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

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

3
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13
14 Running title: *BURSA GRANULARIS* COMPLEX

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17 **ABSTRACT**

18 *Bursa granularis* (Röding, 1798) is a tonnoidean gastropod viewed as broadly
19 distributed throughout the Indo-Pacific and tropical western Atlantic. Because of its variable
20 shell it received no less than thirteen names, now all synonymized under the name *B.*
21 *granularis*. We sequenced a fragment of the *cox1* gene for 82 specimens covering a large part
22 of its distribution and most type localities. Two delimitation methods were applied, one based
23 on genetic distance (ABGD) and one based on phylogenetic trees (GMYC). All analyses
24 suggest that specimens identified as *B. granularis* comprise four distinct species: one limited
25 to the tropical western Atlantic; another to southwestern Western Australia; and two in the
26 Indo-Pacific, from the Red Sea to the open Pacific, partly sympatric - but not syntopic - in
27 Japan, the Philippines, Vanuatu and New Caledonia. Based on shells characters, we applied
28 available names to each of the four species, respectively *B. cubaniana* (d’Orbigny, 1841), *B.*
29 *elisabettae* Nappo, Pellegrini & Bonomolo, 2014, *B. granularis* s.s., and *B. affinis* Broderip,
30 1833, and we provide new standardized conchological descriptions for all of them. Our results
31 demonstrate that a long planktotrophic larval stage, common among Tonnoidea, does not
32 necessarily ensure a circum-tropical species distribution.

33
34 **INTRODUCTION**

35 Tonnoideans are a rather small superfamily of Caenogastropoda (~357 species, WoRMS
36 2017) related to the neogastropods, either as its sister group (Zou *et al.* 2011) or belonging in
37 Neogastropoda (Colgan *et al.*, 2007; Cunha *et al.*, 2009; Hayashi, 2005; Williams *et al.*,
38 2014, Osca *et al.*, 2015). Notwithstanding the non-planktotrophic development of a few
39 Australian species, one of the characteristic features of tonnoidean gastropods is their long to
40 extremely long planktonic larval stages, named teleplanic larvae [based on the Greek *tele*,
41 distant, and *planos*, wandering; Scheltema (1971)]. The record has been observed for a larva
42 of *Fusitriton oregonensis* Redfield, 1846 (Ranellidae), which lived in an aquarium for 4.5
43 years without metamorphosing (Strathmann & Strathmann, 2007). An indirect estimation of
44 the duration of larval life was also proposed by Scheltema (1972) who, based on the extent of
45 the distribution area and the speed of ocean currents, inferred the time it would take for the
46 larvae to cross ocean basins — generally several months. Conversely, and in quite circular
47 reasoning, the duration of this larval time led to the hypothesis that some species may have
48 trans-oceanic dispersal capabilities (e.g., Scheltema, 1966, 1968, 1971, 1972, 1986a, 1986b,
49 1988; Laursen, 1981; Pechenik *et al.*, 1984), resulting in a cosmopolitan distribution.
50 Scheltema (1971, table 1) also kept larvae alive in an aquarium that had been collected in the
51 plankton, and found that some taxa lived as planktonic veliger larvae for several months [e.g.,
52 *Monoplex nicobaricus* (Röding, 1798) lived for 390 days in captivity].

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

67 Among the Tonnoidea, the family Bursidae includes 54 Recent species (WoRMS
68 2017), among which several are potentially species complexes, i.e., species for which

69 alternative hypotheses of delimitation have been proposed in the literature. In particular, the
70 *Bursa granularis* complex, already identified as such by Castelin *et al.* (2012), is typically
71 recognized as a single species by modern authors (Beu, 1998, 2005, 2010), although
72 sometimes with subspecies (Nappo *et al.*, 2014). According to both the literature and the
73 GBIF database (2016) (Fig. 1), *B. granularis* has a subtropical and tropical distribution
74 throughout the Indo-West Pacific, the eastern Pacific, and the tropical western Atlantic. [In
75 the eastern Atlantic, it has only been recorded from the Cape Verde Islands (Garcia-Talavera,
76 1983, cited by Beu 1998), but this record is unconfirmed by Rolán (2005).] This distribution
77 would make it one of the most cosmopolitan species among the Tonnoidea. However, this
78 apparently cosmopolitan species has received no fewer than ten names (Beu, 1998). WoRMS
79 (2017) lists 13 synonyms of *Tritonium granulare* Röding, 1798: *Tritonium jabick* Röding,
80 1798, *Biplex rubicola* Perry, 1811, *Ranella granifera* Lamarck, 1816, *Ranella affinis*
81 Broderip, 1833, *Ranella cubaniana* d'Orbigny, 1841, *Ranella livida* Reeve, 1844, *Bursa*
82 *cumingiana* Dunker, 1862, *Bursa alfredensis* Turton, 1932, *Bursa kowiensis* Turton, 1932, *B.*
83 *cubaniana intermedia* Nowell-Usticke, 1959, *Bursa corrugata lineata* Nowell-Usticke, 1959
84 and *Bursa granularis elisabettae* Nappo, Pellegrini & Bonomolo, 2014. The numerous
85 alternative species hypotheses led to various usages of these names in the literature; whereas
86 19th century authors (e.g. Reeve, 1844b) recognized up to four different species, the last
87 revision proposed to group them all under the name *Bursa granularis* (Beu, 1998). Two of
88 these, however — *B. granularis cubaniana* (d'Orbigny, 1841) and *Bursa granularis*
89 *elisabettae* Nappo, Pellegrini & Bonomolo, 2014 — are accepted by Nappo *et al.* (2014) at
90 the rank of subspecies besides the nominate subspecies *Bursa granularis granularis* (Röding,
91 1798).

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

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

106

107 MATERIAL AND METHODS

108 *Sampling*

109 The material for this study was collected from various localities during a series of shallow-
110 water and deep-sea expeditions to Saudi Arabia (UF 2013), Viet Nam (NT 2014), Vanuatu
111 (UF 2005, Santo Marine biodiversity survey 2006), Mozambique (MAINBAZA 2009,
112 INHACA 2011), Madagascar (UF 2008), the Philippines (PANGLAO 2004, UF 2015),
113 Mariana Island (UF 2008), Micronesia (UF 2008), Okinawa Japan (UF 2010), Guam (UF
114 2010), Marquesas Islands (Pakaihi I Te Moana 2012), Papua New Guinea (PAPUA NIUGINI
115 2012), Marshall Islands (UF 2008), New Caledonia (TERRASSES 2008, UF 2013), Taiwan
116 (UF 2005), Florida, USA (UF 2010), Guadeloupe (KARUBENTHOS 2012), and Western
117 Australia (UF 2009, WESTERN AUSTRALIA 2011). MNHN specimens collected before
118 2012 were anaesthetized with an isotonic solution of MgCl₂ and fixed in 96% ethanol.
119 Specimens collected after 2012 were processed with a microwave oven (Galindo *et al.* 2014);
120 the living molluscs in small volumes of sea water were exposed to microwaves for ca. 30
121 seconds. Bodies were immediately removed from shells and dropped into 96% ethanol. UF
122 specimens were directly put alive into 75 or 95% ethanol. The analysed material includes 82
123 specimens, 42 registered in the MNHN and 40 in the UF collections (Supplementary Material
124 Table 1). The specimens and the corresponding sequences are also registered in the Barcode
125 of Life Datasystem (project BURSA) and GenBank. Maps with the sampling locality of all
126 the specimens were generated using Qgis 2.16.3 (Fig. 1).

127

128 *DNA sequencing*

129 DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the
130 manufacturers' recommendations. A fragment of the cytochrome oxidase subunit I (cox1)
131 gene was amplified using the universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994).
132 PCR reactions were performed in volumes of 20 µl, containing 3 ng DNA, 1X reaction buffer,
133 2.5 mM MgCl₂, 0.26 mM dNTP, 0.3 mM of each primer, 5% DMSO and 1.5 units of
134 Qbiogene Q-Bio Taq. The amplification consisted of an initial denaturation step at 94°C for 5
135 min, followed by 40 cycles of denaturation at 94°C for 30 s, annealing at 47°C for 30 s,

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

138

139 *Species delimitation*

140 All specimens were first separated into morphogroups, using characters of the teleoconch and
141 in particular the outer lip. In a second step, the *cox1* sequences were analysed. Alignment was
142 done by eye. Pairwise genetic distances were calculated using MEGA v. 6 (Tamura *et al.*,
143 2013). Phylogenetic trees were reconstructed using maximum likelihood (ML) and Bayesian
144 inference approaches (BI), with MEGA v. 7 (with Bootstraps 100 replications and default
145 parameters for tree inference options) for ML analysis, and with MrBayes (Huelsenbeck,
146 Ronquist & Hall, 2001) (six Markov chains and 10,000,000 generations, five chains, three
147 swaps at each generation, a sampling frequency of one tree each 1,000 generations, chain
148 temperature set at 0.02) and BEAST v1.8.3 (Drummond *et al.*, 2012) (with uncorrelated
149 relaxed clock, and 10,000,000 generations) for the BI analysis. In all analyses the three codon
150 positions of the *cox1* gene were treated as independent partitions and the substitution model
151 was set to GTR+G and GTR+I+G for the ML and BI analyses, respectively. Convergence for
152 both BI analysis was evaluated using Tracer v. 1.4.1 (Rambaut *et al.*, 2014) to check that all
153 effective sample size values exceeded 200. Consensus trees were calculated after omitting the
154 first 25% trees as burn-in. Nodal support was assessed as posterior probability (PP) in the BI
155 analyses and as bootstraps (BS) for the ML analysis. Closely related bursid species were used
156 as outgroups: *Bursa latitudo* Garrard, 1961, *Bursina ignobilis* (Beu, 1987) and *Tutufa bufo*
157 (Röding, 1798), following Castelin *et al.* (2012).

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

168

169 *Shell description*

170 Once the species were delimited based on molecular data, shells were described using the
 171 methods developed by Merle (2001, 2005) for primary homologies definition. Primary cords
 172 are spiral ornamentations present from the first teleoconch whorl. Secondary cords (S) are
 173 spiral ornamentations appearing later during shell ontogeny. The shoulder cord is designated
 174 as P1. Cords of the convex part of the whorl are added from adapical to abapical (P2 to P6,
 175 Fig. 2A). The primary cord of the infrasutural ramp is designated IP and the secondary cord
 176 IS. Secondary cords on the convex part of the whorl are designated S1 to S6. Cords of the
 177 siphonal canal were not considered. Denticles inside the outer lip are named D1 to D6,
 178 starting under the shoulder cord and added from adapical to abapical; denticles above the
 179 shoulder are designed as ID1 and ID2 added from abapical to adapical (ID2 is not shown in
 180 Fig. 2). Denticles are bifid on most specimens but can merge or further bifurcate. In order to
 181 describe the outer lip we introduce here the outer lip denticles formula (OLDF). It is a four-
 182 digit sequence representing the number of visible denticles (D) between a notch and the
 183 preponderant primary cord (P1, P3 and P5) or between two preponderant primary cords ,
 184 starting from the anal notch towards the siphonal one. For example, in the specimen of *B.*
 185 *granularis* figured in Fig. 2, the OLDF should be read as AN,2, P1, 4, P3, 4, P5, 4, SC or
 186 2,4,4,4 for short.

Fig. 2

187

188

189 ABBREVIATIONS

190 *Depositaries*

191 MAC. ML Museo di Storia Naturale Aquilegia, Cagliari

192 MHNG Muséum d'Histoire naturelle, Geneva, Switzerland

193 MNHN Muséum National d'Histoire Naturelle, Paris, France

194 NHMUK Natural History Museum, London, United Kingdom

195 RASM Russian Academy of Science, Moscow

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

197

198 *Shell characters*

199 AN anal notch

200 SC siphonal canal

201 H height

202 P Primary cord

203 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 (Jousseume, 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, OLF: 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

306 per primary cord between two varices (and secondary cords of infrasutural ramp) and double
 307 this number for secondary ones. Apertural lip well flared, bearing numerous prominent,
 308 narrow, transverse denticles. Outer lip bearing numerous denticles; ID1 bifid, ID2 absent, D1-
 309 4 bifid, D5 bifid but merged in large specimens, D6 bifid (Fig. 5).

310
 311 *Distribution and habitat:* *Bursa granularis* has a tropical distribution throughout the Indo-
 312 West Pacific province (Fig.1), from the Mozambique Channel throughout East Africa and the
 313 Red Sea to the northern Indian Ocean, in the western Pacific from Kii Peninsula and

314 Yamaguchi Prefecture, Honshu, Japan (Beu, 1999), south to Rottneest Island in Western
 315 Australia (Wilson, 1993). Its eastward distribution in the Pacific extends from Japan to
 316 Australia through the Philippines, Vanuatu and New Caledonia. *Bursa granularis* is
 317 commonly found in very shallow water but some specimens were found alive around 100m
 318 deep.

319
 320 *Remarks:* The nomenclatural history of *Bursa granularis* is a particularly complex one. The
 321 types of *Tritonium granulare*, *T. jabick* and *Biplex rubicola* are lost. Beu (1998) designated
 322 the lectotype of *Ranella granifera* as neotype of the three other names. As a consequence
 323 these formerly subjective synonyms became objective synonyms and following ICZN Art.
 324 76.3 they also all share the same type locality, the Red Sea. There is only one species
 325 belonging to the complex in this locality, to which the name *B. granularis* can thus
 326 unambiguously be attributed. Furthermore the type specimen of *Ranella granifera* displays
 327 characters congruent with the description above (Fig. 4,A).

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

337

338

339 *Bursa affinis* (Broderip, 1833)

340 (Fig. 4 E-I,K)

341

342 *Ranella affinis* Broderip, 1833: 179 (“Anaa,” Tuamotu Islands, Lectotype NHMUK
343 1950.11.28.4, designated by Beu, 1998:150); G. B. Sowerby II, 1835: pl. 89, fig. 12; Reeve,
344 1844b: pl. 4, fig. 19; Küster, 1871 [in Küster & Köbelt, 1870-1878]: 142, pl. 38a, fig. 5.

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

346 *Ranella livida* Reeve, 1844a: pl. 6, fig. 28; (“Anaa,” Tuamotu Islands, Lectotype NHMUK
347 1967657_1, designated by Beu, 1998:150); 1844b: 138; Krauss, 1848: 113.

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

350 *Bursa granularis* — Hertlein & Allison, 1960: 15; Salvat & Rives, 1975: 307, fig. 179; Kay,
351 1979: 227, fig. 80A; Severns 2011: 150, pl. 59, fig. 6; Beu *et al.*, 2012: 67, fig. E2 (not of
352 Röding, 1798).

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

354

355 *Material examined:* See Supplementary material table 1.

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

359 *Description:* Protoconch as in *B. granularis*. Teleoconch tall and relatively narrow with 4–5
360 whorls (up to 6 on large specimens). H 40 to 50 mm, up to 80 mm. Spire angle 55°.
361 Proportion of aperture, 50% of the shell width. Proportion of last whorl 52% of the height.
362 Varices strictly aligned for most of spire height, becoming a little displaced only on last whorl
363 or two of large specimens. Abapertural face of each varix deeply excavated, buttressed by
364 spiral cords. Spiral ornamentation as in *B. granularis*. After whorl 2 (varix 4) IP grows in
365 importance to equal other cords, only to reduce again after varix 6, leaving room for
366 development of secondary cord above it. Every primary cord surrounded by secondary cords,
367 growing in importance similarly to primary cords. Spiral ornamentation composed, on last
368 whorl, of 9 nodules per primary cord between two varices with the exception of P1, which
369 bears much bigger nodules, pointing slightly upwards, and decreasing in number with
370 ontogeny, from 9 to 5. Secondary cords bear same number of small nodules as *B. granularis*.
371 Nodules on varices where they meet P1 angulating the shoulder. Apertural lips well flared,
372 bearing numerous prominent, narrow, internal transverse denticles. ID2 present in large

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

375
376 *Distribution and habitat:* *Bursa affinis* has a tropical distribution throughout the Pacific
377 Ocean (Fig. 1), from Okinawa, Japan to Sydney Harbour, New South Wales, Australia, and
378 throughout Polynesia to Hawaii (Beu, 1998). In the eastern Pacific, particularly large
379 specimens are common at Clipperton Island (Hertlein & Allison, 1960; Kaiser, 2007) and
380 specimens were recorded by Emerson (1991) from the Revillagigedo Islands, Cocos Island,
381 and the mainland coast at Bahia Chamela, Jalisco, western Mexico (Beu, 2010). Its westward
382 distribution in the Pacific extends from Japan to Australia through the Philippines, Papua New
383 Guinea, Vanuatu and New Caledonia. *Bursa affinis* is commonly found in very shallow water
384 but specimens are occasionally found alive in around 40 m deep.

385
386 *Remarks:* *Bursa affinis* and *Bursa livida* have the same type locality; “Anaa,” [now Anaa]
387 Tuamotu Islands. The type specimens (Fig. 4 E,G) of both have the same OLDF, and we
388 consider the latter to be a junior synonym of the former. Considering that there is only one
389 MOTU occurring in Outer Oceania in general (Fig. 1), and French Polynesia in particular, we
390 attribute to it the name *affinis*.

391
392 Fig.6 *Bursa cubaniana* (d’Orbigny, 1841)

393 (Fig. 6 A-D,L)

394
395 *Ranella cubaniana* d’Orbigny, 1841: 165, pl. 23, fig. 24 (Ste Lucie, West Indies, Holotype
396 NHMUK 1854.10.4.412); Mörch, 1877: 24.

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

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

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

402 *Bursa cubaniana* — Nowell-Usticke, 1959: 61. Work, 1969: 663; Kaufmann & Gotting,
403 1970: 372, fig. 87; Matthews & Kempf, 1970: 28; de Jong & Coomans, 1988: 214, pl. 16, fig.
404 382.

405 *Bursa cubaniana* var. *intermedia* Nowell-Usticke 1959: 61-62, pl. 3, fig. 13 (North of
406 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; 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,

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

442 *Distribution and habitat:* *Bursa cubaniana* occurs in the western Atlantic (Fig. 1; Rosenberg
 443 2009), where it is recorded from southeastern Florida (Abbott, 1974; this study), Texas and
 444 Louisiana (Garcia, 1999) westwards to Mexico, Costa Rica, Panama and Colombia
 445 (Massemin *et al.* 2009), the Bahamas (Redfern 2013), Guadeloupe (this study), Jamaica, Cuba
 446 and St Lucia (d'Orbigny, 1841) south to French Guiana (Massemin *et al.* 2009), Bahia and
 447 Pernambuco, Brazil (Matthews, 1968; Rios, 1985, 1994, Mello & Perrier 1986). In the eastern
 448 Atlantic, it has been recorded only from the Cape Verde Islands, but this record in
 449 unconfirmed (Rolán, 2005).

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

453

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

456

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

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

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

462

463 *Material examined:* See Supplementary Material table 1.

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

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

468 Teleoconch tall, relatively narrow with 4-5 whorls, H around 50 mm. Spire angle 45°; % of
 469 aperture, 52% of the shell width; % of last whorl 52% of the height. Varices strictly aligned,
 470 although low and hardly visible in some specimens. Spiral ornamentation very reduced to
 471 absent from some specimens. Primary cords P1, 3 and 5 are the only ones visible; each bears
 472 4 nodules between two varices, especially visible on P1. No secondary cords present. Nodules
 473 on varices where they meet P1 angulate shoulder, although not as sharply as in *B. affinis*.

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

477

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

480

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

485

486 DISCUSSION

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

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

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

514 Other anatomical characters and radulae were not considered in the present study but
515 may perhaps provide useful information. Abbott (1958) pointed out differences between *B.*
516 *cubaniana* and *B. granularis* in denticle size and number on the central teeth (Abbott, 1958:
517 figs 1d, 2c), but radular studies are often based on too small a sample size and their results
518 may not be significant. For good pictures of the radula of *B. granularis*, see Barbakova *et al.*
519 (2016) and for insight on the general anatomy of *B. cubaniana* see Simone (2011).

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

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

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

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

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

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

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

602
603

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634

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997

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.

1007 **Figure 3.** Molecular tree for the *cox1* gene. *Bursa granularis* (Röding, 1798) is represented by the
 1008 shell of UF-423792 (marked by a black square on the tree); *Bursa affinis* (Broderip, 1833) is
 1009 represented by the shell of IM-2007-43056 (marked by a white square on the tree); *Bursa cubaniana*
 1010 (d'Orbigny, 1841) is represented by the shell of IM-2009-23406 (marked by a black hexagon) and
 1011 *Bursa elisabettae* Nappo, Pellegrini & Bonomolo, 2014 is represented by the shell of IM-2009-23322
 1012 (marked by a black star). Support for nodes is given as PP/BS, where these exceed 0.95 and 95,
 1013 respectively. PNG: Papua New Guinea.

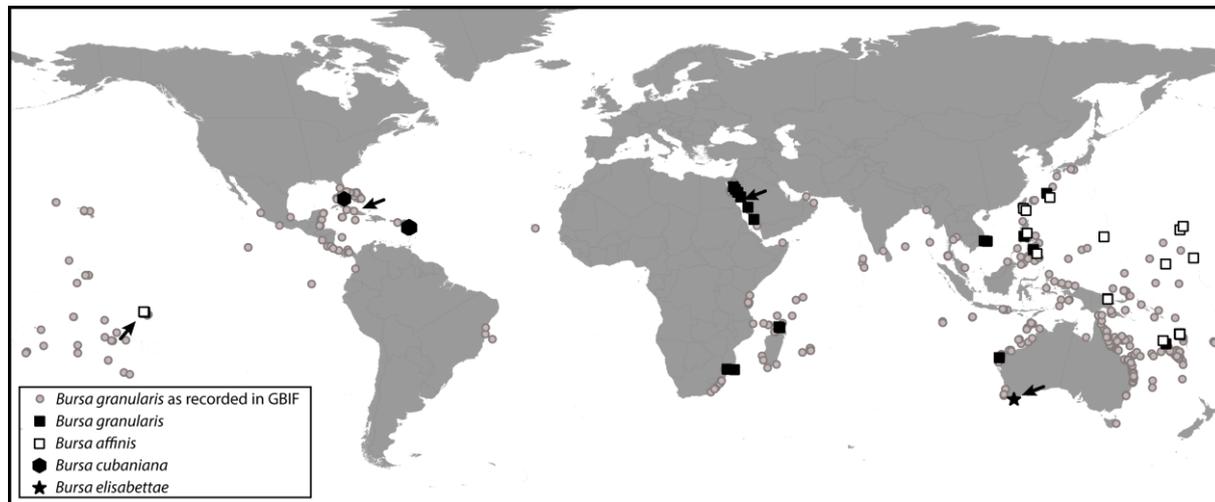
1014 **Figure 4.** Shells of the *Bursa granularis* complex. **A-D.** *Bursa granularis* (Röding, 1798): **A.** MHNG
 1015 1098/85/1, Lectotype of *Ranella granifera* Röding, 1798, Neotype of *Tritonium granulare* Röding,
 1016 1798, of *T. jabick* Röding, 1798, and of *Biplex rubicola* Perry, 1811, from the Red Sea H: 64 mm. **B.**
 1017 IM-2009-5148, MAINBAZA 2009 (Mozambique Channel), stn DW3168, H: 26 mm. **C.** UF-423792,
 1018 UF 2008 (Madagascar), Nosy Komba, NW side.H: 40 mm. **D.** IM-2007-43071, Santo Marine
 1019 Biodiversity Survey 2006 (Vanuatu), stn VM62, H: 25 mm. **E-I.** *Bursa affinis* (Broderip, 1833): **E.**
 1020 MNHUK 1950.11.28.4, Lectotype of *Ranella affinis* Broderip, 1833, supposedly from “Anaa,”
 1021 Tuamotu Islands, H: 62.5 mm **F.** IM-2007-43056, Santo Marine Biodiversity Survey 2006 (Vanuatu),
 1022 stn VM02, H: 37 mm. **G.** NHMUK 1967657 Lectotype of *Ranella livida* Reeve, 1844, supposedly
 1023 from “Anaa,” Tuamotu Islands, H: 56.8 mm **H.** UF-422918, UF 2008 (Federated States of
 1024 Micronesia), Kosrae Letu, in front of Nautilus Hotel, H: 25 mm. **I.** IM-2007-43039, PANGLAO 2004
 1025 (Philippines), stn R24, H: 41mm. **J.** IM-2009-5148 *Bursa granularis* protoconch close-up. **K.** IM-
 1026 2007-43056 *Bursa affinis* protoconch close-up. P1, P3, P5 preponderant primary cords; numbers
 1027 indicates the number of denticles

1028
 1029 **Figure 5.** Synthetic diagrams showing the sequences of appearance of the primary and secondary
 1030 cords in the four species of the *Bursa granularis* complex. In all ontogenies, the primary cords (black
 1031 lines) are numbered following an adapical to abapical order.

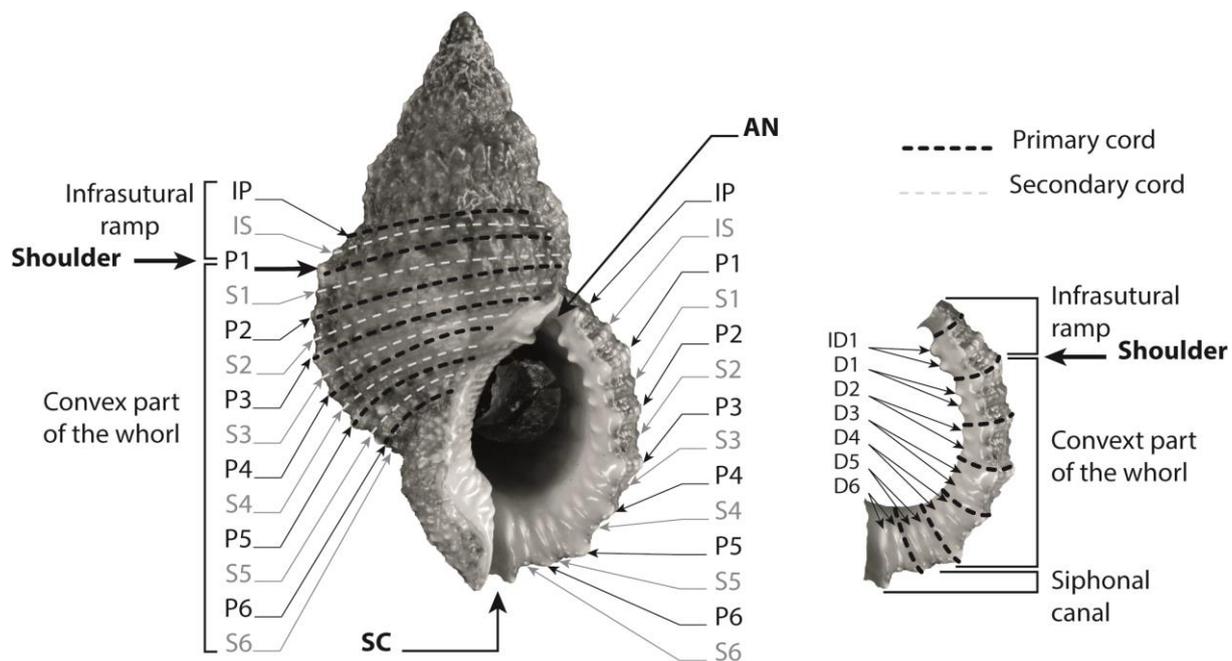
1032
 1033 **Figure 6.** Shells of the *Bursa granularis* complex. **A-D.** *Bursa cubaniana* (d'Orbigny, 1841): **A.**
 1034 NHMUK 1854.10.4.412, Holotype of *Ranella cubaniana* d'Orbigny, 1841, St. Lucie, West Indies, H:
 1035 51.7 mm **B.** IM-2009-23406, Port Louis, Pointe Antisu, Guadeloupe, H: 41mm. **C.** IM-2013-20184,
 1036 KARUBENTHOS 2012 (Guadeloupe), stn GM09, H: 51mm. **D.** UF 437626, UF 2010 (Florida, USA),
 1037 Florida, Monroe County, Florida Keys, Tennessee Reef, H: 3.5 cm. **E-G.** *Bursa elisabettae* Nappo,
 1038 Pellegrini & Bonomolo, 2014 **E.** MAC.ML 1536 Holotype of *Bursa granularis elisabettae* Nappo,
 1039 Pellegrini & Bonomolo, 2014, Flinders Bay, Cape Leeuwin, South West Australia, H: 35 mm. **F.** IM-
 1040 2009-23319, WESTERN AUSTRALIA 2011, stn WA17, H: 31mm. **G.** IM-2009-23313, WESTERN
 1041 AUSTRALIA 2011, stn WB28, H: 28 mm. **H** “deep sea” form of south African *Bursa granularis*
 1042 MNHN ex coll. Aiken, off Richard bay, South Africa, dredge H: 24.8mm-**I** *Bursa aff.kowiensis*
 1043 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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