Just the once will not hurt: DNA suggests species lumping over two oceans in deep-sea snails (Cryptogemma)

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Abstract :

The practice of species delimitation using molecular data commonly leads to the revealing of species complexes and an increase in the number of delimited species. In a few instances, however, DNA-based taxonomy has led to lumping together of previously described species. Here, we delimit species in the genus *Cryptogemma* (Gastropoda: Conoidea: Turridae), a group of deep-sea snails with a wide geographical distribution, primarily by using the mitochondrial COI gene. Three approaches of species delimitation (ABGD, mPTP and GMYC) were applied to define species partitions. All approaches resulted in eight species. According to previous taxonomic studies and shell morphology, 23 available names potentially apply to the eight *Cryptogemma* species that were recognized herein. Shell morphometrics, radular characters and geographical and bathymetric distributions were used to link type specimens to these delimited species. In all, 23 of these available names are here attributed to seven species, resulting in 16 synonymizations, and one species is described as new: *Cryptogemma powelli* sp. nov. We discuss the possible reasons underlying the apparent overdescription of species within *Cryptogemma*, which is shown here to constitute a rare case of DNA-based species lumping in the hyper-diversified superfamily Conoidea.

Keywords : species delimitation, species description, ABGD, GMYC, PTP, deep-sea species, larval dispersal, cosmopolitan species

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1 **Introduction**

2 The advent of integrative taxonomy (Dayrat, 2005; Will *et al.*, 2005), mainly driven by
3 the molecular revolution, has led to a great remodeling of the practice of species
4 delimitation, extending the use of standardized approaches in the field of taxonomy (e.g.
5 Lefébure *et al.*, 2006). Several resulting studies, often primarily based on molecular
6 data, have revealed numerous species complexes, thus increasing the number of
7 delimited species within such groups, commonly referred to as “cryptic species”
8 (Bickford *et al.*, 2007; Fišer *et al.*, 2017). The difficulty in assigning names and/or
9 describe these newly delimited species can constitute an impediment, especially for
10 non-taxonomists. Indeed, when new species are discovered, nearly half of them remain
11 undescribed, at least not described in the publication where they are revealed (Pante *et*
12 *al.*, 2014). Thus, the splitting effect of integrative taxonomy is not accompanied by
13 adequate taxonomic effort, resulting in a plethora of undescribed species. It has been
14 suggested that such lack of appropriate taxonomic procedure can have consequences in
15 various fields, such as ecology and conservation (e.g. Iglésias *et al.*, 2010).
16 Conversely, there have been cases where integrative taxonomy, by incorporating
17 molecular data, has led to the lumping of species that have been originally described
18 using morphological and anatomical characters only (e. g. Chan *et al.*, 2018; Dejacó *et*
19 *al.*, 2016). Such instances may occur when, contrary to the occurrence of “cryptic
20 species”, intra-specific morphological variability is equal to or greater than inter-
21 specific variability (e.g. Puillandre *et al.*, 2010). These phenomena may have biological
22 causes (e.g. sexual dimorphism, allometry during ontogeny, phenotypic plasticity), or in
23 other cases simply be artefacts of a particular taxonomic practice (some taxonomists
24 tend to split more than others). Unfortunately, these cases are difficult to investigate for

taxa where morphological characterization is not formalized, genomic resources are poor, and/or known specimens are rare and deposited in different institutions. Nevertheless, investigating whether or not different forms correspond to different species should rely on a combination of modern species delimitation approaches and solid taxonomic expertise in order to clarify both boundaries and taxonomic status of a given taxon.

The Conoidea (Neogastropoda) is an extremely diversified lineage of marine gastropods, traditionally divided into Terebridae, Conidae and Turridae (Bouchet *et al.*, 2011). Recent molecular phylogenies have significantly redefined boundaries within the superfamily (Puillandre *et al.*, 2011; Abdelkrim *et al.*, 2018a), leading to a redefinition of the turrids. The family Turridae H. Adams & A. Adams, 1853 (1838) is now a monophyletic group that encompasses a few morphologically well-defined monophyletic genera, such as *Gemmuloborsonia*, *Polystira*, *Lophiotoma* or the “*Xenuroturris/Iotyrris* complex”, that have been revised in recent years (Puillandre *et al.*, 2010; Todd & Rawlings, 2014; Puillandre *et al.*, 2017; Abdelkrim *et al.*, 2018b). In some cases, the integrative taxonomy approach has uncovered “cryptic species” that were described in the same studies in which they were revealed. However, a considerable proportion of turrid species are still left in the paraphyletic genus *Gemmula*, for which it was estimated that less than half the number of species has been described so far (Puillandre *et al.*, 2012). Puillandre *et al.* (2012) also called for the complete revision of *Gemmula*, and suggested that the high number of species and the suspected global morphological stasis of the group are likely explanations as to why this group remains unrevised until now. Moreover, revising the *Gemmula* group would be tantamount to revising the entire Turridae, given that independent “*Gemmula*-like”

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lineages are distributed all over the turrid tree (Puillandre *et al.* 2012). Finally, while a high number of undescribed species was estimated in *Gemmula*, it is not clear whether all the independent “*Gemmula*-like” lineages equally include undescribed species, or if some lineages will require splitting of previously described species, while others will imply lumping of previously described species, or a combination of both splitting and lumping. Hence, we propose to partition the taxonomic revision by focusing on smaller monophyletic groups that would be revised one by one, in order to progressively resolve the taxonomic predicament of *Gemmula* as it presently stands. The first group we identified is a clade of deep-water species, hereafter named “*Cryptogemma*”, that has already been used as a case-study to illustrate congruent species hypotheses in the integrative taxonomy framework designed in Puillandre *et al.* (2012, Figure 5), comprising five species of Turridae attributed to three genera. We completed the dataset from Puillandre *et al.* (2012) with recent field sampling and material from museums, and applied an integrative taxonomy approach primarily based on the analysis of barcode fragment of *COI* with additional data on the geography and bathymetry included *a posteriori* to help attributing existing names to the molecular species hypotheses. Furthermore, we significantly improved resolution of morphological studies by carrying out a formalized analysis of the morphology of teleoconch and protoconch, and by examining radulae in all sequenced species. The sequencing of a few type specimens and the formalized morphological analysis allowed us to attribute confidently type specimens to molecular species. Our results enabled a comprehensive revision of *Cryptogemma*: rather than finding the usual splitting effect of molecular-based integrative taxonomy, our study led to an unexpected number of new synonymies and only one new species description.

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74 **Material and Methods**

75 The integrative taxonomy pipeline followed in this study comprises three main steps.

76 First, most samples were sequenced at least for the *COI* gene fragment, without
77 necessary being preliminarily identified morphologically to the species level. Second,
78 automated species delimitation methods were used to delimit molecular operational
79 taxonomic units (MOTUs), resulting in primary species hypotheses. Finally, MOTUs
80 were assessed using alternative gene fragments, morphology, geography and
81 bathymetry, resulting in final species hypotheses.

82 *Sampling*

83 As a part of our background activity, most neogastropods collected during field
84 expeditions organized by the Muséum national d'Histoire naturelle (MNHN) are
85 processed for DNA extraction and sequencing of the Barcode fragment of the *COI* gene.

86 Among the processed material, all specimens for whom the barcode sequences clustered
87 into the *Cryptogemma* clade were included in this study. These samples were collected
88 during field expeditions in the Indo-Pacific and West Atlantic: EBISCO and
89 KANADEEP in the Chesterfield Islands, CONCALIS, EXBODI, KANACONO,
90 TERRASSES and NORFOLK 2 in New-Caledonia, MIRIKY and ATIMO VATAE in
91 Madagascar, MAINBAZA in Mozambique, BIOMAGLO in Mayotte, BIOPAPUA,
92 KAVIENG, MADEEP and PAPUA NIUGINI in Papua New Guinea, AURORA 2007
93 and PANGLAO 2004 in the Philippines, SALOMON 2 and SALOMONBOA 3 in the
94 Salomon Islands, TARASOC in the Société-Tuamotu islands, TAIWAN 2013,
95 NANHAI 2014, DONGHA 2014 and ZHONGSHA 2015 in Taiwan, GUYANE 2014 in
96 French Guyana. Additional samples were collected during Japanese expeditions: T/V

“Nagasaki-maru” cruise N275 and R/V “Tansei-maru” cruise KT-12-32 in Japan. We completed this sampling with specimens from the Australian museum (AMS), Zoological Museum of Moscow State University (ZMMU) and the National Museum of Natural History (USNM) that could potentially belong to this clade, based on their morphology and the available corresponding sequence in GenBank. Twelve specimens from the AMS were collected during the IN2017_V03 - Sampling the Abyss cruise (2017). A paratype of *Ptychosyrinx lordhoweensis* Kantor & Sysoev, 1991 (R/V “Dmitry Mendeleev”, 16th cruise, st. 1245, N° Lc14353; Kantor & Sysoev, 1991) from the ZMMU was used for DNA extraction. Samples from USNM were also selected for molecular analyses: three paralectotypes of *Gemmula benthima* Dall, 1908 (USS Albatross; Stations 2807, 3360, 3365, USNM N° 96485, 123087, 123092; Kabat, 1996) and one specimen of *Ptychosyrinx carynae* (Haas, 1949), USNM 832922. For USNM samples, *G. benthima* specimens were preserved dry, while the *P. carynae* specimen was probably fixed in formalin before conservation in ethanol. MNHN specimens processed before 2012 as well as all AMS specimens chosen for molecular analysis were anaesthetized using the isotonic solution of MgCl₂ prior to fixation in 96% ethanol. MNHN specimens processed after 2012 were microwaved and fixed in 96% ethanol (Galindo *et al.*, 2014). In some cases, shells were subsequently drilled to extract the retracted animals. Japanese specimens were boiled in 70–90°C water for 0.1–0.5 min before preservation in 99% ethanol. ZMMU specimens were probably fixed and preserved in 75–80% ethanol.

DNA sequencing

DNA from MNHN samples was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturers' recommendations. DNA from AMS samples was extracted from small pieces of foot muscle by use of a Bioline Isolate II Genomic DNA extraction kit for animal tissue, following the standard procedure of the manual. DNA from ZMMU and USNM samples was extracted using the EZNA Mollusc DNA Kit (Omega Bio-Tek Inc.), following the manufacturers' recommendations. For most samples, the barcode fragment (658 bp) of the mitochondrial *COI* gene was amplified using the universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994). PCR reactions were performed using a previously well-established protocol (Puillandre *et al.*, 2017). For the ZMMU and USNM samples, the barcode fragment was amplified in two fragments, one with the LCO1490 and a newly designed primer (conoCOIntR: GCNCATGCHGGNGGNTCWGTW) and the other with another newly designed primer (conoCOIntF: TCWTCAGCTGCNGTWGAAAGNGG) and the HCO2198 primer. Both fragments are overlapping over ~50 nucleotides. The PCR mix was the same as for the LCO1490/HCO2198, except that BSA (10 mg/mL) was used instead of DMSO. The amplification procedure was also similar, except that the annealing temperature was 47°C, with 40 cycles instead of 35. A fragment of the mitochondrial *12S* rRNA gene was amplified using the universal primers *12S1/12S3* (Simon, Franke & Martin, 1991) and PCR reactions performed using a previously established protocol (Puillandre *et al.*, 2011). PCR products were purified and sequenced by the Eurofins sequencing facility. *28S* primers used at AMS were C1'/D2 (Dayrat *et al.*, 2001; Jovelín & Justine, 2001). Amplification of *28S* consisted of an initial denaturation step at 94 °C for 4 min, followed by 30 cycles of denaturation at 94 °C for 30 s, with annealing set to

143 57°C for 45 s, followed by extension at 72 °C for 1 min. The final extension was at 72
144 °C for 5 min.

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146 *Species delimitation*

147 *COI* sequences were aligned manually using MEGA X (Kumar *et al.*, 2018); *12S* and
148 *28S* sequences were aligned using Muscle (Edgar, 2004) as implemented in MEGA X
149 and then checked by eye. Phylogenetic reconstruction methods were applied to the *COI*
150 alignment, plus a concatenation of the *COI*, *12S* and *28S* alignments with one specimen
151 per species (see Results section).ABGD, GMYC and mPTP methods were applied to
152 the *COI* dataset. All three methods are exploratory and aim at finding clusters of
153 specimens corresponding to species but differ strongly in several aspects. ABGD is
154 based on genetic distances only and automatically detects the gap (the so-called
155 “barcode gap”) between intra and interspecific distances, then used to delimit species
156 hypotheses. On the contrary, GMYC and mPTP rely on phylogenetic trees. GMYC uses
157 an ultrametric tree and looks for a transition between speciation and coalescent nodes.
158 mPTP also delimit species by identifying the transition between the inter and
159 intraspecific parts of the tree, but requires only a phylogeny with branch length being
160 proportional to the number of substitutions, and relies on the mutation rate instead of the
161 branching rate.

162 For ABGD, the web version (<http://wwwabi.snv.jussieu.fr/public/abgd/>) and the default
163 parameters were used, with a Kimura (K80) TS/TV model implemented. Maximum
164 likelihoods trees were constructed for *COI*, and the concatenated (*COI* + *12S* + *28S*)
165 alignments using IQ-TREE v1.6.3 (Nguyen *et al.* 2014), with 100 bootstraps. For all
166 alignments, *COI* was consistently divided into three partitions, corresponding to the

three codon positions, and 12S and 28S considered each as a single partition. The best model for each partition was evaluated using ModelFinder as implemented in IQ-TREE (Kalyaanamoorthy *et al.*, 2017). The mPTP approach of species delimitation (Kapli *et al.*, 2017) was performed on the *COI* maximum likelihood tree, using both ML delimitation with default parameters and MCMC method with a Markov chain of 200,000,000 generations, a sampling frequency each 2,000 generations and a burnin set at 25%. Bayesian trees were reconstructed using BEAST v2.5.0 (Bouckaert *et al.*, 2019), running 200,000,000 generations on the *COI* dataset with a sampling frequency every 4,000 generations and a burnin set at 10%. The *COI* dataset was partitioned by codon position for model evaluation, and prior values were set as in Puillandre *et al.* (2017). The resulting trees were combined using TreeAnnotator as implemented in BEAST2, with node heights corresponding to mean heights of all trees. The “single threshold” method of GMYC was applied using the resulting tree. Finally, a non-ultrametric Bayesian tree was reconstructed for the *COI*, and concatenated datasets using MrBayes v3.2.6 (Ronquist & Huelsenbeck, 2003), each of the two runs consisting of 8 Markov chains and 20,000,000 generations and a sampling frequency each 2,000. The analysis was performed on the Cipres Science Gateway (<http://www.phylo.org/portal2>). The consensus tree was calculated with burnin set at 20%.

Four species of Turridae were used as outgroups: *Turris babylonia* (Linnaeus, 1758), *Gemmula kieneri* (Doumet, 1840), *Unedogemmula unedo* (Kiener, 1839) and *Turridrupa* sp. The MolD program (Fedosov *et al.*, 2019) was used to identify unique combinations of diagnostic sites for each delimited species.

Shell and radular morphology

Radulae were prepared by standard methods (Kantor & Puillandre, 2012) and examined by scanning electron microscopes JEOL JSM 840A and Tescan VEGA II LSU at the MNHN. Protoconchs and shells were measured in standard position and the number of protoconch whorls counted according to Bouchet & Kantor (2004).

Variation of shell shapes was analyzed through their outlines. Initially, we made a selection of shells of sequenced specimens that were not broken, truncated or aberrant. To complete this dataset, we obtained photographs of 20 name-bearing types (corresponding to 21 species names) that were deemed high-quality, of which 18 were suitable for morphometric analysis (nearly complete shells). In total, shape acquisition was performed for 197 sequenced specimens, 18 types and 8 unsequenced specimens of *C. periscelida*.

Shell shape was acquired from photographs using a Photoshop CC 2019 script. Outlines were reconstructed with the package Momocs (Bonhomme *et al.* 2014) from the R software. We used Elliptical Fourier analysis (Giardina and Kuhl, 1977), which presents many advantages over alternative Fourier analyses (Bonhomme *et al.* 2014), to decompose the closed outlines of the shells into periodic functions. The number of harmonics necessary to describe the shape was selected to reach 99.9% of the cumulative harmonic power, ensuring that the majority of shell shape outlines were considered. Shapes were also checked by eye to ensure that enough complexity was captured. The obtained coefficients were normalized to allow the superposition of the first ellipse and make the shapes comparable. We checked that all the reconstructed outlines were appropriately aligned. A principal component analysis (PCA) was performed on the harmonics coefficients in order to capture an optimal shape variation

with a minimal number of principal components. Finally, a linear discriminant analysis (LDA) was performed to find the linear combination of principal components that maximizes difference between specimens from species delimited with DNA. Fourier analysis does not take size into account; only shapes are compared. As the size of the shells may provide some discriminatory information, we added the length of each specimen as a variable for the LDA. The appropriate number of principal components to use in the LDA model was carefully chosen to find optimal equilibrium between maximizing the differences and overfitting. A leave-one-out cross-validation procedure was used to find the number of PC axes leading to the best percentage of species predictions (see Figure S1). In order to test if our species attribution to each molecular species partition was correct, type specimens were not included in the LDA training set but subsequently added in the LDA morphospace. Another reason not to include the types in the training set was to extract at best the morphological differences between molecular species without the influences of type specimens morphology.

All the material examined for this study is summarized in Table S1.

Results

A total of 303 *COI*, 32 *28S* and 18 *12S* sequences of *Cryptogemma* were used for this study, of which respectively 255, 8 and 16 were newly obtained. The USNM and ZMMU samples yielded poor DNA quality, making them difficult to sequence with a classical Sanger sequencing approach. Nevertheless, the *12S* was obtained for the USNM96485 and USNM123087 paralectotypes of *Gemmula benthima* collected 128 years ago. For the ZMMU paratype, the USNM123092 paralectotype and the

USNM83292 lot of *Ptychosyrinx carynae*, the *COI* was obtained using the conoCOIntR and conoCOIntF newly designed primers. The USNM123092 lot had previously been sequenced and published by Todd & Rawlings (2014) for the *COI* and *12S* fragments (GenBank accession number KM218745, KM218648), despite the fact that the samples were most probably formalin-fixed. Nevertheless, sequencing an additional specimen from the same lot was necessary as the lot might include specimens from different species.

All ABGD, mPTP and GMYC analysis (see Figure S2) on the *COI* dataset resulted in the same partition with eight species hypotheses. Both *COI* and *28S* proved, in this clade, to be appropriate markers for species delimitation, confirming the five *COI*-based species hypothesis (*C. praesignis*, *C. timorensis*, *C. tessellata*, *C. unilineata* and *C. powelli* sp. nov.) in Puillandre *et al.* (2012). However, new *28S* sequences were not produced here. The *28S* sequencing of *C. aethiopica* and *C. periscelida* failed, but these two species are well recognizable morphologically and are not genetically close to a sister species, making it less probable that the *COI*-based species hypotheses are incorrect. The case of *C. praesignis* and *C. phymatias* could be considered problematic as they are found to be sister species and are separated bathymetrically. However, the single sequence of *28S* recovered for *C. phymatias* (C571715) showed a divergence with the available *28S* sequences of *C. praesignis* comparable to the divergence between other sister species (results not shown herein; see Puillandre *et al.*, 2012; Puillandre *et al.*, 2017).

For these eight species hypotheses, we searched for all names available and potentially applicable (see also the Taxonomy section). By consulting with the relevant literature

on Turridae (e.g. Powell, 1964; Tucker, 2004) and by comparison of type specimens or their images to shells of sequenced specimens, we found 23 names (see Taxonomy section) that we applied tentatively to this partition. A total of 18 name-bearing types corresponding to 19 names were of sufficient quality to be included in the morphometric study. The other name-bearing types were discussed and assigned to molecular species using only the shell photographs or drawings and extrinsic parameters such as the bathymetry or geography (see Taxonomy section).

Despite considerable intraspecific morphological heterogeneity, the morphometric analysis yielded instructive results: using shape alone, the leave-one-out cross-validation procedure successfully predicted correct species attribution of 84% of sequenced specimens and confirmed placement of 14 types out of 18 *a priori* attributed to our species hypotheses (see Figure S3). By adding shell size, we increased the score of the leave-one-out cross-validation procedure to 90.64% of the sequenced specimens, and 15 out of 18 types (Fig. 1). The three type specimens whose placement was incorrectly *a priori* attributed were *Bathybermudia carynae* (only representative of its species), *Pleurotoma praesignis* and *Ptychosyrinx bisinuata japonica* (see also taxonomic section). The most discriminant axis (Fig. 1, axis 1: 71.92% of trace) corresponds to the variation range of the siphonal canal length and the width of the shell, while variation along the second axis (15.57% of trace) mainly corresponds to the intensity of the curvature of the outer aperture lip.

The phylogenetic trees resulting from the *COI* (Fig. 2) and concatenated-gene analyses (Fig. 3) showed poorly supported interspecific relationships, except for the *Cryptogemma phymatias*/*C. praesignis* sister relationship and the (*C. unilineata*, *C. timorensis*, *C. powelli*) clade. Thus, the two molecular species PSH 11 and PSH 14 in

the study of Puillandre *et al.* (2012), which were attributed to the genus *Ptychosyrinx* Thiele, 1925, did not form a monophyletic group. The genera *Cryptogemma* Dall, 1918 (type species: *Gemmula benthima* Dall, 1908), *Ptychosyrinx* Thiele 1925 (type species: *Pleurotoma (Subulata) bisinuata* Martens, 1901) and *Pinguiggemula* McNeil, 1961 (type species: *Pinguiggemula okinavensis* McNeil, 1960), despite being easily recognizable morphologically, showed a level of molecular divergence among them that was similar to, or even lower than, the level of divergence found among species in most other turrid genera, thus suggesting synonymization of the two latter genera with *Cryptogemma*.

All species showed large, oceanic or transoceanic, sympatric distributions. Despite having large sympatric distribution, the *C. phymatias*/*C. praesignis* sister species are found in different bathymetric zones, ~1400–3000 m and ~300–1400 m respectively, with the exception of two specimens, one for each species, found at the same station CP2752 (1378–1436 m) during the AURORA 2007 expedition, off Luzon Island, in Philippines (see Table S1). All species geographic (Fig. 4) and depth (Fig. 5) ranges were represented using only sequenced specimens, except for *C. periscelida*. For the latter, the *COI* sequencing did not work for the 13 MNHN samples available but information on geography and bathymetry was included nonetheless.

Abbreviations

Museums and repositories

AMS: Australian Museum of Sydney, Sydney, Australia.

AWMM: Auckland War Memorial Museum, Auckland, New Zealand

BPBM: Bernice Pauahi Bishop Museum, Honolulu, USA.

- 311 FMNH: Field Museum of Natural History, Chicago, USA.
- 312 MNHN: Muséum national d'Histoire naturelle, Paris, France.
- 313 NHMUK: Natural History Museum of United Kingdom, London, UK.
- 314 USNM: National Museum of Natural History, Smithsonian Institution, Washington,
315 DC, USA.
- 316 ZMB: Museum für Naturkunde, Humboldt-Universität, Berlin, Germany.
- 317 ZMMU: Zoological museum of Moscow University, Moscow, Russian Federation.
- 318 ZSIC: Zoological Survey of India, Calcutta, India.
- 319
- 320 *Others*
- 321 AL: Shell aperture length.
- 322 PD: Protoconch diameter.
- 323 PL: Protoconch length.
- 324 R/V: research vessel.
- 325 St.: station.
- 326
- 327 **Taxonomy**
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- 329 **Superfamily Conoidea Fleming, 1822**
- 330 **Family Turridae H. & A. Adams, 1853 (1838)**
- 331 **Genus *Cryptogemma* Dall, 1918**
- 332
- 333 Type species: *Gemmula benthima* Dall, 1908 (OD)
- 334 *Ptychosyrinx* Thiele, 1925 (type species *Pleurotoma bisinuata* Martens, 1901 – OD)

335 *Bathybermudia* Haas, 1949 (type species *Bathybermudia carynae* Haas, 1949 – OD)

336 †*Pinguigemmula* McNeil, 1960 (type species †*Pinguigemmula okinavensis* McNeil,
337 1960 – OD)

338

339 *Included species:* *Cryptogemma aethiopica* (Thiele, 1925); *C. periscelida* (Dall, 1889);

340 *C. phymatias* (Watson, 1886); *C. powelli* sp. nov.; *C. praesignis* (Smith, 1895); *C.*

341 *tessellata* (Powell, 1964); *C. timorensis* (Tesch, 1915); *C. unilineata* (Powell, 1964).

342

343 *Remarks:* According to WoRMS (checked July 2019), *Cryptogemma* comprises 11

344 species, and has never been revised. A consultation of available type photos and

345 published images on *Cryptogemma* species indicated that all of 11 species except the

346 type species *C. benthima* and *C. phymatias*, the senior synonym of *C. benthima*, should

347 be excluded from the genus, as the majority of them lack key characters such as the

348 narrow fusiform shell and the well-marked peripheral anal sinus. Moreover, studied

349 samples from Japan most certainly corresponding to the *Cryptogemma corneus* as

350 pictured in Hasegawa (2009: figs 335–338), showed closer affinity to other conoidean

351 families (e.g. Horaiclavidae) than to the Turridae, based on both, the sequence of the

352 barcode fragment of *COI*, and radular morphology (results not shown). The eight

353 species of *Cryptogemma* listed herein have wide distributions, most of them covering

354 the whole Indo-Pacific tropical region, and are not found at depths shallower than

355 200m.

356 Protoconch consisting of 4 to 5.25 whorls. Shell shape of the teleoconch combined with

357 size is an important factor to distinguish species (see Results section), despite high

358 intra-specific variability. Widest variability range observed in shell proportions, with

shells with wide last whorl and long siphonal canal being at one extreme of the range,
and more elongated shells with short siphonal canal on the other.

***Cryptogemma phymatias* (Watson, 1886)**

(Fig. 6)

Pleurotoma phymatias R. B. Watson, 1886. 1920 m, Philippine Islands, 16°42'N,
119°22'E (Expedition H.M.S. *Challenger* on November 13, 1874, st. 205).

Gemmula benthima Dall, 1908. 2323 m, Gulf of Panama.

Gemmula benthina – Dall, 1918: 318 (lapsus calami); Powell, 1964: 279 (lapsus
calami).

Pleurotoma truncata Schepman, 1913. 2798 m, Banda Sea, Indonesia, 6°24'S,
124°39'E.

Bathybermudia carynae Haas, 1949. 3109 m, off Bermuda, 32°08.2'N, 64°33'W.

Remarks: This species was not present in the sampling of Puillandre *et al.* (2012) but
was included in the phylogeny of Puillandre *et al.* (2011) under the name *Ptychosyrinx*
carynae.

Due to the frequent loss of the shell apex, there are very few available protoconchs for
this species. Only the eroded protoconch of the type specimen of *Bathybermudia*
carynae could be measured, with PD= 1.3 mm and PL > 1.6 mm, consisting of more
than 3 whorls.

Radula medium long, about 2.6 mm in length (0.44 of AL), composed of 74 transverse
rows of teeth. Marginal teeth 118–128 µm long (mean 120 µm, n = 5), duplex. Anterior

(inner) 1/3 of tooth length solid, very narrow in dorsal view, pointed, in posterior 2/3 major and accessory limbs broadly bifurcating, accessory limb with clear constriction at about half tooth length, slightly shorter than major limb. Central formation with distinct narrow carinated cusp and lateral inconspicuous flaps with indistinct lateral and anterior margins (Fig. 7B–C).

Although this species can be distinguished from its congeners by the frequent loss of the first whorls, and from its sister species *Cryptogemma praesignis* by the slightly larger diameter of the shell, the bathymetry is its most distinct characteristic. *C. praesignis* is found between ~300 and ~1400 m depth, while *Cryptogemma phymatias* is the only Turridae to our knowledge to be exclusively found below ~1400 m deep. Moreover, it is the only Turridae so far, and possibly the first reported benthic gastropod, to have a Pacific–Atlantic distribution (Fig. 4; see Discussion). Most studied type specimens have very eroded shells, but the variability of the last whorls, siphonal twist and aperture among them is in agreement with the variability in the sequenced specimens. Noteworthy, the etymology of this species combines “*Cryptogemma*” (hidden gems) and “*phymatias*” (one who has tubercles), resulting in a confusing combination.

List of COI diagnostic sites (position: character state): [379: T, 493: C, 622: C].

Counting starts right next to the 3' end of the LCO1490 primer (from 1 to 658).

Distribution: From the Central Indo-Pacific (Banda Sea) to the North Atlantic Ocean (Bermuda Is.) (Fig. 4A), from ~1400 to ~3000 meters depth (Fig. 5). This species is expected to be found in the Indian Ocean, as is the case with other Indo-Pacific species

of *Cryptogemma*, but it has not been documented there, due presumably to a lack of sampling at bathyal depths.

***Cryptogemma praesignis* (Smith, 1895)**

(Fig. 8A–K)

Pleurotoma praesignis Smith, 1895. 1234 m, off Colombo, Ceylon.

? *Pleurotoma microscelida* Dall, 1895. 642 m, South of Oahu Island Albatross st. 3475

Pleurotoma (Subulata) bisinuata Martens, 1901. 1134 m, off East Africa, 1°49'N, 45°29'E.

Pleurotoma rotatilis Martens, 1902. 1134 m, off Mogadishu, Somalia, East Africa, 1°49'N, 45°29'E.

Pleurotoma (Surcula) lobata G. B. Sowerby III, 1903. 805 m, off Cape Natal, Durban and 567 m, off Buffalo River, East London, S. Africa. E. A. Smith, 1906.

Ptychosyrinx bisinuata japonica Okutani, 1964. 620 m, Sea of Enshu-nada, Japan, 34°25.7'N, 137°58.5'E.

Ptychosyrinx lordhoweensis Kantor & Sysoev, 1991:205, figs. 1, 2. 1210 m, Lord Howe Rise, off eastern Australia, 30°24'S, 161°51'E.

Remarks: This species corresponds to PSH 11 in Puillandre *et al.* (2012).

The protoconch exhibits a wide size range, with PD = 1.05–1.38 mm and PL = 1.4–1.93 mm, and from 4 to 5.2 whorls.

Radula long, about 3.4 mm in length (0.44 of AL), formed of 72 transverse rows of teeth. Marginal teeth 142–151 µm long (mean 149 µm, n = 5, or 1.9% of AL), duplex.

Anterior (inner) 1/3 of tooth length solid, narrow in dorsal view, pointed, in posterior 2/3 major and accessory limbs broadly bifurcating, accessory limb with clear constriction and bent at about half tooth length, shorter than major limb. Central formation with distinct narrow carinated cusp and lateral inconspicuous flaps with indistinct lateral and anterior margins (Fig. 7A).

This species is morphologically close to *Cryptogemma timorensis*, although it differs from that species in its generally smaller size (~15–35mm SL), in having a narrower last whorl, and the presence of a tertiary apertural notch in mature females. *Cryptogemma praesignis* also differs from *C. timorensis* in having a much longer radula (0.44 vs 0.2 of AL) and relatively longer marginal teeth (1.9% of AL vs 1.35%). Anatomical examination of Australian material (C571714 and C571704) shows that mature males (SL 29.4 and 34.9 mm respectively) can obtain an extremely large and muscular penis, with a width almost equal to the width of the animal itself, and with a very large, long lateral appendage situated distally. The penial tip is rather blunt, with the opening situated distally. A third, smaller Australian specimen (C571757; SL 25.7 mm), did not possess a well-developed papilla, suggesting that such a feature may develop with increasing maturity and therefore not be present in subadults. Furthermore, the shells of C571714 and C571704 did not possess a tertiary apertural notch. The observation of C571714 and C571704 supplements the findings of Kantor & Sysoev (1991) that the mature females of this species develop a tertiary apertural notch. The authors hypothesized that this structure was possibly connected with the process of fertilization. Such a feature has been observed in *C. aethiopica* specimens as well (Fig. 9G, I), but not in other *Cryptogemma* species.

The general morphology, and more specifically the presence of a tertiary apertural notch in *Pleurotoma bisinuata* and *Ptychosrynx bisinuata japonica*, supports the synonymization of these names with *C. praesignis*. Because the holotype of *P. bisinuata japonica* is a comparatively large specimen (39 mm), the result of the LDA and the leave-one-out cross-validation procedure attributed it to *C. timorensis*. Possibly for this same reason, the holotype of *P. praesignis* (42 mm) also fell into the *C. timorensis* range. The result of the LDA analysis and the leave-one-out cross-validation procedure when considering only shape predicted the two holotypes as *C. praesignis*, (see Figure S3) thus justifying the attribution of *P. praesignis* to this molecular species. The sequencing of a paratype of *P. lordhoweensis* confirmed its conspecificity with *C. praesignis*. The name *Pleurotoma lobata*, although conchologically very similar to *P. bisinuata*, has never been synonymized based on the reportedly different morphology of the radula: the absence of a central tooth (= central formation as understood herein) in the specimens of *P. lobata* examined by Barnard (1958), contrasting with the large unicuspid rectangular-based central tooth described in *P. bisinuata* by Thiele (1929, p. 359). Powell (1964) suggested that Thiele could have mixed his radular preparations, but in light of the radulae type of *Cryptogemma* (Fig. 8), all composed of a unicuspid central formation, it is more likely that either it was Barnard, who mixed up the radula preparation, or that the specimens examined by Barnard are not *Cryptogemma* specimens. The holotype of *Pleurotoma rotatilis* is almost identical conchologically to a sequenced juvenile from the East African coast (MNHN-IM-2013-62900; Fig. 8J). Some doubts remain as to the status of *Pleurotoma microscelida*, but the size and overall last whorl morphology of the type specimen show a stronger resemblance to *C. praesignis* than to any other *Cryptogemma* species.

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478 *List of COI diagnostic sites (position: character state):* [232: A, 319: T, 407: C, 409: T]

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480 *Distribution:* This species is known to occur from the West Indian Ocean to the East

481 Pacific Ocean (Fig. 4B), from ~300 to ~1400 m of depth (Fig. 5).

482

483 ***Cryptogemma timorensis* (Tesch, 1915)**

484 (Fig. 8L-P)

485

486 †*Pleurotoma timorensis* Tesch, 1915. Timor. Pliocene.

487 †*Pleurotoma ktolemandoënsis* K. Martin, 1933. Ktolemando. Miocene.

488 *Ptychosyrinx timorensis teschi* Powell, 1964: 291 (22–853), pl. 223, figs. 5, 6. 759 m,

489 NW off Sipadan Island, Borneo.

490

491 *Type locality:* Pliocene of Timor Island.

492

493 *Remarks:* This species corresponds to PSH 14 of Puillandre *et al.* (2012).

494 Protoconch commonly eroded, with PD = 1–1.2 mm and PL = 1.3–1.675 mm and

495 number of whorls varying from 4 to 4.5.

496 Radula medium short, about 2.5 mm in length (0.2 of AL), formed of 45 transverse

497 rows of teeth. Marginal teeth 162–172 µm long (mean 168 µm, n = 5, or 1.35% of AL),

498 duplex. Anterior (inner) 1/3 of tooth length solid, medium broad in dorsal view,

499 lanceolate, in posterior 2/3 major and accessory limbs broadly bifurcating, accessory

500 limb with clear constriction and bent at about half tooth length, nearly the same length

as major limb. Central formation with short and obtuse cusp and lateral inconspicuous flaps with indistinct lateral and anterior margins. Posterior margin thickened and uninterrupted along its length (Fig. 7I).

This type of this species, *Pleurotoma timorensis*, is a fossil specimen from Timor island (Indonesia) described by Tesch, and Martin described another very similar specimen from Buton island (Indonesia), *Pleurotoma ktolemandoënsis*, without reference to the work of Tesch. However, Martin furtherly recognized the affinities between *P. timorensis* and *P. ktolemandoënsis* (Martin, 1935). Finally, Robba *et al.* (1989) synonymized *P. ktolemandoënsis* with *P. timorensis*. Powell (1964) described the subspecies *Ptychosyrinx timorensis teschi* based on an extant specimen, which Sysoev (1996) elevated to species rank. Both authors' arguments for separating the fossil species from the extant was the 'much broader' shell of the extant *Ptychosyrinx timorensis teschi* specimen. Examination of the morphological variability of the sequenced specimens showed that dimensions and shape of fossil specimens is close to the inferred average breadth of the species; some specimens show broader aperture and a taller last whorl than others, despite having the same number of teleoconch whorls. The results of the LDA showed that *P. timorensis* and *P. timorensis teschi* fall into the variability of the sequenced specimens. The broader last whorl and the generally larger size (~30-55mm) are characteristic for *C. timorensis* when compared to *C. praesignis*.

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521 *List of COI diagnostic sites (position: character state):* [73: G, 214: G, 334: G, 511: G]

522

Distribution: Found in the West Indian Ocean to the Central Indo-Pacific (Fig. 4C), from ~300 to ~1200 meters depth (Fig. 5). Curiously, this species has not been found in New-Caledonia, despite considerable sampling effort in this region.

***Cryptogemma aethiopica* (Thiele, 1925)**

(Fig. 9)

Pleurotoma aethiopica Thiele, 1925. 638 m, off Somalia, East Africa, 0°27'S,

42°47.3'E. (Expedition Deutschen Tiefsee, st. 253).

Pleurotoma fusiformis Thiele, 1925:176(210), pl. 22(34), fig. 24. 614 m, Nias-südkanal,

0°15.2'N, 98°08.8'E.

Gemmula thielei Finlay, 1930. (nom. nov. for *Pleurotoma fusiformis* Thiele, 1925).

†*Pleurotoma trincincta* Martin, 1935:113, pl. 2, figs. 2, 2a. Buton Island, SE Celebes.

Oligocene.

†*Pinguigemmula okinavensis* McNeil, 1960. Okinawa. Shinzato Tuff Member, Miocene

or Pliocene.

Pinguigemmula luzonica Powell, 1964 1964:278(22–790), pl. 215, figs. 3, 4. 326m, off

Hermana, Menor Island, Luzon Island, Philippines.

Pinguigemmula philippinensis Powell, 1964:278(22–790), pl. 215, figs. 5, 6. 512m, off

Santiago, west Luzon Island, Philippines.

Remarks: This species was not included in the study by Puillandre *et al.* (2012).

Protoconch commonly eroded, with PD = 1.05–1.25, PL = 1.375–1.75 and number of

whorls ranging from 4.2 to 5.

Radula long, about 3.4 mm in length (0.37 of AL), composed of 77 transverse rows of teeth. Marginal teeth 150-159 μm long (mean 155 μm , $n = 5$, or 1.66% of AL), duplex. Anterior (inner) 0.4 of tooth length solid, narrow in dorsal view, awl-shaped, in posterior part major and accessory limbs broadly bifurcating, accessory limb with clear constriction and bent at about half tooth length, thin, nearly same length as major limb. Central formation with long, very narrow, sharp, carinated cusp and lateral flaps with distinct posterior and antero-lateral margins. Flaps not completely fused with cusp (Fig. 7E).

The former *Pinguigemmula* genus is easily distinguishable from *Gemmula* in having a broadly conic spire, a strongly constricted base and a long, straight siphonal canal (Powell, 1964). Although expressing a wide variety of forms, the molecular analysis resulted in a single species hypothesis. Several species were described based on the sculptural details such as the number of gemmate cords (1, 2 or none). The sculpture seems to correlate with geography, with the forms from West Indian Ocean having smooth inter-suture sculpture, while the forms from East Indian-West Pacific usually possess two or three gemmate cords. Some large specimens of this species possess a similar 'tertiary notch' to that of *C. praesignis*, suggesting sexual dimorphism also for this species (Kantor & Sysoev, 1991).

List of COI diagnostic sites (position: character state): [115: C, 307: A, 418: G]

Distribution: Found in East Africa to Central Indo-Pacific (Fig. 4E), from ~400 to ~850 meters of depth (Fig. 5).

571 ***Cryptogemma tessellata* (Powell, 1967)**

572 (Fig. 10A-D)

573

574 *Gemmula tessellata* Powell, 1967:439 (22–734a), pl. 315. 183–219m, off Waikiki,

575 Oahu Island, Hawaiian Islands (Collected by Dr. Pat Burgess)

576

577 *Remarks:* This species corresponds to PSH 12 in Puillandre *et al.* (2012). The
578 protoconch of the holotype is 4.5 whorls according to Powell (1967) and PD = 1.22 mm
579 and PL = 1.64 mm according to measurements inferred from photographs of the
580 holotype. Protoconch with high variability, with PD = 1.175–1.3, PL = 1.525–1.975 and
581 consisting of 4 to 5.5 whorls.

582 Radula medium long, about 1.2 mm in length (0.29 of AL), composed of 51 transverse
583 rows of teeth. Marginal teeth 86–91 µm long (mean 89 µm, n = 2, or 2.1% of AL),
584 duplex. Anterior (inner) 1/2 of tooth length solid, medium broad in dorsal view,
585 triangular, accessory limb weak, thin, without constriction, much shorter than major
586 limb, but nearly of same width (the marginal teeth on Fig. 8F are not fully sclerotized).
587 Central formation with long, sharp and carinated central cusp, slightly curved in profile,
588 and with lateral conspicuous flaps with distinct margins. Flaps not completely fused
589 with cusp. Anterior margin of central formation strongly concave (Fig. 7F).

590 The ‘light form’ of *C. tessellata* has been misidentified in Puillandre *et al.* (2012) as
591 *Xenuroturris gemmuloides* Powell, 1967 as it shares superficially similar features such
592 as the white-yellowish shell punctuated with regular brown-orange spots, and the small
593 size (~15–25mm). The ‘brown-orange form’ of *C. tessellata*, closer to the holotype, is
594 quite different from the ‘light form’ not only in coloration, but also in having a stouter

outline and a more tuberculate subsutural fold (Powell, 1964). Although readily distinguished from the other *Cryptogemma* species due to its color pattern and small size, LDA analysis indicates that this species more closely resembles small adults of *C. praesignis*.

List of COI diagnostic sites (position: character state): [46: C, 61: A, 316: T]

Distribution: The sequenced specimens were found in New Caledonia only and the holotype is from the Hawaiian Islands (Fig. 4C), from ~200 to ~500 meters depth (Fig. 5). The protoconch characteristics, similar in shape, size and number of whorls to *C. praesignis*, imply that the species may have a much broader range than what is currently documented, possibly covering the entire Central Indo-Pacific.

***Cryptogemma unilineata* (Powell, 1967)**

(Fig. 10E-H)

Gemmula congener unilineata Powell, 1967:437(22–716a), pl. 313. 366 m, off Waikiki, Oahu Island, Hawaii (Expedition Pele, June 13 1964).

Remarks: This species corresponds to PSH 13 in Puillandre *et al.* (2012).

Protoconch commonly retained, with PD = 1.075–1.275, PL = 1.375–1.925 and number of whorls ranging from 4.75 to 5.5.

Radula long, about 3 mm in length (0.31 of AL), composed of 99 transverse rows of teeth. Marginal teeth 121–127 μ m long (mean 125 μ m, n = 5, or 1.27% of AL), duplex.

Anterior (inner) 0.4 of tooth length solid, very narrow in dorsal view, awl-shaped, in posterior part major and accessory limbs broadly bifurcating, accessory limb with clear constriction and bent at about half tooth length, slightly shorter than major limb. Central formation with long sharp carinated cusp and lateral flaps with distinct posterior and antero-lateral margins. Flaps not completely fused with cusp (Fig. 7G).

This species has been named based on the characteristic carinated brown-orange subsutural band. The brown-orange subsutural band has been found in *C. powelli* n. sp. and in some specimens of *C. praesignis*, as well as in other Turridae such as *Gemmula cosmoi* (Sykes, 1930), but it is generally smoother and thinner to that of *C. unilineata*. The LDA analysis indicated that *C. unilineata* has generally a more angulated shape on the outer aperture lip of the last whorl, indicating a more concave subsutural ramp in comparison to other *Cryptogemma*. However, we note that the convex hulls (Fig. 1) of *C. unilineata* and *C. powelli* sp. nov. are greatly overlapping, so the strong carinated brown-orange subsutural band remains the best suited character for distinguishing *C. unilineata* from *C. powelli*.

List of COI diagnostic sites (position: character state): [172: G, 307: T, 361: G, 370: C]

Distribution: From East Africa to Central Pacific (Hawaiian and Society islands) (Fig. 7D), from ~300 to ~800 meters of depth (Fig. 5).

***Cryptogemma periscelida* (Dall, 1889)**

(Fig. 10I-K)

643

644 *Pleurotoma periscelida* Dall, 1889. 283m (USS Albatross expedition, st. 2143, collected
645 on March 23 1884) and (196m, off Hatteras, North Carolina)

646

647 *Remarks:*

648 The protoconch is unknown, as it is consistently eroded in all examined material, even
649 in younger specimens.

650 Radula medium long (part of youngest section lost), more than 1.9 mm in length (>0.22
651 of AL), composed of more than 50 transverse rows of teeth. Marginal teeth 107-116 μm
652 long (mean 110 μm , $n = 5$, or 1.25% of AL), duplex. Anterior (inner) 0.4 of tooth length
653 solid, narrow lanceolate in dorsal view, in posterior part major and accessory limbs
654 medium broadly bifurcating, accessory limb with clear constriction and bent at less than
655 half tooth length, thin, nearly same length and width as major limb. Central formation
656 with long, narrow, sharp carinated cusp and lateral flaps with distinct posterior and
657 postero-lateral margins. Flaps completely fused with cusp (Fig. 7D).

658 This species has been described from the Gulf of Mexico, although specimens from
659 Suriname and from the MNHN recent expedition GUYANE 2014 (French Guyana)
660 were also collected. This is the only '*Gemmula*'-like species to be found exclusively in
661 the Atlantic Ocean, and it occurs in a 200-800 m depth range.

662

663 *List of COI diagnostic sites (position: character state):* [352: C, 412: G, 655: C]

664

665 *Distribution:* Found in the Gulf of Mexico and further south to French Guyana (Fig.
666 4B), from ~200 to ~500m of depth (Fig. 5).

667

668 ***Cryptogemma powelli* sp. nov.**

669 (Fig. 11)

670

671 *Type material*: Holotype MNHN-IM-2013-68787; Paratype 1, MNHN IM-2007-40795,
672 paratype 2, MNHN-IM- 2007-40765, all live collected and processed for DNA
673 extraction.

674

675 *Type locality*: New-Caledonia, South-West of Ile des Pins, 22°48'S, 167°15'E, 449-465
676 meters depth, sand and debris (Expedition KANACONO, st. DW4697).

677

678 *Etymology*: Named after the New Zealand malacologist A.W.B. Powell (1901-1987),
679 who contributed enormously to the systematics of Conoidea, and in particular, who
680 revised the family Turridae in 1964 and described several species of *Cryptogemma*.

681

682 *Description (holotype)*: Shell narrowly fusiform, with high spire, and medium-long
683 siphonal canal. Protoconch conical, eroded, with a diameter of 1.125 mm, of about 4
684 convex whorls. Teleoconch of 9 whorls; suture shallow, impressed. Shell height 38 mm,
685 aperture height 10.9 mm and shell diameter 12.5 mm. Whorls strongly shouldered, with
686 slightly concave shoulder slope, very weakly convex, nearly cylindrical periphery.
687 Spiral sculpture of fine, broadly spaced, wavy subequal spiral cords on subsutural ramp,
688 10 on last whorl, uppermost being much more pronounced than others, colored light
689 orange-brown. Sinus cord strongly gemmate, with gemmules clearly bisected (39 on the
690 body whorl). Spiral cords becoming thicker on whorl periphery, sometimes nodulose,

some notably wider than others. Axial sculpture of fine growth lines. Last whorl shortly constricted to long siphonal canal, with 32 cords below sinus, of which about 20 on canal. Aperture irregular oval, outer lip thin, simple. Anal sinus moderately deep, U-shaped. Shell color straw-yellow, subsutural cord orange-brown, gemmae slightly lighter than background.

Radula medium long, around 3.1 mm in length (0.28 of AL), composed of 75 transverse rows of teeth. Marginal teeth 129–135 μm long (mean 133 μm , $n = 5$, or 1.22% of AL), duplex. Anterior (inner) 1/3 of tooth length solid, lanceolate in dorsal view, in posterior part major and accessory limbs broadly bifurcating, accessory limb with clear constriction at half tooth length, thin, about half length and width of major limb. Central formation with medium long and medium broad sharp carinated cusp and lateral flaps with distinct posterior and postero-lateral margins. Flaps not completely fused with cusp (Fig. 7H).

Remarks: This species corresponds to PSH 15 in Puillandre *et al.* (2012). *Cryptogemma powelli* sp. nov. exhibits similar intraspecific variation in shell shape to that of its congeners, based on its convex hull area (Fig. 1). Studied specimens vary in shades of shell color, from light yellowish to light orange, occasionally with a patchy pattern. In terms of both size and shape, *C. powelli* can in some cases be undistinguishable from *C. unilineata* (Fig. 1). The morphometric analysis shows considerable overlap of the measured shell features between the two species, with the main distinction between them expressed by the second axis. Interpretation of this result suggests that the *C. powelli* on average possess a more concave curvature of the outer aperture lip, compared to *C. unilineata*. Besides, distinction of *C. powelli* and *C. unilineata* mostly

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715 relies on the degree of pronunciation of the subsutural cord – it is typically not
716 significantly stronger than the succeeding cords in the former species, but is always
717 thick and gemmate in the latter. The subsutural cord is, however, thicker in younger
718 specimens, rendering the distinction of juvenile *C. powelli* and *C. unilineata* specimens
719 problematic.

720
721 *List of COI diagnostic sites (position: character state):* [112: G, 322: T, 433: A]

722
723 *Distribution:* The confirmed distribution of this species based on sequenced specimens
724 ranges from the Indian Ocean to the Central Indo-Pacific (Fig. 4F), from ~400 to ~600m
725 of depth.

726
727 **Discussion**

728 Using an integrative taxonomy approach, by combining DNA-based species
729 delimitation methods with classical morphological taxonomic methods, we reevaluated
730 the *Cryptogemma* group studied in Puillandre *et al.* (2012) with new sequences – in
731 some cases from type material – resulting in eight delimited species. Among the eight
732 delimited species, *C. phymatias*, *C. praesignis*, *C. timorensis* and *C. aethiopica*
733 comprise 20 of the available species names, with *C. powelli* the only one described as
734 new. Our results contrast with the usual tendency in this family toward the discovery of
735 new species (e.g. Puillandre *et al.*, 2017; Abdelkrim *et al.*, 2018b). All the synonymized
736 species names in this group were established before the ‘molecular era of taxonomy’,
737 reinforcing the recommendation – yet not always followed (Bouchet & Strong, 2010) –
738 of systematically relying on molecular analysis, combined with other data, to delimit

species. However, our study also shows that using only molecular delimitation of species while ignoring some key specimens such as types would limit knowledge of intra-specific morphological variability, thus obscuring also the ability to relate such variability to extrinsic parameters, such as geographic and bathymetric ranges. In this study, morphological study and taxonomic expertise on types resulted in the extension of intra-specific variability (Fig. 1; e.g. *C. aethiopica* types). This might be explained because, when describing a new species, there can be a strong subjective effect on the choice of the type specimens (usually the largest of a lot). The recent and promising success in sequencing DNA obtained from empty shells (Villanea *et al.*, 2016; Sarkissian *et al.*, 2017) should assist in attributing names to molecularly-defined species by sequencing type specimens. However, sequencing shells implies destructive sampling, and will therefore possibly not be accepted by many museum curators. Furthermore, identifying and attributing material to species within a species complex still requires considerable taxonomic investigation.

By exploring the intraspecific variability of the shell, in isolation or in relation to interspecific variability, geographical and bathymetric ranges, or ecological data, we here emphasize a few remarks that may provide directions for the future study of this group.

Geographical intra-specific variability. In *C. aethiopica*, for which many species were synonymized, there are significant geographical variations in the spire whorls. Specimens from the West Indian Ocean were found to have very smooth spire whorls, while specimens from the central Indo-Pacific were found with either two or three well-marked gemmate cords. Considering the few available discrete shell features, these distinguishable characteristics were used by authors to justify the creation of several

species names. No such intraspecific variation in shell sculpture was found in the other species of *Cryptogemma*, although other geographically-structured morphological variability has been observed in the Turridae genus *Lophiotoma* (Puillandre *et al.* 2017), with shell color varying from one side of the Indo-Pacific to the other.

Ecological variability. It is shown (e.g. Bierne *et al.*, 2003; Hauquier *et al.*, 2017) that some benthic species have clear preferences with regards to the substrate on which they thrive (e.g. sandy/muddy vs. rocky bottom). However, other species are generalists with respect to the substratum, as seems to be the case for the *Cryptogemma* species. All species were found both on hard and soft substrate, with or without organic matter (e.g. leaves or sunken wood). A remarkable case is *C. tessellata*, for which the three available trawl images showed three very different environments (Fig. 12), and, even more remarkably, correlated with shell morphology (Fig. 10C-D); specimens found in sandy or spongy environments exhibited a light pale color ground while the individual found in a volcanic rock bottom has a reddish color ground. However, the holotype of this species shows an intermediate pattern and was collected “in mud and sand” (Powell, 1964). More material is needed to properly study the potential effects of substrate on shell color.

Sexual dimorphism. *C. praesignis* is the first Turridae turrid species for which apparent sexual dimorphism of the shell has been documented (Kantor & Sysoev, 1991). The (mature) females possess one or several tertiary notches that is probably linked to fertilization according to the authors, since mature males possess an extremely large and muscular penis. The authors proposed the hypothesis that these notches appear periodically during the breeding period, mainly based on the observation of several successive notches on the shells.

Bathymetric zonation. Bathymetric segregation between sister species has been shown in molluscan species (e.g. Clague *et al.*, 2012). In the Turridae, it has been found that a pair of sister species, *Lophiotoma abbreviata* and *L. brevicaudata*, show distinct bathymetric preferences, with the former observed at an average depth of 3 m and the latter at an average depth of 15 m (Puillandre *et al.*, 2017). The present study demonstrates that, at a much wider scale, a similar case was found in the *C. praesignis*/*C. phymatias* species pair, with the former species occurring between ~300 to ~1400 m and the latter between ~1400 to ~3000m depth (Fig. 5). This example could be added to the list of models used for studying speciation processes in benthic species with high dispersal capabilities and large geographic distributions, for which a topographic barrier would not satisfactorily explain genetic isolation (see Etter *et al.*, 2005; Zardus *et al.*, 2006).

Geographical ranges. While an Indo-Pacific distribution is common in benthic species, but so far no – molecularly supported - cases of Pacific-Atlantic distribution have been found in benthic gastropods. There are cases of cosmopolitan pelagic gastropods: *Glaucus atlanticus* (Churchill *et al.*, 2014), *Clione limacina* (Jennings *et al.*, 2010) and *Fiona pinnata* (Trickey *et al.*, 2016). To this extent, *C. phymatias* could be the first documented, molecularly supported, case of a benthic gastropod with a Pacific-Atlantic distribution (Fig. 4A). Cases of such molecularly confirmed cosmopolitan benthic species have been found in other phyla such as Annelida (Meyer *et al.*, 2008; Sun *et al.*, 2016; Tomioka *et al.*, 2016), Arthropoda (Casanova *et al.*, 1998; Havermans *et al.*, 2013) and Algae (Macaya & Zuccarello, 2010). However, human-mediated introduction was strongly suggested for some of these cases, e.g. annelids. Nothing is known of the biological features of *C. phymatias* that would enable such a wide dispersal of larvae.

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811 *Protoconch variability*. As reported in Bouchet & Warren (1979; 1994), many deep-
812 water gastropods' larval shells indicate a planktotrophic larval development, which is
813 generally associated with good dispersal abilities and gene flow. The *Cryptogemma*
814 species are no exception to this, with protoconch varying from 4 to 5.25 whorls.
815 However, no correlation was found between the number of whorls of protoconch in a
816 specimen and its associated depth, implying that, from a certain threshold (e.g. 4), the
817 number of whorls is not the only factor determining the ability to disperse. Furthermore,
818 in other neogastropod species complex for which there is a comparable number of
819 protoconch whorls (e.g. Sanders *et al.*, 2017) the study showed a strict ocean-delimited
820 (e.g. Indian only, Pacific only) distribution. As for *C. phymatias*, the (eroded)
821 protoconch of the holotype of *B. carynae* is to our knowledge the only one preserved
822 (but slightly eroded) in this species, and it shows no major difference
823 (diameter/height/number of whorls) from other *Cryptogemma* species with regards to
824 this character that could explain its very large Pacific-Atlantic distribution.

825 *Morphological stasis in teleoconch*. *C. praesignis* and *C. timorensis*, previously
826 assigned to *Ptychosyrinx* in Puillandre *et al.* (2012), show considerable similarity in
827 shell sculpture despite not being sister species, and the two taxa would be difficult to
828 distinguish without their significant difference in size. These two species represent a
829 clear case of morphological homogeneity in Conoidea, for which other examples have
830 been reported (Kantor *et al.*, 2018). Large-scale morphometrics correlated with
831 phylogeny may serve to better characterize and understand the conserved '*Gemmula*-
832 like' form across geological time. Some specimens from the Mio-Pliocene have been
833 attributed to species of *Cryptogemma* (see 'Taxonomy'), however, an incommensurable
834 number of '*Ptychosyrinx*-like' or '*Gemmula*-like' Turridae from the Paleogene will

probably remain unattributed to a clade until a more comprehensive understanding, characterization and formalization of the family is achieved.

Radular morphology. The radula is an important morphological character in conoidean taxonomy. In Turridae, the radula is seemingly quite similar between congeneric species with few exceptions, such as for *Iotyraris* (Abdelkrim et al, 2018b). *Cryptogemma* presently is one of few genera of Turridae for which the radula has been examined for every representative species. Morphology of the marginal duplex teeth is rather similar among all species, except for slight variation in the development of the accessory limb; either shorter or nearly the same in length as the major limb (*C. timorensis*), or much narrower or nearly of the same width as the major limb (*C. tessellata*). However, we note this with the caveat that the shape of the duplex teeth as inferred from SEM images may differ considerably due to the position of the tooth, thus rendering comparison of different specimens and species imperfect. Additionally, there are large variations between species in the morphology of the central formation in terms of the shape of the central cusp and the degree of development and shape of the lateral flaps, in some cases with very distinct elevated edges (*C. tessellata*), in others with the flaps being barely distinguishable (*Cryptogemma phymatias*). Another potentially important character is the relative length of the radula, which may differ greatly between otherwise morphologically close species (e.g. *C. praesignis* and *C. timorensis*), number of transverse rows of teeth (in *Cryptogemma* varying from 45 to 99) and the relative length of the marginal teeth (from 1.22% of AL in *C. powelli* to 1.9% in *C. praesignis*). Unfortunately, little has been published on relative tooth size in different Turridae lineages and other groups of Conoidea to date.

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859 The above-mentioned characteristics of the *Cryptogemma* species have been revealed
860 by the morphological and molecular delimitation of species, a practice strongly advised
861 for future studies on the Turridae. In particular, it is shown here that morphological
862 differences associated with geographical or ecological diversity within the distribution
863 range of a species may lead to erroneous taxonomic conclusions. Unexpectedly wide
864 geographic distributions in particular, such as those documented herein, further add to
865 the challenges of conoidean taxonomy, notably where morphologically heterogenous
866 taxa are concerned. This is because material potentially seen as too widely separated
867 geographically to be considered relevant (or where geographically well-separated taxa
868 have not even been considered), may in fact represent conspecific material, a notion
869 supported by the numerous synonymizations herein. Combined with the fact that
870 sampling of the deep sea is infrequent and geographically severely incomplete
871 (potentially masking the presence of morphological clines which results in the over-
872 emphasis on few, morphologically discrete forms), future studies on deep-sea Conoidea
873 must take such wide distributions into account when embarking upon taxonomic
874 investigation.

875 Finally, the study of shell variability may serve to produce hypotheses regarding the
876 evolutionary processes that lead to such observed diversity. Indeed, the fact that the
877 actual, molecular-based *Cryptogemma* species were previously split by ante-molecular
878 taxonomists in several species each, has led us to a re-evaluation and re-interpretation of
879 the intraspecific morphological diversity that we could have neglected otherwise. In this
880 regard, the words of Darwin (1857) "It is good to have hair-splitters & lumpers." make
881 sense: the splitter reminds lumpers that intraspecific variability should not be ignored,

and the lumpers reminds splitters that intraspecific variability should not be over-interpreted.

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Legends

Figure 1: Projection of specimens along the two first discriminant axes. Convex hulls are drawn to easily observe the range of each species in the morphospace. Triangles are type specimens, with names of species indicated; the background color corresponds to the species attribution from the literature and the border color to the LDA prediction. Type specimens were not included in the LDA training set. Orange segments correspond to the projection of coefficients multiplied by the standard deviation of each raw variable (PC axes and shell length). Outlines of most extreme shapes are drawn with their respective MNHN numbers.

Figure 2: Bayesian Tree (MrBayes) for the *COI*. Posterior probabilities (>0.95) are only shown for specific and inter-specific nodes. Abbreviations next to each specimen number refer to main marine provinces: WIP: Western Indo-Pacific; CIP: Central Indo-Pacific; EIP; Eastern Indo-Pacific; EP: Eastern Pacific; WA: Western Atlantic. Alignment provided in Appendix 1.

Figure 3: Bayesian Tree (MrBayes) of the *COI*, *12S* and *28S* concatenated. Posterior probabilities and bootstrap values are shown for each node. Alignment provided in Appendix 2.

Figure 4: Map showing the species distributions. Filled circles represent localities of sequenced specimens; full triangles represent localities of type specimens.

Figure 5: Candlestick chart of depth distributions of the eight species. The high and low value correspond respectively to the minimum and maximum values of depth recorded for each species, while the open and close values correspond to the confirmed minimum and maximum values of depth. Confirmed minimum and maximum values of depth correspond respectively to the highest depth value of ending of trawl and the highest depth value of beginning of trawl.

Figure 6: *Cryptogemma phymatias* (Watson, 1886). (A) Lectotype of *Gemmula benthima* Dall, 1908, USNM 123089, Gulf of Panama. (B) Paralectotype of *Gemmula benthima* Dall, 1908, USNM 123087, Gulf of Panama. (C) Holotype of *Bathybermudia carynae* Haas, 1949, FMNH 31656, Bermuda. (D) Lateral view of the protoconch of *B. carynae* (E) Holotype of *Pleurotoma phymatias* Watson, 1886, NHMUK 1887.2.9.957, Philippines. (F-G) AMS T0077, IN2017_V03 - Sampling the Abyss, Jervis Commonwealth Marine Reserve. (H) MNHN-IM-2013-49928, R/V Tansei-maru, KT-12-32, Okinawa. (I) MNHN-IM-2009-13476, AURORA 2007, Philippines.

Figure 7: Radulae of studied *Cryptogemma*. (A) *Cryptogemma praesignis* (Smith, 1895). (B-C) *Cryptogemma phymatias* (Watson, 1886). (B) MNHN uncatalogued, Biocal, New-Caledonia, st. CP23 (C) USNM 857019, Venezuela. (D) *Cryptogemma periscelida* (Dall, 1889), R/V Pelican, 28°23.935'N, 89°22.508'W, 675-765 m. (E) *Cryptogemma aethiopica* (Thiele, 1925), MNHN-IM-2013-50175, DONGSHA 2014, Taiwan. (F) *Cryptogemma tessellata* (Powell, 1964), MNHN-IM-2007-40775, EBISCO, Chesterfield Islands. (G) *Cryptogemma unilineata* (Powell, 1964), MNHN-IM-2013-61844, ZhongSha 2015, Taiwan. (H) *Cryptogemma powelli* sp. nov., MNHN-IM-2013-68787, KANACONO, New Caledonia. (I) *Cryptogemma timorensis* (Tesch, 1915), MNHN-IM-2013-09864, PAPUA NIUGINI, Papua. Scale bars 50 µm.

Figure 8: (A-K) *Cryptogemma praesignis* (Smith, 1895) and (L-P) *Cryptogemma timorensis* (Tesch, 1915). (A) Holotype of *Pleurotoma praesignis* Smith, 1895, ZSIC, Sri Lanka. (B) MNHN-IM-2009-13477, AURORA-2007, Philippines. (C) MNHN-IM-2013-62903, BIOMAGLO, Iles Glorieuses. (D) Holotype of *Pleurotoma lobata* Sowerby III, 1903, NHMUK 1903.7.27.49, South Africa. (E) Holotype of *Ptychosyrinx lordhoweensis*, ZMMU Lc-14532, Lord Howe Rise. (F) Syntype of *Pleurotoma bisinuata* von Martens, 1901, ZMB 683, off East Africa. (G) Holotype of *Pleurotoma microscelida* Dall, 1895, USNM 127122, Hawaiian Islands. (H). Holotype of *Pleurotoma rotatilis* von Martens, 1902, ZMB 60070, off East Africa. (I) MNHN-IM-2013-62893, BIOMAGLO, Iles Glorieuses. (J) MNHN-IM-2013-62900, BIOMAGLO, Iles Glorieuses. (K) Lateral view of the protoconch of MNHN-IM-2013-62893. (L) Holotype of *Ptychosyrinx timorensis teschi* Powell, 1964, USNM 239068, Borneo. (M)

1141 MNHN-IM-2009-14860, ATIMO VATAE, South of Madagascar. (N) MNHN-IM-
 1142 2007-40928, SALOMON 2, Salomon Islands. (O) MNHN-IM- 2013-58793,
 1143 KAVIENG, Papua. (P) Lateral view of the protoconch of MNHN-IM-2009-14935.
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 1145 **Figure 9:** *Cryptogemma aethiopica* (Thiele, 1925). (A) Holotype of *Pleurotoma*
 1146 *aethiopica* Thiele 1925, ZMB 109376, off East Africa. (B) Holotype of *Pleurotoma*
 1147 *fusiformis* Thiele, 1925, ZMB 109388, off Sumatra. (C) MNH- IM-2009-14979,
 1148 ATIMO VATAE, South of Madagascar. (D) Lateral view of the protoconch of MNHN-
 1149 IM-2013-48115, KANADEEP, Chesterfield Islands. (E) MNHN-IM- 2009-29301,
 1150 EXBODI, New Caledonia. (F) MNHN-IM- 2009-14778, ATIMO VATAE, South of
 1151 Madagascar. (G) Holotype of *Pinguigemmula luzonica* Powell, 1964, USNM 237784,
 1152 Philippines. (H) Holotype of *Pinguigemmula okinavensis* McNeil, 1960, UNSM MO
 1153 562851, Miocene or Pliocene of Okinawa. (I) MNHN-IM-2013-19950, PAPUA
 1154 NIUGINI, Papua. (J) Holotype of *Pinguigemmula philippinensis* Powell, 1964, USNM
 1155 237563, Philippines.

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 1158 **Figure 10:** (A-D) *Cryptogemma tessellata* (Powell, 1964), (E-H) *Cryptogemma*
 1159 *unilineata* (Powell, 1964) & (I-K) *Cryptogemma periscelida* (Dall, 1889). (A) Holotype
 1160 of *Gemmula tessellata* Powell, 1964, AWMM MA71042, Hawaiian Islands. (B) Lateral
 1161 view of the protoconch of MNHN-IM-2013-48252, KANADEEP, Chesterfield Islands.
 1162 (C) MNHN-IM-2009-24975, EXBODI, New Caledonia. (D) MNHN-IM- 2007-40775,
 1163 EBSICO, Chesterfield Islands. (E) Holotype of *Gemmula congener unilineata* Powell,
 1164 1964, BPBM 8929, Hawaiian Islands. (F) Lateral view of the protoconch of MNHN-

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1165 IM-2007-40786, NORFOLK 2, New Caledonia. (G) MNHN-IM-2009-14953, ATIMO
1166 VATAE, South of Madagascar. (H) MNHN-IM-2007-38340, MAINBAZA, Mozambic
1167 channel. (I) Lectotype of *Pleurotoma periscelida* Dall, 1889, USNM 87391, Columbia.
1168 (J) MNHN-IM- 2013-56285, GUYANE 2014, French Guyana. (K) MNHN-IM- 2013-
1169 56283, GUYANE 2014, French Guyana.
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1172 **Figure 11:** *Cryptogemma powelli* sp. nov. (A-C) Holotype, MNHN-IM- 2013-68787,
1173 KANACONO, New Caledonia. (D) Lateral view of the protoconch of the paratype 1
1174 MNHN-IM- 2007-40765, EBISCO, Chesterfield Islands. (E) Paratype 2, MNHN-IM-
1175 2007-40795, Norfolk 2, New Caledonia. (F) MNHN-IM-2013-55832, TAIWAN 2013,
1176 Taiwan. (G-I) Paratype, MNHN-IM- 2007-40765, EBISCO, Chesterfield Islands.
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1178 **Figure 12:** Pictures of trawls from stations were *Cryptogemma tessellata* (Powel, 1964)
1179 specimens were found.
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1182 **Supplementary Material**
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1184 **Figure S1:** Result of the leave-one-out cross-validation procedure that was used to find
1185 the number of PC axes leading to the best percentage of species predictions.
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1187 **Figure S2:** Results of the ABGD, mPTP and GMYC analysis
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1189 **Figure S3:** Results of the morphometric analysis without taking size in account.

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1191 **Table S1:** Material examined in this study

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Projection of specimens along the two first discriminant axes. Convex hulls are drawn to easily observe the range of each species in the morphospace. Triangles are type specimens, with names of species indicated; the background color corresponds to the species attribution from the literature and the border color to the LDA prediction. Type specimens were not included in the LDA training set. Orange segments correspond to the projection of coefficients multiplied by the standard deviation of each raw variable (PC axes and shell length). Outlines of most extreme shapes are drawn with their respective MNHN numbers.

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Bayesian Tree (MrBayes) of the COI, 12S and 28S concatenated. Posterior probabilities and bootstrap values are shown for each node. Alignment provided in Appendix 2.

155x79mm (300 x 300 DPI)

Map showing the species distributions. Filled circles represent localities of sequenced specimens; full triangles represent localities of type specimens.

188x297mm (300 x 300 DPI)

Candlestick chart of depth distributions of the eight species. The high and low value correspond respectively to the minimum and maximum values of depth recorded for each species, while the open and close values correspond to the confirmed minimum and maximum values of depth. Confirmed minimum and maximum values of depth correspond respectively to the highest depth value of ending of trawl and the highest depth value of beginning of trawl.

276x230mm (300 x 300 DPI)

Cryptogemma phymatias (Watson, 1886). (A) Lectotype of *Gemmula benthima* Dall, 1908, USNM 123089, Gulf of Panama. (B) Paralectotype of *Gemmula benthima* Dall, 1908, USNM 123087, Gulf of Panama. (C) Holotype of *Bathybermudia carynae* Haas, 1949, FMNH 31656, Bermuda. (D) Lateral view of the protoconch of *B. carynae* (E) Holotype of *Pleurotoma phymatias* Watson, 1886, NHMUK 1887.2.9.957, Philippines. (F-G) AMS T0077, IN2017_V03 - Sampling the Abyss, Jervis Commonwealth Marine Reserve. (H) MNHN-IM-2013-49928, R/V Tansei-maru, KT-12-32, Okinawa. (I) MNHN-IM-2009-13476, AURORA 2007, Philippines.

189x231mm (300 x 300 DPI)

Radulae of studied *Cryptogemma*. (A) *Cryptogemma praesignis* (Smith, 1895). (B-C) *Cryptogemma phymatias* (Watson, 1886). (B) MNHN uncatalogued, Biocal, New-Caledonia, st. CP23 (C) USNM 857019, Venezuela. (D) *Cryptogemma periscelida* (Dall, 1889), R/V Pelican, 28°23.935'N, 89°22.508'W, 675-765 m. (E) *Cryptogemma aethiopica* (Thiele, 1925), MNHN-IM-2013-50175, DONGSHA 2014, Taiwan. (F) *Cryptogemma tessellata* (Powell, 1964), MNHN-IM-2007-40775, EBISCO, Chesterfield Islands. (G) *Cryptogemma unilineata* (Powell, 1964), MNHN-IM-2013-61844, ZhongSha 2015, Taiwan. (H) *Cryptogemma powelli* sp. nov., MNHN-IM-2013-68787, KANACONO, New Caledonia. (I) *Cryptogemma timorensis* (Tesch, 1915), MNHN-IM-2013-09864, PAPUA NIUGINI, Papua. Scale bars 50 μ m.

210x210mm (300 x 300 DPI)

(A-K) *Cryptogemma praesignis* (Smith, 1895) and (L-P) *Cryptogemma timorensis* (Tesch, 1915). (A) Holotype of *Pleurotoma praesignis* Smith, 1895, ZSIC, Sri Lanka. (B) MNHN-IM-2009-13477, AURORA-2007, Philippines. (C) MNHN-IM-2013-62903, BIOMAGLO, Iles Glorieuses. (D) Holotype of *Pleurotoma lobata* Sowerby III, 1903, NHMUK 1903.7.27.49, South Africa. (E) Holotype of *Ptychosyrinx lordhoweensis*, ZMMU Lc-14532, Lord Howe Rise. (F) Syntype of *Pleurotoma bisinuata* von Martens, 1901, ZMB 683, off East Africa. (G) Holotype of *Pleurotoma microscelida* Dall, 1895, USNM 127122, Hawaiian Islands. (H). Holotype of *Pleurotoma rotatilis* von Martens, 1902, ZMB 60070, off East Africa. (I) MNHN-IM-2013-62893, BIOMAGLO, Iles Glorieuses. (J) MNHN-IM-2013-62900, BIOMAGLO, Iles Glorieuses. (K) Lateral view of the protoconch of MNHN-IM-2013-62893. (L) Holotype of *Ptychosyrinx timorensis teschi* Powell, 1964, USNM 239068, Borneo. (M) MNHN-IM-2009-14860, ATIMO VATAE, South of Madagascar. (N) MNHN-IM- 2007-40928, SALOMON 2, Salomon Islands. (O) MNHN-IM- 2013-58793, KAVIENG, Papua. (P) Lateral view of the protoconch of MNHN-IM-2009-14935.

210x293mm (300 x 300 DPI)

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Cryptogemma aethiopica (Thiele, 1925). (A) Holotype of *Pleurotoma aethiopica* Thiele 1925, ZMB 109376, off East Africa. (B) Holotype of *Pleurotoma fusiformis* Thiele, 1925, ZMB 109388, off Sumatra. (C) MNH- IM- 2009-14979, ATIMO VATAE, South of Madagascar. (D) Lateral view of the protoconch of MNHN-IM-2013-48115, KANADEEP, Chesterfield Islands. (E) MNHN-IM- 2009-29301, EXBODI, New Caledonia. (F) MNHN-IM- 2009-14778, ATIMO VATAE, South of Madagascar. (G) Holotype of *Pinguigemmula luzonica* Powell, 1964, USNM 237784, Philippines. (H) Holotype of *Pinguigemmula okinavensis* McNeil, 1960, UNSM MO 562851, Miocene or Pliocene of Okinawa. (I) MNHN-IM-2013-19950, PAPUA NIUGINI, Papua. (J) Holotype of *Pinguigemmula philippinensis* Powell, 1964, USNM 237563, Philippines.

210x214mm (300 x 300 DPI)

(A–D) *Cryptogemma tessellata* (Powell, 1964), (E–H) *Cryptogemma unilineata* (Powell, 1964) & (I–K) *Cryptogemma periscelida* (Dall, 1889). (A) Holotype of *Gemmula tessellata* Powell, 1964, AWMM MA71042, Hawaiian Islands. (B) Lateral view of the protoconch of MNHN-IM-2013-48252, KANADEEP, Chesterfield Islands. (C) MNHN-IM-2009-24975, EXBODI, New Caledonia. (D) MNHN-IM-2007-40775, EBSICO, Chesterfield Islands. (E) Holotype of *Gemmula congener unilineata* Powell, 1964, BPBM 8929, Hawaiian Islands. (F) Lateral view of the protoconch of MNHN-IM-2007-40786, NORFOLK 2, New Caledonia. (G) MNHN-IM-2009-14953, ATIMO VATAE, South of Madagascar. (H) MNHN-IM-2007-38340, MAINBAZA, Mozambic channel. (I) Lectotype of *Pleurotoma periscelida* Dall, 1889, USNM 87391, Columbia. (J) MNHN-IM-2013-56285, GUYANE 2014, French Guyana. (K) MNHN-IM-2013-56283, GUYANE 2014, French Guyana.

210x215mm (300 x 300 DPI)

Cryptogemma powelli sp. nov. (A-C) Holotype, MNHN-IM- 2013-68787, KANACONO, New Caledonia. (D) Lateral view of the protoconch of the paratype 1 MNHN-IM- 2007-40765, EBISCO, Chesterfield Islands. (E) Paratype 2, MNHN-IM-2007-40795, Norfolk 2, New Caledonia. (F) MNHN-IM-2013-55832, TAIWAN 2013, Taiwan. (G-I) Paratype, MNHN-IM- 2007-40765, EBISCO, Chesterfield Islands.

192x167mm (300 x 300 DPI)

Pictures of trawls from stations where *Cryptogemma tessellata* (Powel, 1964) specimens were found.

433x947mm (200 x 200 DPI)

Acknowledgments

This work was supported by the Service de Systématique Moléculaire (UMS 2700 CNRS MNHN), the CONOTAX project funded by the French National Research Agency (grant number ANR-13-JSV7- 0013-01), the bilateral cooperation research funding from the Ministry of Science and Technology, Taiwan (grant number MOST 102-2923-B-002-001-MY3) and the French National Research Agency (grant number ANR 12-ISV7-0005-01). The contribution of Y. Kantor and A. Fedosov was supported by the grant from Russian Science Foundation no. 16-14-10118-II (PI Y. Kantor), F. Criscione and A. Hallan supported by a grant from the Australian Biological Resources Study (ABRS grant RF217-57 to PI F. Criscione), and Y. Kano by the Japan Society for the Promotion of Science (KAKENHI grant nos 15H04412 and 18H02494).

The material in this paper originates from numerous shore-based expeditions and deep sea cruises, conducted respectively by MNHN and Pro-Natura International (PNI) as part of the Our Planet Reviewed programme (ATIMO VATAE, MAINBAZA, GUYANE 2014, PAPUA NIUGINI, KAVIENG 2014; PI P. Bouchet)) and/or by MNHN and Institut de Recherche pour le Développement (IRD) as part of the Tropical Deep-Sea Benthos programme (BIOMAGLO, TARASOC, MIRIKY, AURORA 2007, EBISCO, TAIWAN 2013, DongSha 2014, NANHAI 2014, BIOPAPUA, SALOMON 2, SALOMONBOA 3, CONCALIS, EXBODI, NORFOLK 2, TERRASSES, ZHONGSHA 2015, KANACONO, KANADEEP, MADEEP; PIs Bertrand Richer de Forges, Philippe Bouchet, Sarah Samadi, Nicolas Puillandre, Wei-Jen Chen, Tin-Yam Chan). Scientific partners included the University of Papua New Guinea (UPNG); National Fisheries College, Kavieng, Papua New Guinea; the National Museum of the Philippines; Institut d'Halieutique et Sciences Marines (IH.SM), Université de Tuléar,

Madagascar; University of Taipei and University of Keelung, Taiwan; Universidade Eduardo Mondlane, Maputo; the Madagascar bureau of the Wildlife Conservation Society (WCS); and Instituto Español de Oceanografía (IOE). Funders and sponsors included the Total Foundation, Prince Albert II of Monaco Foundation, Stavros Niarchos Foundation, Richard Lounsbery Foundation, Vinci Entrepose Contracting, Fondation EDF, European Regional Development Fund (ERDF), the Philippines Bureau of Fisheries and Aquatic Research (BFAR), the French Ministry of Foreign Affairs, Fonds Pacifique and the Government of New Caledonia. Additional field work included PANGLAO 2004, a joint project of MNHN and University of San Carlos, Cebu City. All expeditions operated under the regulations then in force in the countries in question and satisfy the conditions set by the Nagoya Protocol for access to genetic resources. The authors would like to thank Virginie Héros, Barbara Buge, and Julien Brisset (MNHN) for their help in curating the vouchers; Alexander Sysoev (ZMMU) for photographs and tissue loan; Christine Zorn (ZMB) for photographs and type specimens loan; Ellen Strong, Mark. S. Florence and Kathy Hollis (USNM) for photographs and specimens loan; Jochen Gerber (FMNH) for photographs; Philippe Maestrati (MNHN) for photographs; Regina Kawamoto & Norine Yeung (BPBM) for photographs; Severine Hannam (AWMM) for photographs; Andreia Salvador (NHMUK) for photographs; Jun Hashimoto (Nagasaki University) for organizing the Nagasaki-maru cruise N275; the Plateau Technique de Microscopie Électronique (PtME) of MNHN for SEM pictures. Posthumous thank goes to Richard Kilburn for photograph of *P. praesignis*.