Diversity and systematics of philinid snails (Gastropoda: Cephalaspidea) in West Africa with remarks on the biogeography of the region

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West Africa is often considered one of the least studied regions of the world concerning marine biodiversity. Knowledge about the philinid snails of the region has largely been based on shells, but shells can be insufficient to discriminate between species. In this paper, we review the diversity and revise the systematics of the West African species of Philinidae *sensu lato* based on a comprehensive literature review and the study of shells, anatomy and DNA sequence data of novel specimens obtained by the R/V *Dr Fridtjof Nansen* (2005–2012) between Morocco and Angola. We use scanning electron microscopy together with a cytochrome *c* oxidase subunit I molecular phylogeny and molecular species delimitation methods (ABGD and SDP Geneious Plug In) to define species. Twenty species (19 formally named) were found to occur in the region, including four new species we describe here: ***Laona nanseni* sp. nov., *Philine cerebralis* sp. nov., *Philine schrammi* sp. nov.** and ***Spiniphiline caboverdensis* sp. nov.** We identified a complex of four cryptic species under the name *P. quadripartita* (*P. guineensis*, *P. quadripartita*, ***Philine schrammi* sp. nov.,** *Philine* sp.). A biogeographical break is observed around Cape Verde and the Sahelian upwelling system coinciding with the West African Transition Province; eight species have their northern geographical limit or are restricted to this Province, while ten species have their southern limit here or just further north. Only one species seems to span across this biogeographical breaking point (*P. scabra*), but we speculate that this might result from taxonomic misidentifications.

INTRODUCTION

Western Africa is regarded as one of the regions of the world where knowledge about marine biodiversity is low (Gray, 2001; Costello *et al.*, 2010). Yet the literature on molluscs and in particular on the gastropods of the region is not only prolific but also old, including works like the classic *Histoire naturelle du Sénégal, coquillages* by Adamson (1757). Several major 19th century scientific expeditions sampled along the western coast of Africa, providing some of the first insights into the diversity of molluscs of the region, particularly from greater depths. These expeditions include the *Challenger* (Watson, 1886) and the *Travailleur* and *Talisman* (Locard, 1897). Particularly since the early 20th century, the study of western African molluscs has received considerable attention, chiefly those inhabiting costal and shallow habitats (for lists of references see Hemmen & Groh, 1989; Rolán & Ryall, 1999; Ardovini & Cossignani, 2004). Of note, because of their breadth, descriptions or illustrations, are the works by Nicklès (1950), Marcus & Marcus (1966) and Ardovini & Cossignani (2004), and despite their limited geographical focus the works by

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Bernard (1984, Gabon), Rolán (2005, Cape Verde Islands) and Hernàndez *et al.* (2011, Canary Island).

Philinids are a group of marine infaunal Cephalaspidea gastropods with a dorso-ventrally flattened body. They occur worldwide across all latitudes and inhabit soft substrates of mud and sand from shallow waters to the deep sea (e.g. > 2500 m; Høisæter, 2010; Ohnheiser & Malaquias, 2013). These snails are characterized by the presence of a smooth or sculptured shell with a rounded-squarish 'plate-like' shape, which is often internal and varies between 1 and 40 mm in length (Burn & Thompson, 1998; Ohnheiser & Malaquias, 2013; Oskars, Bouchet & Malaquias, 2015). The body colour of philinids is often whitish, but some species, particularly from tropical waters, exhibit colourful patterns (Burn & Thompson, 1998; Gosliner, Valdés & Behrens, 2015).

All philinid snails were traditionally included in the family Philinidae (Burn & Thompson, 1998; Malaquias *et al.*, 2009), but Oskars *et al.* (2015) recently produced sound evidence for the polyphyly of the family, and proposed a new classification where the traditional Philinidae [herein referred as Philinidae *sensu lato* (*s.l.*) or philinid snails) is divided into four distinct linages of familial status supported not only by molecular phylogenetic data but also by morphological traits.

A total of 15 species (including one described as a subspecies) of Philinidae *s.l.* have been referred previously to this work from West Africa, between Morocco and South Africa including the Canary Islands, Cape Verde Islands and the islands São Tomé and Principe (Table 1). Four of these species have their type localities in African waters: *Philine alternans* van der Linden, 1995, *P. aperta guineensis* Marcus & Marcus, 1966, *P. araneosa* van der Linden, 1995 and *P. gelida* van der Linden, 1995.

However, it is remarkable that only two species have been identified for West Africa based on characters other than those of shells [*P. aperta guineensis* (external morphology, coloration, digestive and reproductive structures) and *P. scabra* O. F. Müller, 1776 (radula, gizzard plates)]. Ohnheiser & Malaquias (2013) have shown that the use of shells alone can be problematic to separate species of philinids and it is known that different species can have similar body plans and colours. This was demonstrated by Price, Gosliner & Valdés (2011) for the *Philine aperta* species-complex and by Ohnheiser & Malaquias (2013) for the *P. scabra-indistincta* complex. Additionally, it is not uncommon that African specimens similar to those occurring in European waters are simply treated as conspecific [e.g. *P. quadripartita* (= *Philine aperta*); Watson, 1910; van der Linden, 1995; Rolán & Ryall, 1999; Rolán, 2005; Hernàndez *et al.*, 2011].

The wide geographical distribution of some philinid species (such as *P. quadripartita* and *P. scabra* collected from both Norway and Angola) conflicts with the assumption of latitudinal biogeographical boundaries along the eastern Atlantic coastline, raising the question of whether they are really conspecific. Recognition of significant regional differences in the marine fauna and flora has resulted in a system of bio-regionalization of coastal and shelf marine areas of the world (e.g. Ekman, 1953; Briggs, 1995; Spalding *et al.*, 2007; Briggs & Bowen, 2012). Spalding *et al.* (2007), based on the assumption of distinct cohesive biotas over evolutionary time frames, proposed a system of biogeographical units for coastal and shelf marine areas of the world, which recognized seven biogeographical provinces in the eastern Atlantic Ocean: (1) the Arctic (from Greenland to the north of the Barents Sea including northern Iceland), (2) the Northern European Seas (from southern Iceland to the Celtic Seas including Norway and the Baltic Sea), (3) the Lusitanian (from the southern European Atlantic shelf to the Saharan upwelling system including the archipelagos of the Azores, Madeira and Canaries), (4) the Mediterranean Sea, (5) the West Africa Transition (including the Cape Verde islands and the Sahelian upwelling system zone), (6) the Gulf of Guinea (the Gulf of Guinean countries and islands, and Angola) and (7) Benguela (with the Namib and Namaqua areas).

The impact of climate change and anthropogenic activities (e.g. habitat alteration, shipping, mariculture) poses a challenge to the delimitation of biogeographical boundaries. Nevertheless, the geographical area that Spalding *et al.* (2007) called the 'West African Transition', and Briggs & Bowen (2012) referred to as the border between the Lusitanian and Tropical Eastern Atlantic biogeographical provinces at around Cap Juby in southern Morocco seems to be a strong barrier for dispersal of many marine species. About 30% endemism among fish (Floeter *et al.*, 2008), 36% endemism among 'opisthobranch' gastropods (García & Bertsch, 2009) and 31% endemism among tunicates (Naranjo, Carballo & García Gómez, 1998) are recognized in the Tropical Eastern Atlantic biogeographical province (*sensu* Briggs & Bowen, 2012).

Since 1975 the Institute of Marine Research of Norway (IMR) together with FAO (United Nations) and funded by the Norwegian Agency for Development Cooperation (NORAD) have been responsible for the Nansen Programme dedicated to the evaluation, monitoring and management of fisheries resources in Africa, Asia and South America. The programme aims to promote sustainable utilization of marine living resources and improved protection

Table 1. Summary of most useful characters used for diagnosis of philinid snails occurring in West Africa, including geographical distributions and type localities

Character/species	*Philine araneosa* van der Linden, 1995	*P. catena* (Montagu, 1803)	***P. cerebralis* sp. nov.**	*P. gelida* van der Linden, 1995	*P. guineensis* Marcus & Marcus, 1966	*P. intricata* Monterosato, 1884
Family assignment	Philinidae	Philinidae	Philinidae	Philinidae	Philinidae	Philinidae
Animal	?	Body pale brown with brown dots.	Body white	?	Body whitish. Maximum height c. 16.6 mm	Whitish speckled with brown dots
Shell	Spaced spiral grooves. Maximum height 1.8 mm	Internal, squarish, flat, wide aperture; spiral grooves chain-like with oval pits. Maximum height 4 mm	Internal, elongated, cylindrical, narrow aperture; spiral lines with chainlike sculpture. Maximum height c. 4 mm	Spiral lines of micro-pits and rings. Maximum height c. 1.3 mm	Internal, smooth with growth lines and faint spiral lines	Internal, spiral lines of fused pits forming grooves. Maximum height c. 2 mm
Radula	?	1.1.0.1.1; inner lateral denticulate, outer lateral smooth	1.1.0.1.1; inner lateral denticulate, outer lateral smooth	?	1.0.1; inner lateral denticulate	3.1.0.1.3
Gizzard plates	?	Calcified; three equal pointed gizzard plates	Chitinous; three equal spindle shaped plates	?	Calcified; paired plates almost round; unpaired plate smaller with variable shape; ventral holes narrow	Absent
Male reproductive system	?	Feather duster-shaped prostate	Prostate brain shaped, separated from tubular penial region	?	Blind caecum present; hammer shaped penial papilla with pointed subequal lobes	Bilobed prostate, separated from penial sheath.
Ecology	20–430 m	Tidal zone to 2000 m	29 m deep; soft bottom	18 m	37–98 m	80–620 m
Type locality	West of Boavista I., Cape Verde Is	Bigberry Bay, south coast of Devon, England, UK	Off Nikine, Senegal	Off Mauritania	Gulf of Guinea; between São Tomé and Príncipe and Nigeria	Palermo, Italy
Geographical range	Cape Verde Is	From Norway to, Mediterranean Sea, Madeira I., Canaries Is	As type locality	As type locality	Western Sahara, Mauritania, between Ivory Coast and Nigeria; São Tomé and Príncipe	From northern Brittany, Mediterranean Sea, Azores, Madeira I., Canary Is, Western Sahara, Cape Verde Is

Table 1. *Continued*

Character/species	*Philine araneosa* van der Linden, 1995	*P. catena* (Montagu, 1803)	***P. cerebralis* sp. nov.**	*P. gelida* van der Linden, 1995	*P. guineensis* Marcus & Marcus, 1966	*P. intricata* Monterosato, 1884
Biogeographical province(s)	West African Transition	Northern European Seas + Lusitanian + Mediterranean Sea	West African Transition	West African Transition	West African Transition + Gulf of Guinea	Northern European Seas + Mediterranean Sea + Lusitanian + West African Transition
Main references for the area	van der Linden (1995), Rolán (2005)	Ardovini & Cossignani (2004), Thompson (1988), Hernàndez *et al.* (2011), Segers, Swinnen & Abreu (2009)	Present study	van der Linden (1995)	Marcus & Marcus (1966), Marcus (1974), Rolán & Ryall (1999)	van der Linden (1994, 1995), Oliverio & Tringali (2001), Rolán (2005), Segers *et al.* (2009)
Remarks	Only known from shells	References to the region based on shells	New species here described	Known from a single shell	Described as a subspecies of *Philine aperta*	Shell similar to those of *P. angulata* and *P. catena*

Character/species	*P. iris* Tringali, 2001	*P. quadripartita* Ascanius, 1772	*P. scabra* (O. F. Müller, 1776)	***P. schrammi* sp. nov.**	***Spiniphiline caboverdensis* sp. nov.**	*Laona alternans* van der Linden, 1995
Family assignment	Philinidae	Philinidae	Philinidae	Philinidae	Philinidae	Laonidae
Animal	Reddish-orange	Body white	Body white	Body whitish	Body white	
Shell	Spiral lines of small pits moderately oblong. Maximum height c. 3 mm	Internal, smooth with faint spiral growth lines. Maximum height c. 30 mm	Internal, with chainlike spirals. Maximum height c. 10 mm	Internal, smooth. Maximum height c. 10 mm	Internal, with three spines on posterior outer lip. Maximum height c. 1 mm	? Spiral grooves with ovals, alternated with white bands. Maximum height 1.4 mm
Radula	2.1.0.1.2; inner lateral denticulate	1.0.1.; inner lateral denticulate	1.0.1; inner lateral denticulate; outer lateral smooth	1.0.1; inner lateral denticulate	?	?
Gizzard plates	Absent	Calcified; elongated, spindle-shaped; central plate smaller. Ventral holes narrow	Partially calcified; three equal, spindle-shaped plates	Calcified; spindle shaped; central plate smaller. Ventral holes wide	Two paired and one unpaired plates	?

Table 1. *Continued*

Character/ species	*P. iris* Tringali, 2001	*P. quadripartita* Ascanius, 1772	*P. scabra* (O. F. Müller, 1776)	***P. schrammi* sp. nov.**	***Spiniphiline caboverdensis* sp. nov.**	*Laona alternans* van der Linden, 1995
Male reproductive system	?	Long, thin, convoluted, prostate; blind caecum present; hammer shaped penial papilla with sub-equal lobes	Long, thin convoluted prostate; penial papilla cone shaped, verrucose	Prostate convoluted; blind caecum present; hammer shaped penial papilla with two long, slim equal lobes	?	?
Ecology	2–50 m	20–140 m	Down to 900 m deep; coarse and fine sand and mud	32 m deep; soft bottom	53 m deep; soft bottom	38 m
Type locality	Torres de Alcalá, Morocco, eastern Mediterranean Sea	Arendal, Norway	Not specified; Denmark and/ or Norway	Off Ilha de Orango, Guinea-Bissau	Off Baia das Gatas, São Vicente I., Cape Verde Is.	Off Banc d'Arguin, Mauritania
Geographical range	Malta, Spain, Morocco (Eastern Mediterranean Sea), Canaries	From Norway to, Mediterranean Sea, Madeira, Canary Is, ?off Mauritania; ?Cape Verde Is; ?Angola	Norway to Mediterranean Sea, Madeira I., Canary Is, off Mauritania; Gulf of Guinea, Benin, Angola	As type locality	As type locality	As type locality
Biogeographical province(s)	Mediterranean Sea + Lusitanian	Northern European Seas + Lusitanian	Northern European Seas + Mediterranean Sea + Lusitanian + West African Transition + Gulf of Guinea	Gulf of Guinea	West African Transition	West African Transition
Main references for the area	Moreno & Templado (1998), Tringali (2001); Ortea *et al.* (2002)	van der Linden (1995), Rolán & Ryall (1999), Thompson (1988), Rolán (2005), Hernández *et al.* (2011), Segers *et al.* (2009)	Marcus & Marcus (1966), van der Linden (1995), Rolán & Ryall (1999), Thompson (1988), Hernández *et al.* (2011)	Present study	Present study	van der Linden (1995)
Remarks	–	This NE Atlantic species probably has its southern geographical limit around Mauritania/ Senegal/Cape Verde	It is possible that all records south of Morocco refer to the new species here described as *P. cerebralis*	New species here described	New species here described	Only known from a single shell

Table 1. *Continued*

Character/ species	*L. condensa* van der Linden, 1995	*L. nanseni* **sp. nov.**	*L. quadrata* (S. Wood, 1839)	*L. rugosula* Dautzenberg & H. Fischer, 1896	*'Philine' angulata* Jeffreys, 1867 *i. s.*	*'P.' calva* van der Linden, 1995 *i. s.*	*'P.' retifera* (Forbes, 1844) *i. s.*
Family assignment	Laonidae	Laonidae	Laonidae	Laonidae	?Philinidae	?Philinidae	?Philinidae
Animal	?	Body yellowish	Body white	?	Body with black dots; cephalic shield lacks median groove	?	Body pale yellow
Shell	Chain-like spirals of regular microscopic rings. Maximum height 3 mm	External, nearly smooth with faint rugose sculpture. Maximum height c. 2 mm	Spirals chain-like of rings and pits. Maximum height c. 7 mm	Wrinkled pattern of spiral and axial lines	Internal, wing-like protrusion in upper lip, spiral lines with fused pits. Maximum height 2.3 mm	Spirals of irregular rings and dots. Maximum height c. 3 mm	With network of reticulated pattern. Maximum height c. 7 mm
Radula	?	Absent	2.1.0.1.2; inner lateral denticulate, outer lateral smooth	?	2.1.0.1.2; inner lateral denticulate. Outer lateral smooth	?	?
Gizzard plates	?	Absent	Absent	?	Chitinous; two paired and one smaller unpaired plate with rounded expansion on dorsal side	?	?
Male reproductive system	?	Tubular, no obvious separation between prostate and penial sheath	Short, thick, wrinkly prostate emerging from tubular penial sheath	?	?	?	?
Ecology	110–620 m	92 m deep; soft bottom	20–2355 m; coarse and fine soft bottoms	450–1167 m	15–160 m	60–405 m	22–300 m; muddy-sand bottoms
Type locality	SW of Hierro I., Canary Is	Off Cintra Bay, Western Sahara	Corraline Crag, Sutton, England, UK	Azores	Not specified; along the North cost of UK	North of Faial I., Azores	Serifos, Greece Aegean Sea

Table 1. *Continued*

Character/species	L. condensa van der Linden, 1995	L. nanseni sp. nov.	L. quadrata (S. Wood, 1839)	L. rugosula Dautzenberg & H. Fischer, 1896	'Philine' angulata Jeffreys, 1867 i. s.	'P.' calva van der Linden, 1995 i. s.	'P.' retifera (Forbes, 1844) i. s.
Geographical range	Azores, Canary Is	As type locality	Greenland, Barents and White Seas, Norway, to the Mediterranean Sea, Azores, W. of Cape Jubi Morocco	Azores, São Tiago I., Cape Verde	Norway to Mediterranean Sea. Canary Is, Morocco, off Mauritania	Mediterranean Sea, Azores, Madeira I., Canary Is, NW Africa Cape Verde Is	Mediterranean Sea and adjacent Atlantic, Madeira I., West Africa, off Mauritania
Biogeographical province(s)	Lusitanian	West African Transition	Northern European Seas + Mediterranean Sea + Lusitanian	Lusitanian + West African Transition	Northern European Seas + Lusitanian + Mediterranean Sea + West African Transition	Lusitanian + Mediterranean Sea + West African Transition	Mediterranean Sea + Lusitanian + West African Transition
Main references for the area	van der Linden (1995), Hernández et al. (2011)	Present study	van der Linden (1995)	van der Linden (1995), Rolán (2005)	van der Linden (1995), Hernández et al. (2011)	van der Linden (1995), Rolán (2005), Hernández et al. (2011), Segers et al. (2009)	van der Linden (1995), Segers et al. (2009)
Remarks	Only known from shells	New species here described	African records based on shells only	Only known from shells	References to the region apparently based on shells	Only known from shells	African records based on shells only

Classification according to Oskars *et al.* (2015). '*i.s.*' (*incertae sedis*) is used for species of uncertain generic and familial placement.

of the marine environment. Since 2005 the IMR and the Natural History Museum of Bergen (University of Bergen) have collaborated to extend the sampling activities to also include benthic invertebrate macrofauna.

In this paper we revise the diversity and systematics of the West African species of the Philinidae *s.l.* based on the study of material collected during the Nansen Project and bibliographical data. A taxonomic integrative approach combining morphological characters and molecular phylogenetics is used to aid in species delimitation. The biogeographical affinities of the West African species of philinid snails are discussed.

MATERIAL AND METHODS

SAMPLING OF TAXA

African specimens were obtained during scientific cruises carried out between 2005 and 2012 on board the Norwegian R/V *Dr Fridtjof Nansen* along the western coast of Africa between Morocco and Angola. The samples were collected by grab, trawl and epibenthic sled from 19 to 877 m depth. The sediment samples were fixed on board in either formalin or ethanol and later sorted to species level under a dissecting microscope at the University Museum of Bergen (Department of Natural History; ZMBN, Norway). Specimens were used for both anatomical dissection and DNA extraction. Geographical distributions are based on examined material and reliable literature records. All studied specimens have been deposited at the Systematic Invertebrate Collections, ZMBN, Norway.

ANATOMICAL AND SCANNING ELECTRON MICROSCOPY WORK

Photographs of the whole animal were taken with an auto-montage camera (Leica M205 C) or macrophotography equipment. The cephalic shield was cut open and the buccal mass, gizzard and male reproductive system removed. Shell height (H) was measured with a digital calliper and the various anatomical pieces were drawn with a *camera lucida* and photographed with an auto-montage system. Radulae were cleaned in proteinase K-solution after Holznagel (1998) while shells and gizzard plates were cleaned in either proteinase K-solution or in a 10% bleach solution. The penial papillae were cut and critical point dried prior to mounting on carbon sticky tabs together with the radulae and gizzard plates for scanning electron microscopy (SEM). The stubs were then coated with gold–palladium and images taken with a Zeiss Supra 55VP scanning electron microscope.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Tissue was cut from the foot or parapodial lobes. Molecular work was performed both by ourselves at the University of Bergen and by the Canadian Centre for DNA Barcoding (CCDB) in Guelph. In our lab we used the Qiagen DNeasy Blood and Tissue Kit protocol for extraction. Partial sequences of the COI gene (*c.* 660 bp) were amplified according to the method described by Malaquias & Reid (2009) using universal primers (Folmer *et al.*, 1994). For samples that did not amplify with Qiagen Taq, additional 25-μL reactions were set with TaKaRa Ex Taq Polymerase HS (250 U) following the protocols described by Oskars *et al.* (2015). The quality and quantity of PCR products were assessed by gel electrophoresis following standard methods and successful PCR products were purified according to the EXO-SAP method described by Eilertsen & Malaquias (2013). Sequence reactions were run on an ABI 3730XL DNA Analyser (Applied Biosystems). As for the sequencing in CCDB, we submitted tissue samples and data according to the routines in BOLD (http://www.boldsystems.org). CCDB used their tissue lysis protocol and applied the forward primer cocktail C_GasF1_t1 and the reverse primer GasR1_t1 COX1 (S. Prosser, unpublished data) for PCR amplification and the primer pair M13F/M13F (Messing, 1983) for sequencing.

PHYLOGENETIC ANALYSES AND MOLECULAR SPECIES DELIMITATION

Sequences (Table 2) were assembled and aligned with the software package Geneious (version 8.1.2) (Kearse *et al.*, 2012). The nucleotide reads were translated to amino acids to check for potential stop codons and 'numts' (Bensasson *et al.*, 2001). The best-fit evolutionary model for phylogenetic analysis was selected with jModeltest2 (Darriba *et al.*, 2012) using the Akaike information criterion (AIC) yielding the GTR+I+G model. Phylogenetic inference was performed with MrBayes v3.2.4 (Ronquist *et al.*, 2012) using the species *Scaphander lignarius* as outgroup. MrBayes was run with four chains and two parallel runs for two million generations. We used flat Dirichlet priors on all model parameters, sampling trees and posteriors every 500 generations. Tree graphics were made with FigTree 1.4 (Rambaut, 2006–2014) and with R using SPIDER (Brown *et al.*, 2012). Pairwise Kimura two-parameter (K2P) distances were calculated with MEGA 6 (Tamura *et al.*, 2013).

Table 2. Samples included in the phylogenetic and species delimitation analyses with geographical localities, voucher numbers and GenBank or BOLD accession numbers

Taxa	Locality	Voucher no	GenBank (GB)/ BOLD Accession No
Laona confusa	Norway	ZMBN 94153	BOLD, NBC100-14
Laona confusa	Norway	ZMBN 95223	BOLD, NBC082-14
Laona nanseni sp. nov.	Western Sahara	ZMBN 105808	BOLD, MIWAM194-15
Laona nanseni sp. nov.	Western Sahara	ZMBN 105809	BOLD, MIWAM193-15
Laona ventricosa	Norway	ZMBN 81820	BOLD, NBC003-14
Laona ventricosa	Norway	ZMBN 88008	BOLD, NBC006-14
Laona sp.2	Norway	ZMBN 95212	BOLD, NBC071-14
Laona sp.2	Norway	ZMBN 95213	BOLD, NBC072-14
Laona sp.2	Norway	ZMBN 95214	BOLD, NBC073-14
Laona sp.2	Norway	ZMBN 95217	BOLD, NBC076-14
Philine aperta	Simon's Bay, Cape Peninsula, South Africa	CASIZ176345	GB, JN825187
Philine aperta	Simon's Bay, Cape Peninsula, South Africa	CASIZ176332	GB, JN825186
Philine finmarchica	Norway	ZMBN 95209	BOLD, NBC068-14
Philine finmarchica	Norway	ZMBN 95210	BOLD, NBC069-14
Philine finmarchica	Norway	ZMBN 95208	BOLD, NBC067-14
Philine finmarchica	Norway	ZMBN 95207	BOLD, NBC066-14
Philine guineensis	Western Sahara	ZMBN 91994	BOLD, MIWAM006-13
Philine guineensis.	Western Sahara	ZMBN 105810	BOLD, MIWAM192-15
Philine guineensis	Nigeria	ZMBN 92420	BOLD, MIWAM047-13
Philine guineensis.	Nigeria	ZMBN 92421	BOLD, MIWAM048-13
Philine guineensis	Nigeria	ZMBN 92003	BOLD, MIWAM008-13
Philine guineensis	Nigeria	ZMBN 92419	BOLD, MIWAM046-13
Philine guineensis	Mauritania	ZMBN 92426	BOLD, MIWAM053-13
Philine guineensis	Mauritania	ZMBN 91989	BOLD, MIWAM003-13
Philine guineensis	Mauritania	ZMBN 92424	BOLD, MIWAM051-13
Philine guineensis	Mauritania	ZMBN 92425	BOLD, MIWAM052-13
Philine guineensis	Mauritania	ZMBN 92427	BOLD, MIWAM054-13
Philine indistincta	Norway	ZMBN 95204	BOLD, NBC063-14
Philine intricata	Western Sahara	ZMBN 105807	BOLD, MIWAM195-15
Philine quadripartita	Tjärnö, Sweden	MCZ:DNA101778	GB, GQ160767
Philine quadripartita	Murcia, Spain	-	GB, AY345016
Philine scabra	Norway	ZMBN 95202	BOLD, NBC061-14
Philine scabra	Norway	ZMBN 95205	BOLD, NBC064-14
Philine scabra	Norway	ZMBN 87077	BOLD, NBC001-14
Philine scabra	Norway	ZMBN 81821	BOLD, NBC002-14
Philine scabra	Norway	ZMBN 95203	BOLD, NBC062-14
Philine schrammi sp. nov.	Guinea Bissau	ZMBN 92413	BOLD, MIWAM041-13
Philine sp.	Guinea Bissau	ZMBN 92416	BOLD, MIWAM044-13
Spiniphiline caboverdensis sp. nov.	São Tiago I., Cape Verde Is	ZMBN:DNA92171	BOLD, MIWAM191-15
Scaphander lignarius	Norway	ZMBN 95233	BOLD, NBC092-14

To examine the molecular distinctiveness of different morpho-species, we used ABGD (Automatic Barcode Gap Discovery) (Puillandre *et al.*, 2012) via the web interphase at http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html (version of 11 April 11 2013). ABDG was run by selecting K2P with transition/transversion ratio (TS/TV) equal to 2 and with a fasta file input of the alignment. We applied default values for P_{min} and P_{max}, but the relative gap width was lowered from 1.5 to 1, because the default relative gap value returned just one single group for all the sequences in the initial run. This gap adjustment resulted in the identification of 15 groups (Fig. S1, Supporting Information).

The groups resulting from the ABGD analysis were subsequently used to assign the sequences as

members of groups in the Species Delimitation Plugin (SDP version 1.4.3; Masters, Fan & Ross, 2010) of the software Geneious. The species delimitation plugin is based on the method by Ross, Murugan & Li (2008) and execution of the program generates the following statistics based on predefined clades: IntraDist – average pairwise patristic distance among members of a group of interest; InterDist – average pairwise patristic distance between members of the group and its sister taxa; Intra/Inter – the ratio of IntraDist to InterDist; PID(Liberal) –the mean probability with a 95% confidence interval for a prediction of making a correct identification of an unknown specimen being sister to or within the group of interest; PID(Strict) – the mean probability with a 95% confidence interval for a prediction of making a correct identification of an unknown specimen being found only in the group of interest; AvMA – the mean distance between the most recent common ancestor of the species and its members; Rodrigo's P (RD) – the probability that a clade has the observed degree of distinctiveness due to a random coalescent process (Rodrigo *et al.*, 2008); and Rosenberg's P(AB) – the probability that a species *A* represented by *n* sequences, in a clade of *n* + *m* sequences, will be reciprocally monophyletic with the remaining *m* sequences under the null model of random coalescence (Rosenberg, 2007). The null hypothesis in this test is that lineages evolve according to a Yule model with random branching. If the null hypothesis is rejected it is assumed that the branching may be due to some barrier to gene flow (Rosenberg, 2007). We did not include Rodrigo's (RD) parameter because it is not a relevant measure of the degree of distinctness when the underlying tree is not estimated under a strict molecular clock (Masters *et al.*, 2010). Additionally, the measurement may be oversensitive to taxonomic distinctness (Rodrigo *et al.*, 2008; Boykin *et al.*, 2012).

The tree for the SDP computations was estimated with the PhyML (Guindon & Gascuel, 2003; Guindon *et al.*, 2010) plugin in Geneious, using the GTR+G+I model and SPR-search with 250 bootstrap replicates for estimating branch support. Rosenberg's test was also performed with the R-package SPIDER (Brown *et al.*, 2012), using the same maximum-likelihood (ML) tree.

The ML tree was additionally used to calculate the Genealogical Sorting Index (*gsi*), which quantifies the degree of exclusive ancestry of a particular group on a rooted phylogeny (Cummings, Neel & Shaw, 2008; Cranston, 2010). The *gsi* is a quantitative assessment of the extent to which a genealogical relationship departs from random polyphyly expected under panmixis in the population. A *gsi* index of 1 means monophyly. The statistical significance of the *gsi* is computed with random permutation of the group labels of terminal branches while the tree topology is kept constant. These calculations were done with 10 000 permutations using the web service at http://www.genealogicalsorting.org/index.php. Sequential Holm–Bonferroni correction of *P*-values for multiple test bias was subsequently computed with a procedure prepared by Gaetano (2013) using a α-level of 0.05.

RESULTS

We here adopt the classification proposed by Oskars *et al.* (2015) for the Philinidae *s.l.* The latter study showed that Philinidae is an artificial taxon and introduced several other families and genera for 'philinid snails'. However, not all philinid species have features consistent with the systematic scheme proposed by Oskars *et al.* (2015). This is the case of the species *P. angulata* and *P. retifera*, which are here provisionally ascribed to the family Philinidae and genus *Philine* (*incertae sedis*).

SYSTEMATIC DESCRIPTIONS

CLASS GASTROPODA CUVIER, 1795
ORDER CEPHALASPIDEA FISCHER, 1883
FAMILY PHILINIDAE GRAY, 1827
GENUS *PHILINE* ASCANIUS, 1772
PHILINE ANGULATA J. G. JEFFREYS, 1867 INCERTAE SEDIS
(FIG. 1A–O)

See Ohnheiser & Malaquias (2013: 279) for a list of synonymies.

Diagnosis: Shell internal, white, square-oval, upper outer lip flattened and keeled, outer keel ending in

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Figure 1. *Philine angulata* (ZMBN 92170, H = 1.6 mm). A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (SEM). E, ventral view of shell (automontage image). F, detail of dorsal view of shell (SEM). G, sculpture on dorsal surface of shell (SEM). H, gizzard (automontage image). I, dorsal view of gizzard plates (SEM). J, ventro-lateral view of gizzard plate (SEM). K, detail of dorsal hump on gizzard plate (SEM). L, ventral surface of gizzard plate (SEM). M, dorsal surface of gizzard plate (SEM). N, dorsal surface of gizzard plate (SEM). O, jaws (SEM). lk, larval kidney. Scale bars: A–C = 500 μm; E = 250 μm; D, H = 200 μm; F = 100 μm; G, J, K = 20 μm; I = 30 μm; L, O = 10 μm; M = 2 μm; N = 5 μm.
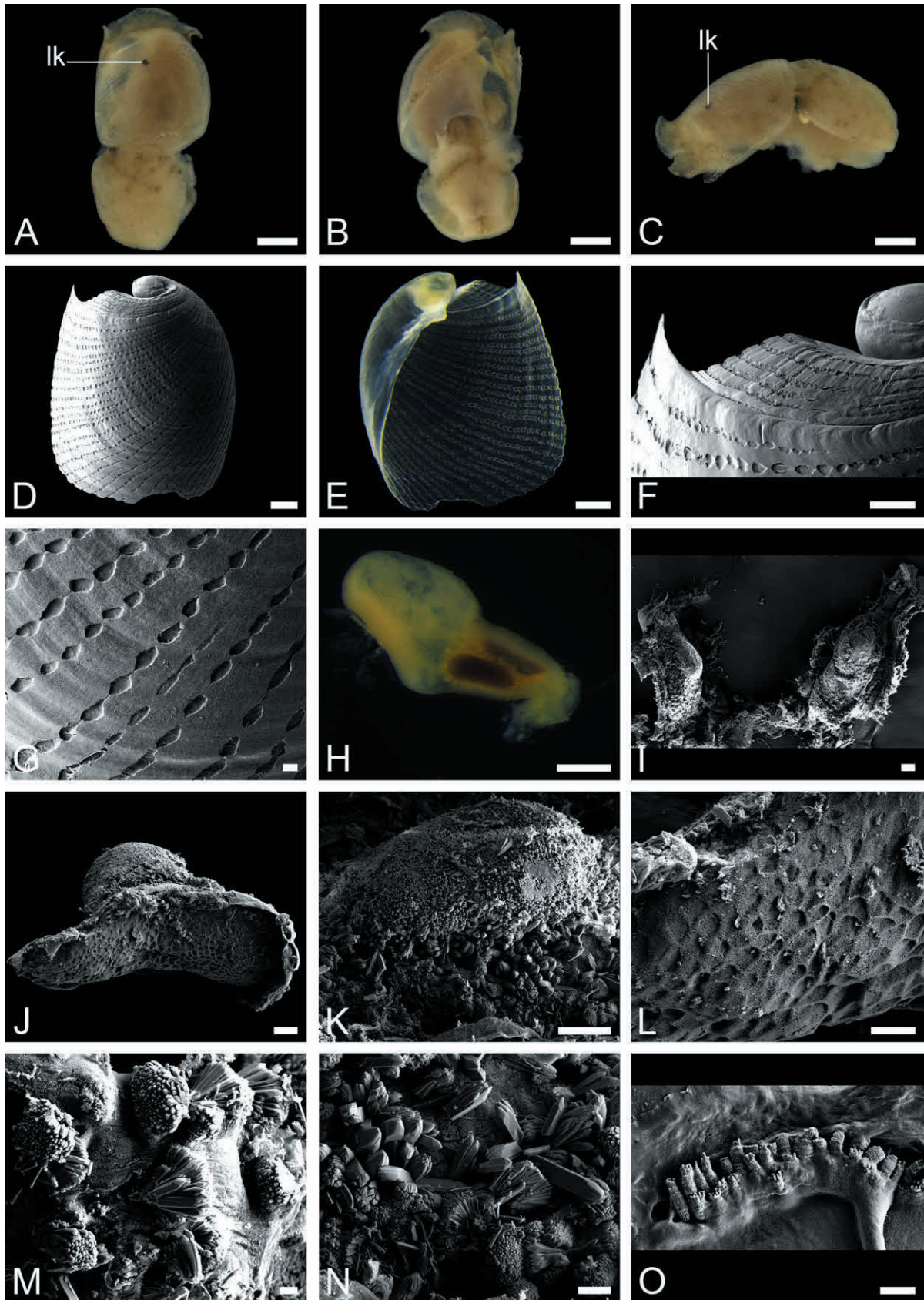
wing-like extension; sculpture of mostly fused pits arranged in transverse lines. Body with small black dots, larval kidney visible. Rachidian tooth absent, one inner lateral, two outer lateral teeth. Jaws present. Gizzard not surrounded by muscle fibres. Three gizzard plates of equal size, chitinous, kidney-bean shaped, rounded elevated bump on dorsal side of plates present.

Type locality: North of UK (Larne, Antrim, Hebrides, Shetland).

Material examined: Off El Quatia, Morocco, 29°00′09.00″N, 011°13′06.24″W, 1 spec., dissected, ZMBN 92170, H = 1.6 mm.

Shell (Fig. 1D–G): Maximum H = 2.3 mm (Ohnheiser & Malaquias, 2013). Thin; white; square–oval in shape, aperture wide with thin parietal callus, upper outer lip flattened and keeled, outer keel ending in wing-like extension, five rows of spiral striae between the keels, apex obtuse, not umbilicated; sculpture consisting of transverse lines of pits mostly, but not always connected to form chains or grooves.

Animal (Fig. 1A–C): Body with small black dots on cephalic shield and pallial lobe in preserved specimen; mantle thin. Larval kidney visible through shell. Cephalic shield blunt, median groove absent, eyes present.

Jaws (Fig. 1O): Made of two to three rows of columnar elements inserted in tegument with apical short pointed finger-like extensions.

Radula: 16 × 2.1.0.1.2; rachidian tooth absent. Inner and outer lateral teeth curved with broad base.

Gizzard (Fig. 1H–N): Gizzard globose, not surrounded by muscle fibres; contains three kidney-bean-shaped chitinous plates of equal size. Plates uniformly brown; all plates with an elevated rounded bump on dorsal side; bump located posteriorly in one plate, centrally in the other two. Microsculpture on ventral surface consisting of irregular pits with net-like appearance; bundles of broad, long 'crystal-like' rods on dorsal surface. Gizzard not surrounded by muscle fibres.

Male reproductive system: Unknown.

Ecology: Occurs in depths down to 160 m (Thompson, 1988; present study) on sand, mud and gravel (Moreno & Templado, 1998; Sneli *et al.*, 2005; Høisæter, 2009).

Distribution: North-east coast of America, Norway south of Tromsø, the Faeroes, Shetlands, British Isles (J. G. Jeffreys, 1867; Thompson, 1988; Høisæter, Sneli & Brattegard, 2001; Sneli *et al.*, 2005; Ohnheiser & Malaquias, 2013). Mediterranean Sea (Thompson, 1988), Morocco, Mauretania and south of Lanzarote, Canary Islands (van der Linden, 1995; present study).

Remarks: This is a species described originally from the northern coasts of the UK with a ubiquitous distribution spanning across the entire European coastline southwards to Mauritania in West Africa where it seems to have its southern geographical limit. The reproductive system of this species is unknown and no DNA sequences are available. Unfortunately, the minute size of the specimen hampered the successful preparation of the radula for SEM and ultrastructural details of this structure could not be studied. It is the first time that the presence of jaws is reported in philinid snails.

PHILINE CEREBRALIS SP. NOV.
(FIGS 2A–O, 3A–E)

Diagnosis: Shell internal, translucent, elongate-oval in shape, with chain-like sculpture in transverse lines. Body white. Rachidian tooth absent, one curved inner lateral tooth with sharp, developed denticulation along inner edge, one outer lateral tooth. Gizzard surrounded by muscle fibres, contains

Figure 2. *Philine cerebralis* sp. nov. (ZMBN 105802, H = 3.6 mm, holotype). A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (SEM). E, ventral view of shell (automontage image). F, detail of dorsal view of shell (SEM). G, sculpture on dorsal surface of shell (SEM). H, head region of animal, gizzard, eyes (arrow), cephalic shield removed (automontage image). I, dorsal, ventral and lateral view of gizzard plate (automontage image). J, dorsal and lateral view of gizzard plate (SEM). K, detail of dorsal view of gizzard plate (SEM). L, detail of lateral view of gizzard plate (SEM). M, ventral surface of gizzard plate (SEM). N, ventral surface of gizzard plate (SEM). O, dorsal surface of gizzard plate (SEM). Scale bars: A–C, E, H = 500 μm; D, J = 200 μm; F = 100 μm; G, K, N = 20 μm; I = 250 μm; L = 30 μm; M = 10 μm; O = 2 μm.
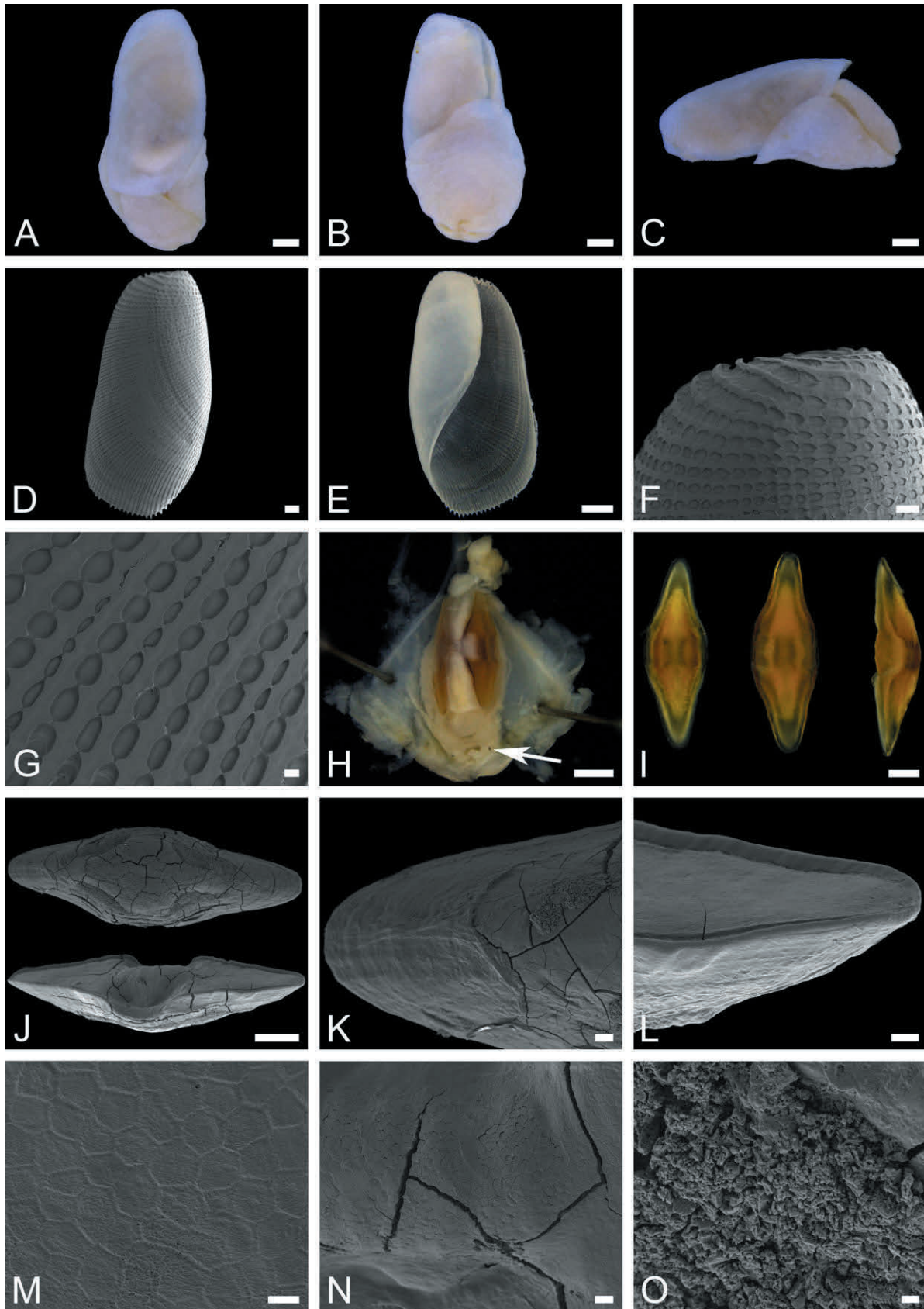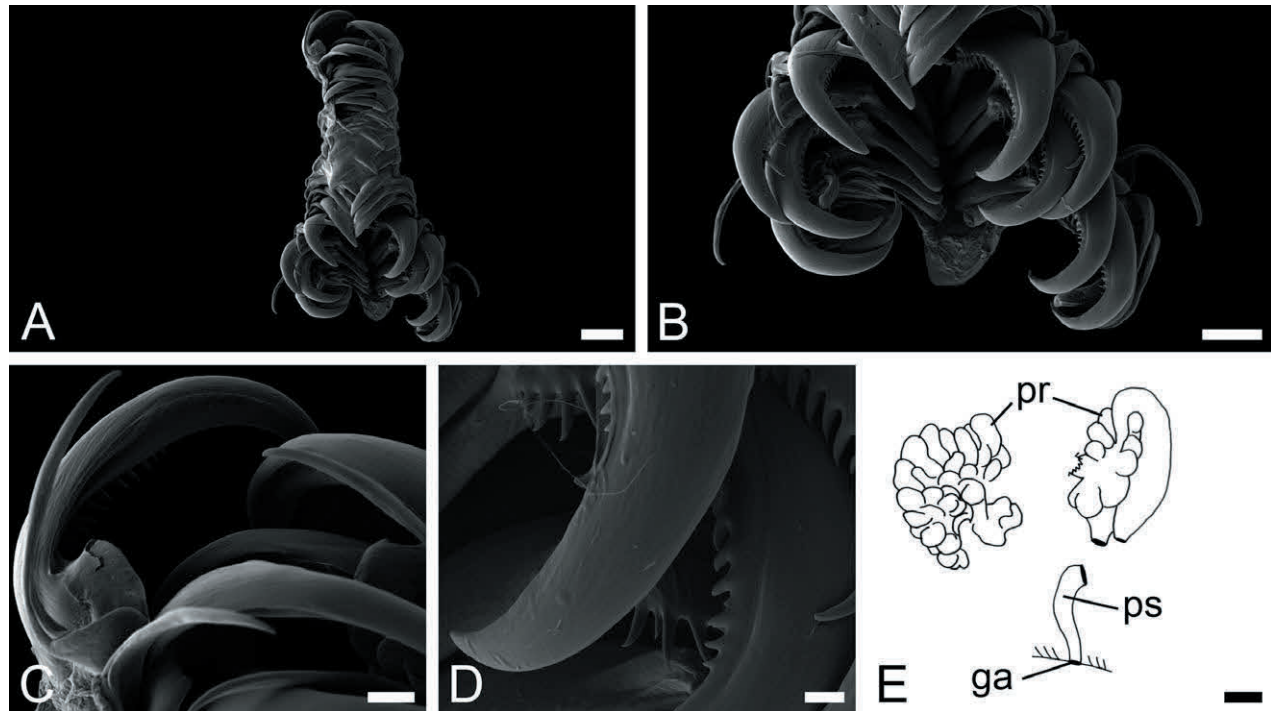
Figure 3. *Philine cerebralis* sp. nov. (ZMBN 105802, H = 3.6 mm, holotype). A, radula (SEM). B, detail of radula (SEM). C, outer lateral tooth (SEM). D, detail of denticles (SEM). E, male reproductive system. ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A = 50 µm; B = 30 µm; C = 10 µm; D = 5 µm; E = 250 µm.

three equal chitinous spindle-like gizzard plates. Prostate highly lobate, emerging from tubular penial sheath.

ZooBank registration: urn:lsid:zoobank.org:act:D3 FC6EEC-729D-477D-AEAE-D3022BC6C154

Etymology: The name of this species stems from the shape of the prostate, which is highly lobate, resembling a vertebrate brain.

Type locality: Off Nikine, Senegal, 12°33′53.28″N, 017°21′18.36″E.

Material examined: Off Nikine, Senegal, 12°33′53.28″N, 017°21′18.36″E, 1 spec. (holotype), dissected, ZMBN 105812, H = 3.6 mm.

*Shell (Fig. 2D–G):* Maximum H = 3.6 mm. Internal, thin; translucent; elongated-oval cylindrical in shape, aperture wide with thin whitish parietal callus, outer lip scalloped, apex obtuse, not umbilicated; sculpture visible through mantle, consisting of transverse lines of pits connected to form chains.

Animal (Fig. 2A–C): Body white in preserved specimen, mantle thin. Cephalic shield indented, median groove present. Larval kidney not visible through shell.

Radula (Fig. 3A–D): Radular formula 17 × 1.1.0.1.1. Rachidian tooth absent. Inner lateral teeth with broad base, curved; inner edge with sharp and developed denticulation. Outer lateral teeth straight, with broad base.

Gizzard (Fig. 2H–O): Gizzard elongate cylindrical, surrounded by muscle fibres, contains three equal chitinous spindle-like plates with two longitudinal depressions on ventral surface. Dorsal surface inside the

Figure 4. *Philine guineensis.* A, dorsal view of complete animal. B, ventral view of complete animal. C, dorsal view of shell (automontage image). D, ventral view of shell (automontage image). E, radula (SEM). F, detail of radula (SEM). G, detail of denticulation on inner lateral teeth (SEM). H, top view of penial papilla (automonatge image). I, side view of penial papilla (automontage image). J, side view of penial papilla (SEM). K, male reproductive system (automontage image). bc, blind caecum; ed, ejaculatory duct; ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A–D = 2 mm; E = 100 µm; F = 50 µm; G = 10 µm; H, I = 500 µm; J = 200 µm; K = 1 mm.
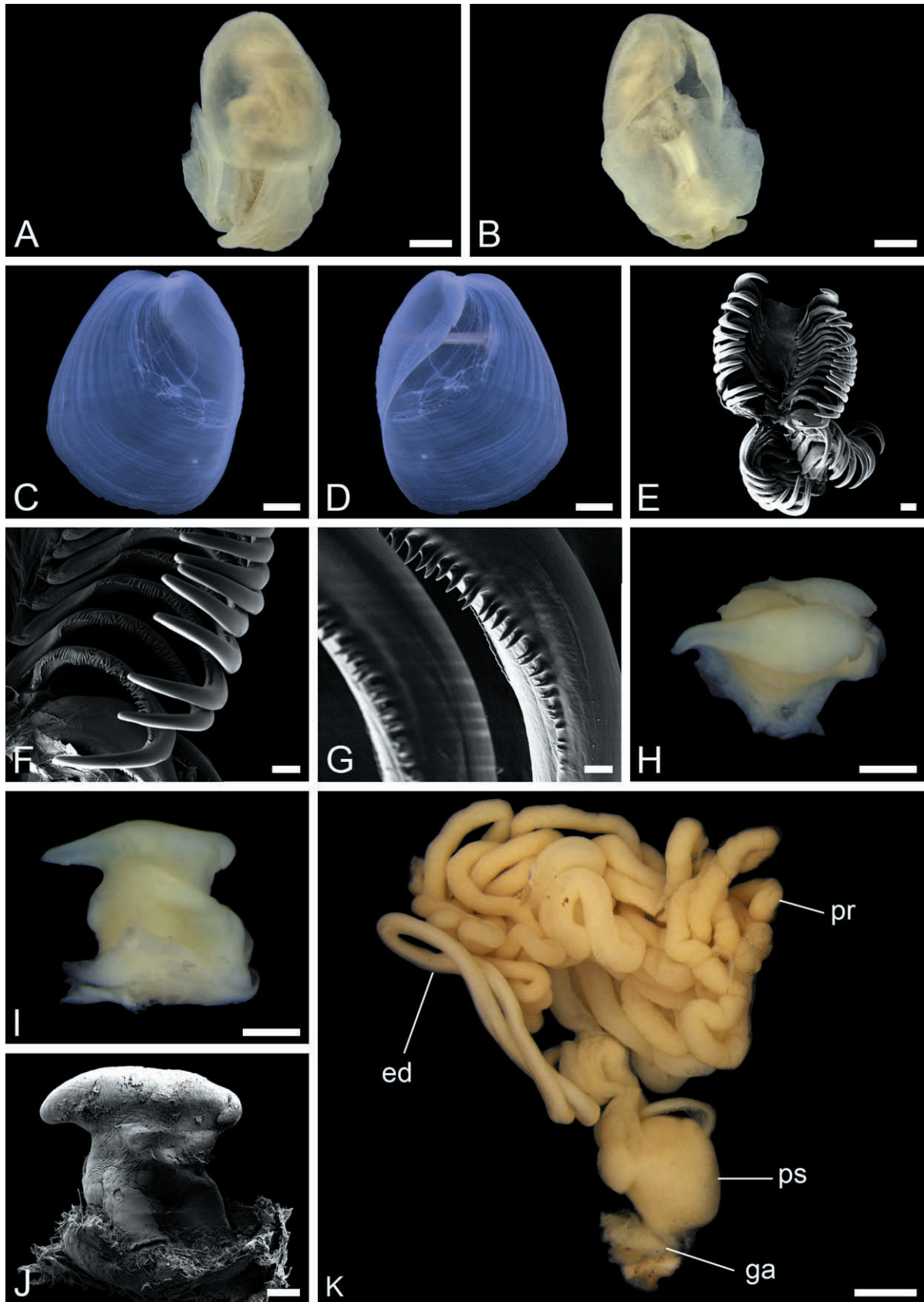
gizzard of amber colour, ventral surface more whitish, surrounded by translucent margin. Microsculpture on ventral surface, dorsal surface with crystalline needles.

Male reproductive system (Fig. 3E): Obvious separation between long, thin, lobate brain like-shaped prostate and elongate tubular penial sheath.

Ecology: Soft bottom, 29 m depth.

Distribution: See type locality.

Remarks: The shell of this new species resembles those of *Philine scabra* and *P. indistincta*, but the male reproductive system of the three species is different with an unusual configuration (Ohnheiser & Malaquias, 2013; present work). During dissection the reproductive system of the new species *P. cerebralis* broke into three different parts and thus full reconstruction and interpretation was not entirely possible; however, the highly lobate shape of the prostate and the tubular penial region were recognizable. The only species that has somehow a similar reproductive system is *P. catena* (Montagu, 1803), yet its shell is quite distinct and the gizzard plates are calcified (Thompson, 1976; Ohnheiser & Malaquias, 2013; Table 1). The combination of shell type with the unique male reproductive system separates *P. cerebralis* sp. nov. from all other species occurring in the eastern Atlantic. It is possible that previous records of *P. scabra* in West Africa correspond to *P. cerebralis* sp. nov.

PHILINE GUINEENSIS MARCUS & MARCUS, 1966
(FIGS 4A–K, 5A–O, 6)

Philine aperta guineensis Marcus & Marcus, 1966: 159, figs 9–18. Marcus, 1974: 360; fig. 104. Rolán & Ryall, 1999: 58.
Philine aperta–Price *et al.*, 2011: 4.

Diagnosis: Shell oval, aperture wide, smooth, whitish translucent, internal. Body whitish translucent. Rachidian tooth absent, one rounded inner lateral tooth with developed, sharp denticulation along inner edge. Gizzard not surrounded by muscle fibres; plates calcareous; paired plates rounded with wide central region; unpaired plate smaller spindle shape; all with deep narrow holes. Long, thin, convoluted, prostate emerging from sack-like penial sheath tapering towards genital aperture; blind caecum present, separate ejaculatory duct, hammer shaped penial papilla with pointed subequal lobes; one about twice the length of the other.

Type locality: Off Atijere, Nigeria, 06°10′02.28″N, 04°17′19.32″W.

Barcode: BOLD: MIWAM048-13 (ZMBN 92421).

Material examined: Off Cintra Bay, Western Sahara, 23°01′30.72″N, 17°01′50.52″W, 1 spec., sequenced, ZMBN 105810, H = 1.2 mm. Off Dakhla, Western Sahara, 23°48′33.12″N, 016°04′46.92″W, 1 spec., dissected and sequenced, ZMBN 91994, H = 13.6 mm. Off Nouamghar, Mauritania, 19°17′44.88″N, 016°48′33.12″W, 1 spec., dissected and sequenced, ZMBN 91989, H = *c.* 8.3 mm. Off Nouakchott, Mauritania, 18°17′05.28″N, 016°27′46.08″W, 1 spec., dissected, ZMBN 92009, H = 16.6 mm; 2 specs, one sequenced, ZMBN 92427, H = 15.2, 15.4 mm; 1 spec., sequenced, ZMBN 92424, H = 17.1 mm; 1 spec., sequenced, ZMBN 92425, H = 23.2 mm; 1 spec., sequenced, ZMBN 92426, H = 21.9 mm. Off Atijere, Nigeria, 06°10′02.28″N, 04°17′19.32″E, 2 specs, one sequenced, ZMBN 92419, H = 11.6, 13.7 mm. Off Atijere, Nigeria, 06°10′02.28″ N, 04°17′19.32″E, 1 spec., sequenced, ZMBN 92420, H = 21.3 mm; 1 spec., dissected and sequenced, ZMBN 92421, H = 13.7 mm. Nigeria, 5°21′56.52′N, 4°57′50.4′E, 1 spec., sequenced, ZMBN 92003, H = 16.4 mm. Gulf of Guinea, 3 specs, one dissected, MZSP 75104, H = 35 mm (total animal length). Gulf of Guinea, station 62 (4°22′31″N, 6°14′10″E), 2 spcs, USNM 576260, H = 2.6, 2.2 mm (syntypes).

Figure 5. *Philine guineensis*. A, lateral view of gizzard and buccal mass (automontage image). B, ventral view of gizzard and buccal mass (automontage image). C, ventral view of gizzard and buccal mass, muscles removed (automontage image). D, dorsal view of gizzard plates (automontage image). E, dorsal (left) and ventral (right) views of paired gizzard plates (topotype specimen; MZSP 75104). F, dorsal (left) and ventral (right) views of unpaired gizzard plate (topotype specimen; MZSP 75104). G, dorsal view of gizzard plates (automontage image). H, ventral view of gizzard plates, same specimen (automontage image). I, lateral view of gizzard plate, same specimen (automontage image). J, dorsal view of gizzard plates (automontage image). K, ventral view of gizzard plates, same specimen (automontage image). L, dorsal and ventral views of paired gizzard plates, ventral view of unpaired plate, same specimen as D–F, (SEM). M, detail of ventral view of gizzard plate (SEM). N, ventral view of gizzard plate surface, central part (SEM). O, ventral gizzard plate surface, outer part (SEM). bm, buccal mass; c, crop; g, gizzard; gp, gizzard plate; sg, salivary gland. Scale bars: A–C, G–K = 1 mm; D = 500 μm; E, F = 2 mm; L = 400 μm; M = 100 μm; N, O = 5 μm.
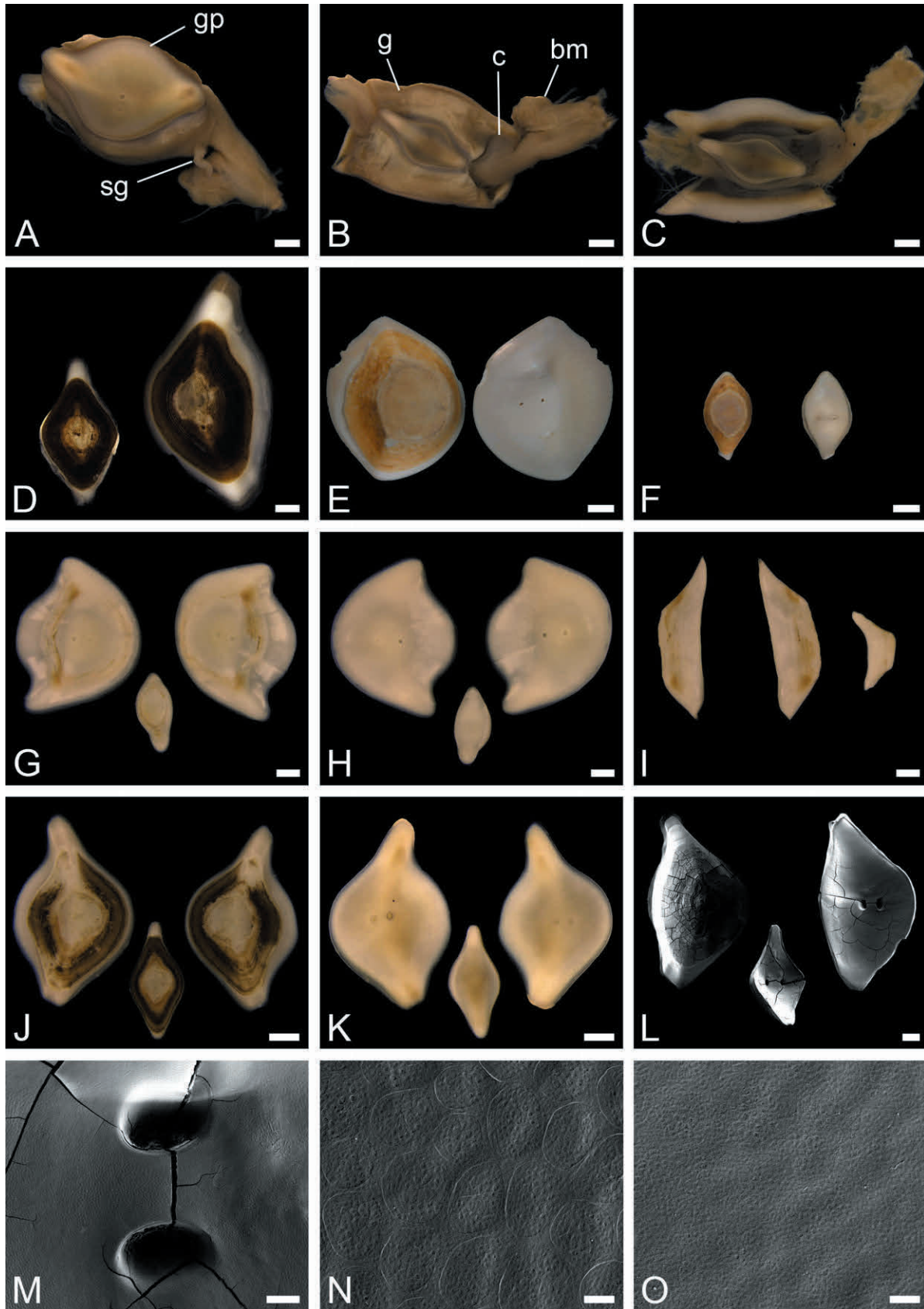
Figure 6. Two syntypes of *Philine aperta guineensis* Marcus & Marcus, 1966 (USNM 576260) from off the Gulf of Guinea (4°22′31″N, 6°14′10″E). A, shell H = 26 mm. B, shell H = 22 mm.

Shell (Fig. 4C, D): Maximum H = 33 mm (Marcus & Marcus, 1966). Internal; smooth; whitish translucent; oval in shape, aperture wide, with parietal callus, outer lip smooth, apex obtuse, slightly sunken, not umbilicated.

Animal (Figs 4A, B, 6): Body whitish translucent in preserved specimens, mantle thick. Cephalic shield sometimes slightly indented, median groove present, posterior pallial lobe with dorsal notch. Larval kidney not visible through shell. Salivary glands as long as buccal mass.

Radula (Fig. 4E, G): Radular formula 20–23 × 1.0.1 Rachidian tooth absent. Inner lateral teeth with broad base; curved and rounded tips; inner edge with developed, sharp denticulation.

Gizzard (Fig. 5A–O): Gizzard elongate cylindrical, not surrounded by muscle fibres. Plates calcareous; two wide, rounded paired plates with short ends and one smaller symmetrical unpaired spindle-like plate; unpaired plate about 1/3–2/3 of the size of paired plates; two deep narrow holes on ventral surface of all plates. Dorsal surface of all plates brown–yellowish, ventral surface creamy. Microsculpture present on ventral surface only.

Male reproductive system (Fig. 4H–K): Pronounced separation between long, thin, convoluted prostate and sack-shaped penial sheath with blind caecum; tapering towards the genital aperture. Separate ejaculatory duct. Penial papilla hammer shaped, both lobes pointed, one about twice the length of the other; upper part contained in blind caecum, flat or rounded, lower part either straight or forming a flap.

Ecology: Known from between 32 and 109 m depth.

Distribution: Western Sahara, Mauritania, off Ghana, Benin and Nigeria (Marcus & Marcus, 1966; present study).

Remarks: Marcus & Marcus (1966), Marcus (1974) introduced the sub-species name *Philine aperta guineensis* for African specimens based on the presence of 'strikingly broad' paired gizzard plates and a thicker penial papilla. Price *et al.* (2011) claimed that the penial morphology of *P. a. guineensis* (= *Philine quadripartita sensu* Price *et al.*, 2011) is more similar to the true *P. aperta* from South Africa rather than to that of *P. quadripartita* from European seas.

Yet, based on available data it is difficult to ascertain the extent and significance of these differences; all three species have sub-equal penial lobes, apparently with differences on the thickness and relative length of the lobes (Marcus & Marcus, 1966; Marcus, 1974; Price *et al.*, 2011; Ohnheiser & Malaquias, 2013; current study), but the true extent of the taxonomic value of these dissimilarities remains to be thoroughly evaluated. In both *P. guineensis* and *P. quadripartita* the penial papilla extend into the blind caecum (Ohnheiser & Malaquias, 2013: 307; current study), a structure that seems to be absent in *P. aperta* (Price *et al.*, 2011).

The main morphological difference between *P. guineensis* and the southern African *P. aperta*, and European *P. quadripartita* is undoubtedly the configuration of the gizzard plates. *Philine guineensis* has wider paired plates nearly rounded in the central region leading to short ends and the unpaired plate is always smaller, one-third to two-thirds the size of the paired plates. This was confirmed by our results and by the analysis of a topotypic specimen from the original series studied by the Marcus and deposited in the collections of the Museu de Zoologia of the University of São Paulo, Brazil (MZSP 75104). The gizzard plates of this

specimen are here illustrated in Figure 5E, F. In *P. aperta* and *P. quadripartita* the plates are typically spindle-like with expanded ends and the unpaired plate is of similar configuration always about three-quarters the length of the paired plates. The microsculpture of the gizzard plates is similar between *P. aperta* and *P. quadripartita* with hexagonal-like deep indentations, whereas is *P. guineensis* the hexagonal pattern is shallower, nearly not indented.

Price *et al.* (2011) suggested that African specimens from the Gulf of Guinea could be conspecific with those from southern Africa (from Saldanha Bay to Mozambique) but stating that the addition of molecular data would be necessary to draw definitive conclusions. As discussed above, the detailed study of West African specimens revealed discrete differences in both the gizzard plates and the reproductive system between these two species matching the description of *P. a. guineensis* by Marcus & Marcus (1966). In addition, our molecular phylogenetic analysis clearly differentiated between the three species (Fig. 14) and the genetic distances between them are unequivocal (22.7% between *P. guineensis* and *P. quadripartita*; 21.1% between *P. aperta* and *P. guineensis*; 21.4% between *P. aperta* and *P. quadripartita*; Table 3). Therefore, we here raise the sub-species status of *P. a. guineensis* to species level.

PHILINE INTRICATA MONTEROSATO, 1884
(FIG. 7A–I)

Philine intricata Monterosato, 1875: 47 (*nomen nudum*). Monterosato, 1884: 47. Nordsieck & García-Talavera, 1979: 171, pl. 43 (as *P. monterosatoi*). van der Linden, 1994: figs 1–6. van der Linden, 1995: 73. Oliverio & Tringali, 2001: 134–137, figs 59–60. Tringali, 2001: 216, figs 33, 41, 48, 49a, b.
?*Philine desmotis* Watson, 1897: 237–238. Malaquias, 2004: 238, fig. 4A–D.

Diagnosis: Shell internal, translucent, elongate-oval, cylindrical, with sculpture of fused pits arranged in transverse lines, forming a fan in the apical part. Body white with brown dots. Larval kidney visible. Radula with three outer lateral teeth and one inner lateral tooth, rachidian tooth absent. Gizzard plates absent. Thick globose bilobed prostate clearly separated from penial sheath.

Barcode: MIWAM195-15 (ZMBN 105807).

Type locality: Palermo, Italy.

Material examined: Off Cintra Bay, Western Sahara, 23°01′30.72″N, 17°01′50.52″W, 1 spec.,

dissected and sequenced, ZMBN 105807, H = 1.7 mm.

Shell (Fig. 7D–H): H = 1.7 mm. Internal, thin, translucent; elongate-oval, cylindrical in shape; aperture wide with thin white parietal callus, outer lip scalloped, apex obtuse, slightly umbilicated; sculpture visible through mantle, consisting of transverse lines of pits fused to form grooves, new chains forming a fan in the apical part.

Animal (Fig. 7A–C): Body white with brown dots, mantle thin. Cephalic shield blunt, median groove absent. Larval kidney visible through shell. Eyes present.

Radula: Radular formula ?15 × 3.1.0.1.3.

Gizzard: Gizzard plates absent.

Male reproductive system (Fig. 7I): Prostate thick, globose and bilobed, clearly separated from penial sheath.

Ecology: The species occurs between 85 and 620 m depth (van der Linden, 1994; present study).

Distribution: From Brittany southwards to Cape Verde, Morocco including the archipelagos of the Azores and Canaries; western Mediterranean Sea (France, Italy) (van der Linden, 1994, 1995; present study).

Remarks: This is a difficult species because of the poor original description and of several later odd definitions and personal interpretations (see for reviews van der Linden, 1994; Oliverio & Tringali, 2001). van der Linden (1994) has redescribed *P. intricata* and referred that the shell has a similar chain-like sculpture to that of *P. catena* and a similar narrow and elongated spire to that of *P. angulata*; however, exhibits consistent differences in many other features of the shell (see van der Linden, 1994 for a thorough description). We tentatively here ascribe our specimen to *P. intricata* because of the presence of a folded (umbilicated) columella and we provide the first anatomical data on this species. Oliverio & Tringali (2001) have suggested that the description and illustrations by Vayssiére (1885: 35–38, figs 25–34) of *Philine catena* could refer to *P. intricata* because of the apparent folded columella. Yet, based on the evidence available this remains speculative and our observations depart substantially from the description by Vayssiére (1885) where a single outer-marginal tooth is
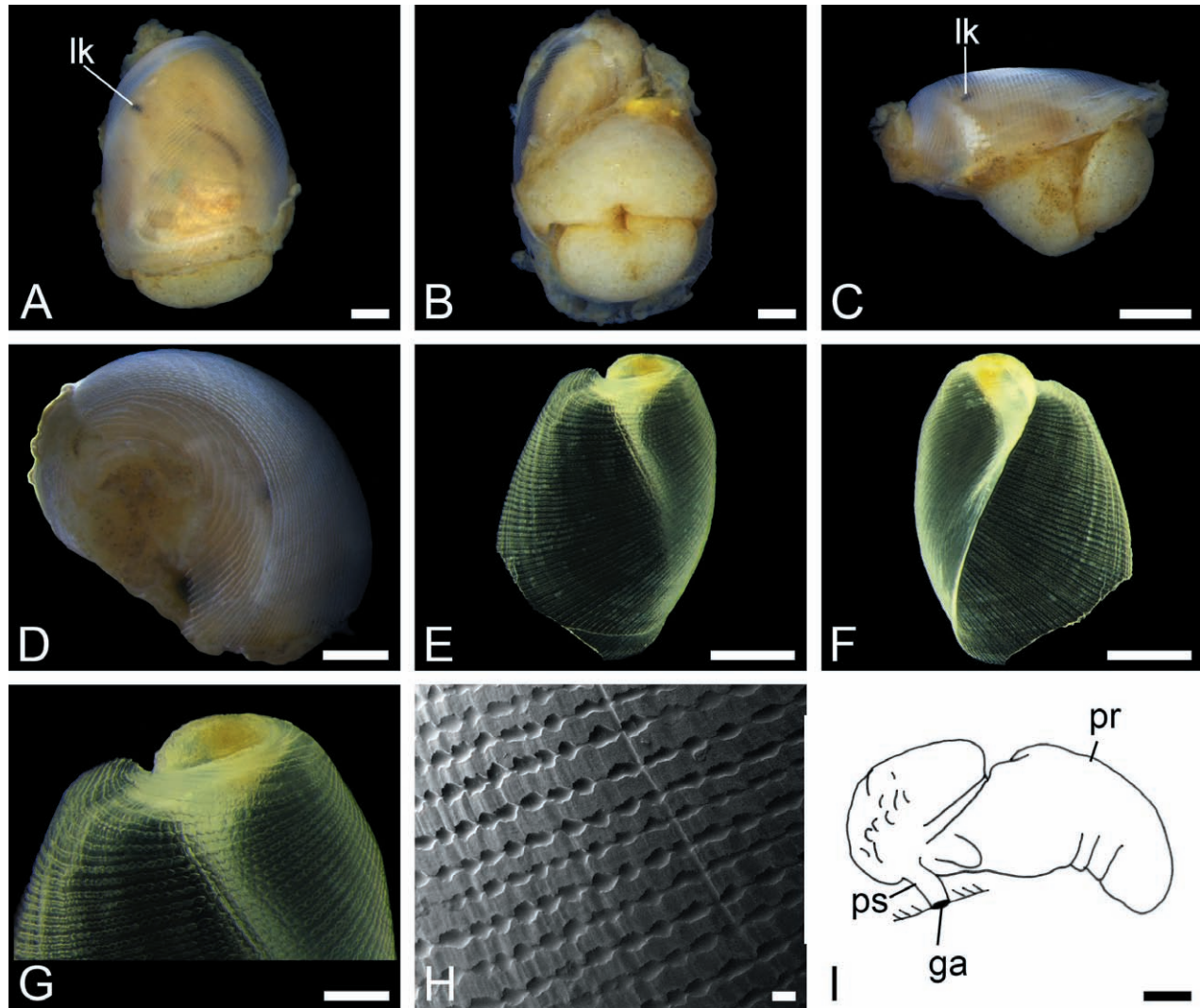
Figure 7. *Philine intricata* (ZMBN 105808, H = 1.7 mm). A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, apical view of complete animal. E, dorsal view of shell (automontage image). F, ventral view of shell (automontage image). G, detail of dorsal posterior part of shell (automontage image). H, sculpture on dorsal surface of shell (SEM). I, male reproductive system. ga, genital aperture; lk, larval kidney; pr, prostate; ps, penial sheath. Scale bars: A–D = 250 μm; E, F = 500 μm; G = 200 μm; H = 20 μm; I = 100 μm.

referred to be present as well as three calcified gizzard plates. Regrettably, we did not succeed in preparing the radula of the only specimen available for SEM and ultrastructural details cannot be provided at this time.

PHILINE RETIFERA (FORBES, 1844) INCERTAE SEDIS
(FIG. 8A–D)

See Ohnheiser & Malaquias (2013: 309) for a list of synonymies.

Diagnosis: Shell external, elongate, square–oval, with sculpture of raised longitudinal and transverse lines forming a white reticulate pattern on dark background. Body pale yellow.

Type locality: Serifos, Greece, Aegean Sea.

Material examined: Off Conakry, Guinea, 09°15′36.36″N, 014°19′19.56″W, 1 shell, ZMBN 105811, H = 2.3 mm. Funchal Bay, Madeira I., 2 shells, NMW.1955.158.02421 (lectotype) and NMW.1955.158.02467, H = 1.77, 3.0 mm (paralectotype).

Shell (Fig. 8A–D): Maximum H = 3.0 mm. External; elongate, squared–oval in shape, aperture wide with

Table 3. Kimura two-parameter distances (K2P) between and within groups for putative species of Philinidae *s.l.* (n/c = not computed)

	Between groups 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Within groups	
1 P. aperta															P. aperta	0.013
2 L. confusa	0.255														L. confusa	0.002
3 P. finmarchica	0.247	0.250													P. finmarchica	0.003
4 P. guineensis	0.211	0.308	0.259												P. guineensis	0.033
5 P. indistincta	0.262	0.229	0.196	0.257											P. indistincta	n/c
6 P. intricata	0.268	0.202	0.195	0.265	0.167										P. intricata	n/c
7 L. nanseni	0.298	0.186	0.232	0.276	0.173	0.193									L. nanseni	0.005
8 P. quadripartita	0.214	0.266	0.240	0.227	0.241	0.258	0.259								P. quadripartita	0.022
9 P. scabra	0.227	0.207	0.183	0.257	0.082	0.152	0.176	0.250							P. scabra	0.003
10 Philine sp.	0.295	0.308	0.271	0.251	0.281	0.284	0.296	0.238	0.280						Philine sp.	n/c
11 Laona sp.2	0.261	0.203	0.258	0.275	0.233	0.220	0.225	0.261	0.220	0.288					Laona sp.2	0.007
12 P. schrammi	0.266	0.318	0.268	0.207	0.255	0.280	0.294	0.251	0.248	0.151	0.291				P. schrammi	n/c
13 L. ventricosa	0.248	0.194	0.235	0.280	0.246	0.250	0.202	0.260	0.231	0.294	0.206	0.290			L. ventricosa	0.000
14 Scaphander	0.317	0.265	0.273	0.284	0.250	0.268	0.237	0.268	0.249	0.272	0.262	0.289	0.249		Scaphander	n/c
15 Spiniphiline	0.265	0.272	0.274	0.273	0.218	0.261	0.274	0.267	0.233	0.298	0.308	0.298	0.271	0.301	Spiniphiline	n/c

parietal callus, apex obtuse, slightly sunken, umbilicated; white sculpture consisting of raised longitudinal and transverse lines forming a reticulate pattern.

Animal: Body pale yellow (Philippi, 1844).

Radula: Unknown.

Gizzard: Unknown.

Male reproductive system: Unknown.

Ecology: Between 45 and 100 m on muddy-sand with decaying algae (Mifsud, 2007; present study).

Distribution: Mediterranean Sea (Monterosato, 1884), Madeira I. (Watson, 1897; Malaquias, 2004), off Mauritania (van der Linden, 1995), and Guinea Conakry (present study).

Remarks: This species has a distinct shell with a deep reticulated sculpture, but almost nothing is known concerning its anatomical features. Whether Mediterranean/Lusitanian specimens are conspecific with the African counterparts is difficult to confirm, but based on present shell evidence we ascribe our specimen to this species. The occurrence of *P. retifera* in Guinea Conakry represents a considerable extension of its southern range.

PHILINE SCHRAMMI SP. NOV.
(FIGS 9A–L, 10A–E)

Diagnosis: Shell internal, smooth, whitish translucid, oval; aperture wide. Body whitish. Rachidian tooth absent, one rounded inner lateral tooth with developed, sharp denticulation along inner edge. Gizzard not surrounded by muscle fibre; with two paired and one smaller unpaired spindle-shaped plates; all with wide deep holes. Long, thin, convoluted, prostate emerging from sack-like penial sheath which is tapering towards genital aperture, with blind caecum, separate ejaculatory duct, thin hammer shaped penial papilla with two long, slim pointed lobes, of similar length.

ZooBank registration: urn:lsid:zoobank.org:act:EE 4EA80B-842B-40CE-AF98-1E253EDD16D5

Barcode: BOLD: MIWAM041-13 (ZMBN 92413).

Etymology: This species is named after Jacob Robert Schramm whose endowments led to the
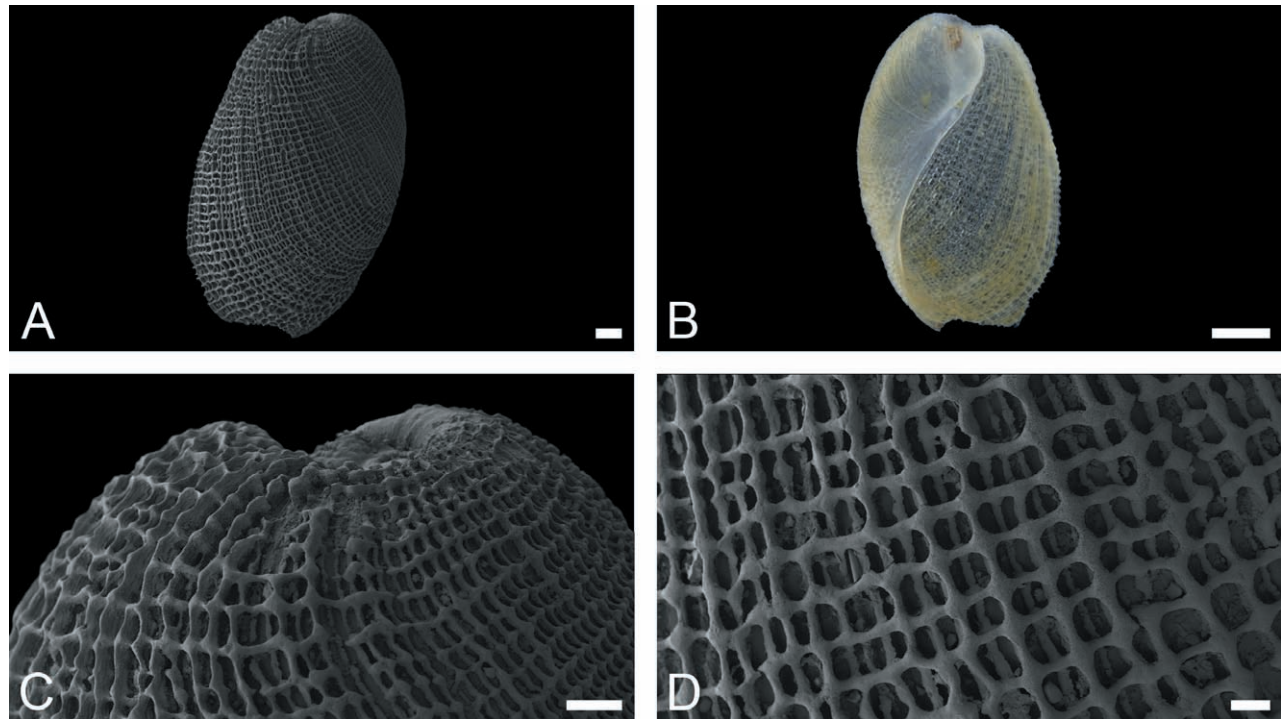
Figure 8. *Philine retifera* (ZMBN 105811, H = 23 mm). A, dorsal view of shell (SEM). B, ventral view of shell (automontage image). C, detail of dorsal posterior part of shell (SEM). D, sculpture on dorsal surface of shell (SEM). Scale bars: A = 200 μm; B = 500 μm; C = 100 μm; D = 50 μm.

birth of the JRS Biodiversity Foundation, a co-funding organization of the present research initiative that made possible this contribution.

Type locality: Off Ilha de Orango, Guinea-Bissau, 10°48′29.88″N, 016°34′57.72″W.

Material examined: Off Ilha de Orango, Guinea-Bissau, 10°48′29.88″N, 016°34′57.72″W, 1 spec., dissected and sequenced, ZMBN 92413, H = 7.3 mm (holotype).

Shell (Fig. 9D, E): H = 7.3 mm. Internal; smooth; whitish translucid; oval in shape, aperture wide, parietal callus present, outer lip smooth, apex obtuse, slightly sunken, not umbilicated.

Animal (Fig. 9A–C): Body whitish in preserved specimens; mantle thick. Cephalic shield blunt, median groove present, posterior pallial lobe with dorsal notch. Larval kidney not visible through shell.

Radula (Fig. 10A, B): Radular formula 19 × 1.0.1. Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips; developed, sharp denticulation along inner edge.

Gizzard (Fig. 9F–L): Gizzard elongate cylindrical, not surrounded by muscle fibres, contains two broad curved paired and one smaller symmetrical unpaired spindle-like plates; two deep wide holes on ventral surface of all plates. Dorsal surface brown–yellowish, ventral surface creamy. Microsculpture on ventral surface only.

Male reproductive system (Fig. 10C–E): Clear separation between long, thin, convoluted prostate and sack-shaped penial sheath with blind caecum, tapering towards the genital aperture. Separate ejaculatory duct. Penial papilla thin, hammer shaped with lobes of similar length, upper part smooth, contained in blind caecum.

Ecology: Soft bottom at 32 m depth.

Distribution: Off Ilha de Orango, Guinea-Bissau.

Remarks: Externally this species resembles *P. quadripartita*, *P. aperta* and *P. guineensis*. However, it exhibits several anatomically unique features. The spindle-like gizzard plates (characters also present in *P. aperta* and *P. quadripartita*) separates this species from *P. guineensis*. The presence of a blind caecum in the penial sack
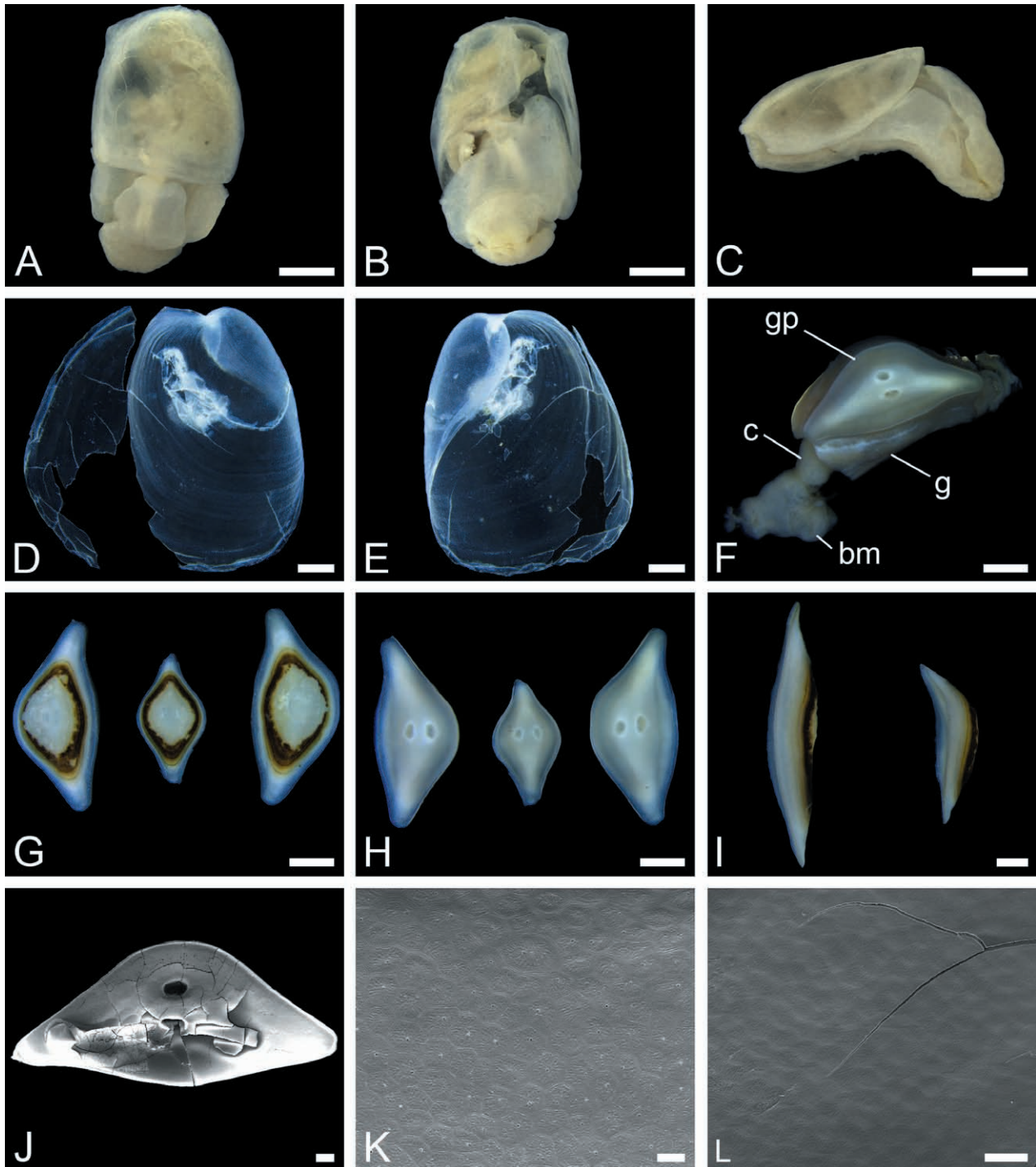
Figure 9. *Philine schrammi* **sp. nov.** (ZMBN 92413, H = 7.3 mm, holotype). A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (automontage image). E, ventral view of shell (automontage image). F, lateral view of gizzard and buccal mass (automontage image). G, dorsal view of gizzard plates (automontage image). H, ventral view of gizzard plates (automontage image). I, lateral view of gizzard plates (automontage image). J, ventral view of paired gizzard plate (SEM). K, ventral gizzard plate surface, central part (SEM). L, ventral gizzard plate surface, outer part. bm, buccal mass; c, crop; g, gizzard; gp, gizzard plate. Scale bars: A–C = 2 mm; D–H = 1 mm; I = 500 μm; J = 200 μm; K = 10 μm; L = 20 μm.
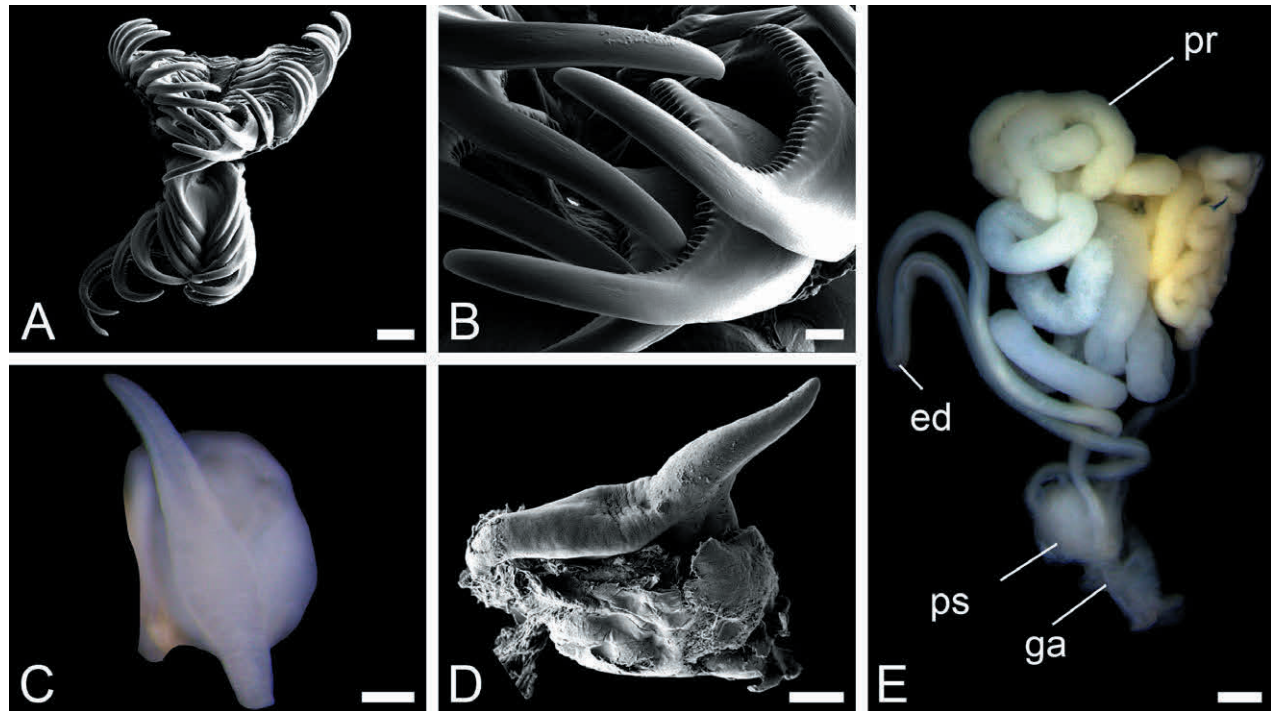
Figure 10. *Philine schrammi* sp. nov. (ZMBN 92413, H = 7.3 mm, holotype). A, radula (SEM). B, detail of radula (SEM). C, top view of penial papilla (automonatge image). D, side view of penial papilla (SEM). E, male reproductive system (automontage image). ed, ejaculatory duct; ga, genital aperture; pr, prostate; ps, penial sheath. Scale bars: A, D = 100 μm; B = 20 μm; C = 125 μm; E = 250 μm.

(characters also present in *P. guineensis* and *P. quadripartita*) distinguishes it from *P. aperta*. The thin penial papilla of *Philine schrammi* sp. nov. with equal lobes separates this species from the other three which possess sub-equal penial lobes. Moreover, the ventral holes in the gizzard plates are comparatively wider than those present in *P. aperta*, *P. guineensis* and *P. quadripartita*. Additionally, all four species are well separated in our molecular phylogenetic analysis (Fig. 14) with COI genetic distances varying from 20.7% between the pair *P. guineensis* and *P. schrammi* and 26.6% between the pair *P. aperta* and *P. schrammi* (K2P; Table 3).

The species *P. guineensis* and *P. schrammi* sp. nov. possibly share overlapping distributions at least around Guinea Bissau, whereas the other two species have disjunct geographies; *P. quadripartita* occurs from Norway, the Mediterranean Sea, southwards most likely until Morocco, but the southern limit of this species needs now to be further investigated. *Philine aperta* is a western Indian Ocean species (Price *et al.*, 2011).

PHILINE SP.
(FIG. 11A–L)

Diagnosis: Shell internal, whitish translucent, smooth. Body whitish translucent (in preserved specimens). Rachidian tooth absent, one rounded inner lateral tooth with developed, sharp

Figure 11. *Philine* sp. (ZMBN 92416, H = 6.8 mm). A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (automontage image). E, ventral view of shell (automontage image). F, lateral view of gizzard and buccal mass (automontage image). G, dorsal view of gizzard plates (automontage image). H, ventral view of paired gizzard plate (SEM). I, ventral gizzard plate surface, central part (SEM). J, radula (SEM). K, detail of radula (SEM). L, male reproductive system (automontage image). bm, buccal mass; c, crop; ed, ejaculatory duct; g, gizzard; ga, genital aperture; gp, gizzard plate; pr, prostate; ps, penial sheath; sg, salivary gland. Scale bars: A–C = 2 mm; D–G = 1 mm; H = 200 μm; I, K = 20 μm; J = 100 μm; L = 250 μm.
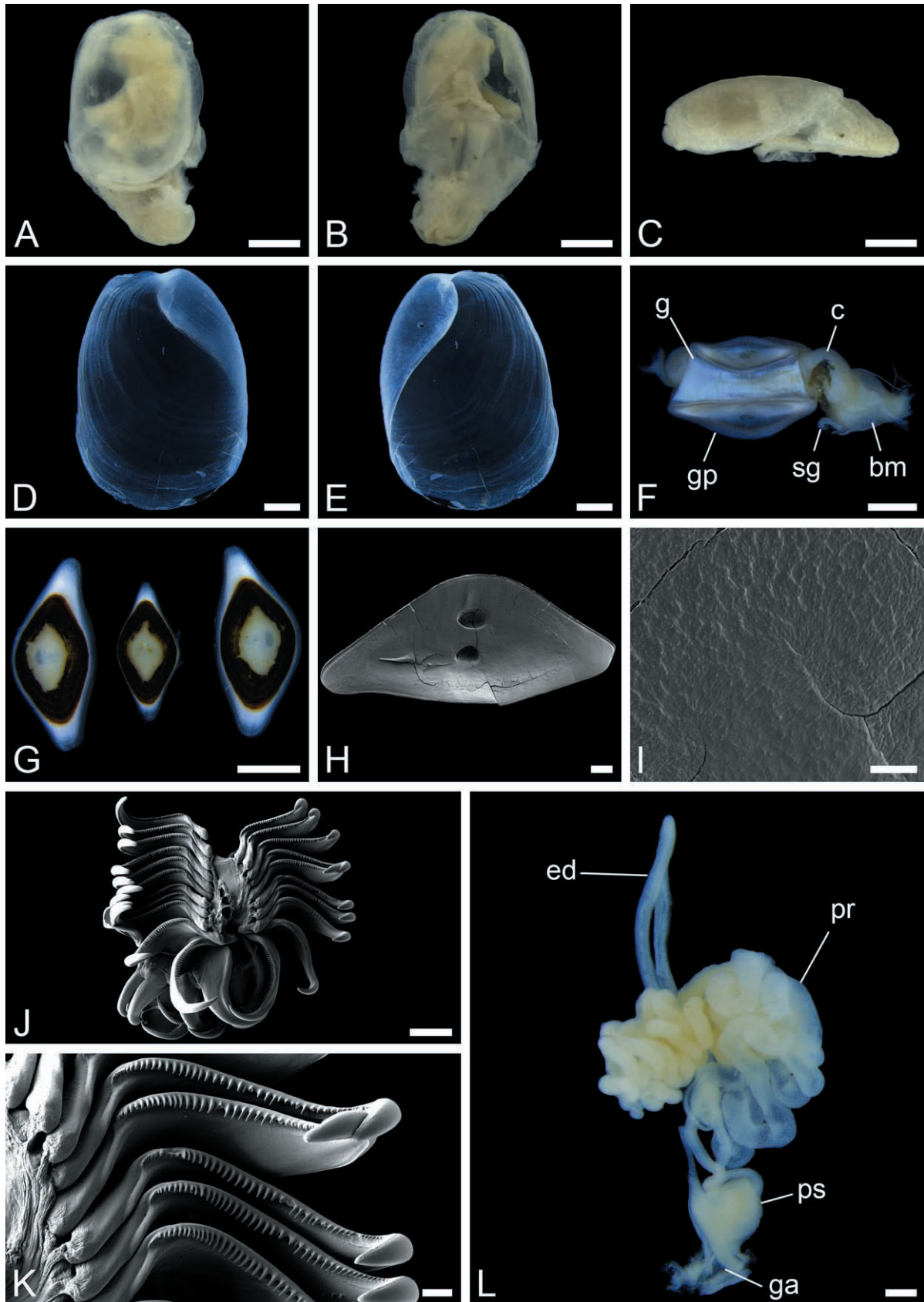
denticulation along inner edge. Gizzard not surrounded by muscle fibres, contains two paired and one unpaired spindle-shaped gizzard plates with deep wide holes. Long, thin, convoluted, prostate emerging from sack-like penial sheath which is tapering towards genital aperture, with blind caecum, separate ejaculatory duct, hammer-shaped penial papilla.

Barcode: BOLD: MIWAM044-13 (ZMBN 92416).

Material examined: Off Ilha de Orango, Guinea-Bissau, 10°48′29.88″N, 016°34′57.72″ W, 1 spec., dissected and sequenced, ZMBN 92416, H = 6.8 mm.

Shell (Fig. 11D, E): H = 6.8 mm. Internal; whitish translucent; oval in shape, aperture wide, with parietal callus, outer lip smooth, apex obtuse, slightly sunken, not umbilicated; smooth.

Animal (Fig. 11A–C): Body whitish translucent in preserved specimens, mantle thick. Cephalic shield blunt, median groove present, posterior pallial lobe with dorsal notch. Larval kidney not visible through shell. Salivary glands shorter than buccal mass.

Radula (Fig. 11J, K): Radular formula 15 × 1.0.1. Rachidian tooth absent. Inner lateral teeth with broad base, curved and rounded tips; developed, sharp denticulation along inner edge.

Gizzard (Fig. 11F–I): Gizzard elongate cylindrical, not surrounded by muscle fibres, contains two broad curved paired and one smaller symmetrical unpaired spindle-like; two deep wide holes on ventral surface of all plates. Dorsal surface brown–yellowish, ventral surface creamy. Microsculpture on ventral surface only.

Male reproductive system (Fig. 11L): Obvious separation between long, thin, convoluted prostate and sack-shaped penial sheath with blind caecum, tapering towards the genital aperture. Separate ejaculatory duct. Penial papilla hammer shaped, upper part contained in blind caecum.

Ecology: Soft bottom at 32 m depth.

Distribution: Off Ilha de Orango, Guinea-Bissau.

Remarks: We could not detect any external and anatomical differences between this species and the sympatric and topotypic *Philine schrammi* sp. nov., but genetic distances showed both to be unequivocally distinct (15.1% K2P, Table 3). Additional material is required to study in detail the anatomy of these species and clarify the taxonomic status of *Philine* sp.

SPINIPHILINE GOSLINER, 1988
***SPINIPHILINE CABOVERDENSIS* SP. NOV.**
(FIG. 12A–E)

Diagnosis: Shell internal, translucent, squarish-oval, with three spiny elements on posterior upper outer lip. Body white in preserved specimen. Gizzard with two paired and one unpaired plates.

ZooBank registration: urn:lsid:zoobank.org:act:1401 945E-2E2C-4246-9402-59522547E161

Barcode: MIWAM191-15 (ZMBN:DNA92171).

Etymology: Named after its type locality, the Cape Verde Islands.

Type locality: Off Baía das Gatas, São Vicente I., Cape Verde Is, 16°53′28.32″N, 024°53′27.96″W.

Material examined: Off Baía das Gatas, São Vicente I., Cape Verde Is, 16°53′28.32″N, 024°53′27.96″W, 1 spec., dissected and sequenced, H = 0.7 mm. Holotype: ZMBN:DNA92171 (extracted DNA in buffer. Animal dissected).

Shell: H = 0.7 mm. Internal, thin; translucent; squarish-oval in shape, aperture wide, upper outer lip with three spiny elements.

Animal (Fig. 12A–E): Body white semi-translucent, mantle thin. Cephalic shield blunt, median groove absent. Larval kidney not visible through shell.

Radula: Unknown.

Gizzard: With two paired elongated plates and one round unpaired plate.

Male reproductive system: Unknown.

Ecology: Found at 53 m depth.

Distribution: Off Baía das Gatas, São Vicente I., Cape Verde Is.

Remarks: The small size of the only specimen available hindered a detail study of the anatomy of this species and features such as the radula, male reproductive system and structure of the gizzard plates remain unknown. This is the first occurrence of the genus *Spiniphiline* in the Eastern Atlantic Ocean. Gosliner (1988) first described this rare tropical genus from the Aldabra Atoll in the Indian Ocean and Caballer & Ortea (2015) described a second species from the
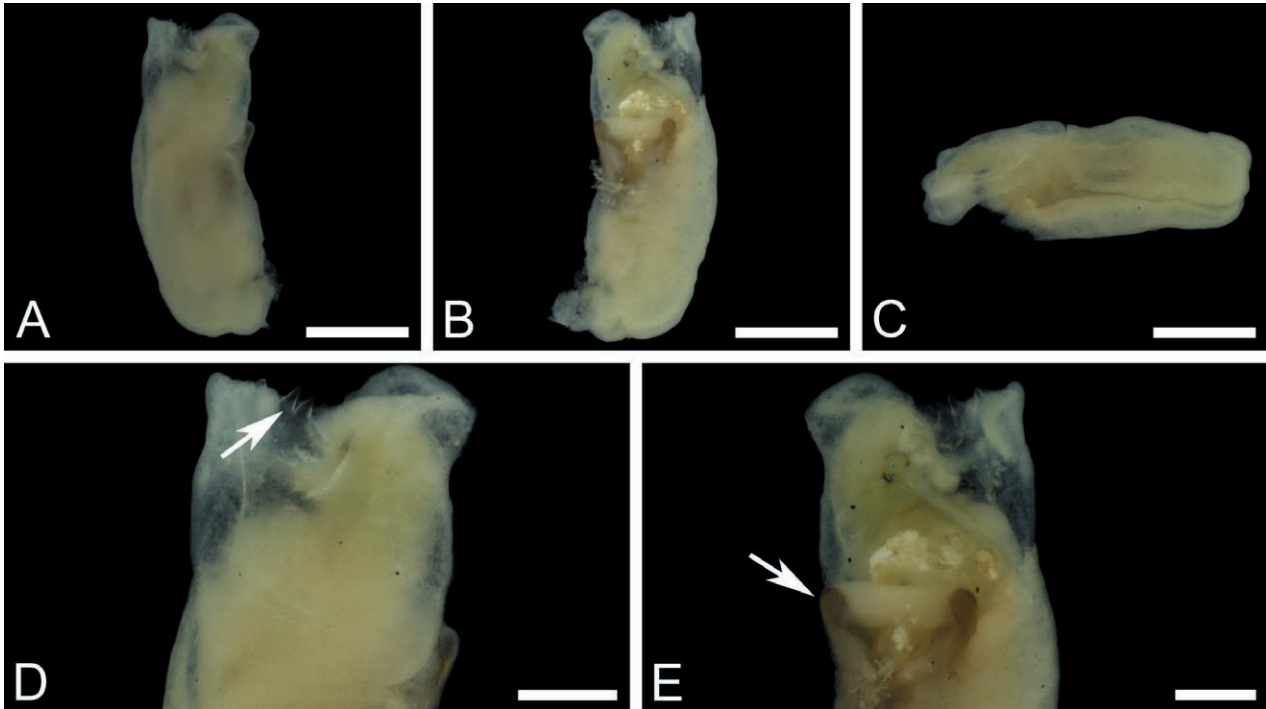
Figure 12. *Spiniphiline caboverdensis* **sp. nov.** (ZMBN:DNA92171, H = 0.7 mm, holotype). A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, detail of posterior part of animal with shell (arrow), dorsal view (automontage image). E, detail of posterior part of animal with shell and gizzard plates (arrow), ventral view (automontage image). Scale bars: A–C = 500 μm; D, E = 200 μm.

Caribbean island of Guadeloupe in the western Atlantic. Our specimen can easily be distinguished from these two by the presence of only three spiny elements in the shell [4–6 spines in *S. kensleyi* Gosliner, 1988 (Aldabra Atoll) and six spines in *S. persei* Caballer & Ortea, 2015 (Guadeloupe Is.)]. Additionally, a preliminary molecular phylogenetic analysis showed that the two Atlantic species are genetically distinct (uncorrected *P*-distance = 6%; T. R. Oskars & M. A. E. Malaquias, unpublished data).

LAONIDAE PRUVOT-FOL, 1954
LAONA A. ADAMS, 1865
LAONA NANSENI SP. NOV.
(FIG. 13A–J)

Diagnosis: Shell external, translucent, oval, apex obtuse, with faint rugose sculpture. Body yellowish. Larval kidney visible. Radula absent. Gizzard not surrounded by muscle fibres, gizzard plates absent.

ZooBank registration: urn:lsid:zoobank.org:act:43 6C1635-0E2A-46A2-86F7-C530985FEAC1

Barcode: BOLD: MIWAM193-15 (ZMBN 105809).

Etymology: This species is named after Fridtjof Nansen, Norwegian scientist and curator at Bergen Museum (University Museum of Bergen) between 1882 and 1889, where he developed pioneering comparative work on the nervous systems of marine animals. Both the project and the research vessel used to collect the material studied in the current contribution are named after Fridtjof Nansen.

Type locality: Off Cintra Bay, Western Sahara, 23°01′30.72″N, 017°01′50.52″W.

Material examined: Off Cintra Bay, Western Sahara, 23°01′30.7″N, 017°01′50.52″W, 2 specs (paratypes), both dissected and one sequenced, ZMBN 105808, H = 1.6 mm, 1.7 mm (sequenced). Off Cintra Bay, Western Sahara, 23°01′30.72″N, 017°01′50.52″W, 1 spec. (holotype), dissected and sequenced, ZMBN 105809, H = 1.7 mm.

Shell (Fig. 13D–F): Maximum H = 1.7 mm. Internal, thin; translucent; oval in shape, aperture wide with thin parietal callus; parietal wall slightly
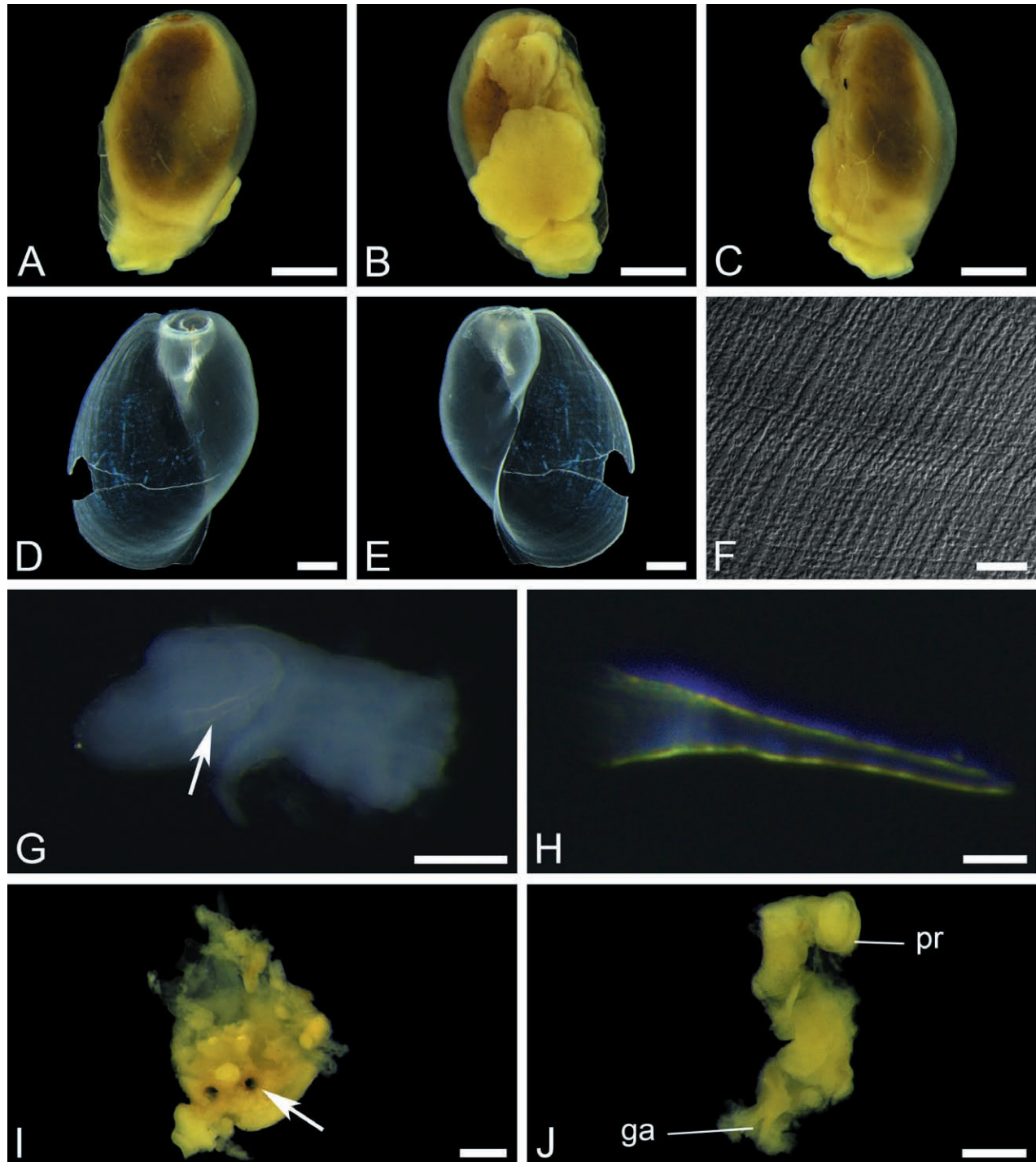
Figure 13. *Laona nanseni* **sp. nov.** A, dorsal view of complete animal. B, ventral view of complete animal. C, right lateral view of complete animal. D, dorsal view of shell (automontage image). E, ventral view of shell (automontage image). F, sculpture on dorsal surface of shell (SEM). G, buccal mass with needle-like structure (arrow) (automontage image). H, needle-like structure (automontage image). I, head region with eyes (arrow), cephalic shield removed (automontage image). J, male reproductive system (automontage image). ga, genital aperture; pr, prostate. Scale bars: A–C = 500 µm; D, E, I = 250 µm; F, H = 20 µm; G = 100 µm; J = 200 µm.

protruding into the posterior half of aperture; outer lip smooth, apex obtuse, slightly sunken; sculpture faintly rugose, consisting of fine transverse and longitudinal lines.

Animal (Fig. 13A–C, I): Body yellowish in preserved specimens. Larval kidney visible through shell. Eyes present.

Radula (Fig. 13G–H): Radula absent; needle-like cuticularized structure present.

Gizzard: Gizzard plates absent.

Male reproductive system (Fig. 13J): Flat tube, no obvious separation between prostate and penial sheath.

Ecology: Specimens collected at 92 m depth in soft bottom.

Distribution: Off Cintra Bay, Western Sahara.

Remarks: This new species has a distinct shell from all other eastern Atlantic philinids, with a nearly smooth appearance masking a fine rugose surface. *Laona nanseni* sp. nov. lacks radula, but a cuticularized structure with needle-shape was found inside the buccal bulb and could be a remnant of this digestive structure. Moreover, our phylogeny rendered this species distinct (Fig. 14) and nested among all other representatives of the genus *Laona*. This species exhibits several distinctive features of the family Laonidae, namely the ovaloid rounded shape of the shell, a parietal wall protruding into the posterior half of aperture and absence of gizzard plates (Oskars *et al.*, 2015).

The shell illustrated and named '*Philine*' cf. *ventricosa* by van der Linden (1995: 81, figs 29, 30) from the Cape Verde Islands might be *L. nanseni* sp. nov.

MOLECULAR SPECIES DELIMITATION AND PHYLOGENETIC ANALYSES

The recursive ABGD analysis identified 15 groups given a series of prior values from 0.001 to 0.049 (Fig. S1, Supporting Information). These groups correspond to the morpho-species that also returned maximum or nearly maximum posterior probabilities in the Bayesian phylogenetic analysis and bootstrap supports of 80–100% in the ML analysis (Fig. 14).

K2P distances between and within groups are given in Table 3. The mean distance between the species was computed to be 22.4% (SE 1.3%). The smallest distance of 8.2% was found between *P. indistincta* and *P. scabra*, and the largest of 31.8% between *L. confusa* and *P. schrammi* sp. nov. The highest intraspecific distance was found in *P. guineensis* (3.3%).

The Bayesian runs converged towards an average standard deviation of split frequencies (ASDSF) of 0.01 after 500 000 generations, indicating that the subsequent samples had been taken from around the likelihood equilibrium. Effective sample sizes (ESS) for all diagnostic statistics showed recommended values of > 200 when the run was terminated (Drummond & Bouckaert, 2015) (http://beast.bio.ed.ac.uk/increasing-esss). The samplings were then summarized with a 'burnin' of 25%. The consensus tree showed posterior probabilities of 1 for all putative species clades with sequence numbers $n \geq 2$ (Fig. 14). There was a topology conflict between a neighbour-joining (NJ, not depicted) tree produced from K2P distances and the ML and Bayesian trees regarding the placement of *L. nanseni* sp. nov. With NJ, *L. nanseni* sp. nov. was rendered sister to *L. confusa*, whereas with ML and Bayesian inference, *L. nanseni* sp. nov. was sister to *L. confusa*, *L. ventricosa* and *Laona* sp. 2 [posterior probability (PP) = 0.96, bootstrap support (BS) = 67%; Fig. 14].

Statistics from calculations with different species distinctness approaches can be found online in Table S1 and Fig. S2 (Supporting Information). The values from tests including ABGD, Rosenberg's and *gsi* indicate good support for all *a priori* recognized species. The P(AB) reciprocal monophyly test is not valid for those under-sampled clades represented by singletons, namely *Spiniphiline caboverdensis* sp. nov., *P. intricata*, *P. indistincta*, *P. schrammi* sp. nov. and *Philine* sp. The species *L. confusa* and *L. ventricosa* show no intraspecific variability and there is also no phylogenetic support for a sister relationship between the two (PP < 0.5; BS = 35; Fig. 14), which may be why the pair fails the test for reciprocal monophyly [P(AB) = 0.11]. The relationship between *Laona* sp. 2, *L. confusa* and *L. ventricosa* should better be described as a trichotomy at present due to a lack of resolution of these clades.

Mapping of the geographical distribution of all species present in West Africa shows a clear discontinuity in the West African Transition Province (WAT) (*sensu* Spalding *et al.*, 2007), around Mauritania–Senegal–Cape Verde Islands. Ten species are distributed northwards of this province with six of those extending their range into the WAT. Eight species are known from either the WAT or southern latitudes only. A single species has a geographical
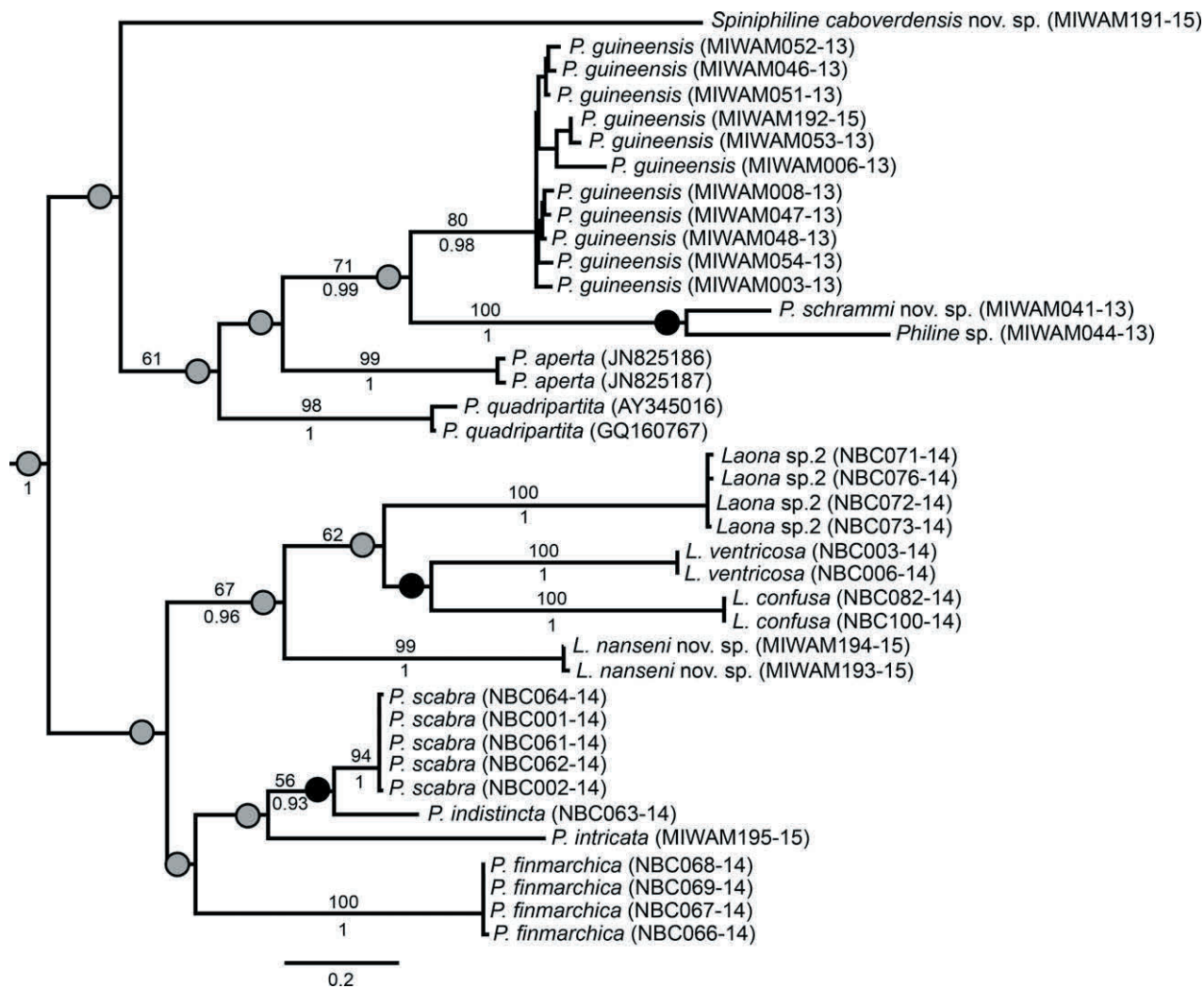
Figure 14. Maximum-likelihood tree indicating significant (grey dots) and non-significant (black dots) results of Rosenberg's test for reciprocal monophyly. Numbers above branches are bootstrap support from maximum-likelihood analysis (≥ 75%) and below branches Bayesian posterior probabilities (≥ 0.90).

distribution that spans north- and southwards across the WAT (Fig. 15).

DISCUSSION

PHYLOGENY AND MOLECULAR SPECIES DELIMITATION

The main aim of our phylogenetic analysis was to aid in the recognition of the African species and not to determine sister species relationships. Therefore, only a reduced taxon set consisting mostly of Atlantic species was included. This may explain (together with the use of only a single gene) the fact that *Philine* was not rendered monophyletic. In contrast, all species attributed to the genus *Laona* based on morphological features were recovered as monophyletic by the Bayesian analysis (PP = 0.96; Fig. 14).

The support for our putative species clusters was always high both with ML and Bayesian inference (Fig. 14) and was additionally supported by the ABGD species delimitation method (Fig. S1, Supporting Information). Moreover all species yielded a *gsi* of 1, indicating monophyly (see Table S1, Supporting Information). The species clusters were also distinct in terms of pairwise K2P distances, with a mean distance of 22.4% (SE 1.3%) (Table 3). This is up to ten times higher than the cut-off values suggested for species recognition using COI barcoding (Hebert *et al.*, 2003). Only *P. indistincta* showed a distance of < 10% from its closest neighbour *P. scabra*, a result also obtained by Ohnheiser & Malaquias (2013). Yet, despite this lower genetic distance, the latter authors have demonstrated that they have distinctive male reproductive systems. Additionally, there is also compelling
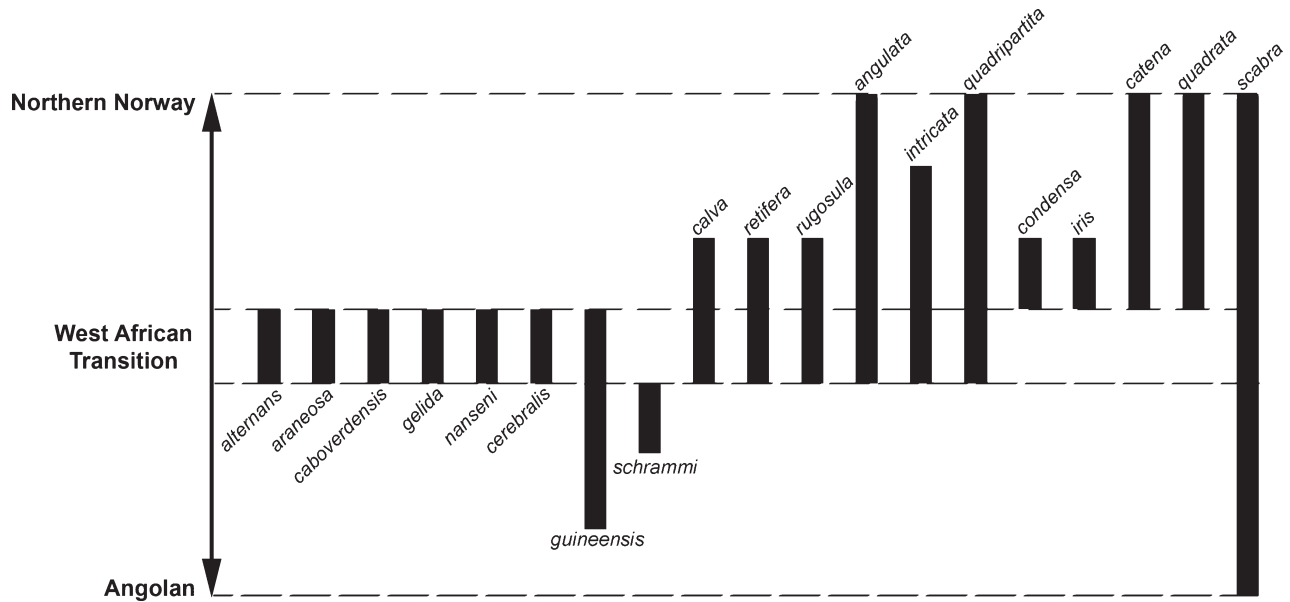
Figure 15. Diagrammatic representation of the latitudinal range of Philinidae *s.l.* species present in West Africa, highlighting the WAT Province (West African Transition) as a breaking point in the distribution of species. For accurate distributions see Table 1.

evidence from morphological characters to recognize all species identified by the molecular methods (see species descriptions and Table 1).

Rosenberg's P(AB) and *gsi* tests depend on the provided tree topology, and the use of an NJ tree instead of an ML tree on these data did not change the support for these groups being separate units. Gene trees can depart from their species tree as a result of horizontal gene transfer, hybridization, gene duplication or incomplete lineage sorting, the last named being particularly important in early phases of speciation (e.g. Avise, 1989; Maddison, 1997; Templeton, 2001; Funk & Omland, 2003). According to the Yule model, each of two evolving lineages has equal chance of branching and, accordingly, there is a possibility that shared ancestral polymorphism can be sorted at random to each branch (Yule, 1925). The rationale of Rosenberg's test for reciprocal monophyly is that random sorting may be the source of the monophyly. Therefore, sample size must be sufficiently large to eliminate chance. This is certainly not the case when we deal with singletons as in *P. indistincta*, *P. intricata*, *P. schrammi* sp. nov. and *Philine* sp. (Figs 14, S2, Supporting Information).

DIVERSITY OF PHILINIDAE *S.L.* IN WEST AFRICA

The Philinidae snails were recently the focus of several taxonomic studies that have used characters other than the shell. A common denominator to all these works was the discovery of cryptic diversity; for example, Price *et al.* (2011) addressed the systematics of the Indo-Pacific *Philine aperta* species-complex and described four new species; Ohnheiser & Malaquias (2013) in a study focused on the Scandinavian fauna described two new species; and Gonzales & Gosliner (2014) added six new lineages to the tropical Indo-Pacific fauna mainly from deep waters. Caballer & Ortea (2015) described the second species of *Spiniphiline* from the western Atlantic, and Oskars *et al.* (2015) unravelled the complex phylogenetic relationships of philinid snails and hinted the occurrence of a multitude of undescribed species in the Indo-Pacific, most of them from the deep sea (T. R. Oskars & M. A. E. Malaquias, unpublished data).

Before the present contribution, 15 species of philinids were known in West Africa, five of which resulted from the work of van der Linden (1995) alone and were described based on shells only (see Table 1). van der Linden (1995) referred to the possible occurrence of an additional species – *P. ventricosa* – but he cast doubt on the identity of the single juvenile damaged shell collected at 420 m depth off São Tiago Island, Cape Verde, and therefore we disregard the occurrence of this species in West Africa until sound evidence is available.

In the present monograph, we refer to an additional putative five new species, four of which are here formally described (*P. cerebralis* sp. nov., *L. nanseni* sp. nov., *P. schrammi* sp. nov., *Philine*

sp., *Spiniphiline caboverdensis* sp. nov.) and we provide the first data on the occurrence of the genus *Spiniphiline* in the eastern Atlantic Ocean. This raises the number of known and named species of Philinidae *s.l.* in West Africa to 19.

Price *et al.* (2011) have reinstated the name *P. quadripartita* for the white and large Atlantic philinid form, broadly named by authors as *P. aperta* (e.g. Thompson, 1988; Poppe & Goto, 1991; Cervera *et al.*, 2004). Similarly, in this work we also provide evidence for the existence of a complex of at least four species that have been reported under the name *P. quadripartita* in the eastern Atlantic Ocean. Beside the latter species, our results confirmed the taxonomic validity of *P. guineensis* (originally described as *P. aperta guineensis*) and have unravelled the existence of two additional lineages; one of them is formally described here as *P. schrammi* sp. nov. All these species are indistinguishable by their external morphology, but show subtle differences in their anatomy, mostly in the shape of the gizzard plates and in male reproductive system (see Remarks sections of these species).

BIOGEOGRAPHY OF WEST AFRICAN PHILINIDS

A striking biogeographical break was observed around Cape Verde and the Sahelian upwelling system between Mauritania and Guinea Bissau. This coincides with a classical transition zone between the northern cold-temperate fauna of the Lusitanian (including the Canaries, Azores and Madeira archipelagos) and northern European seas provinces and a more southern fauna inhabiting the Tropical Eastern Atlantic/Gulf of Guinea Provinces (the WAT *sensu* Spalding *et al.*, 2007; Briggs & Bowen, 2012).

Of the 19 named species of Philinidae in West Africa, eight have their northern geographical range in this area or are geographically restricted to the WAT Province, and ten species have their southern limit here or just further north (Fig. 15; see Table 1 for detailed distributions of species). Only *P. scabra* seems to span across this biogeographical break point (Fig. 15). Nevertheless, as pointed out in the Remarks section for *P. cerebralis* sp. nov. (Taxonomic Results), the previous use of the name *P. scabra* for West African specimens might result from a misidentification as the shells of the latter two species are nearly indistinguishable. Likewise, the citations of *P. quadripartita* south of Morocco are doubtful, as they probably refer to one of its southern cryptic species described in this work.

García & Bertsch (2009) have suggested a similar discontinuity for the 'opisthobranch' gastropods in general (*sensu* Burn & Thompson, 1998). The authors have found a break roughly in this same area separating a predominantly Atlanto-Mediterranean fauna confined southwards by the cold-temperate Canary current (Artic and Temperate Northern Atlantic realms; *sensu* Spalding *et al.*, 2007) with an apparent limited capacity to extend into warm waters, and a southern fauna restricted in the north by the warm Senegalese waters and in the south by the cold waters of the Benguela current.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article:

Fig. S1. Results from recursive automatic barcode gap detection (ABGD) based on COI sequences.
Fig. S2. Cladogram of the ML tree in Figure 13 with node numbers and table with Rosenberg's P(AB) for each node.
Table S1. Statistics for species computed with the Species Delimitation Plugin in the software Geneious and with the gsi-web service.