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The first species of *Spiniphiline* Gosliner, 1988 (Gastropoda: Cephalaspidea) in the Atlantic Ocean, with notes on its systematic position

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ABSTRACT

The Indo-Pacific genus *Spiniphiline* Gosliner, 1988 was erected for a rare species of Cephalaspidea characterized by an internal shell with spines. *Spiniphiline kensleyi* Gosliner, 1988 was until now the only known species. During the 'Karubenthos' expedition to the archipelago of Guadeloupe (Lesser Antilles, Caribbean Sea) coordinated by the Muséum national d'Histoire naturelle, Paris, a small philinid was captured on a mäerl bed. This specimen is here described as a new species of *Spiniphiline*—*S. persei*. Its occurrence in Guadeloupe is the first record of the genus in the Atlantic Ocean. The systematic position of *Spiniphiline* is discussed and evidence given for its inclusion in the family Philinidae *s. s.*

INTRODUCTION

The Indo-Pacific genus *Spiniphiline* Gosliner, 1988 was established for a rare cephalaspidean characterized by an internal shell with a "large posteriorly directed wing bearing 4–6 elongate spines" (Gosliner, 1988: 88). *Spiniphiline kensleyi* Gosliner, 1988, the only species known until now, was described based on six specimens collected from coralline algal rubble at up to 3 m depth from Aldabra Atoll, an isolated island in the western Indian Ocean between the Seychelles, East Africa and northern Madagascar. No new records of this species have since been published.

Despite the external resemblance of *S. kensleyi* to species of the family Aglajidae, *Spiniphiline* was placed in Philinidae because of the presence of gizzard plates and the absence of a posterior yellow gland and sensorial bristles on the head (Gosliner, 1988). In an attempt to test the monophyly of the genus *Philine* based on morphological characters, Price, Gosliner & Valdés (2011) indicated the possibility that *Spiniphiline* and *Philine* were synonyms. Since then, several authors have addressed the phylogeny of *Philine* using molecular methods (Krug *et al.*, 2012; Ohnheiser & Malaquias, 2013; Gonzales & Gosliner, 2014; Oskars, Bouchet & Malaquias, 2015) and it has been shown that the Philinidae as traditionally defined are polyphyletic (Oskars *et al.*, 2015). Unfortunately *Spiniphiline* was not included in these studies and the systematic position of the genus has not so far been tested with molecular data.

The 'Karubenthos' expedition to the archipelago of Guadeloupe (Lesser Antilles, Caribbean Sea) took place in May and December 2012. A small cephalaspidean was collected in sublittoral beds of mäerl of the genus *Lithothamnion* (Peña *et al.*, 2014), which resembled a species of Aglajidae, but it bore a bilobate posterior shield and a distinctive internal shell crowned with spines, and had three large gizzard plates and radular teeth bearing denticles. Thus, although Guadeloupe is more than 12,000 km from Aldabra, it was provisionally identified as belonging to the genus *Spiniphiline*.

In this paper, a second species of the genus *Spiniphiline* is described and the genus is recorded for the first time in the Atlantic Ocean. Additionally, the systematic position of *Spiniphiline* within the Philinidae *s. s.* (*sensu* Oskars *et al.*, 2015) is discussed.

MATERIAL AND METHODS

Sampling and morphological studies

The fieldwork was coordinated by the Muséum national d'Histoire naturelle (MNHN), Paris and included 92 stations from the shore to 258 m depth. Samples were obtained by direct search or by scraping, brushing, underwater vacuuming, dredging or examination of various substrates that were collected by wading, snorkelling or scuba diving. The collected material was processed and examined onshore in a temporary laboratory installed by the MNHN in the Marine Biology facility of the Université des Antilles et de la Guyane. The sole specimen (holotype) of *Spiniphiline persei* n. sp. came from a sample obtained by submarine vacuuming in a maërl bed. It was photographed alive in an aquarium and preserved in 98% ethanol for molecular analysis. Internal shell, gizzard plates, radula and gut content were dissected, cleaned by placing them in NaOH solution and rinsed in clean water. To compare with other Philinidae species, diagrams and photos were made using a stereomicroscope with 80× magnification and a camera attachment. Shell, gizzard plates,

radula and gut content were removed, dried and sputter-coated with gold using a Jeol JFC-1200 fine-coater SEM-coating system. Micrographs were obtained on the Jeol 840A low-vacuum scanning electron microscope.

DNA extraction, amplification and sequencing

Extraction and PCRs were carried out at the Service de Systématique Moléculaire (MNHN-UMS 2700). Extraction was done using the QIAamp DNA Micro Kit (Qiagen, Stanford, CA, USA). Fragments of 658 bp of the cytochrome *c* oxidase I (COI) mitochondrial gene, 829 bp of the 28S rRNA nuclear gene, 408 bp of the 16S rRNA mitochondrial gene and 324 bp of the histone H3 nuclear gene were amplified using the COI universal primers LCO1490 and HCO2198 (Folmer *et al*., 1994), the 28S primers C1′ and D2 (Chisholm *et al*., 2001), the 16S primers 16SA and 16SB (Palumbi, 1996) and the H3 primers H3F and H3R (Colgan *et al*., 1998). PCR reactions were performed in 20.5 µl volume, containing: 1 µl of DNA, 15 µl of H_2O, 2 µl of 1X reaction buffer (2.5 mM $MgCl_2$), 0.8 µl dNTP (6.6 mM), 0.3 µl of each primer (10 µM), 1 µl of bovine serum albumin (10 mg/l) and 0.12 µl of Q-Bio Taq (QBiogene, Carlsbad, CA, USA). Annealing temperatures and number of cycles were 48 °C and 40 cycles for COI, 58 °C and 40 cycles for 28S, 53 °C and 35 cycles for 16S and 55 °C and 35 cycles for H3. PCR products were purified with Agencourt® AMPure® XP (Massachusetts, USA) in 384-well plates following the Beckman protocol. Molecular sequencing was carried out at the EUROFINS sequencing facility (France). Both directions were sequenced to confirm accuracy of each sequence. Sequence editing and alignment were done using BioEdit Sequence Alignment Editor software v. 7.2.5. Once the sequences had been validated by Blast search in the NCBI database, the vouchers were submitted to the Barcode of Life Database (BOLD) and the corresponding sequences to GenBank. References to the sequences obtained are included in the description of the species.

Phylogenetic analyses

The main objective of the molecular analyses was to determine the systematic position of *Spiniphiline* within the Cephalaspidea. Thus, we compiled a dataset of COI, 28S and 16S sequences for each representative of the families in the order and for two outgroups, *Aplysia parvula* (Anaspidea) and *Hypselodoris infucata* (Nudibranchia), as available in GenBank (Table 1). The best-fitting partitioning scheme and the nucleotide substitution models were selected using PartitionFinder v. 1.1.1. (Lanfear *et al*., 2012): GTR+I+G (COI_pos1, COI_pos3, 28S_pos1, 16S_pos1) and SYM+G (COI_pos2).

A Bayesian analysis (BA), consisting of two Markov chain runs with eight chains each was performed using MrBayes v. 3.2 (Ronquist & Huelsenbeck, 2003). After 30 million generations, the log-likelihood scores stabilized, convergence was checked using Tracer v. 1.6. (Rambaut *et al*., 2014) and a consensus tree was calculated after omitting the first 25% of the trees as burn-in. A maximum likelihood (ML) analysis was performed in parallel using RAxML-HPC2 on XSEDE in the CIPRES Science Gateway (Miller, Pfeiffer & Schwartz, 2010), with a random starting tree and 1,000 rapid bootstraps.

SYSTEMATIC DESCRIPTION

Order Cephalaspidea Fischer, 1883
Family PHILINIDAE Gray, 1850 (1815)
Genus *Spiniphiline* Gosliner, 1988

Type species: Spiniphiline kensleyi Gosliner, 1988: 79–100, figs 6–8 (holotype California Academy of Sciences CASIZ063253; Lagoon between Passe Femme and Passe du Bois, Aldabra Atoll, Republic of Seychelles).

Diagnosis: Body white, elongate. Head shield longer than posterior shield. Posterior shield bilobate. Internal shell bearing

Table 1. GenBank accession numbers of sequences used in phylogenetic analysis.

Species	Family	COI	28S	16S
Hypselodoris infucata	Nudibranchia	JQ727891.1	FJ917467.1	FJ917426.1
Aplysia parvula	Anaspidea	KJ522466.1	DQ237971.1	JX560139.1
Aglaja tricolorata	Aglajidae	JN825149.1	DQ927215.1	JN825078.1
Navanax aenigmaticus	Aglajidae	JN402027.1	–	JN402120.1
Navanax inermis	Aglajidae	JN402045.1	–	JN402154.1
Chelidonura sandrana	Aglajidae	JN825166.1	AM421945.1	JN825113.1
Atys curta	Haminoeidae	DQ974672.1	DQ927229.1	–
Atys cylindricus	Haminoeidae	DQ974671.1	DQ927228.1	–
Bullacta exarata	Haminoeidae	HQ834118.1	–	HQ833986.1
Haminoea japonica	Haminoeidae	KF615822.1	KF615787.1	–
Cylichna gelida	Cylichnidae	–	EF489374.1	EF489326.1
Philinoglossa praelongata	Philinoglossidae	–	AY427475.1	HQ168411.1
Bulla ampulla	Bullidae	DQ974656.1	DQ927207.1	DQ986588.1
Diaphana sp.	Diaphanidae	EF489394.1	EF489373.1	EF489325.1
Retusa sp.	Retusidae	DQ974679.1	DQ927238.1	–
Sagaminopteron psychedelicum	Gastropteridae	AM421856.1	DQ927225.1	AM421815.1
Siphopteron tigrinum	Gastropteridae	DQ974668.1	DQ927226.1	–
Scaphander mundus	Scaphandridae	KC351565.1	KC351547.1	KC351529.1
Scaphander subglobosus	Scaphandridae	KC351574.1	KC351556.1	KC351539.1
Volvulella sp.	Rhizoridae	DQ974684.1	DQ927244.1	–
*Spiniphiline persei**	Philinidae	KR733277	KR733279	KR733278
Philine aperta	Philinidae	GQ160767.1	DQ279988.1	JN825128.1

*Only *Spiniphiline persei* was newly sequenced for this study.

an extension with spines. Protoconch bearing a small crest on posterior end. Three gizzard plates, occupying most of the anterior body cavity. Paired gizzard plates dorsal, elongate, curved, with central thickening. Unpaired plate ventral, rounded to elongate, one half to one third of the length of the dorsal plates. Radular formula 1.1.0.1.1. Innermost lateral teeth denticulate. Outermost lateral teeth simple and very small. Penis unarmed.

Remarks: The type species was found in the intertidal, in a lagoon, under coralline algal rubble. This kind of habitat appears to be typical for the genus.

***Spiniphiline persei* n. sp.**

(Figs 1, 2)

Holotype: MNHN_IM_2013-52190, partially dissected, 3 mm long, fixed. Shelf on outer side of Îlet à Fajou (stn GS31), 16°21.6′N, 61°34.73′W, 29 m deep, Guadeloupe. Coll. 24 May 2012. BOLD number: SIG001-15.

ZooBank registration: urn:lsid:zoobank.org:act:D7C50D53-E8C9-4CD9-90A9-0FC8D78B2D5B

Etymology: to honour the local Marie-René-Auguste-Alexis Leger, born in Pointe-à-Pitre, Guadeloupe, on 31 May 1887, winner of the Nobel Prize in Literature in 1960, whose pseudonym was Saint-John Perse.

Diagnosis: Body white with white spots, elongate. Head shield over posterior shield. Posterior shield bilobate; lobes palp-shaped, directed ventrally, right one larger. Internal shell bearing an extension with 6 spines oriented posteriorly, partially external. Paired gizzard plates yoke-shaped. Unpaired gizzard plate flattened and lemon-shaped. Radular formula 28 × 1.1.0.1.1; innermost radular teeth bearing 49–50 denticles; outermost radular teeth simple. Penis unarmed. Barcodes: COI (KR733277); 28S (KR733279); 16S (KR733278); H3 (KR733280).

Animal: Body translucent white, with opaque white spots (Fig. 1A), elongate, 3 mm long preserved (Fig. 1C). Eyes not visible through dorsum. Visceral mass yellowish, visible through skin. Head lacking sensorial bristles. Head shield tapering posteriorly, overlapping posterior shield. Posterior shield half as long as head shield. Parapodia short, barely covering the shields. Part of internal shell protruding at end of posterior shield like a 'claw' (Fig. 1A, C, D). Anus ventral, at posterior end of body mass, central (Fig. 1D). Gill leaflets 4, tightly arranged, small, reddish-pink, on right side of anus (Fig. 1B). Posterior shield bilobate. Posterior shield lobes palp-shaped, directed ventrally; right one larger, protecting gill (Fig. 2B–D). Penis unarmed.

Shell: Partially external (not due to damage), 1,193 μm long, bearing long posterior extension with 6 reinforced spines (Figs 1E, 2A). Sutural area between protoconch and extension of teleoconch bearing spines, with porous surface (Fig. 2E). Protoconch partially embedded in teleoconch, bearing a crest on top (Figs 1E, 2A).

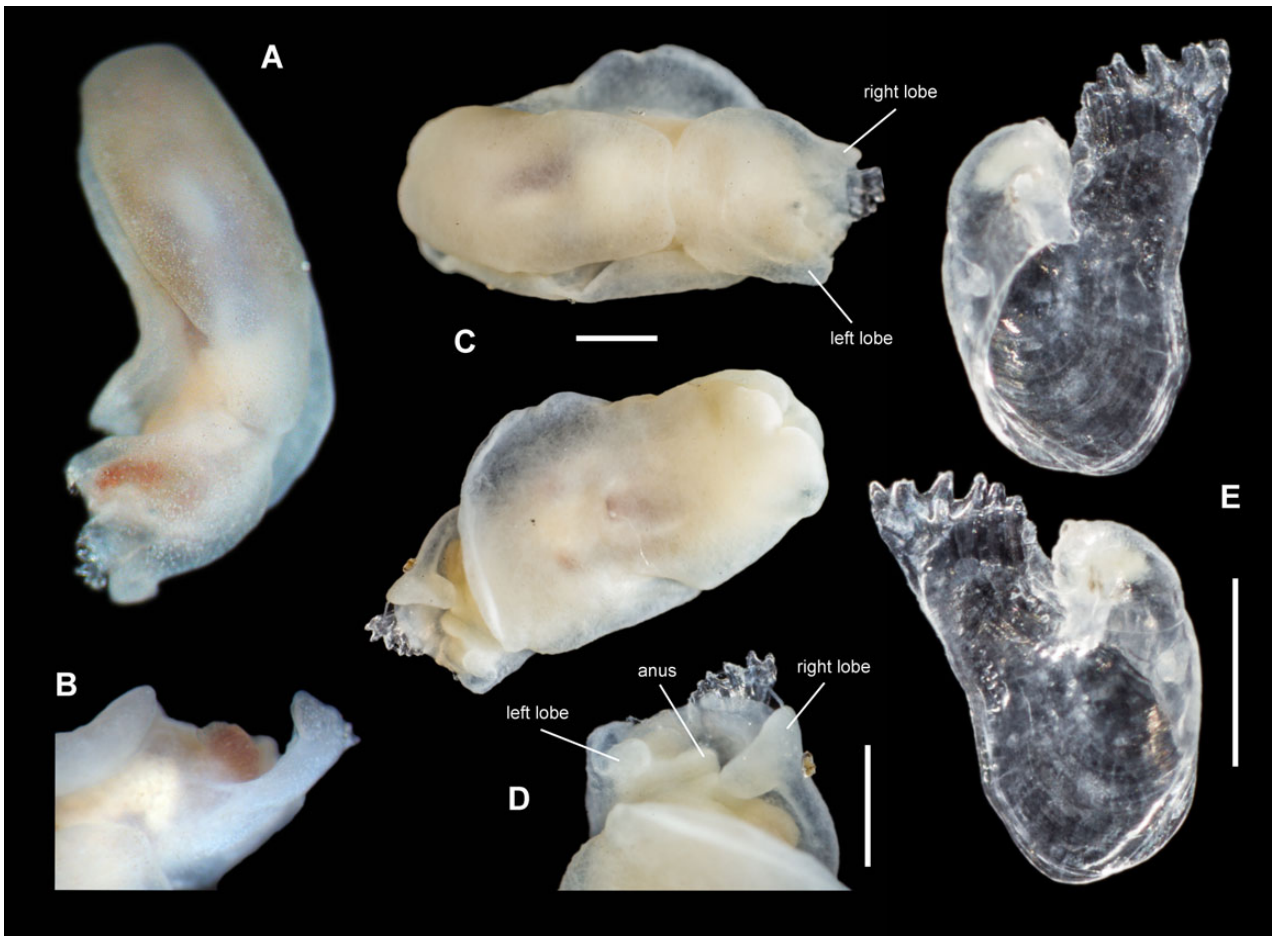

Figure 1. *Spiniphiline persei* n. sp. **A, B.** Living animal. **A.** Dorsal view. **B.** Ventral view of posterior end. **C, D.** Preserved specimen. **C.** Dorsal and ventral view. **D.** Ventral view of posterior end. **E.** Ventral and dorsal view of shell. Scale bars = 500 μm.

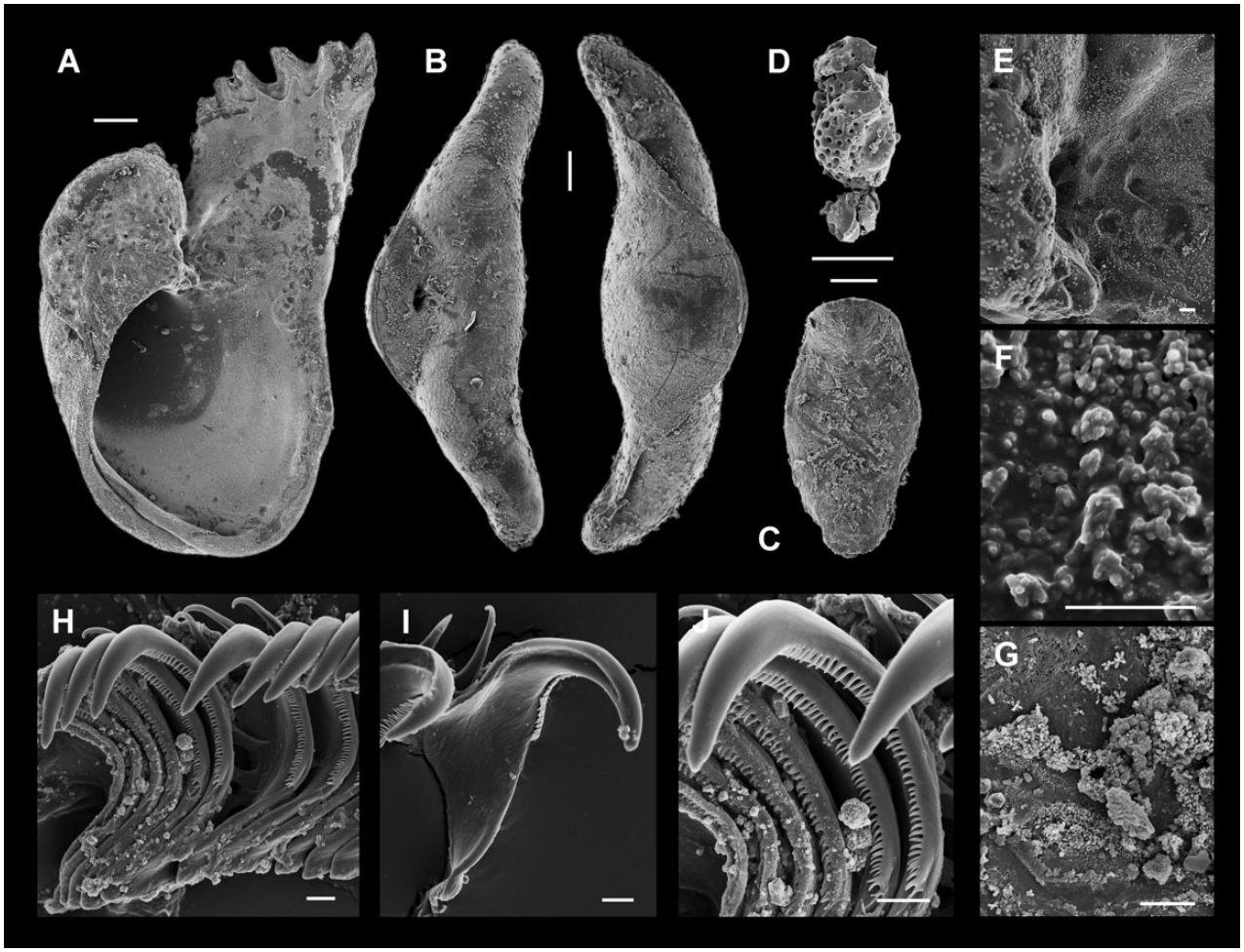

Figure 2. *Spiniphiline persei* n. sp. **A.** Ventral view of shell. **B.** Paired dorsal gizzard plates. **C.** Unpaired ventral gizzard plate. **D.** Foraminifera found in digestive system of holotype. **E.** Detail of ventral side of shell. **F.** Surface of paired gizzard plates. **G.** Surface of unpaired gizzard plate. **H.** Dorsal side of innermost radular teeth. **I.** Ventral side of innermost and outermost radular teeth. **J.** Detail of innermost radular teeth. Scale bars: **A–D** = 100 μm; **E–J** = 10 μm.

Gizzard: Of 3 plates, occupying most of anterior body cavity. Paired gizzard plates 1,300 μm long, dorsal, elongate, curved, yoke-shaped, with roughened surface (Fig. 2F), bearing central thickening on one side and groove on the other (Fig. 2B). Unpaired gizzard plate 560 μm long (Fig. 2C), ventral, lemon-shaped, flattened, slightly roughened (Fig. 2G), one half to one third of length of dorsal plates.

Radula: Radular formula 28 × 1.1.0.1.1. Innermost lateral teeth with 49–50 elongate denticles forming a comb (Fig. 2H, J). Outermost lateral teeth small, attached to innermost teeth, needle-shaped, curved, smooth at top and broader at base (Fig. 2I). Jaws absent.

Habitat and biology: On mäerl bottom, 29 m depth. Feeds on benthic foraminiferans; an almost intact foraminiferan was found inside the gizzard (Fig. 2D).

Remarks: Despite the type localities of *S. kensleyi* (Aldabra, Indo-Pacific) and *S. persei* (Guadeloupe) being far apart and in different oceans, their autopomorphies (see diagnosis of genus) are striking, suggesting that they are congeneric.

S. persei is distinguished from *S. kensleyi* by the following characters: the internal shell, which is partially external in *S. persei*, is nearly twice as big, with proportionally smaller protoconch and spines; the larger radula has more teeth and bears more denticles (innermost); the paired gizzard plates are not so flattened and have a groove; the unpaired gizzard plate is more elongated; the gill has four reddish-pink leaflets; the eyes are not visible through the dorsum. Additionally, the head shield of *S. persei* is proportionally larger, tapered posteriorly and overlaps the posterior shield dorsally.

Phylogenetic analysis

The analysis was based on the alignment of 1,921 bp of 22 sequences from COI, 28S and 16S genes. The resulting BA and ML molecular phylogenetic trees (Fig. 3) confirm that *S. persei* clusters with *Philine aperta* (Philinidae) (posterior probability PP = 1; bootstrap percentage BS = 100) which, together with the Aglajidae, form a monophyletic group (PP = 1; BS = 93). The ML and BA analyses were nearly congruent in their topology and the few differences were not supported. The position of the Diaphanidae (represented by *Diaphana* sp.) as a sister group to all the other families of the Cephalaspidea was supported in both cases (PP = 1; BS = 100).

DISCUSSION

Malaquias *et al.* (2009) produced a molecular phylogeny of the Cephalaspidea *s. l.* in which the Philinidae formed a monophyletic group sister to the Aglajidae. However, the first molecular

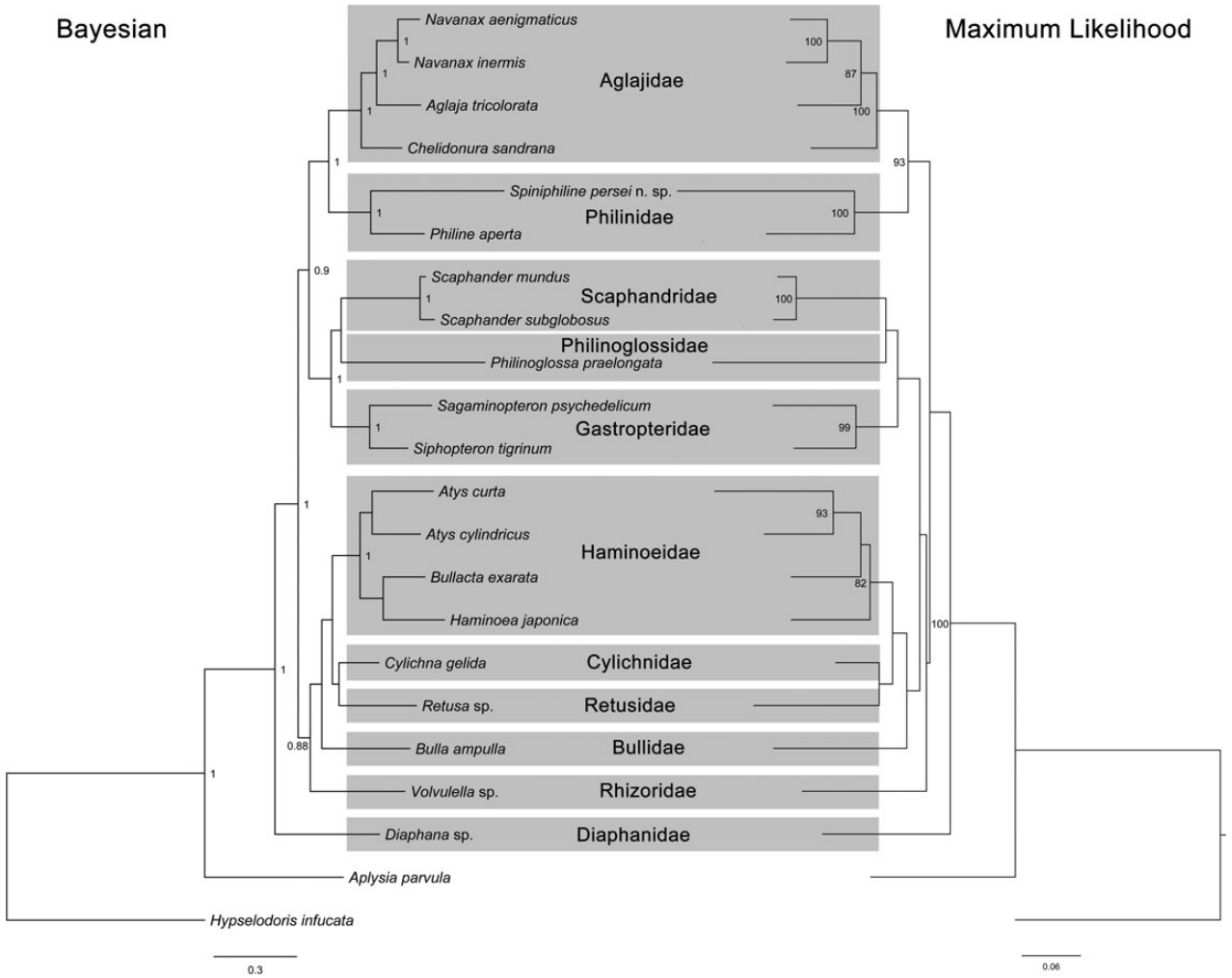

Figure 3. Phylogenetic hypothesis for systematic position of *Spiniphiline* within the Cephalaspidea based on Bayesian inference (left) and maximum likelihood (right) analyses of COI, 28S and 16S concatenated gene sequences.

phylogeny (based on 16S gene) of *Philine* species was that of Krug *et al.* (2012) and their results were consistent with the monophyly of the genus *Philine* and family Philinidae. Based on a COI phylogeny, Ohnheiser & Malaquias (2013) proposed the synonymization of several genera of the Philinidae—namely *Johania*, *Laona* and *Praephiline*—with *Philine*, again supporting both the monophyly of *Philine* and Philinidae. Subsequently, in a molecular phylogeny using the 16S marker and including several tropical Indo-Pacific members of the Philinidae and Aglajidae, Gonzales & Gosliner (2014) retrieved the species *P. rubrata* and *P. orca* nested with the Aglajidae, suggesting the potential nonmonophyly of the Philinidae. Although this result did not receive statistical support, it is nevertheless noteworthy that these two species of *Philine* have pigmented bodies and plate-less muscular gizzards, features that characterize all members of the Aglajidae.

The work of Oskars *et al.* (2015) first soundly demonstrated the polyphyly of Philinidae *s. s.*, these authors recognizing four different clades of familial status: Philinidae *s. s.*, Laonidae, Philinorbidae and a fourth unnamed clade. Unfortunately no representatives of *Spiniphiline* were studied. The taxon sampling in our molecular analysis did not allow us to test the relationships of *Spiniphiline* with other species of Philinidae *s. s.* Nevertheless the morphology of both known species of *Spiniphiline* (*S. kensleyi* and *S. persei*) strongly suggest membership of the family Philinidae *s. s.* (*sensu* Oskars *et al.*, 2015), because of the shared presence of two mirrored gizzard plates and a single outer lateral radular tooth, features that are unique to the Philinidae *s. s.* (Oskars *et al.*, 2015).

One of the most recognizable characters of *Spiniphiline* is its shell, with a "large posteriorly directed wing bearing 4–6 elongate spines", "... distinct from that of any described gastropod" (Gosliner, 1988: 88). The shell has long been the base for the classification of molluscs, but with the advent of molecular and morphometric tools it become clear that the use of shells alone can lead to misleading taxonomic conclusions (Mynhardt *et al.*, 2014; Hirano *et al.*, 2015). Yet, there are several examples in the Cephalaspidea where the shell in combination with other characters has great taxonomic value (Malaquias & Reid, 2008; Ohnheiser & Malaquias, 2013, 2014; Ortea *et al.*, 2014). Ohnheiser & Malaquias (2013) considered that reliance on the shell alone was largely responsible for the confused taxonomy of Philinidae, but showed that when the external morphology was combined with shell features it was possible to diagnose most philinid species.

Price *et al.* (2011) have suggested the possible synonymization of *Spiniphiline* with *Philine*, but the uniqueness of the shell of *Spiniphiline* and its morphological features (see Systematic description) suggest otherwise. Until the phylogenetic affiliation of the genus is thoroughly tested in a molecular framework we propose to maintain its validity.

Spiniphiline seems to be habitat-specific, being restricted to shallow mäerl-coral rubble habitats. More evidence is obviously necessary to confirm this ecological association, but it is striking that the only two species know so far were collected in the same habitat in two different oceans. Additional efforts focussed on these little studied habitats could result in finding new species of *Spiniphiline*; this would certainly help to untangle the systematics and biogeography of the group. Unfortunately, the information about the geographic ranges of coralline algal species is scarce (Peña *et al*., 2015).

Prior to this paper no data have been published on the genus *Spiniphiline* since its original description 37 years ago. The genus is composed of two rare species, known from two ocean basins, with a unique kind of shell distinct from all the remaining members of the Philinidae *s. s*., supporting the validity of the genus. However, further assessment of the systematic position of *Spiniphiline* in a molecular phylogenetic framework is desirable, despite the fact that its taxonomic position within the Philinidae *s. s*. is strongly supported by morphological characters.

With *S. persei* n. sp., the number of sea slugs (Opisthobranchia *s. l*.) known in Guadeloupe is increased to 151 species (Ortea *et al*., 2012, 2013; Caballer & Ortea, 2014; present study).

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