An assessment of the genus *Columbella* Lamarck, 1799 (Gastropoda: Columbellidae) from eastern Atlantic

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Published on 30 June 2017

urn:lsid:zoobank.org:pub:57395522-BE12-40AC-B504-C448A31F8A8D

Russini V., Fassio G., Modica M. V., deMaintenon M. J. & Oliverio M. 2017. — An assessment of the genus *Columbella* Lamarck, 1799 (Gastropoda: Columbellidae) from eastern Atlantic. *Zoosystema* 39 (2): 197-212. https://doi.org/10.5252/z2017n2a2

ABSTRACT
Three species of the neogastropod genus *Columbella* Lamarck, 1799 are recognised from the northeastern Atlantic and the Mediterranean. One is the common Mediterranean *C. rustica* (Linnaeus, 1758), with paucispiral protoconch, extending its range in the Atlantic South to Senegal and North to Portugal. *Columbella adansoni* Menke, 1853, with multispiral protoconch is restricted to the Macaronesian archipelagoes. A third species, also with multispiral protoconch, from West Africa is recognised through molecular methods, and the name *C. xiphitella* Duclos, 1840 is employed by correcting the original erroneous locality ("Californie") to Gabon. Except for protoconch features, no major morphological characters are available to separate the three species; however diagnostic species-level differences in specific positions in the cytochrome c oxidase I (COI) sequences are present between all three species.

KEY WORDS
Columbellidae,
East Atlantic,
Mediterranean,
lectotypification,
DNA-Barcoding.

RÉSUMÉ
Étude du genre Columbella *Lamarck, 1799 (Gastropoda: Columbellidae) dans l'Est de l'océan Atlantique.*
Trois espèces du genre de néogastropode *Columbella* Lamarck, 1799 sont reconnues dans le nord est de l'Atlantique et en Méditerranée. L'une est courante en Méditerranée, *C. rustica* (Linnaeus, 1758), au protoconche paucispiralé : son aire de répartition s'étend en Atlantique du Sénégal au nord du Portugal. *Columbella adansoni* Menke, 1853, au protoconche multispiralé, se limite aux archipels Macaronésiens. Une troisième espèce, caractérisée également par un protoconche multispiralé, est originaire d'Afrique de l'Ouest : elle est reconnue par des méthodes moléculaires ; le nom de *C. xiphitella* Duclos, 1840 lui est attribué après correction de la localité originale erronée (« Californie ») en Gabon. Mis à part l'aspect du protoconche, aucun caractère morphologique majeur ne permet de séparer les trois espèces ; cependant des positions précises dans les séquences du cytochrome c oxidase I (COI) présentent des différences supportant des diagnoses spécifiques.

MOTS CLÉS
Columbellidae,
Atlantique de l'est,
Méditerranée,
lectotypification,
DNA-Barcoding.

INTRODUCTION

Columbella Lamarck, 1799 s.s. (type species *Voluta mercatoria* Linnaeus, 1758) is a genus of columbellid neogastropods (dove shells) including 17 recognised species, mostly from tropical America and the East Atlantic/Mediterranean (WoRMS: Bouchet & Gofas 2015). Based on Moolenbeek & Hoenselaar (1991), Oliverio (1995), Rolán (2005), and Rolán & Ryall (1999), two species are currently recorded in the eastern Atlantic and the Mediterranean Sea: *Columbella rustica* (Linnaeus, 1758), ranging over the entire Mediterranean Sea, and extending into the neighbouring Atlantic southward to Senegal, and northward to Portugal (it is absent in Galicia); and *Columbella adansoni* Menke, 1853, described from Cape Verde islands, and assumed to occur across Macaronesia, from the Azores to the Canary Islands, and along the West African coasts from Ghana to Angola (Oliverio 1995; Rolán & Ryall 1999; Rolán 2005). *Columbella rustica* has a paucispiral protoconch, indicating non-planktotrophic development (lecithotrophic, possibly entirely or mostly intracapsular), whereas *Columbella adansoni* has a multispiral protoconch, indicating planktotrophic larval development. This is the only consistent morphological diagnostic feature for the two species, which are otherwise quite variable in shell sculpture, colour and pattern. Preliminary to a study of the bearing of different larval developmental strategies on the genetic structure of populations (Modica *et al.* 2017), we decided to assay samples of *Columbella* from the eastern Atlantic and the Mediterranean to test the currently accepted species boundaries by molecular data. Therefore, we examined specimens collected from localities spanning as much as possible the known range for the genus in the eastern Atlantic. As a result, a third species of *Columbella* was discovered.

MATERIAL AND METHODS

Sampling locality data (Fig. 1), Identification (ID) catalogue numbers of the vouchers, and GenBank accession numbers are reported in Table 1. A total of 29 specimens from the East Atlantic and the Mediterranean were assayed. Specimens were sampled by SCUBA or snorkelling, and fixed in 95 to 100% ethanol. Vouchers are stored in the malacological collection at Department of Biology and Biotechnologies "Charles Darwin" ("La Sapienza" University of Rome) under BAU ID numbers and at Muséum national d'Histoire naturelle (Paris) under MNHN ID numbers. Genomic DNA was extracted using a proteinase K-phenol-chloroform protocol (Oliverio & Mariottini 2001). The DNA-barcode fragment of the mitochondrial cytochrome c oxidase I (COI) and part of the 16S rRNA were amplified by PCR using the universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994) and 16SA (Palumbi *et al.* 2002) and CGLeuUUR (Hayashi 2003), respectively. For some crucial specimens from West Africa, fixed in alcohol but thereafter preserved dried, which were unsuccessfully assayed with the pair HCO2198-LCO1490, we employed HCO2198 with the primer mlCOIint-F (5'-GGWACWGGWTGAACWGTWTAYCCYCC-3') designed to amplify a shorter fragment (*c.* 300 bp) and employed in metabarcoding works (Leray *et al.* 2013). PCR amplifications were performed with the following conditions: initial denaturation of 5' at 94°C, 35 amplification cycles (30"/94°C, 40"/48-52°C, 50"/72°C), followed by a final phase of 7' at 72°C. PCR products were purified by ExoSAP-IT protocol (USB Corporation, Ohio, USA) and Sanger sequenced by Macrogen Inc. (The Netherlands). Forward and reverse sequences were assembled, checked for contamination and edited with Geneious 4.8.5 (Drummond *et al.* 2009).

Species delimitation in Columbellidae Swainson, 1840

A total of 106 COI sequences from columbellid specimens ascribed to the genera *Alia* H. Adams & A. Adams, 1853, *Amphissa* H. Adams & A. Adams, 1853, *Euplica* Dall, 1889, *Graphicomassa* Iredale, 1929, *Indomitrella* Oostingh, 1940, *Mitrella* Risso, 1826, *Pyrene* Röding, 1798, *Sulcomitrella* Kuroda, Habe & Oyama, 1971 and *Zafra* A. Adams, 1860 (plus some labelled as "columbellid indet.") were either provided by Nicolas Puillandre (ID MNHN-IM) or were retrieved from the GenBank (see Table 4). Sequences from *Cancellopollia* sp. (Gastropoda, Buccinoidea, Buccinidae) (EU015666.1; voucher MNHN-IM-2009-17854), and *Pisania striata* Duclos, 1840 (MNHN-IM-2009-30664, Gastropoda, Buccinoidea, Buccinidae) were retrieved from Genbank to be used as outgroups. COI sequences were manually aligned and checked for stop codons; 16S sequences were aligned using MAFFT 7 (Katoh *et al.* 2002), using the Q-INS-i algorithm (Katoh & Toh 2008), which accounts for secondary structures. Highly variable regions, resulting in gap-rich fragments with ambiguous alignment, were discarded using Gblocks 0.91b (Castresana 2000). All alignments are available from the authors on request.

To define species, we used Automatic Barcode Gap Discovery (ABGD, available at http://wwwabi.snv.jussieu.fr/public/abgd/), a distance-based method designed to detect the so-called "barcode gap" in the distribution of pairwise distances estimated in a COI alignment (Puillandre *et al.* 2012a, b), and the criteria of divergence and reciprocal monophyly (Knowlton 2000; Wheeler & Meier 2000; Reid *et al.* 2006; Malaquias & Reid 2009). The COI sequence alignments were processed in ABGD (excluding the outgroups) using the Kimura-2-parameter (K2p) model and the following settings: a prior for the maximum value of intraspecific divergence between 0.001 and 0.1, 25 recursive steps within the primary partitions defined by the first estimated gap, and a gap width of 0.1.

We ran ABGD on the whole columbellid dataset of 136 COI sequences, to define partition scheme(s) based on distance distribution. Then, species hypotheses as derived from ABGD were tested against taxonomic recognition for the assayed specimens and for phylogenetic congruence. Phylogenetic analyses of the COI, 16S and combined sequence alignments were conducted using Maximum likelihood (ML:

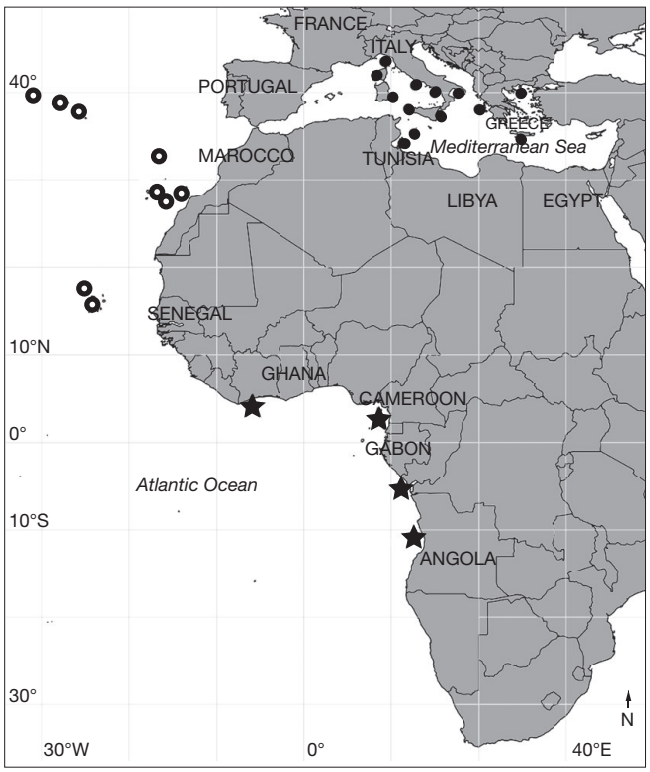

Fig. 1. — Map of the collecting sites (for details see Table 1). Symbols: ●, *Columbella rustica* (Linnaeus, 1758); ○, *Columbella adansoni* Menke, 1853; ★, *Columbella xiphitella* Duclos, 1840.

with 1000 bootstrap replicates) by PhyML3.0 (http://www.atgc-montpellier.fr/phyml/) and Bayesian inference (BI: four-chain Markov chain Monte Carlo (MCMC) analysis, run twice in parallel for 10^7 generations; trees sampled every 1000 generations, burn-in 2500) by MrBayes 3.2.3 on the XSEDE resources on CIPRES Science Gateway V.3.3 portal (https://www.phylo.org/), both with the HKY + I + G (Hasegawa *et al.* 1985) nucleotide substitution model, as selected by jModelTest2. Same analyses (ABGD, ML and BI) were performed on a reduced dataset including sequences from the eastern Atlantic specimens (including full length and shorter COI sequences), sequences from *Columbella mercatoria* (Linnaeus, 1758) (type species of the genus *Columbella*) and *Columbella major* Sowerby, 1832, while those from *Euplica turturina* (Lamarck, 1822) (JQ950207.1 and JQ950143.1, voucher MNHN-IM-2007-33524) were used as outgroup.

Abbreviations

ABGD	Automatic Barcode Gap Discovery;
ICZN	International Commission on Zoological Nomenclature;
sh	shell(s).

Institutions

MNHN	Muséum national d'Histoire naturelle, Paris;
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt.

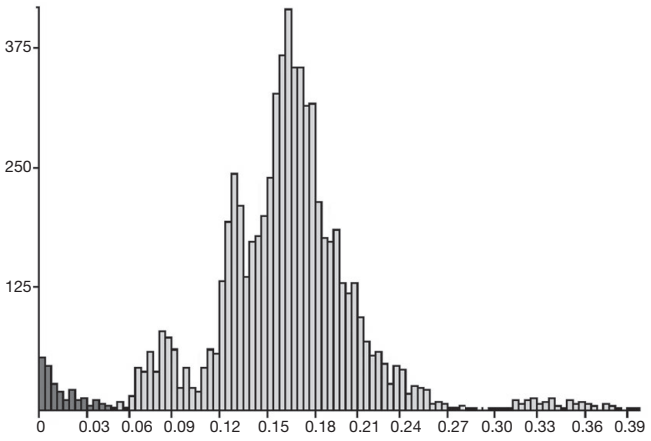

Fig. 2. — Histogram of the distribution of the pairwise estimated genetic distances (K2p) in intraspecific (left, dark grey) and interspecific (right, light grey) comparisons among Columbellidae Swainson, 1840.

RESULTS

For the eastern Atlantic/Mediterranean *Columbella* specimens, a total of 14 specimens from the Mediterranean, nine specimens from the Macaronesia, six specimens from Gabon, three from Ghana and one each from Angola and São Tomé, yielded full length 16S (723bp). Full length COI (658bp) were obtained from 14 specimens from the Mediterranean, nine specimens from Macaronesia, six specimens from Gabon; shorter COI sequences (288bp) were obtained from two specimens from Ghana and one specimen from Angola.

Species delimitation in worldwide Columbellidae

The 30 recursive steps in the ABGD analysis of the COI alignment converged toward a 46-species partition scheme, with the corresponding 46 species hypotheses largely congruent with the *a priori* morphological identification of the worldwide columbellid specimens included (Table 4). Accordingly, the intraspecific genetic divergence estimated on the COI dataset ranged from 0 to 5%, the interspecific ones from 5 to 30% (Fig. 2: K2p matrices available from the authors). ML and BI phylogenetic analyses of the same dataset recovered all 25 species with multiple specimens as monophyletic with very high bootstrap (> 95%) and BI (> 0.99) support.

Species delimitation in eastern Atlantic *Columbella*

The 658bp COI sequences of the eastern Atlantic/Mediterranean *Columbella* were split into three groups: 1) the Mediterranean specimens (corresponding to *Columbella rustica*); 2) the Macaronesian specimens (corresponding to *C. adansoni*); and 3) the specimens from Gabon. The pattern was exactly the same when the shorter sequences of specimens from Ghana and Angola were included.

Intraspecific distance ranged 0-1.5% in *C. adansoni*, 0.2-3% in *C. rustica*, and 0.5-1.6% in the West African species (see Table 2 for K2p indices). The estimated genetic distance was 4% between *C. rustica* and *C. adansoni*, and 7% between the new West African species and the other two (Table 2).

TABLE 1. — List of the examined material with ID numbers for voucher lots (**BAU**, Department of Biology and Biodiversity, Sapienza University of Rome; **MNHN**, Museum national d'Histoire naturelle, Paris), data on collecting sites (in parentheses the number used in Figure 1), and GenBank accession numbers for the sequences.

ID	Site	Coordinates	Accession numbers	
			COI	16S
Columbella rustica (Linnaeus, 1758)				
BAU 1608	(1) Galeria, Corsica, France: 1-5 m depth	42°25'16"N, 8°37'26"E	KX639980	
BAU 1670	(2) S. Isidoro, Italy: 1-5 m depth	40°12'15"N, 17°55'12"E	KX639897	
BAU 1755	(3) Palinuro, Italy: 1-7 m depth	40°01'53"N, 15°16'07"E	KX639898	
BAU 1779	(4) Cape Tenafo, Greece: 1 m depth	36°23'07"N, 22°28'58"E	KX639914	KX664064 KX664065 KX664066
BAU 1794	(5) Sidi Jmour, Djerba, Tunisia: 0-1 m depth	33°49'53"N, 10°44'50"E	KX639919	
BAU 807	(6) Ognina Cuba, Sicily, Italy: 0-1 m depth	36°58'20"N, 15°14'55"E	KX639923 KX639925	
BAU 811	(7) Giraglia, Corsica, France: 0-1 m depth	43°00'37"N, 009°25'27"E	KX639976	KX664073 KX664074 KX664075
BAU 816	(8) Isola dei conigli, Lampedusa, Italy: 0-2 m depth	35°30'35"N, 12°33'27"E	KX639933	
BAU 818	(9) Marsala, Sicily, Italy: 0-1 m depth	37°47'32"N, 12°25'50"E	KX639940	KX664076 KX664077 KX664078
BAU 819	(10) Agios Georgos, Corfù, Greece: 1-3 m depth	39°43'07"N, 19°39'44"E	KX639946	
BAU 822	(11) Agia Pelagia, Crete, Greece: 0-3 m depth	35°24'25.6"N, 25°01'05.5"E	KX639959	
BAU 829	(12) Zannone Island, Italy: 0-10 m depth	40°58'10"N, 13°02'44"E	KX639983	
BAU 831	(13) Arbatax, Sardinia, Italy: 0-12 m depth	39°55'19.0"N, 9°42'54.9"E	KX639987	
Columbella adansoni Menke, 1853				
BAU 1123	(14) Mindelo, São Vicente, Cape Verde: intertidal	16°54'08"N, 24°59'51"W	KX639833	KX664059
BAU 1124	(15) Arguineguin, Gran Canaria, Canary Islands: 0-1 m depth	27°45'18"N, 15°41'04"W	KX639835	
BAU 1694	(16) Sal Rei, Boavista, Cape Verde: intertidal	16°11'5.18"N, 22°55'26.70"W	KX639841	KX664061 KX664062 KX664063
BAU 708	(17) Caloura, São Miguel, Azores: 0-3 m depth	37°42'26.8"N, 25°30'16.4"W	KX639851	
BAU 716	(18) Lajes, Pico, Azores: 0-2 m depth	38°23'05.7"N, 28°15'04.2"W	KX639859	KX664067 KX664068 KX664069
BAU 718	(19) Santa Cruz, Flores, Azores: 0-2 m depth	39°27'07.3"N, 31°07'26.6"W	KX639867	
BAU 802	(20) Puertito de Guimar, Tenerife, Canary Islands: 1-2 m depth	28°17'11"N, 16°22'48"W	KX639885	
BAU 804	(21) Funchal, Madeira: 1-2 m depth	32°38'22"N, 16°55'24"W	KX639888	
BAU 805	(22) Ajuy, Fuerteventura, Canary Islands: 0-1 m depth	28°24'14"N, 14°09'20"W	KX639890	KX664070 KX664071 KX664072
Columbella xiphitella Duclos, 1840				
BAU 1120	(23) Cape Santa Clara, Libreville, Gabon: intertidal to 1 m depth	0°30'18"N, 9°19'07"E	KX639827	KX664053
MNHN-IM-2000-32497/32498			KX639828 KX639829 KX639830 KX639831 KX639832	KX664054 KX664055 KX664056 KX664057 KX664058
BAU 1118	(24) Praia da Corimba, Luanda, Angola: dredged in c. 20 m depth	8°51'S, 13°10'E	KY464898	KX664049
BAU 1119	(25) Miemia, Ghana: 1-10 m depth	4°47'39"N, 2°10'15"W	KY464900 KY464899	KX664050 KX664051 KX664052
BAU 1693	(26) Lagoa Azul, São Tomé: 1-10 m depth	0°24'22"N, 6°36'29"E		KX664060
Columbella major Sowerby, 1832				
184659143	Venado Is., Panama.		KY464894	KY464896
Columbella mercatoria (Linnaeus, 1758)				
184659120	Guadeloupe		KY464895	KY464897
Euplica turturina (Lamarck, 1822)				
MNHN-IM-2007-33524	Vanuatu, SW Tutuba Is., SANTO 2006 Stn. NR04	15°34'59.52"S, 167°15'23.7"E	JQ950207.1	JQ950143.1

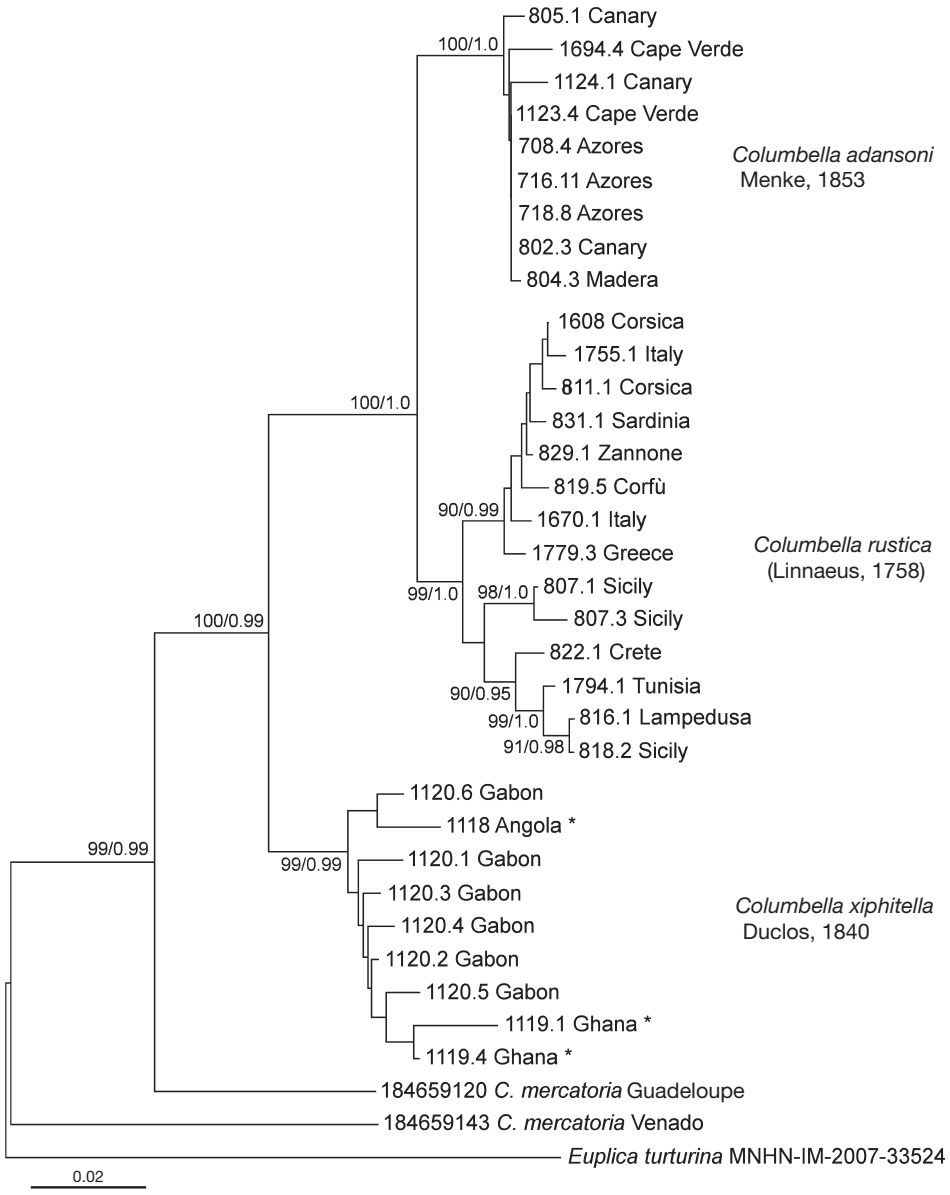

FIG. 3. — ML tree based on the COI dataset (HKY + I + G model of evolution). Numbers at nodes indicate the support by BI Bps (10^7 generations and 25% burnin) and ML bs (1000 replicates). Asterisks indicate shorter sequences (288 bp).

TABLE 2. — K2p genetic distance between East Atlantic and Mediterranean species of *Columbella* (standard deviation in parentheses).

	intraspecific			interspecific	
	min	max	mean		
C. adansoni Menke, 1853	0.000	0.015	0.005 (0.00)		
C. rustica (Linnaeus, 1758)	0.002	0.030	0.020 (0.01)	0.04 (0.00)	
C. xiphitella Duclos, 1840	0.005	0.016	0.011 (0.00)	0.07 (0.01)	0.07 (0.01)
				C. adansoni	*C. rustica*

TABLE 3. — Autapomorphic (diagnostic) position in the COI sequences of the three species.

species	Diagnostic positions
C. adansoni Menke, 1853	61 [G], 91 [G], 160 [C], 181 [T], 352 [C], 549 [A], 586 [T].
C. rustica (Linnaeus, 1758)	238 [C], 310 [T], 447 [G].
C. xiphitella Duclos, 1840	34 [T], 55 [T], 78 [G], 100 [T], 115 [T], 117 [A], 130 [A], 133 [C/G], 178 [C], 309 [C], 346 [C], 385 [T], 430 [C], 463 [T], 472 [G], 565 [T], 598 [T], 619 [T].

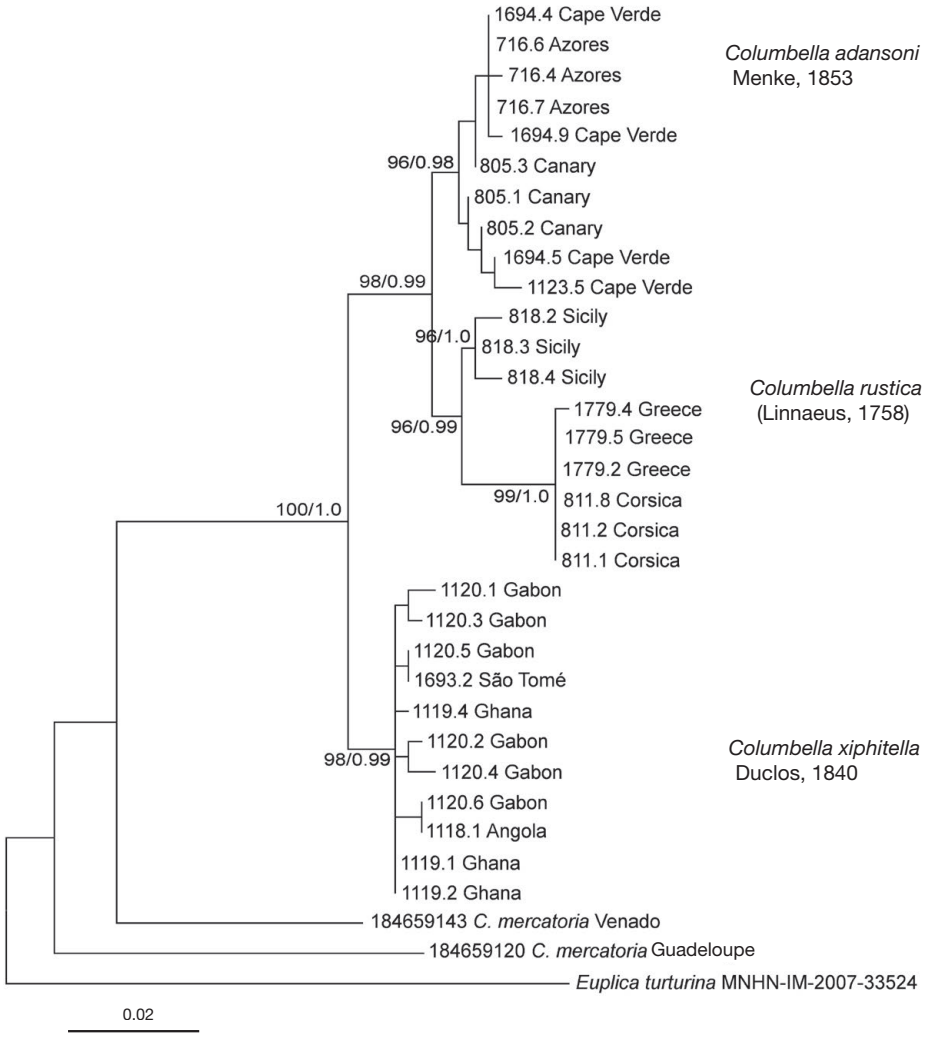

Fig. 4. — ML tree based on the 16S dataset (HKY+I+G model of evolution). Numbers at nodes indicate the support by BI Bps (10^7 generations and 25% burn in) and ML bs (1000 replicates).

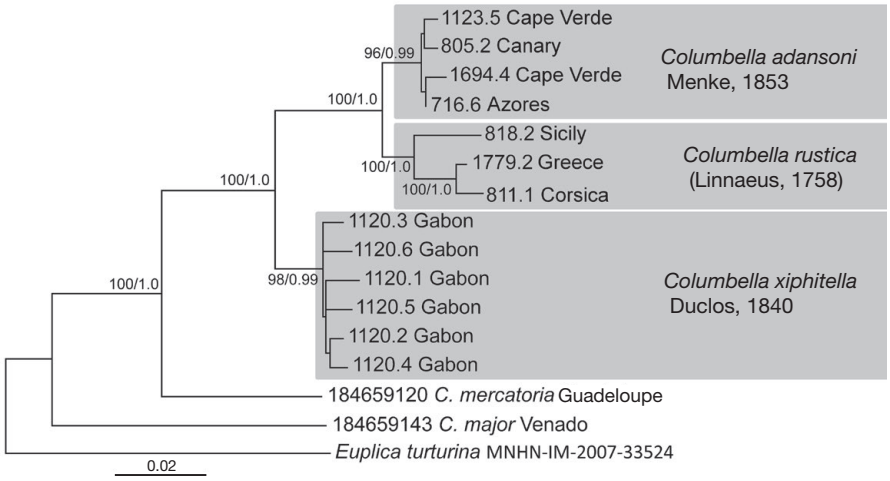

Fig. 5. — ML tree based on the combined COI-16S dataset (HKY+I+G model of evolution). Numbers at nodes indicate the support by BI Bps (10^7 generations and 25% burn in) and ML bs (1000 replicates).

All phylogenetic analyses (ML and BI) of the single gene (16S, COI: including shorter sequences) and of the combined datasets of the eastern Atlantic/Mediterranean *Columbella* retrieved the same topology, with the sequences corresponding to the species hypotheses of ABGD grouped as reciprocally monophyletic clades with high bootstrap values and posterior probabilities (ML bootstrap ≥ 96%, BI support ≥ 0.99: Figs 3-5). In all trees, *C. adansoni* was restricted to the Macaronesian specimens, *C. rustica* to the Mediterranean specimens, and the African specimens comprised a third lineage. The pair including *C. adansoni*/*C. rustica* (ML bootstrap ≥ 98%, BI support ≥ 0.99) was the sister to the African species, which according to the phylogenetic patterns from COI and 16S, included samples from Ghana, São Tomé, Gabon and Angola. Autapomorphic (diagnostic) nucleotides were scored for each species by comparing their COI sequences and are reported in Table 3.

SYSTEMATICS

Family COLUMBELLIDAE Swainson, 1840
Genus *Columbella* Lamarck, 1799

TYPE SPECIES. — *Voluta mercatoria* Linnaeus, 1758, by monotypy.

REMARK

The list of available names for eastern Atlantic *Columbella* is rather long. According to Tryon (1883) and updated with more recent works (e.g., Moolenbeek & Hoenselaar 1991; Bouchet & Gofas 2010; Monsecour & Gofas 2010a, b), we have scored 26 nominal taxa (some under the incorrect subsequent spelling *Colombella*) referable to the *Columbella rustica* complex. All nominal taxa with an explicit Macaronesian type locality can be ascribed to *C. adansoni*: *Columbella adansoni* Menke, 1853, *C. rufa* Menke, 1853, *C. rustica* var. *azorica* Drouët, 1858, *C. striata* var. *minor* Dautzenberg, 1900. All nominal taxa with an explicit type locality from Senegal to Mediterranean (where a single species is known) and/or with a paucispiral protoconch are easily ascribed to *Columbella rustica*. This is the case of *Voluta rustica* Linnaeus, 1758, *C. rustica* var. *elongata* Philippi, 1836, *C. spongiarum* Duclos, 1840, *C. striata* Duclos, 1840, *C. fustigata* Kiener, 1841, *C. striata* Duclos *in* Chenu, 1846, *C. simpronia* Duclos *in* Chenu, 1846, *C. rustica* var. *cuneatiformis* Pallary, 1900, *C. rustica* var. *lutea* Pallary, 1900, *C. rustica* var. *minor* Pallary, 1900, *C. rustica* var. *obesula* Pallary, 1900. The other synonymies currently implemented in WoRMS for this complex are almost all accepted (where necessary by correcting or imposing Mediterranean as type locality, see below) since they maintain stability of current usage, with two exceptions: *C. xiphitella* Duclos, 1840 and *C. nucleus* Kiener, 1841. Among ten potential syntypes of the latter at MHNG, eight have eroded apices, while two have protoconchs partly eroded but clearly multispiral; if we imposed a Macaronesia type locality, this would make *C. nucleus* a senior synonym of *C. adansoni* (which has been the accepted valid name for the Macaronesian species for the last 25 years: Moolenbeek & Hoenselaar, 1991). The same holds for *C. xiphitella* Duclos, 1840: two of the 16 syntypes at MNHN have clearly multispiral protoconchs, the locality indicated ("Californie") is clearly erroneous, and imposing a Macaronesian type locality would make *C. xiphitella* also a senior synonym of *C. adansoni*. Therefore, to preserve nomenclatural stability in this group, we have decided to impose as first reviewers, "Gabon" as type locality to both *C. xiphitella* Duclos, 1840 and *C. nucleus* Kiener, 1841.

Columbella rustica (Linnaeus, 1758)
(Figs 6A, B; 7A-D; 8C)

Voluta rustica Linnaeus, 1758: 731.

Columbella reticulata Lamarck, 1822: 295.

Columbella gualteriana Risso, 1826: 206, n°533.

Columbella rustica var. *elongata* Philippi, 1836: 228.

Colombella tumida Duclos, 1840: pl. 1, figs 13, 14.

Colombella spongiarum Duclos, 1840: pl. 3, figs 13-16.

Columbella striata Duclos, 1840: pl. 6, figs 5-8 (not Menke 1829).

Columbella ambigua Kiener, 1840: 11, pl. 2, fig. 3 [note: plate issued in 1840].

Columbella fustigata Kiener, 1841: 20-21, pl. 5, fig. 3.

Columbella modesta Kiener, 1841: 22, pl. 11, fig. 2.

Colombella aureola Duclos *in* Chenu, 1846: pl. 6, figs 17, 18.

Colombella simpronia Duclos *in* Chenu, 1846: pl. 15, figs 19, 20.

Colombella vestalia Duclos *in* Chenu, 1846: pl. 15, figs 15, 16.

Colombella zulmis Duclos *in* Chenu, 1848: pl. 24, figs 21, 22.

Columbella rustica var. *cuneatiformis* Pallary, 1900: 278, pl. 6, fig. 17.

Columbella rustica var. *lutea* Pallary, 1900: 278.

Columbella rustica var. *minor* Pallary, 1900: 277.

Columbella rustica var. *obesula* Pallary, 1900: 278, pl. 6, fig. 18.

TYPE MATERIAL. — *Voluta rustica*: 6 sh in the Linnaean Society (LSL.348 [Dance label image ref: P-Z 0010728] http://linnean-online.org/17388/). — Type locality: Mediterranean.
Columbella reticulata: 5 probable syntypes MHNG-MOLL-92487. — Type locality: Mediterranean (imposed herein, ICZN 1999: rec. 76A.1.4).
Columbella gualteriana: lectotype (Arnaud 1978) MNHN-IM-2000-6899. — Type locality: Mediterranean (imposed herein, ICZN 1999: rec. 76A.1.4).
Columbella rustica var. *elongata*: lectotype ZMB 13.994, 2 paralectotypes ZMB 112.717. — Type locality: Palermo (Sicily).
Colombella tumida: 2 syntypes MNHN-IM-2000-6373. — Type locality: "China", erroneous, corrected to Mediterranean (ICZN 1999: rec. 76.A.2).
Colombella spongiarum: 2 syntypes, MNHN-IM-2000-6385. — Type locality: Senegal.
Columbella striata: syntypes, 15 sh without locality label

MNHN-IM-2000-6381, and 5 sh from Senegal MNHN-IM-2000-6382. — Type locality: Senegal.
Columbella ambigua: 6 syntypes MNHN-IM-2000-6935. — Type locality: "Asia", erroneous, corrected to Mediterranean (ICZN 1999: rec. 76.A.2).
Columbella fustigata: 7 syntypes MNHN-IM-2000-6904. — Type locality: "Iles Saintes" (Îles des Saintes, Antilles), erroneous, corrected to Mediterranean (ICZN 1999: rec. 76.A.2).
Columbella modesta: MHNG-MOLL-95504 (5 probably not types from Delessert coll. and not "Mus coll" as in description). — Type locality: Mediterranean (imposed herein, ICZN 1999: rec. 76A.1.4).
Colombella aureola: 1 shell MNHN-IM-2000-6346). — Type locality: "Californie", erroneous, corrected to Mediterranean (ICZN 1999: rec. 76.A.2).
Colombella simpronia: 4 syntypes MNHN-IM-2000-6389. — Type locality: Mediterranean.
Colombella vestalia: Not found, not present in MNHN. — Type locality: Mediterranean (imposed herein, ICZN 1999: rec. 76A.1.4).
Colombella zulmis: MNHN-IM-2000-9609. — Type locality: "China", erroneous, corrected to Mediterranean (ICZN 1999: rec. 76.A.2).
Columbella rustica var. *cuneatiformis*: not found at MNHN. — Type locality: Oran, Algeria.
Columbella rustica var. *lutea*: not found at MNHN. — Type locality: Oran, Algeria.
Columbella rustica var. *minor*: not found at MNHN. — Type locality: Oran, Algeria.
Columbella rustica var. *obesula*: not found at MNHN. — Type locality: Oran, Algeria.

DISTRIBUTION. — According to the present data, *Columbella rustica* ranges throughout the entire Mediterranean Sea, and extends in the Atlantic South to Senegal, and North to Portugal.

DIAGNOSIS. — Shell of medium size for the family 12-20 mm long, biconic/strombiform.
Protoconch of 1.5-1.6 smooth, convex whorls; protoconch-teleoconch boundary marked by a slightly opisthocline scar.
Teleoconch of 7-9 almost straight-sided whorls, penultimate whorl slightly convex, body whorl rounded and inflated, about ⅔ to ¾ shell length.
Sculpture of nodulose axial ridges on the first whorls, fading after 2-3 whorls, and very weak, irregular spiral striae. Aperture narrow, elongate and sinuous.
Outer lip angulate posteriorly in some, thickened, especially medially, with 13-16 denticles, and rust coloured markings between denticles. Columellar wall with two weak ridges medially; parietal wall with 5-7 denticles anteriorly, sometimes with rust coloured markings between. Siphonal canal open.
Colour very variable, with white-whitish background and yellow, orange, brown, grey or black irregular spots, sometimes arranged into axial flames or sinuous bands.
Periostracum thin, brown.
Animal with whitish to yellowish background and tawny-orange spots, very dense on propodium, head and mantle; tip of cephalic tentacles white; siphon grey. Radula rachiglossate, with central tooth reduced to a slightly arched plate with no cusps. One pair of massive lateral teeth with a small, basal, outer cusp and a tall, sinuous inner primary cusp with three secondary cusps along the posterior edge: a narrow, pointed distal cusp, a flat central cusp slightly enlarged at the base, and a quadrangular and apically curved basal cusp.

REMARKS

We correct herein (ICZN 1999: rec. 76.A.2) to "Mediterranean" the evidently erroneous localities indicated for *Colombella tumida*, *Columbella ambigua*, *Columbella fustigata*, *Colombella aurola*, *Colombella zulmis*; and impose (ICZN 1999: rec. 76A.1.4) "Mediterranean" for *Colombella vestalia*, *Columbella modesta*, *Columbella reticulata*, *Columbella gualteriana*. The five possible syntypes of *Columbella reticulata* Lamarck (MHNG-MOLL-92487, ex Delessert collection) bear "Bresil" as locality, quite probably a posthumous erroneous labelling.

Very variable in coloration, but also in size, with some populations of very small adult size (12 mm) and others attaining much larger length (20 mm).

Franc (1943) described the egg capsules and embryos of *C. rustica*: the capsules contained 39-57 eggs, 250-280 µm in diameter, of which most were nurse eggs to nourish the 1-2 developing embryos (shell length at hatching 660-850 µm). See also Bandel (1975) for a description of the protoconch in specimens from Banyuls. Pelorce & Boyer (2005: fig. 11) described samples from Central Senegal as 10-14 mm long, with paucispiral protoconch of 1.5-2 whorls, the animal milky white or cream with amber-brown speckles, which matches remarkably the appearance of Mediterranean samples.

As already noticed by Moolenbeek & Hoenselaar (1991), *Columbella striata* Duclos (originally described from Senegal) is a junior homonym of *Columbella striata* Menke, 1829 and therefore is not usable as the valid name for any species. In Senegal two distinct protoconch types have been sometimes cited and interpreted as multispiral and paucispiral, respectively (Thorsson 2003). However, based on Oliverio (1995), Rolán & Ryall (1999), Hernández & Boyer (2005) and Pelorce & Boyer (2005), all intact protoconchs of *Columbella* from Morocco to Mauritania, including Senegal, are paucispiral. Unfortunately, material from Senegal or Mauritania properly fixed for DNA extraction was not available for this study and the actual identity of the *Columbella* from this area could not be unequivocally assessed herein.

Three autapomorphic positions were scored in the COI sequences: 238 [C], 310 [T], 447 [G].

Columbella adansoni Menke, 1853
(Figs 6C, D; 7G-H; 8A)

Columbella Adansoni [sic] Menke, 1853: 74, 75.

Columbella rufa Menke, 1853: 75.

Columbella rustica var. *azorica* Drouët, 1858: 169.

Columbella striata var. *minor* Dautzenberg, 1900: 183.

TYPE MATERIAL. — *Columbella adansoni*: lectotype (Moolenbeek & Hoenselaar 1991) SMF. — Type locality: Cape Verde Islands.
Columbella rufa: lectotype (Moolenbeek & Hoenselaar, 1991) SMF. — Type locality: Cape Verde Islands.
Columbella rustica var. *azorica*: unknown (Moolenbeek & Hoenselaar, 1991). — Type locality: Azores.
Columbella striata var. *minor*. — Type locality: Ilhéu Branco (Cape Verde Islands).

DISTRIBUTION. — According to the data presented herein, *Columbella adansoni* ranges throughout Macaronesia, and is not present in continental African waters.

DIAGNOSIS. — Shell of medium size for the family, 16-25 mm long, biconic/strombiform.

FIG. 6. — *Columbella* spp. types: **A**, **B**, *Columbella rustica* (Linnaeus, 1758), syntype of *Voluta rustica* (LSL.348), Mediterranean (permission of The Linnean Society of London); **C**, **D**, *Columbela adansoni* Menke, 1853, lectotype SMF, Cape Verde (after Moolenbeek & Hoenselaar 1991, figs 1, 2); **E**-**G**, *Columbella xiphitella* Duclos, 1840, lectotype (**F**, **G**) and paralectotypes (**E**) from lot MNHN-IM-2000-9599, Gabon; **H**-**L**, *Columbella xiphitella*, lectotype (**H**, **J**, **K**) and paralectotypes (**I**, **L**) of *C. nucleus* Kiener, 1841 from lot MHNG-MOLL-95502. Symbols: ⋆, the selected lectotypes; ○, the paralectotype with close-up of the protoconch (**L**). Scale bars: 10 mm; G, H, L, not to scale.

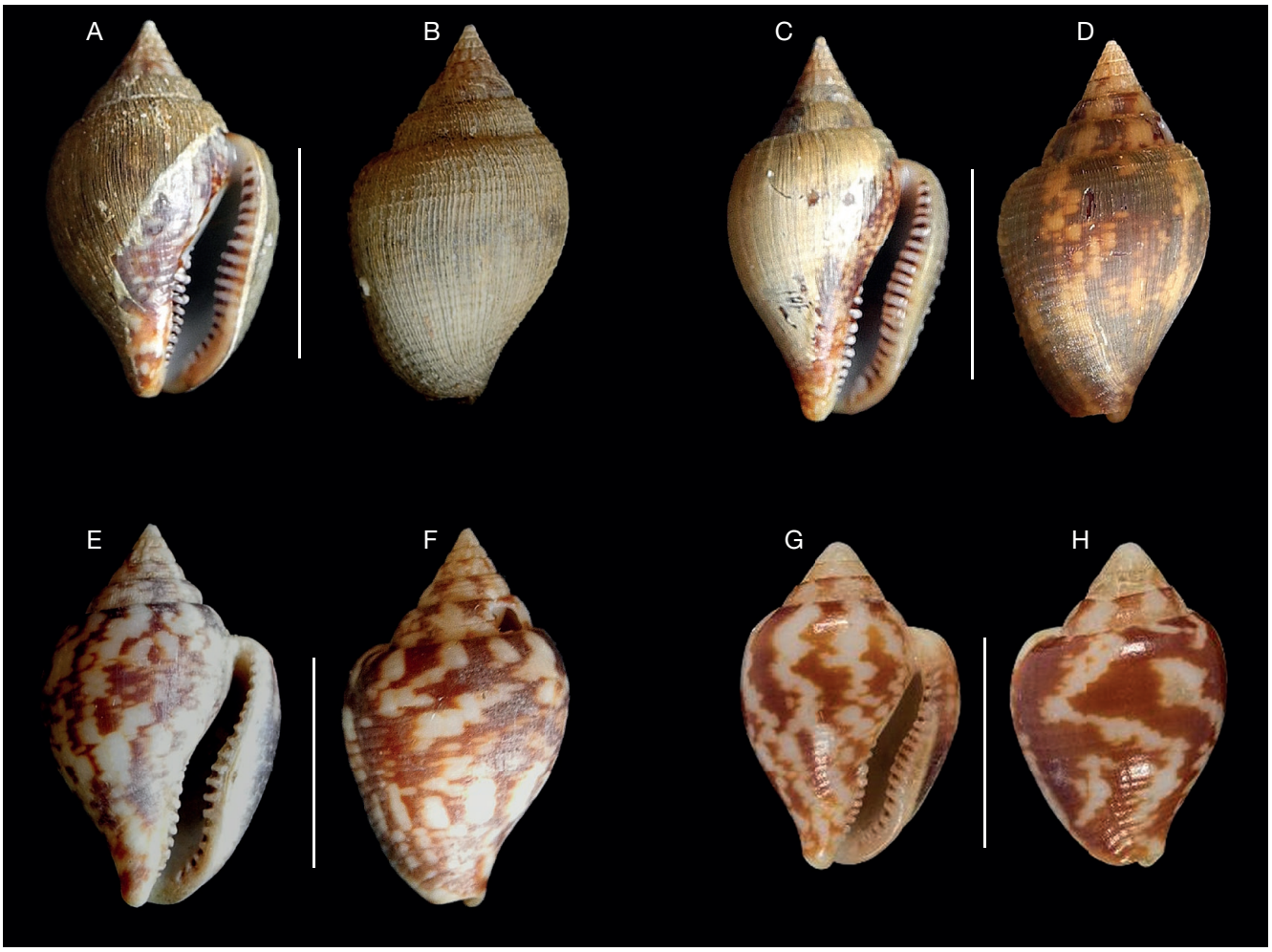

Fig. 7. — *Columbella xiphitella* Duclos, 1840 Gabon: **A**, **B**, MNHN IM-2000-32498; **C**, **D**, MNHN IM-2000-32498; **E**, **F**, BAU 1120.7; **G**, **H**, paralectotype from lot MNHN-IM-2000-9599. Scale bars: 10 mm.

Protoconch of 2.5-2.6 convex whorls, entirely covered by densely spaced microgranules; embryonic shell (protoconch I) of 0.8-0.9 whorls, and larval shell (protoconch II) of 1.6-1.7 whorls; protoconch-teleoconch boundary marked by a sinusigera scar.
Teleoconch of 7-9 almost straight-sided whorls, penultimate whorl slightly convex, body whorl rounded and inflated, about ⅔ to ¾ shell length.
Sculpture of nodulose axial ridges on the first whorls, fading after 2-3 whorls, and very weak, irregular spiral striae. Aperture narrow, elongate and sinuous.
Outer lip angulate posteriorly in some, thickened, especially medially, with 13-16 denticles, and rust coloured markings between denticles. Columellar wall with two weak ridges medially; parietal wall with 5-7 denticles anteriorly, and rust coloured markings between. Siphonal canal open.
Colour very variable, with white-whitish background and yellow, orange, brown, grey or black irregular spots, sometimes arranged into axial flames or sinuous bands. Periostracum thin, brown.
Animal yellowish with tawny-orange spots, very dense on propodium, head and mantle; tip of cephalic tentacles white, siphon grey. Radula rachiglossate, with central tooth reduced to a slightly arched plate with no cusps. One pair of massive lateral teeth with a small, basal, outer cusp and a tall, sinuous inner primary cusp with three secondary cusps along the posterior edge: a narrow, pointed distal cusp, a flat central cusp slightly enlarged at the base, and a quadrangular and apically curved basal cusp.

Remarks

Knudsen (1995) summarized his own (Knudsen 1950) and Gunnar Thorson's (unpublished) notes on the egg capsules of *C. adansoni* from Cape Verde Islands and Canary Islands, respectively. The egg capsules contained 39-73 eggs, *c.* 200 µm in diameter, developing into pelagic larvae attaining at metamorphosis 450 µm shell width (1000 µm length).

Seven autapomorphic positions were scored in the COI sequences: 61 [G], 91 [G], 160 [C], 181 [T], 352 [C], 549 [A], 586 [T].

Columbella xiphitella Duclos, 1840
(Figs 6E-L; 7A-H; 8B; 9A, B)

Colombella xiphitella Duclos, 1840: pl. 9, figs 13, 14.

Columbella nucleus Kiener, 1841: 14-15, pl. 3, fig. 4.

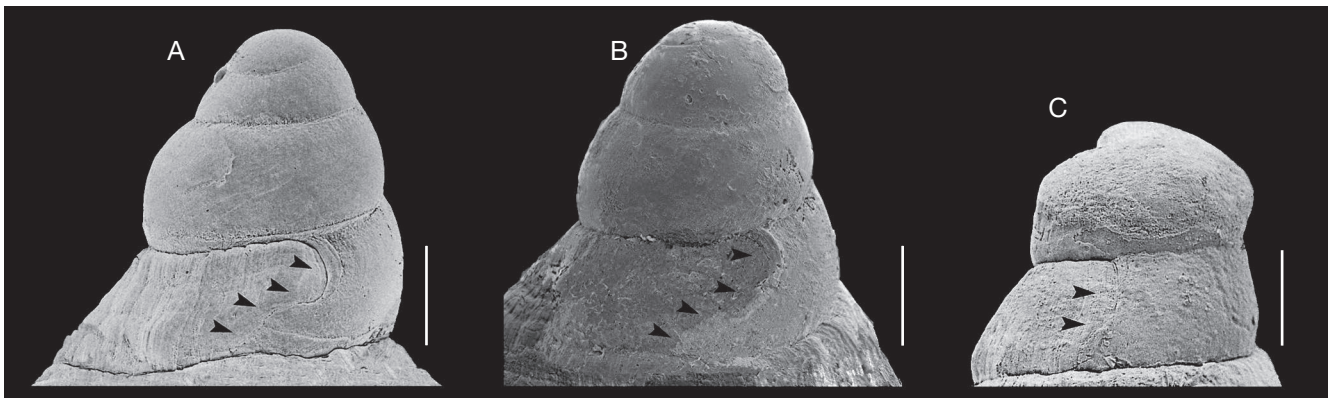

FIG. 8. — Protoconchs of *Columbella* spp.: **A**, *Columbella adansoni* Menke, 1853, Tenerife Is., Canary Islands; **B**, *Columbella xiphitella* Duclos, 1840, Miemia, Ghana; **C**, *Columbella rustica* (Linnaeus, 1758), San Domino Is., Italy. Arrows indicate the protoconch-teleoconch boundary. Scale bars: 100 µm.

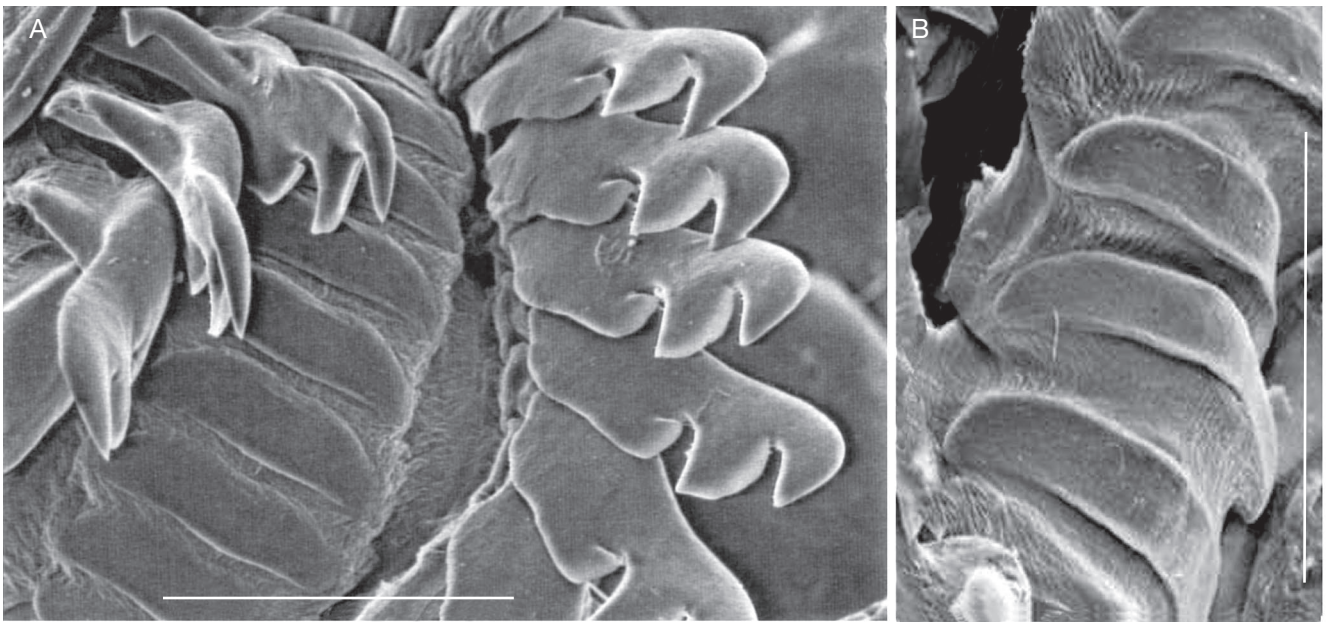

FIG. 9. — Radula of *Columbella xiphitella* Duclos, 1840: **A**, Miemia, Ghana; **B**, Lagoa Azul, São Tomé, detail of the rachidian. Scale bars: 100 µm.

TYPE MATERIAL. — *Colombella xiphitella*: lectotype (here designated: Fig. 6F, G) and 11 paralectotypes MNHN-IM-2000-9599, 4 paralectotypes MNHN-IM-2000-9598. — Type locality: "Californie", erroneous, corrected to Gabon (ICZN 1999: rec. 76.A.2).
Columbella nucleus: MHNG-MOLL-95502 lectotype (here selected: Fig. 6H, J, K) and 9 paralectoypes (from Delessert collection). — Type locality: Gabon (imposed herein, ICZN 1999: rec. 76A.1.4).

DISTRIBUTION. — According to the material examined genetically herein, *Columbella xiphitella* ranges along West African coasts from Ghana to Angola, including *São Tomé and Principe*.

DIAGNOSIS. — Shell of medium size for the family, 10-18 mm long, biconic/strombiform.
Protoconch of 2.5-2.6 convex whorls, entirely covered by densely spaced microgranules; embryonic shell (protoconch I) of 0.8 whorls, and larval shell (protoconch II) of 1.7 whorls; protoconch-teleoconch boundary marked by a sinusigera scar.
Teleoconch of 7-9 almost straight-sided whorls, penultimate whorl slightly convex, body whorl rounded and inflated, about ¾ shell length. Sculpture of nodulose axial ridges on the first whorls, fading after 2-3 whorls, and very weak, irregular spiral striae. Aperture narrow, elongate and sinuous.
Outer lip angulate posteriorly in some, thickened, especially medially, with 14-19 strong denticles, and rust coloured markings between denticles. Columellar wall with two weak ridges medially; parietal wall with 5-8 strong denticles anteriorly, usually with rust coloured markings between. Siphonal canal open.
Colour very variable, with white-whitish background and yellow, orange, brown, grey or black irregular spots, sometimes arranged into axial flames or sinuous bands. Periostracum thin, brown.
Animal observed only in alcohol preserved specimens: whitish background and dark brown to dark tawny spots, dense on propodium and head, very dense on mantle; tip of cephalic tentacles white, siphon dark grey. Radula rachiglossate, with central tooth reduced to a slightly arched plate with no cusps. One pair of massive lateral teeth with a small, basal, outer cusp and a tall, sinuous inner primary

TABLE 4. — COI sequences of worldwide columbellids, with the ABGD group assignation (alternate grey/white lines, according to ABGD groups numbers), voucher ID (or GenBank accession number), a-priori morphological identification, a-posteriori MOTU assignation.

ABGD group	Voucher ID	a priori morphological identification	a posteriori MOTU assignation
1	IM-2007-33580	*Aesopus cumingii* (Duclos, 1846)	*A. cumingii*
1	IM-2007-33581	*Aesopus cumingii*	*A. cumingii*
2	KF643896.1	*Amphissa columbiana* (Dall, 1916)	*A.* aff. *columbiana*
2	KF644010.1	*Amphissa columbiana*	*A.* aff. *columbiana*
2	KF644101.1	*Amphissa columbiana*	*A.* aff. *columbiana*
2	KF643694.1	*Amphissa versicolor* (Dall, 1871)	*A.* aff. *columbiana*
3	KF644285.1	*Amphissa reticulata* (Dall, 1916)	*A. reticulata*
4	KF643489.1	*Alia carinata* (Hinds, 1844)	*A. carinata*
4	KF643493.1	*Alia carinata*	*A. carinata*
4	KF643566.1	*Alia carinata*	*A. carinata*
4	KF643846.1	*Alia carinata*	*A. carinata*
4	KF643937.1	*Alia carinata*	*A. carinata*
4	KF644175.1	*Alia carinata*	*A. carinata*
4	KF644247.1	*Alia carinata*	*A. carinata*
4	KF644276.1	*Alia carinata*	*A. carinata*
4	KF643354.1	*Alia carinata*	*A. carinata*
5	IM-2009-11313	*Anachis* sp.	*Anachis* sp.
6	BAU 710_7	*Columbella adansoni* Menke, 1853	*C. adansoni*
6	BAU 726_7	*Columbella adansoni*	*C. adansoni*
6	BAU 741_11	*Columbella adansoni*	*C. adansoni*
7	BAU 1120_1	*Columbella adansoni*	*C. xiphitella*
7	BAU 1120_2	*Columbella adansoni*	*C. xiphitella*
7	BAU1120_3	*Columbella adansoni*	*C. xiphitella*
8	BAU 817_1	*Columbella rustica* (Linnaeus, 1758)	*C. rustica*
8	BAU 818_5	*Columbella rustica*	*C. rustica*
8	BAU 821_2	*Columbella rustica*	*C. rustica*
9	IM-2009-18927	columbellid indet.	columbellid indet.
9	IM-2007-35775	columbellid indet.	columbellid indet.
10	IM-2007-35599	columbellid indet.	columbellid indet.
11	IM-2007-33570	columbellid indet.	columbellid indet.
12	IM-2007-33521	*Euplica borealis* (Pilsbry, 1904)	*E . borealis*
13	IM-2007-33515	*Euplica scripta* (Lamarck, 1822)	*E. scripta*
14	JN052985.1	*Euplica scripta*	*E. scripta*
15	JN052986.1	*Euplica scripta*	*E. scripta*
15	JN052987.1	*Euplica scripta*	*E. scripta*
15	HQ834054.1	*Euplica scripta*	*E. scripta*
16	IM-2007-33519	*Euplica turturina* (Lamarck, 1822)	*E. turturina*
16	IM-2007-33522	*Euplica turturina*	*E. turturina*
16	IM-2007-33524	*Euplica turturina*	*E. turturina*
16	IM-2007-33539	*Euplica turturina*	*E. turturina*
16	JQ950207.1	*Euplica turturina*	*E. turturina*
17	IM-2007-33537	*Euplica varians* (Sowerby, 1832)	*E. varians*
17	IM-2007-33583	*Euplica varians*	*E. varians*
18	IM-2007-33493	*Graphicomassa albina* (Kiener, 1841)	*G. adiostina* (Duclos, 1840)
18	IM-2007-33494	*Graphicomassa albina*	*G. adiostina*
19	IM-2007-33514	*Graphicomassa ligula* (Duclos, 1835)	*G. ligula*
19	IM-2007-33517	*Graphicomassa ligula*	*G. ligula*
19	IM-2007-33523	*Graphicomassa ligula*	*G. ligula*
19	IM-2007-33534	*Graphicomassa ligula*	*G. ligula*
19	IM-2007-33542	*Graphicomassa ligula*	*G. ligula*
19	JQ950206.1	*Graphicomassa ligula* as *Mitrella ligula* (Duclos, 1840)	*G. ligula*
20	IM-2007-35779	*Indomitrella* cf. *conspersa* (Gaskoin, 1851)	*I.* cf. *conspersa*
21	IM-2007-33532	*Indomitrella puella* (Sowerby, 1844)	*I. puella*
22	IM-2007-33548	*Indomitrella schepmani* K. Monsecour & D. Monsecour, 2007	*I. schepmani*
22	IM-2007-35594	*Indomitrella schepmani*	*I. schepmani*
23	HM180683.1	*Mitrella bicincta* (Gould, 1860)	*M.* aff. *bicincta*
23	HM180684.1	*Mitrella bicincta*	*M.* aff. *bicincta*
23	HM180685.1	*Mitrella bicincta*	*M.* aff. *bicincta*
23	HM180687.1	*Mitrella bicincta*	*M.* aff. *bicincta*
23	HM180688.1	*Mitrella bicincta*	*M.* aff. *bicincta*
23	HM180690.1	*Mitrella bicincta*	*M.* aff. *bicincta*
23	HM180691.1	*Mitrella bicincta*	*M.* aff. *bicincta*
23	HM180692.1	*Mitrella bicincta*	*M.* aff. *bicincta*
23	JN053028.1	*Mitrella burchardi* (Dunker, 1877)	*M.* aff. *bicincta*
23	HQ834098.1	*Mitrella burchardi*	*M.* aff. *bicincta*
24	JN052988.1	*Mitrella bicincta* (Gould, 1860)	*M. bicincta*
24	JN052989.1	*Mitrella bicincta*	*M. bicincta*
24	JN052990.1	*Mitrella bicincta*	*M. bicincta*
24	JN052991.1	*Mitrella bicincta*	*M. bicincta*

Table 4. — Continuation.

ABGD group	Voucher ID	a priori morphological identification	a posteriori MOTU assignation
24	HQ834055.1	*Mitrella bicincta* (Gould, 1860)	*M. bicincta*
24	HM180686.1	*Mitrella bicincta*	*M. bicincta*
24	HM180689.1	*Mitrella bicincta*	*M. bicincta*
25	IM-2007-30282	*Mitrella* cf. *philia* (Duclos, 1846)	*M.* cf. *philia*
26	IM-2007-35498	*Mitrella essingtonensis* (Reeve, 1859)	*M. essingtonensis*
27	IM-2007-33485	*Metanachis jaspidea* (Sowerby, 1844)	*M. jaspidea*
27	IM-2007-33529	*Metanachis jaspidea*	*M. jaspidea*
27	IM-2007-33585	*Metanachis jaspidea*	*M. jaspidea*
28	IM-2007-33490	*Mitrella moleculina* (Duclos, 1835)	*M. moleculina*
29	IM-2007-33504	*Mitrella nympha* (Kiener, 1841)	*M. nympha*
29	IM-2007-33565	*Mitrella nympha*	*M. nympha*
30	IM-2007-35750	columbellid indet.	*Mitrella* sp.
30	IM-2007-35749	*Mitrella* cf. *moleculina* (Duclos, 1840)	*Mitrella* sp.
30	IM-2007-35495	*Mitrella* sp.	*Mitrella* sp.
31	KF643804.1	*Mitrella* cf. *tuberosa* (Carpenter, 1865)	*Mitrella* sp.
32	IM-2007-33582	*Mitrella* sp.	*Mitrella* sp.
33	IM-2007-35626	*Mitrella* sp.	*Mitrella* sp.
34	IM-2013-20589	*Nassarina metabrunnea* (Dall & Simpson, 1901)	*N. metabrunnea*
35	IM-2007-36625	*Pyrene flava* (Bruguière, 1789)	*P. flava*
35	IM-2007-36760	*Pyrene flava*	*P. flava*
35	IM-2007-36685	*Pyrene flava*	*P. flava*
36	IM-2007-33560	*Pyrene punctata* (Bruguiere, 1789)	*P. punctata*
36	IM-2007-33578	*Pyrene punctata*	*P. punctata*
37	HQ834097.1	*Pseudamycla* sp.	*Pseudamycla* sp.
38	IM-2007-39377	columbellid indet.	*S.* cf. *kanamaruana* A
38	IM-2007-32142	*Sulcomitrella* cf. *kanamaruana* (Kuroda, 1953)	*S.* cf. *kanamaruana* A
38	IM-2007-33555	*Sulcomitrella* sp.	*S.* cf. *kanamaruana* A
39	IM-2009-11298	*Sulcomitrella* cf. *kanamaruana* (Kuroda, 1953)	*S.* cf. *kanamaruana* B
39	IM-2009-11301	*Sulcomitrella* cf. *kanamaruana*	*S.* cf. *kanamaruana* B
39	IM-2007-32150	*Sulcomitrella* cf. *kanamaruana*	*S.* cf. *kanamaruana* B
39	IM-2007-33479	*Sulcomitrella* cf. *kanamaruana*	*S.* cf. *kanamaruana* B
39	IM-2007-33482	*Sulcomitrella* cf. *kanamaruana*	*S.* cf. *kanamaruana* B
39	IM-2007-33574	*Sulcomitrella* cf. *kanamaruana*	*S.* cf. *kanamaruana* B
39	IM-2007-33575	*Sulcomitrella* cf. *kanamaruana*	*S.* cf. *kanamaruana* B
39	IM-2007-33540	*Sulcomitrella circumstriata* (Schepman, 1911)	*S.* cf. *kanamaruana* B
39	IM-2007-36339	*Sulcomitrella circumstriata*	*S.* cf. *kanamaruana* B
40	IM-2007-35773	*Sulcomitrella* cf.. *monodonta* (Habe, 1958)	*S.* cf.. *monodonta* A
41	IM-2009-11304	*Sulcomitrella monodonta* (Habe, 1958)	*S.* cf.. *monodonta* B
42	IM-2007-33551	*Sulcomitrella circumstriata* (Schepman, 1911)	*S. circumstriata*
42	IM-2007-33552	*Sulcomitrella circumstriata*	*S. circumstriata*
43	IM-2007-30246	*Zafra* cf. *pumila* (Dunker, 1858)	*Z.* cf. *pumila*
44	IM-2007-33480	*Zafrona isomella* (Duclos, 1840)	*Z. isomella*
45	IM-2007-30355	*Zafra pumila* (Dunker, 1858)	*Z. pumila*
46	IM-2007-33535	*Metanachis laingensis* Sleurs, 1985	*Mitrella* sp.
46	IM-2007-33536	*Mitrella* cf. *alizonae* (Melvill & Standen, 1901)	*Mitrella* sp.
46	IM-2007-33488	*Mitrella chinoi* Monsecour & Dekkers, 2013	*Mitrella* sp.

cusp with three secondary cusps along the posterior edge: a narrow, pointed distal cusp, a flat central cusp slightly enlarged at the base, and a quadrangular and apically curved basal cusp.

Remarks

Dunker (1853: 24) used *Columbella striata* Duclos for his specimens from Luanda and Annobon, quite certainly referring to this species. However, *Columbella striata* Duclos (described from Senegal and here provisionally included in the synonymy of *C. rustica*) is preoccupied by *Columbella striata* Menke 1829, a nomen dubium without type(s) availables. The 10 syntypes of *Columbella nucleus* Kiener at MHNG are to be considered as syntypes as they originate from the Delessert collection, as reported for this species in the original description.

C. xiphitella differs from *Columbella rustica* by its multispiral protoconch (v. paucispiral in *C. rustica*). Morphological (including colour pattern) variation in the teleoconch of the three eastern Atlantic species (*C. rustica*, *C. adansoni* and *C. xiphitella*) largely overlaps with no evident diagnostic characters. All shells of *C. xiphitella* examined (including the type series) have strong dentition on columellar and outer lips, and very dark marks between the denticles, features only occasionally present in the other two species. However, the three species are unequivocally separated by molecular data from COI and 16S. Eighteen autapomorphic positions were scored in the COI sequences: 34 [T], 55 [T], 78 [G], 100 [T], 115 [T], 117 [A], 130 [A], 133 [C/G], 178 [C], 309 [C], 346 [C], 385 [T], 430 [C], 463 [T], 472 [G], 565 [T], 598 [T], 619 [T].

DISCUSSION

The combined use of molecular data with morphological, geographical and ecological attributes is revealing a growing number of cases of hidden biodiversity in gastropods, often with virtually no morphological distinction in shell characters, among genetically well-separated species (e.g., Modica *et al.* 2013). In the present case, the three species of *Columbella* detected in the eastern Atlantic and the Mediterranean are virtually indistinguishable by their teleoconch features, whereas they are neatly separated by genetic data.

Two species were previously accepted after Moolenbeek & Hoenselaar (1991), Oliverio (1995) and Rolán & Ryall (1999): *Columbella rustica* Linnaeus, 1758, ranging through the entire Mediterranean Sea, and extending into the neighbouring Atlantic South to Senegal and Mauritania, and North to Portugal (it is absent in Galicia); and *Columbella adansoni* Menke, 1853, described from Cape Verde islands, and assumed to occur across Macaronesia, from the Azores to the Canary Islands, and along the West African coast from Mauritania to Angola (Oliverio 1995).

Based on the present data, *Columbella adansoni* is restricted with certainty only to populations from Macaronesia. West African populations from Mauritania and Senegal North to Morocco (with paucispiral protoconch) are conservatively included in *Columbella rustica* pending genetic analysis; those from Ghana South to Angola belong to *Columbella xiphitella* (type locality corrected herein), while those from Mauritania to Ghana should also be assayed genetically, since *C. adansoni* and *C. xiphitella* (albeit clearly defined genetically) are indistinguishable morphologically.

As already highlighted by Moolenbeek & Hoenselaar (1991) and Oliverio (1995), *Columbella adansoni* has a multispiral protoconch indicating planktotrophic larval development, whereas *Columbella rustica* has a paucispiral protoconch, indicating non-planktotrophic development. *Columbella xiphitella*, which is phylogenetically the sister to the other two species, has a multispiral protoconch (similar to *Columbella adansoni*), thus suggesting that the plesiomorphic state in this group was a planktotrophic larva, as is typical of most (if not all) caenogastropod lineages. This is also paralleled by *Columbella moinensis* deMaintenon, 2000, from the Pliocene to Pleistocene(?) of Costa Rica and Colombia, with planktotrophic development (and multispiral protoconch); this is a clear sibling of *Columbella mercatoria* (Pliocene to Recent, Caribbean) with lecithotrophic development (and a paucispiral protoconch) (deMaintenon 2000). Within columbellids, sibling species differing mainly or only in their larval development (and thus in their protoconch morphology) are known also in the genera *Zafrona* Iredale, 1916, *Mitrella* and *Euplica*.

The study of large geographic samples in the species involved herein may yield crucial data to analyse the genetic structure and dynamics of populations from closely related species with contrasting larval ecology. These may in turn prove important to define larval ecology drivers in speciation events related to the loss of planktotrophy (Oliverio 1996b), which has produced pairs of sibling species in many lineages of caenogastropods (e.g., Oliverio 1996a, 1997; Duda & Palumbi 1999).

Acknowledgements
Emilio Rolán (Vigo) provided samples from West Africa. Laurent Charles (Muséum Sciences et Nature, Bordeaux), Andrea Deneau (The Linnean Society, London), Virginie Héros (MNHN, Paris), Alan J. Kohn (University of Washington, Seattle), Gary Rosenberg (ANSP, Philadelphia), Emmanuel Tardy (MHNG, Genève), are thanked for bibliographic help and precious information on and pictures of type material. Nicolas Puillandre (MNHN) gave us access to unpublished sequences obtained from MNHN expedition material. Serge Gofas (University of Malaga) and Kevin Monsecour (Aarschot) provided very useful criticisms.

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Submitted on 21st June 2016;
accepted on 24 January 2017;
published on 30 June 2017.