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

MANUEL ANTÓNIO E. MALAQUIAS*, LENA T. OHNHEISER, TROND R. OSKARS and ENDRE WILLASSEN

Phylogenetic Systematics and Evolution Research Group, Section of Taxonomy and Evolution, Department of Natural History, University Museum of Bergen, University of Bergen, PB 7800, 5020 Bergen, Norway

Received 16 December 2015; revised 19 April 2016; accepted for publication 17 May 2016

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.

© 2016 The Authors. Zoological Journal of the Linnean Society published by John Wiley & Sons Ltd on behalf of The Linnean Society of London, Zoological Journal of the Linnean Society, 2017
doi: 10.1111/zoj.12478


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 coastal and shallow habitats (for lists of references see Hemmen & Groh, 1989; Rolän & Ryall, 1999; Ardovini & Cossignani, 2004). Of note, because of their breadth, descriptions or illustrations, are the works by Nicklés (1950), Marcus & Marcus (1966) and Ardovini & Cossignani (2004), and despite their limited geographical focus the works by
Bernard (1984, Gabon), Rolán (2005, Cape Verde Islands) and Hernández et al. (2011, Canary Island).

Philinids are a group of marine infaunal Cephalopoda 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 lineages 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. quadrirpartita (= Philine aperta); Watson, 1910; van der Linden, 1995; Rolán & Ryall, 1999; Rolán, 2005; Hernández et al., 2011].

The wide geographical distribution of some philinid species (such as P. quadrirpartita 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, Carballe & Garcia 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

<table>
<thead>
<tr>
<th>Character/species</th>
<th>Philine araneosa van der Linden, 1995</th>
<th>P. catena (Montagu, 1803)</th>
<th>P. cerebralis sp. nov.</th>
<th>P. gelida van der Linden, 1995</th>
<th>P. guineensis</th>
<th>P. intrinsica Monterosato, 1884</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Family assignment</strong></td>
<td>Philinidae</td>
<td>Philinidae</td>
<td>Philinidae</td>
<td>Philinidae</td>
<td>Philinidae</td>
<td>Philinidae</td>
</tr>
<tr>
<td><strong>Shell</strong></td>
<td>Spaced spiral grooves.</td>
<td>Internal, squarish, flat, wide aperture; spiral grooves.</td>
<td>Internal, elongated, cylindrical, narrow aperture; spiral lines with chainlike sculpture.</td>
<td>Spiral lines of micro-pits and rings.</td>
<td>Internal, smooth with growth lines and faint spiral lines.</td>
<td>Internal, spiral lines of fused pits forming grooves.</td>
</tr>
<tr>
<td><strong>Radula</strong></td>
<td>?</td>
<td>1.1.0.1.1; inner lateral denticulate, outer lateral smooth</td>
<td>?</td>
<td>1.0.1; inner lateral denticulate</td>
<td>3.1.0.1.3</td>
<td></td>
</tr>
<tr>
<td><strong>Gizzard plates</strong></td>
<td>?</td>
<td>Calcified; three equal pointed gizzard plates</td>
<td>Chitinous; three equal spindle shaped plates</td>
<td>?</td>
<td>Absent</td>
<td></td>
</tr>
<tr>
<td><strong>Male reproductive system</strong></td>
<td>?</td>
<td>Feather duster-shaped prostate</td>
<td>Prostate bladelike shaped, separated from tubular penial region</td>
<td>?</td>
<td>Bipedal prostate, separated from penial sheath.</td>
<td></td>
</tr>
<tr>
<td><strong>Ecology</strong></td>
<td>20–430 m</td>
<td>Tidal zone to 2000 m</td>
<td>29 m deep; soft bottom</td>
<td>18 m</td>
<td>37–98 m</td>
<td>80-620 m</td>
</tr>
<tr>
<td><strong>Type locality</strong></td>
<td>West of Boavista L, Cape Verde Is</td>
<td>Bigberry Bay, south coast of Devon, England, UK</td>
<td>Off Nikine, Senegal</td>
<td>Off Mauritania</td>
<td>Gulf of Guinea; between São Tomé and Principe and Nigeria</td>
<td>Palermo, Italy</td>
</tr>
<tr>
<td><strong>Geographical range</strong></td>
<td>Cape Verde Is</td>
<td>From Norway to, Mediterranean Sea, Madeira L., Canaries Is</td>
<td>As type locality</td>
<td>As type locality</td>
<td>Western Sahara, Mauritania, between Ivory Coast and Nigeria; São Tomé and Principe</td>
<td>From northern Brittany, Mediterranean Sea, Azores, Madeira L., Canary Is, Western Sahara, Cape Verde Is</td>
</tr>
</tbody>
</table>

© 2016 The Linnean Society of London, Zoological Journal of the Linnean Society, 2017, 180, 1-95
### Table 1. Continued

<table>
<thead>
<tr>
<th>Character/species</th>
<th>Philine ammosa van der Linden, 1995</th>
<th>P. catena (Montagu, 1803)</th>
<th>P. cerebralis sp. nov.</th>
<th>P. geisla van der Linden, 1995</th>
<th>P. guineensis Marcus &amp; Marcus, 1966</th>
<th>P. intricata Monterosato, 1884</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biogeographical province(s)</td>
<td>West African Seas + Lusitianian Sea + Mediterranean Sea</td>
<td>West African Transition</td>
<td>West African Transition</td>
<td>West African Transition + Gulf of Guinea</td>
<td>West African Transition</td>
<td>Northern European Seas + Mediterranean Sea + Lusitianian + West African Transition</td>
</tr>
<tr>
<td>Remarks</td>
<td>Known from a single shell</td>
<td>Described as a subspecies of Philine aperta</td>
<td>New species here described</td>
<td>Known from a single shell</td>
<td>Described as a subspecies of Philine aperta</td>
<td>Shell similar to those of P. angulata and P. catena</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Character/species</th>
<th>P. iris Tringali, 2001</th>
<th>P. quadrupartita Ascanius, 1772</th>
<th>P. scabra (O. F. Müller, 1776)</th>
<th>P. schrammi sp. nov.</th>
<th>Spiniphiline caboerdensis sp. nov.</th>
<th>Loona alternans van der Linden, 1995</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family assignment</td>
<td>Philinidae</td>
<td>Philinidae</td>
<td>Philinidae</td>
<td>Philinidae</td>
<td>Philinidae</td>
<td>?</td>
</tr>
<tr>
<td>Animal assignment</td>
<td>Reddish-orange</td>
<td>Body white</td>
<td>Body white</td>
<td>Body whitish</td>
<td>Body white</td>
<td>Spiral grooves with ovals, alternated with white bands.</td>
</tr>
<tr>
<td>Shell</td>
<td>Spiral lines of small pits moderately oblong. Maximum height c. 3 mm</td>
<td>Body white; Internal, smooth with faint spiral growth lines. Maximum height c. 30 mm</td>
<td>Body whitish; Internal, smooth. Maximum height c. 10 mm</td>
<td>Body whitish; Internal, with three spines on posterior outer lip. Maximum height c. 1 mm</td>
<td>?</td>
<td>Maximum height 1.4 mm</td>
</tr>
<tr>
<td>Radula</td>
<td>2.1.0; 2.1.2; inner lateral denticulate</td>
<td>1.0.1; inner lateral denticulate; outer lateral smooth</td>
<td>1.0.1; inner lateral denticulate</td>
<td>1.0.1; inner lateral denticulate</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Gizzard plates</td>
<td>Absent</td>
<td>Partly calcified; three equal, spindle-shaped plates</td>
<td>Ventral holes narrow</td>
<td>Calcified; spindle shaped; central plate smaller. Ventral holes wide</td>
<td>Two paired and one unpaired plates</td>
<td>?</td>
</tr>
</tbody>
</table>
Table 1. Continued

<table>
<thead>
<tr>
<th>Character/species</th>
<th>P. iris (Tringali, 2001)</th>
<th>P. quadripartita Ascanius, 1772</th>
<th>P. sabro (O. F. Müller, 1776)</th>
<th>P. schrammi sp. nov.</th>
<th>Spiniaphileinas caboverdensis sp. nov.</th>
<th>Lavastra alternans van der Linden, 1995</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male reproductive system</td>
<td>?</td>
<td>Long, thin, convoluted, prostate; blind caecum present; hammer shaped penial papilla with sub-equal lobes</td>
<td>Long, thin, convoluted prostate; penial papilla cone shaped, verrucose</td>
<td>Prostate convoluted; blind caecum present; hammer shaped penial papilla with two long, slim equal lobes</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Ecology</td>
<td>2-50 m</td>
<td>20-140 m</td>
<td>Down to 900 m deep; coarse and fine sand and mud</td>
<td>32 m deep; soft bottom</td>
<td>53 m deep; soft bottom</td>
<td>38 m</td>
</tr>
<tr>
<td>Type locality</td>
<td>Torres de Alcalá, Morocco, eastern Mediterranean Sea</td>
<td>Arendal, Norway</td>
<td>Not specified; Denmark and/or Norway</td>
<td>Off Ilha de Orango, Guinea-Bissau</td>
<td>Off Baia das Gatas, São Vicente L, Cape Verde Is.</td>
<td>Off Banc d’Arguin, Mauritania</td>
</tr>
<tr>
<td>Geographical range</td>
<td>Malta, Spain, Morocco (Eastern Mediterranean Sea, Madeira, Canary Is, ?off Mauritania; ?Cape Verde Is, ?Angola</td>
<td>Norway to Mediterranean Sea, Madeira, Canary Is, off Mauritania; Gulf of Guinea, Benin, Angola</td>
<td>Norway to Mediterranean Sea, Madeira, Canary Is, off Mauritania; Gulf of Guinea, Benin, Angola</td>
<td>As type locality</td>
<td>As type locality</td>
<td>As type locality</td>
</tr>
<tr>
<td>Biogeographical province(s)</td>
<td>Mediterranean Sea + Lusitanian</td>
<td>Northern European Seas + Lusitanian</td>
<td>Gulf of Guinea, + Mediterranean Sea + Lusitanian + West African Transition + Gulf of Guinea</td>
<td>Northern European Seas + Lusitanian + West African Transition + Gulf of Guinea</td>
<td>Gulf of Guinea</td>
<td>West African + Mediterranean Sea + Lusitanian + West African Transition + Gulf of Guinea</td>
</tr>
<tr>
<td>Remarks</td>
<td>–</td>
<td>This NE Atlantic species probably has its southern geographical limit around Mauritania/Senegal/Cape Verde</td>
<td>It is possible that all records south of Morocco refer to the new species described as P. cerebralis</td>
<td>New species here described</td>
<td>New species here described</td>
<td>Only known from a single shell</td>
</tr>
</tbody>
</table>
Table 1. Continued

<table>
<thead>
<tr>
<th>Character/species</th>
<th>L. condensa</th>
<th>L. nanseni</th>
<th>L. quadralata</th>
<th>'Philiné' angulata</th>
<th>'P.' calva</th>
<th>'P.' retifera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shell</td>
<td>Chain-like spirals of regular microscopic rings. Maximum height 3 mm</td>
<td>External, nearly smooth with faint rugose sculpture. Maximum height c. 2 mm</td>
<td>Spirals chain-like of rings and pits. Maximum height c. 7 mm</td>
<td>Wrinkled pattern of spiral and axial lines</td>
<td>Internal, wing-like protrusion in upper lip, spiral lines with fused pits. Maximum height c. 3 mm</td>
<td>Spils of irregular rings and dots. Maximum height c. 3 mm</td>
</tr>
<tr>
<td>Radula</td>
<td>?</td>
<td>Absent</td>
<td>?</td>
<td>2.1.0.1.2; inner lateral denticulate, outer lateral smooth</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Gizzard plates</td>
<td>?</td>
<td>Absent</td>
<td>Absent</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Male reproductive system</td>
<td>?</td>
<td>Tubular, no obvious separation between prostate and penial sheath</td>
<td>Short, thick, wrinkly prostate emerging from tubular penial sheath</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Ecology</td>
<td>110–630 m</td>
<td>92 m deep; soft bottom</td>
<td>20–2355 m; coarse and fine soft bottoms</td>
<td>450–1167 m</td>
<td>15–160 m</td>
<td>60–405 m</td>
</tr>
<tr>
<td>Type locality</td>
<td>SW of Hierro I., Canary Is</td>
<td>Off Cintia Bay, Western Sahara</td>
<td>Corraline Crag, Sutton, England, UK</td>
<td>Azores</td>
<td>North of Faial L, Azores</td>
<td>Serifos, Greece</td>
</tr>
</tbody>
</table>
Table 1. Continued

<table>
<thead>
<tr>
<th>Character/species</th>
<th>( L. ) condensa ( ) van der Linden, 1995</th>
<th>( L. ) nanseni sp. nov.</th>
<th>( L. ) quadrata ( ) Dautzenberg &amp; H. Fischer, 1896</th>
<th>'Philine' angulata ( ) Jeffreys, 1867 i. s.</th>
<th>'P.' calva ( ) van der Linden, 1995</th>
<th>'P.' retifera (Forbes, 1844)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geographical range</td>
<td>Azores, Canary Is</td>
<td>As type locality</td>
<td>Greenland, Barents and White Seas, Norway, to the Mediterranean Sea, Azores, W. of Cape Jubi Morocco</td>
<td>Azores, Sio Ío L., Cape Verde</td>
<td>Norway to Mediterranean Sea, Azores, Madeira I., Canary Is, NW Africa Cape Verde Is off Mauritania Mediterranean Sea, and adjacent Atlantic, off Mauritania Mediterranean Sea</td>
<td>Mediterranean Sea, Azores, Madeira I., Canary Is, NW Africa Cape Verde Is</td>
</tr>
<tr>
<td>Biogeographical province(s)</td>
<td>Lusitanian</td>
<td>West African</td>
<td>Lusitanian</td>
<td>Lusitanian</td>
<td>Lusitanian</td>
<td>Lusitanian</td>
</tr>
<tr>
<td></td>
<td></td>
<td>African Transition</td>
<td>+ West African Transition</td>
<td></td>
<td>+ Mediterranean Sea + West African Transition</td>
<td>+ Mediterranean Sea + West African Transition</td>
</tr>
<tr>
<td>Remarks</td>
<td>Only known from shells New species here described</td>
<td>African records based on shells only</td>
<td>Only known from shells</td>
<td>References to the region apparently based on shells</td>
<td>Only known from shells African records based on shells only</td>
<td></td>
</tr>
</tbody>
</table>

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 RV 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 caliper 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 Holzner-Gel (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

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Locality</th>
<th>Voucher no</th>
<th>GenBank (GB)/BOLD Accession No</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laona confusa</td>
<td>Norway</td>
<td>ZMBN 94153</td>
<td>BOLD, NBC100-14</td>
</tr>
<tr>
<td>Laona confusa</td>
<td>Norway</td>
<td>ZMBN 95223</td>
<td>BOLD, NBC082-14</td>
</tr>
<tr>
<td>Laona nanseni sp. nov.</td>
<td>Western Sahara</td>
<td>ZMBN 105808</td>
<td>BOLD, MIWAM194-15</td>
</tr>
<tr>
<td>Laona nanseni sp. nov.</td>
<td>Western Sahara</td>
<td>ZMBN 105809</td>
<td>BOLD, MIWAM193-15</td>
</tr>
<tr>
<td>Laona ventricosa</td>
<td>Norway</td>
<td>ZMBN 81820</td>
<td>BOLD, NCB003-14</td>
</tr>
<tr>
<td>Laona ventricosa</td>
<td>Norway</td>
<td>ZMBN 88008</td>
<td>BOLD, NCB006-14</td>
</tr>
<tr>
<td>Laona sp.2</td>
<td>Norway</td>
<td>ZMBN 95212</td>
<td>BOLD, NCB071-14</td>
</tr>
<tr>
<td>Laona sp.2</td>
<td>Norway</td>
<td>ZMBN 95213</td>
<td>BOLD, NCB072-14</td>
</tr>
<tr>
<td>Laona sp.2</td>
<td>Norway</td>
<td>ZMBN 95214</td>
<td>BOLD, NCB073-14</td>
</tr>
<tr>
<td>Laona sp.2</td>
<td>Norway</td>
<td>ZMBN 95217</td>
<td>BOLD, NCB076-14</td>
</tr>
<tr>
<td>Philine aperta</td>
<td>Simon's Bay, Cape Peninsula, South Africa</td>
<td>CASIZ176345</td>
<td>GB, JN825187</td>
</tr>
<tr>
<td>Philine aperta</td>
<td>Simon's Bay, Cape Peninsula, South Africa</td>
<td>CASIZ176332</td>
<td>GB, JN825186</td>
</tr>
<tr>
<td>Philine finmarchica</td>
<td>Norway</td>
<td>ZMBN 95209</td>
<td>BOLD, NCB068-14</td>
</tr>
<tr>
<td>Philine finmarchica</td>
<td>Norway</td>
<td>ZMBN 95210</td>
<td>BOLD, NCB069-14</td>
</tr>
<tr>
<td>Philine finmarchica</td>
<td>Norway</td>
<td>ZMBN 95208</td>
<td>BOLD, NCB067-14</td>
</tr>
<tr>
<td>Philine finmarchica</td>
<td>Norway</td>
<td>ZMBN 95207</td>
<td>BOLD, NCB066-14</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Western Sahara</td>
<td>ZMBN 91994</td>
<td>BOLD, MIWAM006-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Western Sahara</td>
<td>ZMBN 105810</td>
<td>BOLD, MIWAM192-15</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Nigeria</td>
<td>ZMBN 92420</td>
<td>BOLD, MIWAM047-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Nigeria</td>
<td>ZMBN 92421</td>
<td>BOLD, MIWAM048-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Nigeria</td>
<td>ZMBN 92003</td>
<td>BOLD, MIWAM008-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Nigeria</td>
<td>ZMBN 92419</td>
<td>BOLD, MIWAM046-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Mauritania</td>
<td>ZMBN 92426</td>
<td>BOLD, MIWAM053-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Mauritania</td>
<td>ZMBN 91989</td>
<td>BOLD, MIWAM003-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Mauritania</td>
<td>ZMBN 92424</td>
<td>BOLD, MIWAM051-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Mauritania</td>
<td>ZMBN 92425</td>
<td>BOLD, MIWAM052-13</td>
</tr>
<tr>
<td>Philine guineensis</td>
<td>Mauritania</td>
<td>ZMBN 92427</td>
<td>BOLD, MIWAM054-13</td>
</tr>
<tr>
<td>Philine indistincta</td>
<td>Norway</td>
<td>ZMBN 95204</td>
<td>BOLD, NCB063-14</td>
</tr>
<tr>
<td>Philine intricata</td>
<td>Western Sahara</td>
<td>ZMBN 105807</td>
<td>BOLD, MIWAM195-15</td>
</tr>
<tr>
<td>Philine quadripartita</td>
<td>Tjärnö, Sweden</td>
<td>MCZ:DNA101778</td>
<td>GB, GQ160767</td>
</tr>
<tr>
<td>Philine quadripartita</td>
<td>Murcia, Spain</td>
<td>-</td>
<td>GB, AY345016</td>
</tr>
<tr>
<td>Philine scabra</td>
<td>Norway</td>
<td>ZMBN 95202</td>
<td>BOLD, NCB061-14</td>
</tr>
<tr>
<td>Philine scabra</td>
<td>Norway</td>
<td>ZMBN 95205</td>
<td>BOLD, NCB064-14</td>
</tr>
<tr>
<td>Philine scabra</td>
<td>Norway</td>
<td>ZMBN 87077</td>
<td>BOLD, NCB001-14</td>
</tr>
<tr>
<td>Philine scabra</td>
<td>Norway</td>
<td>ZMBN 81821</td>
<td>BOLD, NCB002-14</td>
</tr>
<tr>
<td>Philine scabra</td>
<td>Norway</td>
<td>ZMBN 95203</td>
<td>BOLD, NCB062-14</td>
</tr>
<tr>
<td>Philine schrammi sp. nov.</td>
<td>Guinea Bissau</td>
<td>ZMBN 92413</td>
<td>BOLD, MIWAM041-13</td>
</tr>
<tr>
<td>Philine sp.</td>
<td>Guinea Bissau</td>
<td>ZMBN 92416</td>
<td>BOLD, MIWAM044-13</td>
</tr>
<tr>
<td>Spinophilina caboverdensis sp. nov.</td>
<td>São Tiago I., Cape Verde Is</td>
<td>ZMBN:DNA92171</td>
<td>BOLD, MIWAM191-15</td>
</tr>
<tr>
<td>Scaphander lignarius</td>
<td>Norway</td>
<td>ZMBN 95233</td>
<td>BOLD, NBC092-14</td>
</tr>
</tbody>
</table>

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 2013). ABGD 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 $P_{\text{min}}$ and $P_{\text{max}}$, 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 (Cummins, 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 Philinididae 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 CEPHALASPIDA 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

Figure 1. The tree for the SDP computations was estimated with random branching. If the null hypothesis is that lineages evolve according to a Yule model of speciation, sequences under the null model of random coalescence will be monophyletic. IntraDist to InterDist; PID(Liberal) 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 server plugin Genealogical Sorting Index (SDP version 1.4.3; Masters, Fan & Ross, 2010) plugin in Geneious, using the GTR model and SPR-search with 250 bootstrap replicates.

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)**

**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, 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.
Microsculpture on bump on dorsal side; bump located posteriorly in one uniformly brown; all plates with an elevated rounded surface consisted of muscle fibres; contains three kidney-bean-shaped bases. Inner and outer lateral teeth curved with broad Radula: short pointed finger-like extensions. Jaws (Fig. 1O): presence of eyes. Shell (Fig. 1D): Cephalic shield blunt, median groove absent, specimen; mantle thin. Larval kidney visible through cephalic shield and pallial lobe in preserved Animal (Fig. 1A). Distribution: north of UK (Larne, Antrim, north of Tromsø, the Faeroes, Shetlands, British Isles (J. G. Jeffreys, 1867; Thompson, 1988; present study) on sand, mud and gravel (Moreno & Templado, 1998; Sneli et al., 2005; Høisæter, 2009). Thin; white; square decussate test. Remarks: The presence of jaws is reported in philinid snails. Unfortunately, the minute size of the specimen hampered the successful preparation of the radula. The mouth could not be studied. It is the first time that the presence of jaws is reported in the family. Southern distribution spanning across the entire European coastline southwards to Mauritania in West Africa, and the North-east coast of America, Norway, the Arctic, and the North Sea (Thompson, 1988), Morocco, Mauretania and south of Lanzarote, Canary Islands (van der Linden, 1995; present study). Slow-moving, the species is usually found in areas where it seems to have its southern geographical range in the Mediterranean. The Linnean Society of London, Zoological Journal of the Linnean Society, 2017, 180, 1–35.

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


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


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′018.36″E.

Material examined: Off Nikine, Senegal, 12°33′53.28″N, 017°21′018.36″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 17^9^1.1.0.1.1. 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...
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*–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 specs, 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, lateral 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.
Diagnosis: Ryall, 1999: 58.

Distribution:

Ecology:

Remarks:

Type locality: The length of the other. papilla with pointed subequal lobes; one about twice separate ejaculatory duct, hammer shaped penial sheath. blind caecum present, emerging from sack-like penial sheath tapering narrow holes. Long, thin, convoluted, prostate shaped prostate and elongate tubular penial sheath.

Material examined: Barcode: H. sp. nov. from all other species

Soft bottom, 29 m depth.

P. cerebralis

Philine aperta guineensis

Marcus, 1974: 360; fig. 104. Rol

H. guineensis

Marcus & Marcus, 1966: 315–330; figs 9–10;

plates; two deep narrow holes on ventral surface of all plates. Dorsal surface of all plates brown–yellowish, ventral surface creamy. Microstructure 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 toptype 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

---

**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.
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)


**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, rachidain 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, translucence; elongate-oval, cylindrical in shape; aperture wide with thin white parietal callus, outer lip scalloped, apex obtuse, slightly umbilicate; 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, exhibit 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 (umbilicate) 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
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
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:EE4EA80B-842B-40CE-AF98-1E253EDD16D5

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

**Etymology:** This species is named after Jacob Robert Schramm whose endowments led to the
Birth of the JRS Biodiversity Foundation, a cofunding 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.
Type locality: Off Ilha de Orango, Guinea-Bissau, 10° 48' 29.88" N, 016° 34' 057.72" W.

Material examined: Off Ilha de Orango, Guinea-Bissau, 10° 48' 29.88" N, 016° 34' 057.72" 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 9 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 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 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 edges.
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).

**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 lm; I, K = 20 lm; J = 100 lm; L = 250 lm.

**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 (automontage 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 lm; B = 20 lm; C = 125 lm; E = 250 lm.
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 callos, 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:1401945E-2E2C-4246-9402-59522547161


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...
Remarks:

Ecology:

Upper part contained in blind caecum.

Separation between long, thin, convoluted prostate surrounded by muscle fibres, contains two broad curved Rachidian tooth absent. Inner lateral teeth with Radula (Fig. 11J, K):

Slightly sunken, not umbilicated; smooth.

Dissected and sequenced, ZMBN 92416, H 26–N, 016 34 945E-2E2C-4246-9402-59522547E161

Round unpaired plate. Squarish-oval in shape, aperture wide, upper outer unknown.


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 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:436C1635-0E2A-46A2-86F7-C530985FEAC1

Laona nanseni

sensu L. nanseni Verde Islands. Ten species are Body yellowish in preserved show no intraspecific variability and

Zoological Journal of the Linnean Society

Radula absent; needle-like 2016 The Authors.

0.96, bootstrap support – = L. confusa recognized 2016 The Authors.

29 100

sp. nov. sp. nov.

sp. L. nanseni

35; L. ventricosa sp. nov. lacks radula, but a = L. confusa et al. and et al.


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.


Downloaded from https://academic.oup.com/zoolinnean/article-abstract/180/1/1/3799574 by Universitetsbiblioteket i Bergen user on 05 December 2017
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-ess). 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 ≥ 2 (Fig. 14). There was a topology conflict between a neighbouring group (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 obtained 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
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
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.

Garcia & 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.

**Acknowledgements**

We extend our gratitude to the NORAD-funded EAF-Nansen programme and the Guinea Current Large Marine Ecosystem (GCLME) and Canary Current Large Marine Ecosystem (CCLME) partners for depositing unsorted and unidentified samples in the University Museum of Bergen. We particularly thank Jens-Otto Krakstad (Institute of Marine Research, Norway) for his coordinating role in the cooperation between EAF-Nansen and our museum. Many crew members contributed to the collecting efforts, but Emmanuel Lamptey (Accra), Akambi Bamikole Williams (Lagos), and Frøydis Lygre and Jon A. Kongsrud (Bergen) played particularly prominent roles in securing benthic samples from GCLME and CCLME. This research also benefited from the collection activities of the Norwegian National programme MAREANO. At the University of Bergen (UoB) F. Lygre, J. A. Kongsrud and Katrine Kongshavn especially invested much time in sorting and in curatorial processing of the samples. We thank Egil Erichsen for help with SEM, and Louise Lindblom and Kenneth Meland for help with the molecular lab work. We also thank the staff of technicians at CCDB and in BOLD for their sequencing and databasing services. We thank Carlo Cunha (Museu de Zoologia, Universidade de São Paulo, Brazil) for the data and images of a topotype specimen of *P. guineensis* housed at the Museu de Zoologia and Ellen Strong (Smithsonian National Museum of Natural History, USA) for images of type material of *P. guineensis*. Lawrence Kirkendall (UoB) helped to improve the English text. This work was produced with financial support from the EAF-Nansen Project, MAREANO, the Norwegian Biodiversity Information Centre, the JRS Biodiversity Foundation, and the University of Bergen.

**References**


The shell-bearing, benthic gastropods on the southern part of the central continental slope off Norway. Journal of Molluscan Studies 76: 234–244.


Jeffreys JG. 1867. British Conchology, or an account of the Mollusca which now inhabit the British Isles and the surrounding seas Vol. IV Marine shells, in continuation of the Gastropoda as far as the Bulla family. J. van Voorst.


Montagu G. 1803. Testacea Britannica or Natural History of British Shells, Marine, Land and Freshwater, including the most minute: systematically arranged and embellled with figures. Romsey: Hollis JS.


**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.