUK 1967657_1, designated by Beu, 1998: 150); Reeve, 1844b: 138; Krauss, 1848: 113.

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

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

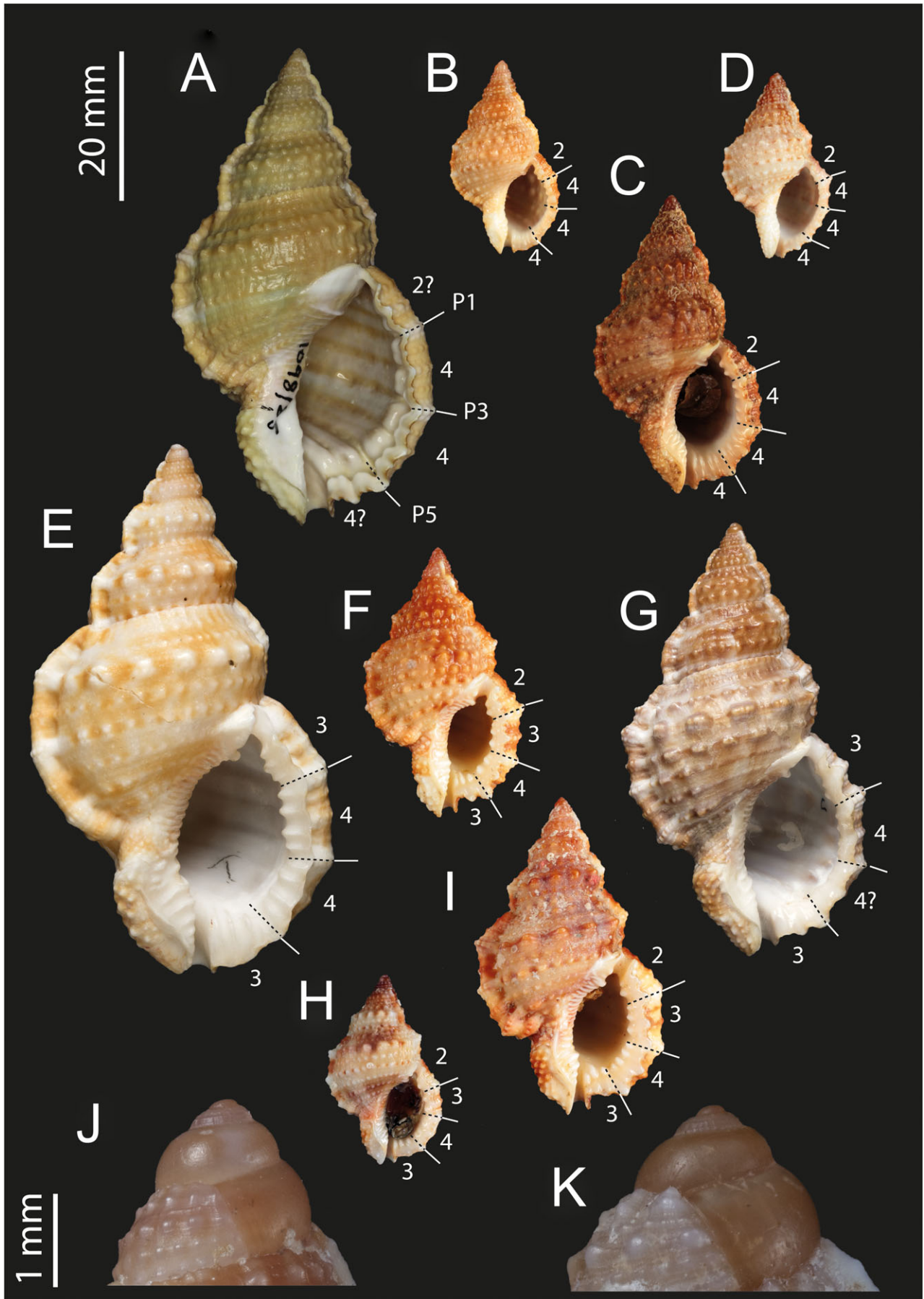
Bursa (Colubrellina) granularis—Kaiser, 2007: 39, pl. 26, fig. 7a–b (not Röding, 1798).

Material examined: Supplementary Material Table S1.

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

Description: Protoconch as in *B. granularis*. Teleoconch tall, relatively narrow, with 4–5 whorls (up to 6 on large specimens). H 40–50 mm, up to 80 mm. Spire angle 55°. Aperture comprising 50% of W. Last whorl comprising 52% of H. Varices strictly aligned for most of spire height, becoming slightly displaced only on last 1 or 2 whorls 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 increasing in importance to equal other cords, diminishing again after varix 6, allowing development of secondary cord above. Each primary cord bounded by two secondary cords, increasing in importance similarly to primary cords. On last whorl, spiral ornamentation composed of 9 nodules per primary cord between two varices except P1, which bears much bigger nodules, pointing slightly upwards, decreasing in number with ontogeny from 9 to 5. Secondary cords bearing same number of small nodules as *B. granularis*. Nodules on varices where they meet P1 angulating shoulder. Apertural lip well flared, bearing numerous prominent, narrow, internal transverse denticles. ID2 present in large specimens, ID1

Figure 3. Molecular tree for the *cox1* gene of the *Bursa granularis* complex. *Bursa granularis* is represented by shell of UF-423792 (indicated by black square); *B. affinis* by shell of IM-2007–43056 (white square); *B. cubaniana* by shell of IM-2009–23406 (black hexagon) and *B. elisabettiae* by shell of IM-2009–23322 (black star). Support for nodes is given as PP/BS, where these exceed 0.95 and 95, respectively. Abbreviation: PNG, Papua New Guinea.



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 about 40 m depth.

Remarks: *Bursa affinis* and *B. livida* have the same type locality, 'Annaa' [now Anaa], Tuamotu Islands. The type specimens (Fig. 4E, G) of both have the same OLF 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 *B. affinis*.

***Bursa cubaniana* (d'Orbigny, 1841)**

(Fig. 6A–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, 1962: 103, pl. 18, fig. i; Rios, 1970: 70;

Coelho & Matthews, 1971: 52, figs 11, 12; Humfrey, 1975: 126, pl. 14, fig. 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.

Bursa corrugata var. *lineata* Nowell-Usticke 1959: 61-62, pl. 3, fig. 12 (North of Fredericksted, St. Croix, Virgin Islands); Boyko & Cordeiro, 2001: 24.

Bursa granularis cubaniana—Abbott, 1974: 167, pl. 7, fig. 1781 (as *B. granularis* in caption); Rios, 1975: 81, pl. 23, fig. 331; Finlay, 1978: 149; Bandel, 1984: 102, pl. 10, figs 3, 8; Diaz & Gotting, 1988: 156; Diaz, 1990: 19; Diaz & Puyana, 1994: 174, fig. 650; Redfern, 2001: 58, pl. 29, fig. 247 A, B. Nappo et al., 2014: pl. 5, figs 2, 3, pl. 6, figs 1–3, pl. 7, fig. 2.

Bursa (Colubrellina) granularis cubaniana—Rios, 1975: 81, pl. 23, fig. 331; Beu, 1985: 64; Cossignani, 1994: 78.

Bursa (Colubrellina) granularia (sic) *cubaniana*—Rios, 1994: 92, pl. 31, fig. 365.

Bursa granularis—Leal, 1991: 111, pl. 16, figs C, D; Lipe & Abbott, 1991: 14-15, illus.; Beu 2010: 48, pl. 3, figs 1, 3; Redfern, 2013: 83, fig. 241 (not Röding, 1798).

Bursa (Colubrellina) granularia (sic)—Rios, 1985: 79, pl. 28, fig. 347 (not Röding, 1798).

Gyrineum affine—Dall, 1903: 132 (not Broderip, 1833).

Ranella (Bursa) affinis—Trechmann, 1933: 39 (not Broderip, 1833).

Material examined: Supplementary Material Table S1.

Diagnosis: Shell biconic, varices strictly aligned, varices abaperturally deeply excavated, relatively numerous nodules on all primary cords, particularly large one on P1, beige stripes following primary cords, OLF: 3,5,4,3 or 3,5,5,4 in particularly large specimens.

Description: Protoconch similar to other species in the complex (see above). Teleoconch tall, relatively narrow with 4–5 whorls (up to 6 for larger specimens). H about 50 mm, up to 60 mm. Spire angle 55°. Aperture comprising 50% of W. Last whorl comprising 47% of H. Varices strictly aligned for most of spire height, becoming slightly displaced only on 1 or 2 last whorls in large specimens. Abapertural face of each varix deeply excavated, buttressed by spiral cords. Spiral ornamentation much reduced compared to *B. granularis* and *B. affinis*. P1, 3 and 5 much more pronounced than others. Primary cords (IP included) bearing 4 rather large nodules, with small nodules overlying large ones in large specimens. Secondary cords not visible on shell after whorl 1, except slightly visible at intersections with varices. Nodules on varices where they meet P1 angulating shoulder, not as sharp as on *B. affinis*. Apertural lip well flared, bearing numerous prominent, narrow transverse internal denticles; ID2 single, ID1 bifid, trifurcated in large specimens, D1 bifid, trifurcated in large specimens, D2 bifid, D3 bifid, trifurcated in large specimens, D4 bifid, D5 single, bifid in large specimens, D6 bifid (Fig. 5). Shells bearing distinctive beige-cream bands following 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 (Massemín et al., 2009), the Bahamas (Redfern, 2013), Guadeloupe (this study), Jamaica, Cuba and St Lucia (d'Orbigny, 1841) south to French Guiana (Massemín 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 is unconfirmed (Rolán, 2005).

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

***Bursa elisabettae* Nappo et al. 2014**

(Fig. 6E–G, M)

Bursa granularis elisabettae Nappo et al. 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 Borson, 1823).

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

Figure 4. Shells of *Bursa granularis* complex. **A–D.** *Bursa granularis* (Röding, 1798). **A.** MHNG 1098/85/1, lectotype of *Ranella granifera* Röding, 1798 and neotype of *Tritonium granulare* Röding, 1798, of *T. jabick* Röding, 1798 and of *Biplex rubicola* Perry, 1811, from Red Sea, H 64 mm. **B.** IM-2009-5148, MAINBAZA 2009 (Mozambique Channel), stn DW3168, H: 26 mm. **C.** UF-423792, UF 2008 (Madagascar), NW side Nosy Komba, 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.** NHMUK 1950.11.28.4, lectotype of *Ranella affinis* Broderip, 1833, supposedly from 'Annaa,' 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 'Annaa,' Tuamotu Islands, H 56.8 mm. **H.** UF-422918, UF 2008 (Federated States of Micronesia), Kosrae Letu, H 25 mm. **I.** IM-2007-43039, PANGLAO 2004 (Philippines), stn R24, H 41 mm. **J.** IM-2009-5148, *Bursa granularis* protoconch detail. **K.** IM-2007-43056, *Bursa affinis* protoconch detail. Abbreviations: P1, P3, P5, preponderant primary cords; numbers indicates the number of denticles.

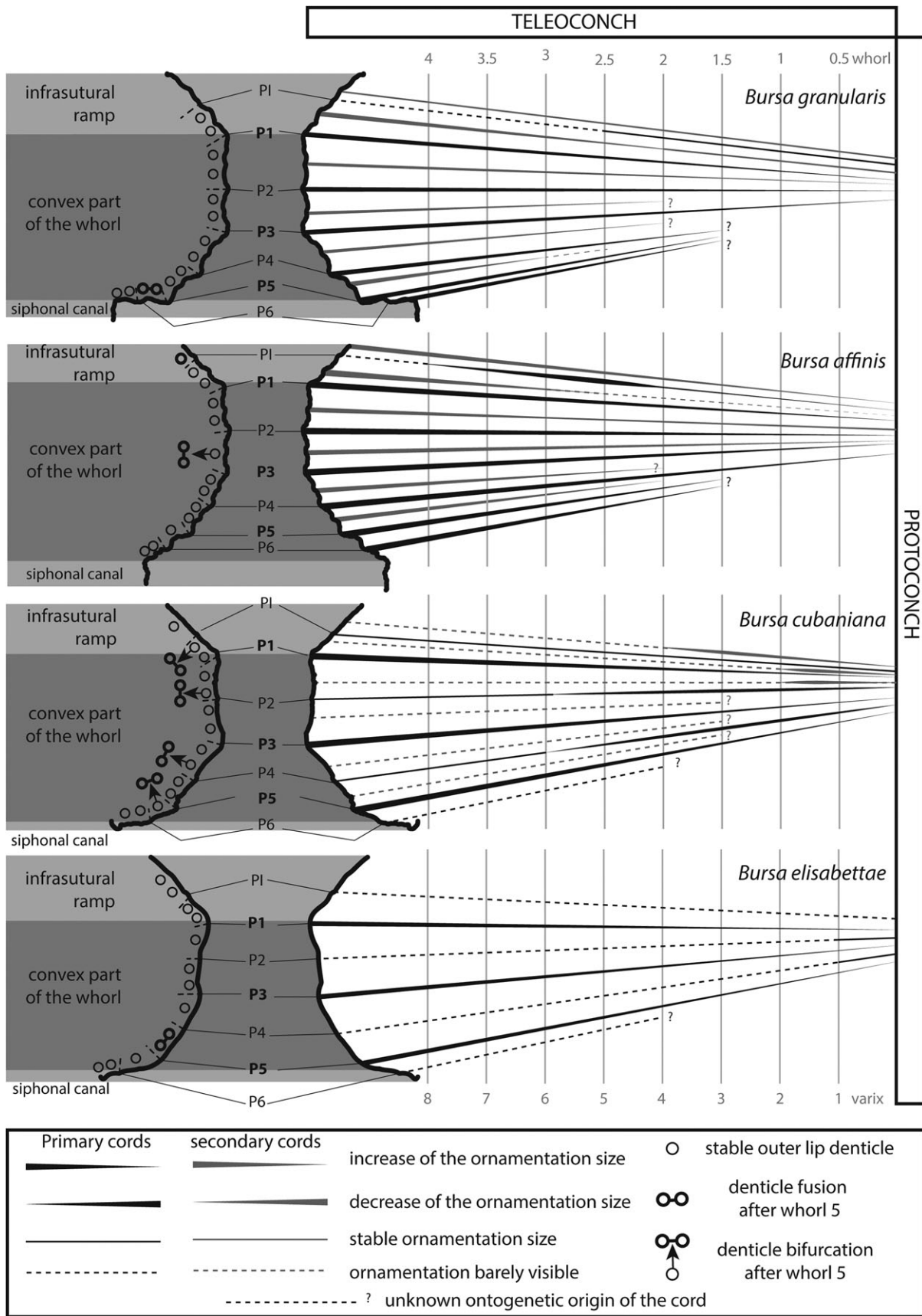


Figure 5. Diagrams showing the sequence of appearance of primary and secondary cords in the four species of the *Bursa granularis* complex. In all ontogenies, the primary cords (black lines) are numbered following their adapical to abapical order.

Material examined: Supplementary Material Table S1.

Diagnosis: Shell biconic, varices strictly aligned, varices abaperturally rather excavated, nodules weak on first primary cords, brown bands following primary cords, outer lip denticles small, OLF: 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 about 50 mm. Spire angle 45°. Aperture comprising 52% of W. Last whorl comprising 52% of H. Varices strictly aligned, although low and indistinct in some specimens. Spiral ornamentation very reduced to absent in some specimens. Only primary cords P1, 3 and 5 visible; each bearing 4 nodules between 2 varices, especially visible on P1. Secondary cords lacking. Nodules on varices where they meet P1 angulating shoulder, although not as sharply as in *B. affinis*. Apertural lip 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 *B. elisabetae* is restricted to southwestern Western Australia, in shallow water.

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

DISCUSSION

Bursa granularis is considered to be easy to identify, although it is highly 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 the single name *B. 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 *B. 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 *cox1* gene corresponds to the species limits.

Among the four delimited species, members of one pair, *B. granularis* and *B. affinis*, are difficult to distinguish morphologically and without molecular evidence there is little to suggest that they are separate species. Furthermore, intraspecific morphological variability sometimes exceeds 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 banded pattern usually attributed to *B. cubaniana* (for which this pattern is stable). Nevertheless, we were able to discriminate this pair of species according to their morphology through the detailed observation of the spiral ornamentation of the shells. The importance of such ornamentation for systematics has previously been recognized in e.g. Muricidae (Merle, Garrigues & Pointier, 2001; Merle & Houart, 2003; Merle, 2005), 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 colour, spire height and sculptural prominence (i.e. considering one cord at a time), are of very little value.

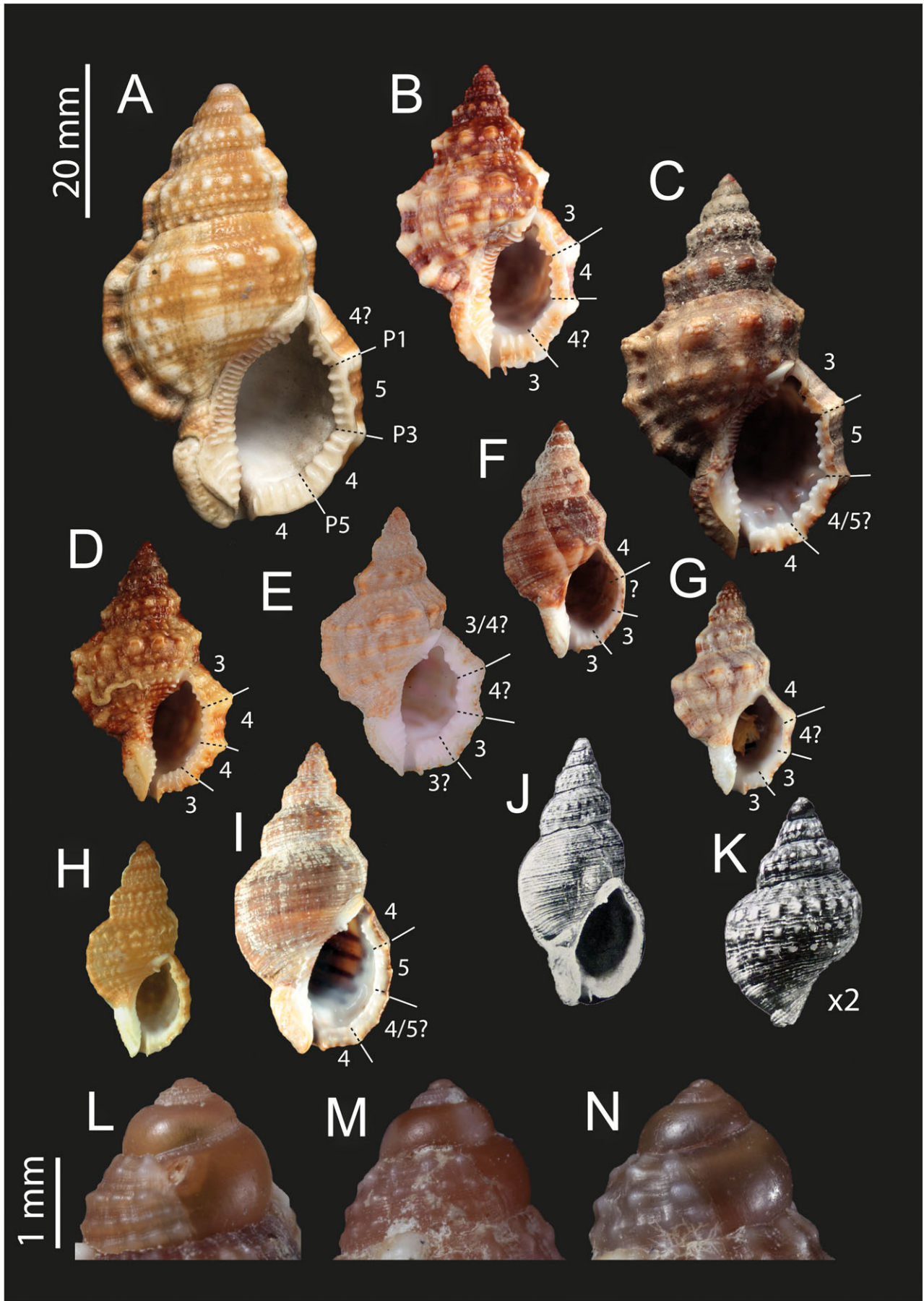
Other anatomical characters and radulae were not considered in the present study, but may perhaps provide useful information. Abbott (1958) pointed out differences between *B. cubaniana* and *B. granularis* in denticle size and number on the central teeth (Abbott, 1958: figs 1d, 2c), but radular studies 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 Barkalova, Fedosov & Kantor (2016) and for insight on the general anatomy of *B. cubaniana* see Simone (2011).

The integrated taxonomic approach followed here was thus effective to propose robust species hypotheses. It is yet another example of the value of molecular characters when species cannot readily be distinguished morphologically, a common pattern in gastropods (e.g. Duda *et al.*, 2008; Puillandre *et al.*, 2012b). However, if proposing putative species using DNA sequences is now a common practice, linking the species hypotheses to available names attached to nonsequenced name-bearing types remains daunting. Indeed, all the species in the *B. granularis* complex were described based on shell characters only, including *B. elisabetae*, which was described as recently as 2014. More generally, most known species of molluscs were described before the molecular era and the application of historical names remains 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 may be recognized in the future. *Bursa alfredensis* and *B. kowiensis* (Fig. 6I–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 MOTUs of this study. The types of both display a loss of fine sculpture early in ontogeny. The adult South African specimen in Fig. 6I (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. elisabetae*. If *B. elisabetae*, *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 consistent with a Pleistocene colonization of the Caribbean from the Indian Ocean around South Africa and which corresponds to the stratigraphic distribution of *B. cubaniana* in the region (Beu, 2010). This scenario was discussed by Vermeij & Rosenberg (1993) for 17 Indo-West-Pacific species.

South African collectors (R. Aiken, personal communication) have also drawn our attention to a small form of *B. granularis* dredged from ‘deep water’ (Fig. 6H). We have not seen this variation anywhere else and the deep-water (100 m?) habitat is very unusual for *B. granularis* *s. s.*, which has only exceptionally been dredged alive in 87–90 m (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 *B. granularis*, *B. cubaniana* and *B. elisabetae* were subspecies of *B. granularis*. We rank them here as full species. Firstly, as we showed above, the two species-pairs *B. granularis*–*affinis* and *B. cubaniana*–*elisabetae* have very distinct distributions and inferred biogeographical histories. Secondly, Castelin *et al.* (2012) demonstrated that the pair *B. granularis*–*affinis* diverged from each other over 11 Mya (the distance between *B. cubaniana* and *B. elisabetae* suggests a comparable time of divergence, although this was not tested). The divergence between the two pairs is necessarily older.



The estimated 11 Mya divergence between *B. granularis* and *B. affinis* corresponds to the Seravallian/Tortonian stages of the Miocene, a period of particularly low sea-level stand (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, disrupting 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 could represent an example of allopatric speciation with secondary contact following recolonization. However, because our results are based only on mitochondrial data, we cannot rule out an alternative scenario in which both groups are still genetically connected. In this latter scenario, the pattern observed with the *cox1* gene would again be the result of an ancient allopatric divergence, but with the secondary contact being too recent to homogenize the two mitochondrial gene pools. Although the large number of sequenced specimens and the high genetic divergence between *B. affinis* and *B. granularis* do not support this hypothesis, nuclear data would help reject one of these scenarios.

One of the main general implications of the systematic revision proposed here is that larval duration alone does not explain geographical distributions. Other factors, such as availability of suitable habitats, may limit distribution areas regardless of dispersal capacity. A striking example is *Fusitriton oregonensis*; it is the only species for which the larval duration has been directly measured (although under laboratory conditions) and estimated at 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 areas of at least two of the members of the *B. granularis* complex are indeed large, we have shown that the range of the classic taxonomic concept of '*B. granularis*' was greatly overestimated. 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—will be found in other tonnoideans. Considering only the Bursidae, *B. corrugata* (Perry, 1811) (with eight subjective synonyms and recorded from Eastern Pacific and Eastern Atlantic Oceans and Caribbean), *B. ranelloides* (Reeve, 1844) (with seven subjective synonyms, recorded from Indian and Atlantic Oceans, and Japan and Hawaii in Pacific) and *B. rhodostoma* (G.B. Sowerby II, 1835) (with six subjective synonyms, recorded from Indo-Pacific and Caribbean) are good candidates for integrative taxonomy-based revision.

However, achieving a representative sampling for molecular taxonomy is becoming 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 trend (Bouchet *et al.*, 2016). For the time being, compliance with regulations on ‘Access and Benefit Sharing’ and ‘Prior Informed

Consent’ is a formidable obstacle to academic researchers investigating the limits and names of species.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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Figure 6. Shells of *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, Pointe Antisu, Port Louis, Guadeloupe, H 41 mm. **C.** IM-2013–20184, KARUBENTHOS 2012 (Guadeloupe), stn GM09, H 51 mm. **D.** UF 437626, UF 2010 (Florida, USA), Tennessee Reef, Monroe Co., FL, H: 35 mm. **E–G.** *Bursa elisabettae* Nappo *et al.* 2014. **E.** MAC.ML 1536, holotype of *Bursa granularis elisabettae* Nappo *et al.* 2014, Flinders Bay, Cape Leeuwin, south Western Australia, H 35 mm. **F.** IM-2009–23319, WESTERN AUSTRALIA 2011, stn WA17, H 31 mm. **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, H 24.8 mm. **I.** *Bursa* aff. *kowiensis* MNHN ex coll. Aiken, Coffee Bay, South Africa, H 40 mm. **J.** Holotype of *Bursa kowiensis* Turton, 1932, H 35 mm (reproduced from Turton, 1932). **K.** Holotype of *Bursa alfredensis* Turton, 1932, H 15 mm (reproduced from Turton, 1932). **L.** IM-2013–20247, *Bursa cubaniana* protoconch detail. **M.** IM-2009–23313, *Bursa elisabettae* protoconch detail. **N.** MNHN ex coll. Aiken, *Bursa* aff. *kowiensis* protoconch detail. Abbreviations: P1, P3, P5, preponderant primary cords; numbers indicates the number of denticles.

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