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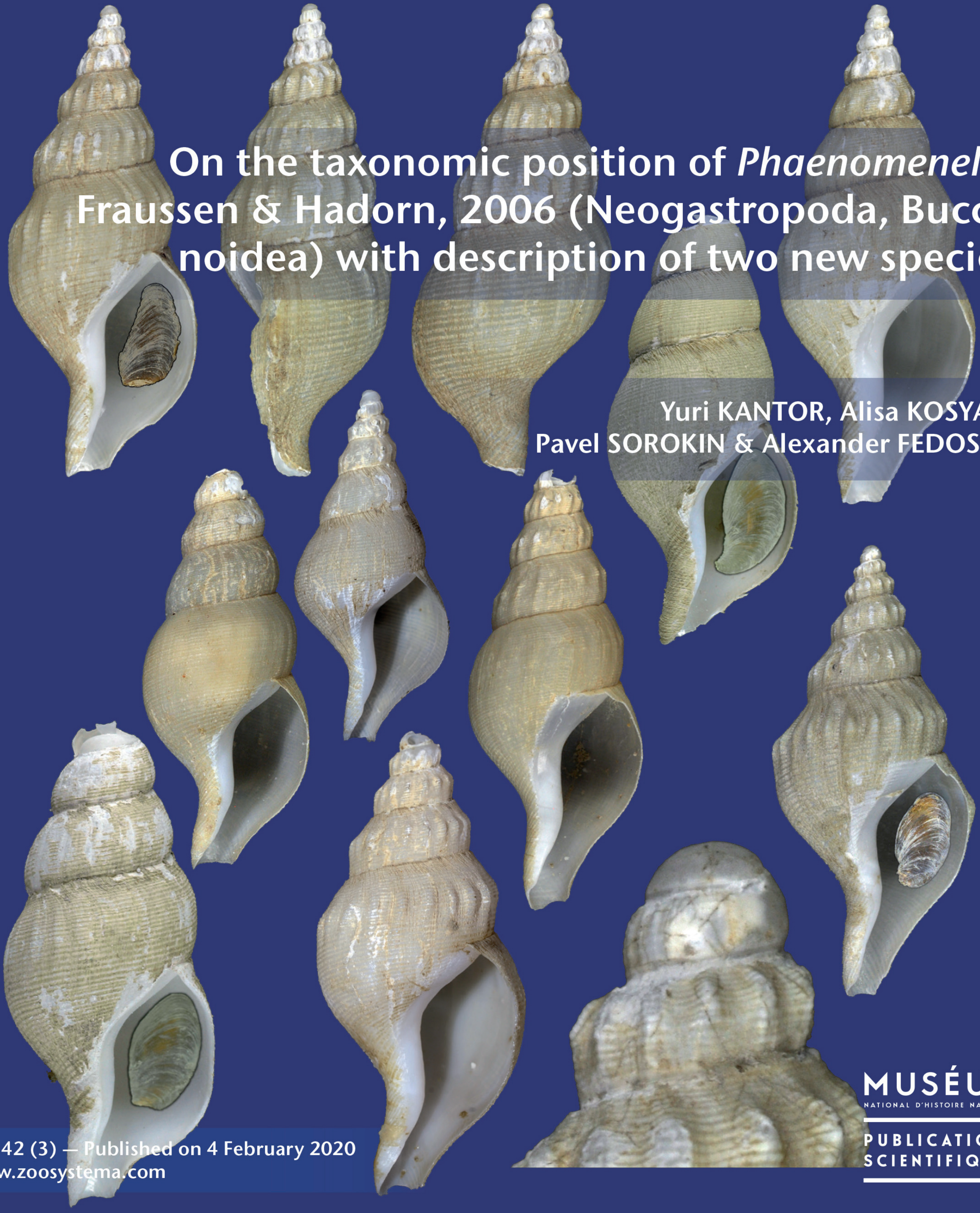

On the taxonomic position of *Phaenomenella* Fraussen & Hadorn, 2006 (Neogastropoda, Buccinoidea) with description of two new species

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Shells of *Phaenomenella nicoi* n. sp.

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On the taxonomic position of *Phaenomenella* Fraussen & Hadorn, 2006 (Neogastropoda, Buccinoidea) with description of two new species

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ABSTRACT

This contribution provides novel information on the anatomy, radula and phylogeny of several species of *Phaenomenella* Fraussen & Hadorn, 2006, a genus of Buccinoidea Rafinesque, 1815 with unclear affinities. Molecular phylogenetic analysis based on sequences of mitochondrial COI and nuclear 28S rRNA genes of different representatives of Buccinoidea revealed close relationships of *Phaenomenella* with *Siphonalia* A. Adams, 1863 both taxa forming a clade with maximal support. The anatomy of two species of the latter genus was examined for the first time for comparative purposes. The subfamily Siphonaliinae Finlay, 1928 was erected for several Recent and fossil genera of Southern Hemisphere Buccinidae Rafinesque, 1815, and is still recognized by current taxonomists (Bouchet *et al.* 2017). Species of all Recent genera of Siphonaliinae were included in our analysis and the monophyly of the subfamily Siphonaliinae in its original scope is rejected. Molecular and morphological data revealed two still unnamed species of *Phaenomenella* from the lower bathyal zone of the South China Sea. These species, *Phaenomenella nicoi* n. sp. and *P. samadiae* n. sp. are described in the present study.

KEY WORDS
Molecular phylogeny,
COI,
28S,
classification,
Siphonaliinae,
new species.

RÉSUMÉ
Position taxonomique de Phaenomenella *Fraussen & Hadorn, 2006 (Neogastropoda: Buccinoidea) et description de deux nouvelles espèces.*
Cette contribution fournit de nouvelles informations sur l'anatomie, la radula et la phylogénie de plusieurs espèces de *Phaenomenella* Fraussen & Hadorn, 2006, un genre de Buccinoidea Rafinesque, 1815 aux affinités peu claires. Une analyse phylogénétique moléculaire basée sur des séquences des gènes mitochondriaux COI et d'ARNr 28S nucléair de différents représentants de Buccinoidea a révélé des relations étroites de *Phaenomenella* avec *Siphonalia* A. Adams, 1863 qui forment un clade avec un soutien maximal. L'anatomie de deux espèces de ce dernier genre a été examinée pour la première fois à des fins de comparaison. La sous-famille Siphonaliinae Finlay, 1928 a été érigée pour plusieurs genres récents et fossiles de Buccinidae Rafinesque, 1815 de l'hémisphère sud, et est toujours reconnue par les taxonomistes actuels (Bouchet *et al.* 2017). Les espèces de tous les genres récents de Siphonaliinae ont été incluses dans notre analyse et la monophylie de la sous-famille Siphonaliinae dans sa définition originelle est rejetée. Les données moléculaires et morphologiques ont révélé deux espèces encore inconnues de *Phaenomenella* de la zone bathyale inférieure du sud de la mer de Chine. Ces espèces, *Phaenomenella nicoi* n. sp. et *P. samadiae* n. sp. sont décrites dans la présente étude.

MOTS CLÉS
Phylogénie moléculaire,
COI,
28S,
classification,
Siphonaliinae,
espèces nouvelles.

INTRODUCTION

The genus *Phaenomenella* Fraussen & Hadorn, 2006, with the type species *Manaria inflata* Shikama, 1971, was established for three species of "Buccinidae" Rafinesque, 1815 from Taiwan and South China Sea (Fraussen & Hadorn 2006). Several additional species were described since and presently the genus includes nine species, all except one from off South East Asia (Fraussen 2008; Fraussen & Stahlschmidt 2012; Fraussen & Stahlschmidt 2013). The anatomy of the genus has never been examined, but the radula was illustrated for two species, *Phaenomenella inflata* (Shikama, 1971) and *Phaenomenella angusta* Fraussen & Hadorn, 2006. The radula is of general buccinid appearance, which gives no clues of the relationships of *Phaenomenella* to other buccinid genera. The position of the genus within Buccinidae was not addressed in previous publications, probably due to still unesolved intrafamiliar classification of the family. The intrageneric shell variability of *Phaenomenella* is high that is hampering providing reliable generic diagnosis.

Among South-East Asian buccinids several genera bear some conchological resemblance to *Phaenomenella*, ie., *Manaria* Smith, 1906, *Eosipho* Thiele, 1929, *Gaillea* Kantor, Puillandre, Fraussen, Fedosov & Bouchet, 2013 (all three genera dwelling on biogenic substrates; Kantor *et al.* 2013) and *Siphonalia* A. Adams, 1863. Buccinidae from biogenic substrates constitute a clade that is well-supported by molecular data, and are characterized by bicuspid lateral teeth (Bouchet & Warén 1986; Kantor *et al.* 2013), while the radula of both *Phaenomenella* and *Siphonalia* is similar and has tricuspid lateral teeth.

Relationships of *Siphonalia* with other Buccinidae are not clear. Its isolated position was recognized by Finlay (1928), who proposed a new subfamily Siphonaliinae in the newly established family Buccinulidae. Having been proposed without diagnosis or discussion, the subfamily originally included several Recent and fossil genera, which were later synonymized with *Penion* Fischer, 1884 (=†*Austrosipho* Cossmann, 1906, *Verconella* Iredale, 1914, *Berylsma* Iredale, 1924), *Aeneator* (=†*Ellicea* Finlay in Marwick 1928, †*Pittella* Marwick, 1928), as well as *Glaphyrina* Finlay, 1926 (presently attributed to Fasciolariidae Gray, 1853; Couto *et al.* 2016) and †*Pomahakia* Finlay, 1927. All genera except the type one are confined to southern hemisphere, mostly to Australian-New Zealand region. The validity and scope of the subfamily have not been revised, although it is recognized in the current taxonomy (Bouchet *et al.* 2017). A recent molecular phylogeny of some southern hemisphere Buccinulinae based on whole mitochondrial genome and nuclear ribosomal sequence data (Vaux *et al.* 2017) revealed that Recent genera included by Finlay into Siphonaliinae do not constitute a monophyletic group. But *Siphonalia* itself was not included in the analysis and therefore its relationships remained unresolved.

In the course of expeditions organized by the Muséum national d'Histoire naturelle, Paris (MNHN) to the South China Sea several specimens of different species of *Phaenomenella* and one species of *Siphonalia* were collected and preserved for DNA sequencing. The examination of this material revealed two still unnamed species. The purpose of the present paper is to provide formal description of the revealed new species, and to clarify relationships of *Phaenomenella* based both on anatomy and on molecular data of extended dataset of Buccinoidea, including groups that are conchologically similar to *Phaenomenella*.

MATERIAL AND METHODS

The material was collected mostly in the research cruises in the South China Sea (DONGSHA 2014, ZHONGSHA 2015) and in the Philippines (AURORA 2007) that were organized respectively by the National Taiwan University and the Muséum national d'Histoire naturelle, Paris (MNHN) with the Philippines Bureau of Fisheries and Aquatic Resources (BFAR).

Specimens collected were processed with a microwave oven (Galindo *et al.* 2014): the living molluscs in small volumes of sea water were exposed to microwaves for 10-30 s, depending on specimen size. Bodies were immediately removed from shells and dropped in 96% ethanol. Specimens processed in this way are suitable for further anatomical studies after soaking them in 70% ethanol. Specimens are registered in the MNHN collection and specimens and sequences are deposited in BOLD (Barcode of Life Datasystem) and GenBank (Table 1).

Due to technical reasons, the sequenced specimens of *Siphonalia spadicea* (Reeve, 1847) were not available for anatomical examination and the material (not suitable for sequencing) on two other species of *Siphonalia* was used for anatomical study.

DNA extraction and PCR

Total DNA was extracted from the piece of foot using either the DNeasy96 Tissue kit or Investigator Kit (Qiagen), following the manufacturer's recommendations. The barcode fragment of the Cytochrome Oxidase I (COI) gene (658 bp) and a 28S rRNA fragment were amplified using the universal primers LCO1490 and HCO2198 (Folmer *et al.* 1994) and C1 and D2 (Jovelin & Justine 2001), respectively. PCRs were performed in 20 µl final volume containing approximately 3 ng template DNA, 1.5 mM MgCl2, 0.26 mM of each nucleotide, 0.3 µl of each primer, 5% DMSO and 0.75 µl of either Taq Polymerase (Qbiogene) or BioHYTaq DNA polymerase (Dialat).

The PCR profile for the COI started with 5 min at 95°C followed by 40 cycles with the denaturation at 95°C (35 sec), annealing at 50°C (35 s) and elongation at 72°C (1 min), with final elongation phase at 72°C (10 min). Similar PCR profiles were set for 28S (annealing at 56°C). COI and 28S genes were sequenced in both directions to confirm accuracy of each sequence. The sequencing was performed by Eurofins or in the SIEE RAS molecular facility on an ABI 3500 Genetic analyser.

Morphology and radula

Radulae were cleaned using diluted bleach (NaOCl), air–dried, coated with gold and examined by scanning electron microscope TeScan TS5130MM in the Institute of Ecology and Evolution of Russian Academy of Sciences, Moscow (IEE RAS). Anatomy was examined on manual dissections.

PHYLOGENETIC ANALYSIS

COI and 28S sequences were aligned using ClustalW implemented in BioEdit v. 7.0.9.0 (Hall 1999); the accuracy of each alignment was checked by eye and if needed modified. COI and 28S sequences of additional 32 buccinoidean taxa, mainly from the datasets of Kantor *et al.* (2013) and Vaux *et al.* (2017) were accessed from GenBank.

Three datasets were analyzed, a single-gene COI dataset (57 taxa) with three codon positions coded as three independent partitions, a nuclear 28S (45 taxa) as single partition, and a concatenated COI–28S dataset (45 taxa), where four partitions corresponded to three codon positions of COI and to the 28S fragment respectively. The single gene datasets were mainly used to evaluate primary species hypotheses (PSHs), proposed based on the shell morphology, whereas the analysis of concatenated dataset allowed us to estimate relationships of *Siphonalia* and remaining genera originally included in Siphonaliinae. The lineage comprising buccinids from the biogenic substrates (Kantor *et al.* 2013) was used to root the tree based on the topology of Buccinidae tree recovered by Galindo *et al.* (2016). In the RAxML analyses (Stamatakis 2006) robustness of nodes was assessed using the Thorough Bootstrapping algorithm (Felsenstein 1985) with 1000 iterations. The Bayesian inference analyses (BI) were performed using MrBayes (Huelsenbeck & Ronquist 2001), running two parallel analyses, consisting each of six Markov chains of 20 000 000 generations with default parameters. Parameters of the substitution model were estimated during the analysis (six substitution categories, a gamma-distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites). The trees from the first 5 000 000 generations (25% from total number of generations) were discarded as burn-in prior to the calculation of consensus trees. Convergence of each analysis was evaluated using Tracer 1.4.1 (Rambaut *et al.* 2014) to check that all ESS values exceeded 200 (with default burning). All analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2), using MrBayes on XSEDE (3.2.6) and RAxML-HPC2 on XSEDE (8.2.10) (Miller *et al.* 2010). The matrix of K2P pairwise genetic distances for COI, was calculated for the *Phaenomenella* and *Siphonalia* taxa in MEGA 6 (Tamura *et al.* 2013) (Table 2).

Abbreviations and conventions

adg	opening of anterior duct of digestive gland;
AL	aperture length;
ao	anterior aorta;
aoe	anterior oesophagus;
ba	buccal artery;
bm	buccal mass;
bn	buccal nerves;
cep.t	cephalic tentacles;
cg	capsule gland;
cm	columellar muscle;
ct	ctenidium;
dd	dead shell;
dg	digestive gland;
eye	eye;
ft	foot;
gl	gland of Leiblein;
gon	gonad;
hd	head;
hg	hypobranchial gland;
int	intestine;
kd	kidney;
lfl	longitudinal fold on inner stomach wall;
lv	live collected specimen;
mrr	medial retractor of radula;
n	nerves;
nr	nerve ring;
od	odontophore;
odn	odontophore nerves;
odr	odontophore retractors;
oeo	oesophageal opening;

TABLE 1. — List of sequenced material used in phylogenetic reconstructions. Exact collection localities of specimens from MNHN (specimen code starts with MNHN-IM-) can be found at MNHN site at https://science.mnhn.fr/institution/mnhn/collection/im/item/****-***** (asterisks correspond to the digital number of specimen).

				Accession numbers			
Specimen code	**Genus**	**species**	**Collection data**	**BOLD**	**Genbank (COI)**	**Genbank (28S)**	**Source**
IM-2007-32673	*Siphonalia*	*spadicea*	TAIWAN 2004, st. CP264	NEOGA544-10	MK567642	–	Present study
IM-2007-32674		*spadicea*	TAIWAN 2004, st. CP264	NEOGA545-10	MK567658	–	Present study
IM-2007-32762		*spadicea*	TAIWAN 2001 st, CP79	NEOGA589-10	MK567643	–	Present study
IM-2007-32856		*spadicea*	TAIWAN 2004, st. CP244	NEOGA601-10	MK567646	–	Present study
IM-2007-32995		*spadicea*	TAIWAN 2001 st, CP109	NEOGA666-10	MK567652	–	Present study
IM-2007-32997		*spadicea*	TAIWAN 2001 st, CP109	NEOGA668-10	MK567664	–	Present study
IM-2007-32996		*spadicea*	TAIWAN 2001 st. CP109	NEOGA667-10	MK567656	MK567635	Present study
IM-2009-11271		*spadicea*	TAIWAN 2004 st. CH257	BUCC001-19	MK567649	MK567632	Present study
IM-2013-41068	*Phaenomenella*	cf *thachi*	TAIWAN 2013 st. CP4090	BUCC007-19	MK567653	–	Present study
IM-2013-41072		*inflata*	TAIWAN 2013 st. CP4090	BUCC008-19	MK567650	–	Present study
IM-2013-41073		*inflata*	TAIWAN 2013 st. CP4090	BUCC009-19	MK567660	–	Present study
IM-2013-50012		cf *thachi*	DONGSHA 2014 st. CP4120	BUCC006-19	MK567654	MK567634	Present study
IM-2013-50203		*insulapratasensis*	DONGSHA 2014 st. CP4129	BUCC002-19	MK567648	MK567631	Present study
IM-2013-50204		*insulapratasensis*	DONGSHA 2014 st. CP4129	BUCC003-19	MK567661	–	Present study
IM-2013-50205		*insulapratasensis*	DONGSHA 2014 st. CP4129	BUCC004-19	MK567655	–	Present study
IM-2013-50260		cf *callophorella*	DONGSHA 2014 st. CP4130	BUCC005-19	MK567665	MK567639	Present study
IM-2013-61674		*samadiae* n. sp.	ZHONGSHA 2015 st. CP4134	BUCC013-19	MK567662	MK567638	Present study
IM-2013-61617		*samadiae* n. sp.	ZHONGSHA 2015 st. CP4133	BUCC015-19	MK567644	MK567628	Present study
IM-2007-34644		*nicoi* n. sp.	AURORA 2007 st. CP2685	NEOGA783-10	MK567663	–	Present study
IM-2013-59398		*nicoi* n. sp.	ZHONGSHA 2015 st. CP4157	BUCC016-19	MK567645	MK567629	Present study
IM-2013-61585		*nicoi* n. sp.	ZHONGSHA 2015 st. CP4132	BUCC014-19	MK567641	MK567627	Present study
IM-2013-61637		*nicoi* n. sp.	ZHONGSHA 2015 st. CP4133	BUCC010-19	MK567647	MK567630	Present study
IM-2013-61639		*nicoi* n. sp.	ZHONGSHA 2015 st. CP4133	BUCC011-19	MK567651	MK567633	Present study
IM-2013-61673		*nicoi* n. sp.	ZHONGSHA 2015 st. CP4134	BUCC012-19	MK567659	MK567637	Present study
IM-2007-34639		*nicoi* n. sp.	AURORA 2007 st. CP2685	NEOGA781-10	MK567657	MK567636	Present study
IM-2007-34635	*Calagrassor*	*aldermenensis*	AURORA 2007 st. CP2673		KC756037	KC755997	Kantor *et al.* 2013
IM-2007-32864	*Manaria*	*clandestina*	PANGLAO 2005 st. CP2389		KC756058	KC756004	Kantor *et al.* 2013
IM-2007-32952		*brevicauda*	SALOMON 2 st. CP2219		KC756055	KC756003	Kantor *et al.* 2013
IM-2009-7079	*Enigmaticolus*	*monnieri*	MIRIKY st. CP3279		KC756034	KC755996	Kantor *et al.* 2013
20140783	*Buccinum*	*undatum*	Reykjanesskagi, Iceland		MK558051	MK543285	Vaux *et al.* 2017
KK12	*Kelletia*	*kelletii*	Santa Barbara, California, USA		MH198161	MH277543	Vaux *et al.* 2017
KL2		*lischkei*	Kansai, Mie Prefecture, Japan		MH198160	MH277544	Vaux *et al.* 2017
SFKH-TMP005	*Pararetifusus*	*carinatus*	Chatham Rise, NZ		MK583342	MK543289	Vaux *et al.* 2017
M.190082/2	*Penion*	*chathamensis*	Chatham Rise, NZ		MH140429	MH277545	Vaux *et al.* 2017
M.190085		*chathamensis*	Chatham Rise, NZ		MH140428	MH277546	Vaux *et al.* 2017
M.183792/1		*cuvierianus*	Red Mercury Island, NZ		MH140431	MH277548	Vaux *et al.* 2017
M.183927		*cuvierianus*	Coromandel, NZ		MH140432	MH277549	Vaux *et al.* 2017
C.456980		*mandarinus*	Gabo Island, Victoria, Australia		MG211145	MH277553	Vaux *et al.* 2017
C.487648		*maximus*	Terrigal, NSW, Australia		MG211144	MH277554	Vaux *et al.* 2017
Phoenix1		*fairfieldae*	Otago Peninsula, NZ		MH198165	MH277547	Vaux *et al.* 2017
Phoenix9		*sulcatus*	Auckland, NZ		MG098232	MG194426	Vaux *et al.* 2017
M.274111	*Aeneator*	*benthicolus*	Cape Palliser, NZ		MK577960	MK543272	Vaux *et al.* 2017
SFKH-TMP015		*elegans*	Chatham Rise, NZ		MH198157	MH277534	Vaux *et al.* 2017
M.279437		*otagoensis*	Tasman Bay, NZ		MK577961	MK543274	Vaux *et al.* 2017
M.190119		*recens*	Cape Turnagain, NZ		MH198159	MH277535	Vaux *et al.* 2017
SFKH-TMP013		*valedictus*	TAN 616/83, NZ		MK577962	MK543276	Vaux *et al.* 2017
M.183832	*Antarctoneptunea*	*benthicola*	Chatham Rise, NZ		MH198156	MH277537	Vaux *et al.* 2017
SFKH-TMP014	*Austrofusus*	*glans*	Island Bay, Wellington, NZ		MK558053	MK543277	Vaux *et al.* 2017
M.302907/2	*Buccinulum*	*fuscozonatum*	Ariel Bank, Gisborne, NZ		MH198158	MH277540	Vaux *et al.* 2017
M.258277/6		*pallidum*	Stewart Island, NZ		MK577963	MK543280	Vaux *et al.* 2017
M.302870/2		*pertinax finlayi*	Point Gibson, NZ		MH198162	MH277541	Vaux *et al.* 2017
M.314755/1		*robustum*	Oneroa Bay, Bay of Islands, NZ		MK577965	MK543282	Vaux *et al.* 2017
SFKH-TMP012		*vittatum vittatum*	Mahia Peninsula, NZ		MK577964	MK543284	Vaux *et al.* 2017
SFKH-TMP009	*Cominella*	*adpsersa*	Urupukapuka Bay, NZ		MH198163	MH277542	Vaux *et al.* 2017
SFKH-TMP010		*virgata*	Spirits Bay, NZ		MK558054	MK543287	Vaux *et al.* 2017
SFKH-TMP004	*Glaphyrina*	*caudata*	Farwell Spit, Golden Bay, NZ		MK558055	MK543288	Vaux *et al.* 2017

op	operculum;
os	osphradium;
p	penis;
pdg	opening of posterior duct of digestive gland;
pma	posterior mixing area;
poe	posterior oesophagus;
pr	proboscis;
prp	propodium;
prpg	propodial groove;
prr	proboscis retractors;
pw	proboscis wall;
r	radula;
rd	rhynchodaeum;
re	rectum;
s	siphon;
sd	salivary duct;
sg	salivary gland;
SL	shell length;
sp	seminal papilla;
st	stomach;
st.	station;
SW	shell width;
va	vagina;
vd	vas deferens;
vl	valve of Leiblein.

Institution

MNHN	Muséum national d'Histoire naturelle, Paris.

RESULTS

Phylogenetic Analysis

Phylogenetic analysis of both the the COI and 28S datasets recovered a well-supported clade comprising sequences of *Siphonalia* and *Phaenomenella* (Figs 1; 2). The K2P pairwise distances distribution for *Phaenomenella* and *Siphonalia* revealed two modes: below 1.1% and above 7.2% that we interpret as corresponding to the intra- and interspecific comparisons respectively (Table 2). The seven revealed clusters also corresponded to the well-supported monophyletic or single specimen lineages on the COI-based tree but relationships among them are mostly poorly resolved. Specimens of only six cluster recognized based on the COI were present in the 28S data set, and they formed five reciprocally monophyletic lineages (Fig. 2). Thus the 28S-based clusters mostly corresponded to those revealed with COI, except for the unresolved relationship of the specimen MNHN-IM-2013-50260. Based on the analysis of single-gene datasets, we conclude that the analyzed specimens of *Phaenomenella* and *Siphonalia* comprise seven MOTUs.

Two of the MOTU can be identified as *Phaenomenella inflata* Shikama, 1971 (Fig. 1 (1)) and *Phaenomenella insulapratasensis* (Okutani & Lan, 1994) (Fig. 1 (5)). One MOTU was represented by a single specimen only in the COI data set (Fig. 1 (3), MNHN-IM-2013-50260). It has strong resemblance to *Phaenomenella callophorella* (Fraussen, 2004), described off Taiwan based on a single specimen from similar depths (500-900 m vs 795-822 m in our specimen) (Fraussen 2004), although it differs in having higher spire and less inflated whorls. Since we are not able to identify the variability of this species we attribute our specimen to *P. callophorella* with some reservation. Two specimens (Fig. 1 (2), MNHN-IM-2013-50012 and MNHN-IM-2013-41068) are subadults (with shell length less than 15 mm) and have some resemblance to *P. thachi* Fraussen & Stahlschmidt, 2012. Although they may represent a different species, the limited material available to us prevents us presently from further taxonomic consideration of the species. Two MOTUs were represented by several well-preserved adult specimens and cannot be attributed to any existing species of *Phaenomenella*. They are described herein as new species, *Phaenomenella samadiae* n. sp. and *P. nicoi* n. sp. Finally one MOTU can be unambiguously identified as *Siphonalia spadicea* (Reeve, 1847).

The analysis of the COI–28S data set (Fig. 3) recovered a well-supported *Phaenomenella-Siphonalia* cluster consistent with the one in the COI tree, except for *P. inflata*, which was not represented in the concatenated data set. Whereas *Phaenomenella* cf. *thachi*, *P.* cf. *calloporella* and *P. nicoi* n. sp. formed a well-supported subclade (BI posterior probability = 0.97), *P. samadiae* n. sp. showed weakly supported affinity to *Siphonalia spadicea* (BI posterior probability = 0.75). This result questions monophyly of *Phaenomenella* in relation to *Siphonalia*. In the absence of the data on *Siphonalia cassidariaeformis*, the type species of the genus, and bearing in mind the conchological differences between the genera, we accept the conservative approach and do not synonymize *Phaenomanella* with *Siphonalia.*

The two major clades of the Southern hemisphere buccinids included in the present study formed a weakly supported clade comprising a well-supported *Buccinulum – Aeneator* grouping (BI posterior probability = 1.00), and a weakly supported *Penion-Kelletia-Antarctoneptunea* clade (BI posterior probability = 0.73). This clade showed no supported relationship to the *Phaenomenella-Siphonalia* cluster. As mentioned above, *Penion* and *Aeneator* were originally included by Finlay (1928) in Siphonaliinae.

SYSTEMATIC ACCOUNT

Order NEOGASTROPODA Wenz, 1938
Family Buccinidae Rafinesque, 1815

Genus *Phaenomenella* Fraussen & Hadorn, 2006

Type species. — *Manaria* (?) *inflata* Shikama, 1971 (OD).

Remarks

The intrageneric shell variability of *Phaenomenella* is high and a few general characters can be mentioned – "broader than high protoconch with flattened tip and (…) a rather sharp angulation just above the suture. The upper teleoconch whorls are shouldered, a shape which is accentuated by the axial knobs or ribs, or have the appearance of being by the presence of obviously convex axial ribs" (Fraussen & Stahlschmidt 2013: 82). Radula with a tricuspid central tooth with rectangular base and laterals with 3 or 4 cusps. Anterior foregut with well-defined valve of Leiblein and large gland of Leiblein.

Table 2. — The matrix of K2P pairwise genetic distances in % (e.g. 133 = 0.133) for COI for the *Phaenomenella* Fraussen & Hadorn, 2006 and *Siphonalia* A. Adams, 1863 species. Within species: min = 0.000, mean = 0.018, max = 0.011. Between species: min = 0.072, mean = 0.157, max = 0.198.

	IM-2013-41072 *Ph. inflata*	IM-2013-41073 *Ph. inflata*	IM-2013-50203 *Ph. insulapratasensis*	IM-2013-50204 *Ph. insulapratasensis*	IM-2013-50205 *Ph. insulapratasensis*	IM-2013-41068 *Ph.* cf *thachi*	IM-2013-50012 *Ph.* cf *thachi*	IM-2013-50260 *Ph.* cf *callophorella*	IM-2007-34639 *Ph. nicoi*	IM-2007-34644 *Ph. nicoi*	IM-2013-59398 *Ph. nicoi*	IM-2013-61585 *Ph. nicoi*	IM-2013-61637 *Ph. nicoi*	IM-2013-61639 *Ph. nicoi*	IM-2013-61673 *Ph. nicoi*	IM-2007-32673 *S. spadicea*	IM-2007-32674 *S. spadicea*	IM-2007-32762 *S. spadicea*	IM-2007-32856 *S. spadicea*	IM-2007-32995 *S. spadicea*	IM-2007-32996 *S. spadicea*	IM-2009-11271 *S. spadicea*	IM-2007-32997 *S. spadicea*	IM-2013-61674 *Ph. samadiae*	IM-2013-61617 *Ph. samadiae*
IM-2013-41072 *Ph. inflata*																									
IM-2013-41073 *Ph. inflata*	000																								
IM-2013-50203 *Ph. insulapratasensis*	133	133																							
IM-2013-50204 *Ph. insulapratasensis*	133	133	000																						
IM-2013-50205 *Ph. insulapratasensis*	139	139	006	006																					
IM-2013-41068 *Ph.* cf *thachi*	130	130	127	127	124																				
IM-2013-50012 *Ph.* cf *thachi*	127	127	127	127	127	002																			
IM-2013-50260 *Ph.* cf *callophorella*	130	130	120	120	123	077	080																		
IM-2007-34639 *Ph. nicoi* n. sp.	140	140	130	130	136	072	072	079																	
IM-2007-34644 *Ph. nicoi* n. sp.	140	140	130	130	136	072	072	079	000																
IM-2013-59398 *Ph. nicoi* n. sp.	140	140	131	131	136	081	082	079	011	011															
IM-2013-61585 *Ph. nicoi* n. sp.	140	140	131	131	136	081	082	079	011	011	000														
IM-2013-61637 *Ph. nicoi* n. sp.	140	140	130	130	136	076	077	079	004	004	006	006													
IM-2013-61639 *Ph. nicoi* n. sp.	143	143	133	133	139	079	079	077	009	009	002	002	004												
IM-2013-61673 *Ph. nicoi* n. sp.	143	143	133	133	139	079	079	077	009	009	002	002	004	000											
IM-2007-32673 *S. spadicea*	195	195	194	194	191	171	174	165	172	172	170	170	169	173	173										
IM-2007-32674 *S. spadicea*	195	195	194	194	191	171	174	165	172	172	170	170	169	173	173	000									
IM-2007-32762 *S. spadicea*	195	195	194	194	191	171	174	165	172	172	170	170	169	173	173	000	000								
IM-2007-32856 *S. spadicea*	185	185	185	185	182	168	171	162	169	169	166	166	166	169	169	006	006	006							
IM-2007-32995 *S. spadicea*	198	198	198	198	194	174	178	168	176	176	173	173	173	176	176	002	002	002	009						
IM-2007-32996 *S. spadicea*	192	192	191	191	188	168	171	162	169	169	167	167	166	170	170	002	002	002	004	004					
IM-2009-11271 *S. spadicea*	195	195	194	194	191	171	174	165	172	172	170	170	169	173	173	000	000	000	006	002	002				
IM-2007-32997 *S. spadicea*	192	192	191	191	188	168	171	162	169	169	167	167	166	170	170	002	002	002	004	004	000	002			
IM-2013-61674 *Ph. samadiae* n. sp.	157	157	157	157	163	172	171	156	176	176	173	173	179	176	176	186	186	186	176	182	183	186	183		
IM-2013-61617 *Ph. samadiae* n. sp.	160	160	159	159	166	169	168	152	167	167	164	164	170	167	167	179	179	179	170	183	176	179	176	006	

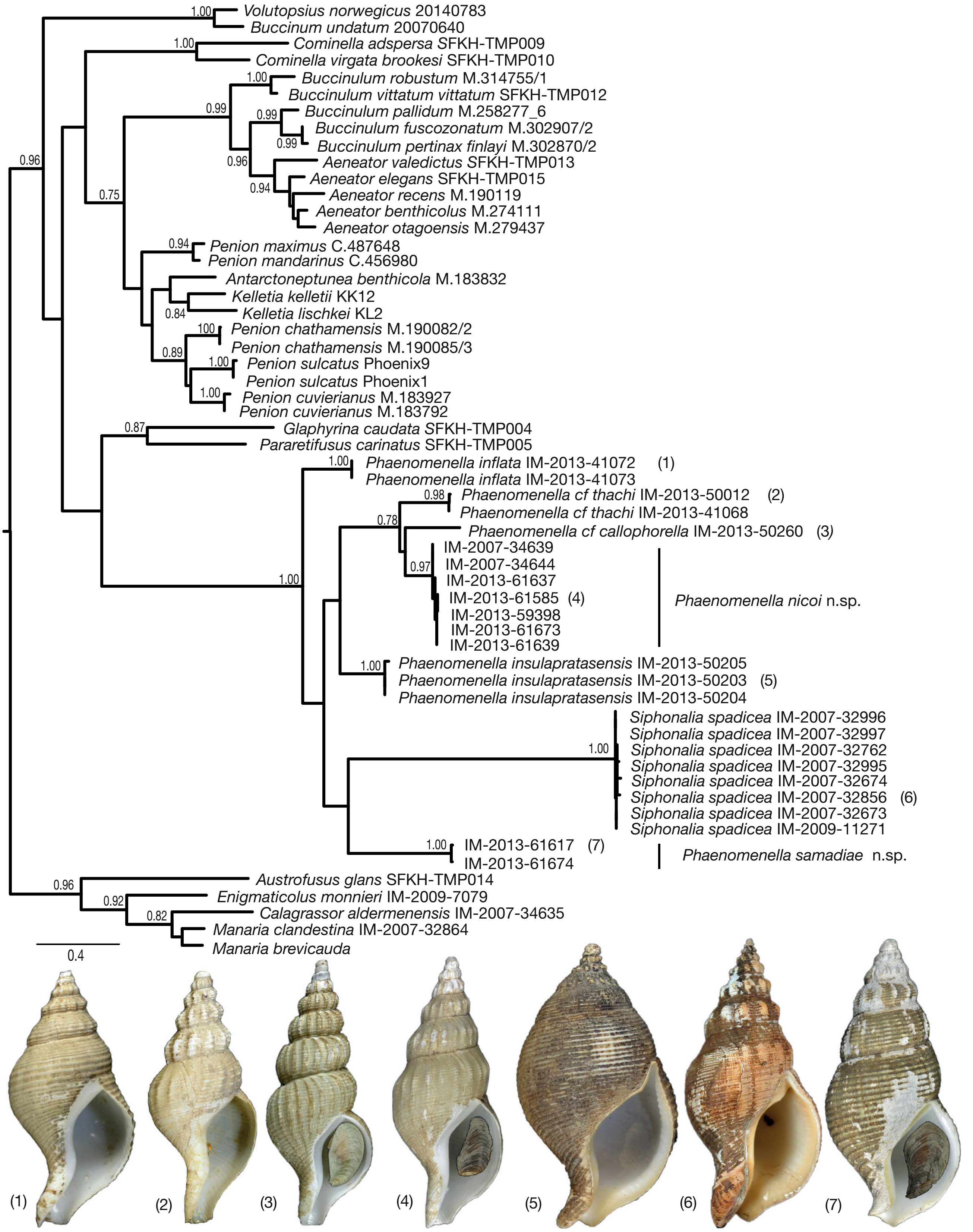

FIG. 1. — Phylogenetic tree of a dataset of Buccinoidea Rafinesque, 1815 obtained with Bayesian analysis of COI gene sequences. Support values shown for the supported nodes with posterior probability values between 0.70 and 1.00 only. The numbers in brackets following the species names correspond to illustrated specimens at the bottom of the figure.

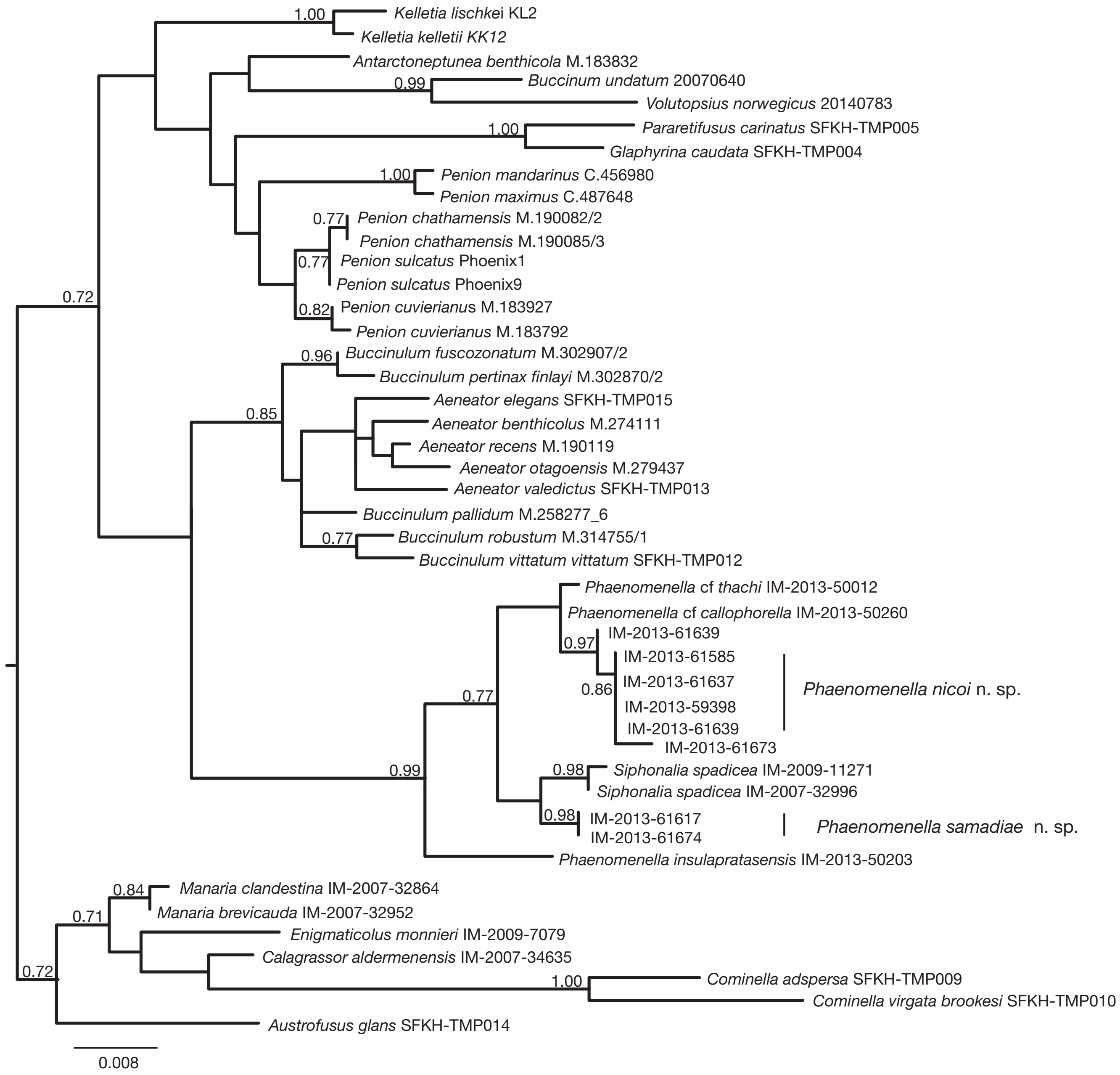

FIG. 2. — Phylogenetic tree of a dataset of Buccinoidea Rafinesque, 1815 obtained with Bayesian analysis of 28S gene sequences. Support values shown for the supported nodes with posterior probability values between 0.70 and 1.00 only.

Phaenomenella samadiae n. sp.
(Figs 4; 5A, B; 6)

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MATERIAL EXAMINED. — **Holotype. South China Sea** • MNHN-IM-2013-61617 (sequenced, Figs 4A-C; 5A; 6A, B, E-G); S.W. off Dong Sha, ZHONGSHA 2015; st. CP4133; 19°59'N, 116°24'E; 999-1070 m.

OTHER SEQUENCED MATERIAL. — **South China Sea** • 1 lv; MNHN-IM-2013-61674 (Figs 4E, F; 5B; 6C, D); S.W. off Dong Sha, ZHONGSHA 2015; st. CP4134; 19°50'N, 116°27'E; 1128-1278 m.

OTHER STUDIED MATERIAL. — **South China Sea** • 1 lv; MNHN-IM-2013-61670; S.W. off Dong Sha, ZHONGSHA 2015; st. CP4134; 19°50'N, 116°27'E; 1128-1278 m • 2 lv; MNHN-IM-2013-59393 (Fig. 4D), MNHN-IM-2013-59665 (Fig. 4G); ZHONGSHA; st. CP4157; 19°48'N, 116°29'E; 1205-1389 m.

ETYMOLOGY. — Named in honour of Sarah Samadi, professor at MNHN, for her leadership in the France-Taiwan research programme in the context of which research cruises in the South China Sea discovered the present new species.

DIAGNOSIS. — Shell large for genus, up to 58.2 mm, broad fusiform with truncated base, short and strongly left reclined siphon canal. Spiral sculpture of distinct cords, more than 20 on last whorl. Radula

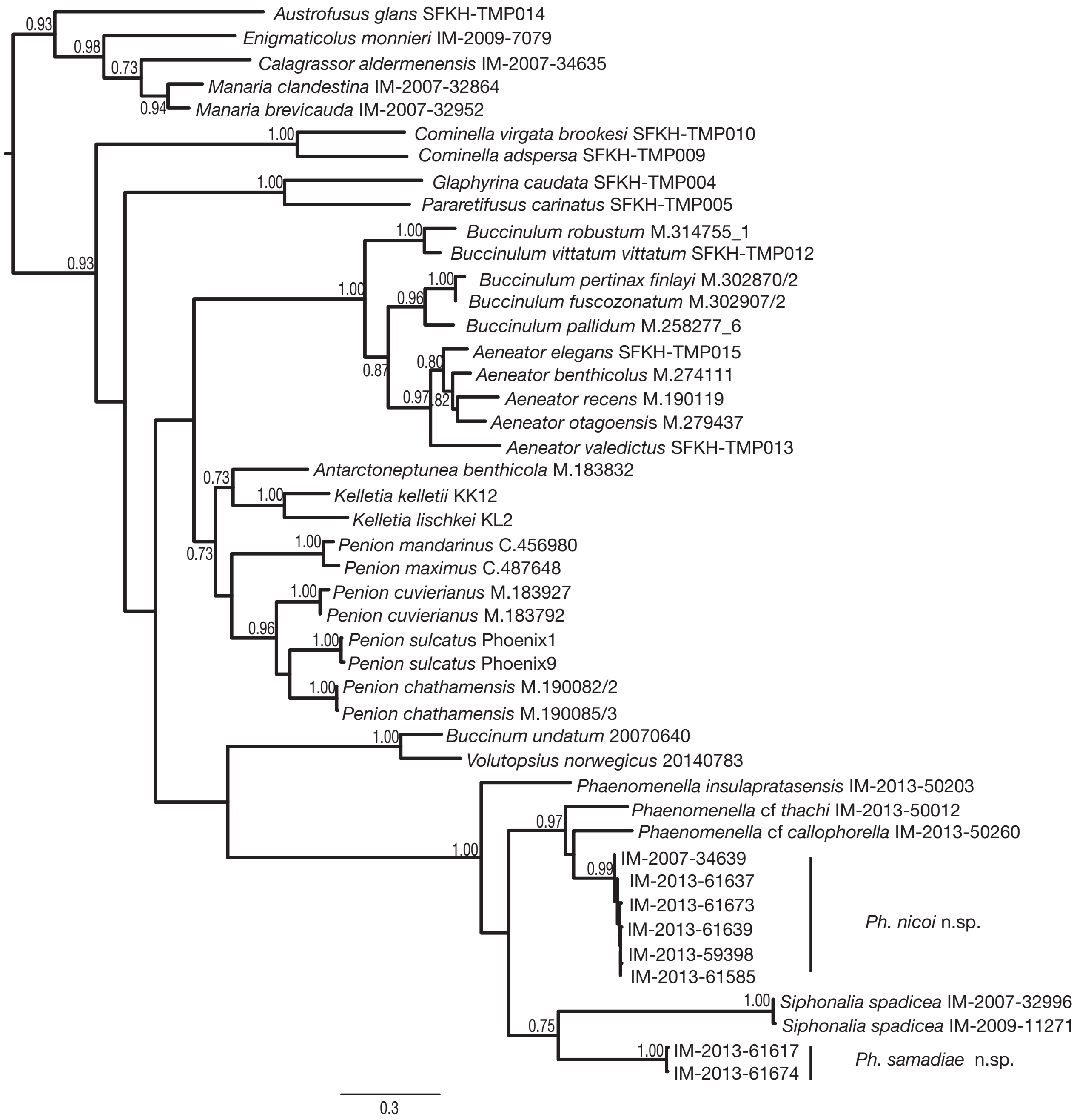

Fig. 3. — Phylogenetic tree of a dataset of Buccinoidea Rafinesque, 1815 obtained with Bayesian analysis of concatenated sequences of COI and 28S. Support values shown for the supported nodes with posterior probability values between 0.70 and 1.00 only.

with tricuspate central teeth with short rectangular basal part and tricuspate lateral teeth with longest outermost cusp.

Distribution. — Presently the species was recorded only in the South China Sea at 1205-1389 m.

Description (Holotype)

Shell

Shell broad fusiform with truncated base (Fig. 4A-C), strong, white under periostracum. Spire high, siphonal canal very short, strongly reclined to left. Protoconch and upper teleoconch whorls eroded, remaining teleoconch whorls 6½ in number. Teleoconch whorls convex, last and penultimate whorls less convex than upper ones. Suture distinct, adpressed. Spiral sculpture of distinct rounded on top spiral cords, on first not eroded teleoconch whorl (3rd remaining) 9 cords, on penultimate 11, on last whorl 24 cords, of which 4 on canal. Cords differing twice in width, the broader ones indistinctly subdivided by shallow spiral groove and with indistinct spiral striation, not visible on most narrow cords. Interspaces between cords from ¼ to more than cord's width. On shell base and canal cords more broadly spaced. Upper teleoconch whorls with axial ribs, disappearing on last and penultimate

Fig. 4. — Shells of *Phaenomenella samadiae* n. sp.: **A**-**C**, holotype, MNHN-IM-2013-61617, SL 58.2 mm; **D**, ZHONGSHA 2015, st. CP4157, non-sequenced spm, MNHN-IM-2013-59393, SL 47.2 mm; **E**, **F**, ZHONGSHA 2015, st. CP4134, sequenced spm, MNHN-IM-2013-61674, SL 51.4 mm; **G**, ZHONGSHA 2015, st. CP4157, non-sequenced spm, MNHN-IM-2013-59665, SL 37.1 mm. Scale bar: 5 cm.

whorls. Ribs nearly orthocline, broadly spaced, 12 on first preserved whorl, 14 on antepenultimate.

Aperture broad ovate, white inside, angulated posteriorly, outer lip thick, slightly reflected. Parietal wall and columella with narrow but thick glossy callus with yellowish band along edge.

Shell covered with light olive adhering periostracum, forming densely spaced low axial lamellae, obsolete on cords, but visible in interspaces.

Operculum spanning most of aperture, with distinctly turned leftwards terminal nucleus and weakly angulate in upper part.

Radula (Fig. 5A, B)

Examined in holotype and sequenced specimen MNHN-IM-2013-61674. Very similar in both specimens; central tooth with rather short rectangular basal part with weakly arcuate anterior margin and three short triangular broad cusps. Lateral teeth tricuspate with weakly curved basal side, attached to membrane. Outermost cusp recurved, medium long, inner cup weakly recurved, about ⅔ of outer cusp length. Intermediate cusp shortest, situated slightly closer to inner cusp.

Measurements

Holotype (largest studied specimen), shell length 58.2 mm, last whorl length 35.8 mm, aperture length (without canal) 23.2 mm, diameter 26.7 mm.

Anatomy

Two specimens studied — MNHN-IM-2013-61674, male, sequenced paratype; MNHN-IM-2013-61617, female, holotype. Soft body partly extracted from the shell. Head rather large, with two thick long tentacles. Eye lobes poorly defined, not pigmented in both examined specimens, eyes obviously absent. Mantle of female (Fig. 6B) approximately square in shape, with long siphon. Ctenidium comprises ¾ of mantle length and in average ⅕ of mantle width; bipectinate symmetric osphradium slightly narrower than ctenidium and ¾ of its length. Capsule gland medium large, covered by thick rectum and terminated by large vagina. In male's mantle, prostate gland well-developed, situated parallel and equal in size to rectum. Penis (Fig. 6 C) flattened, terminating in seminal papilla shifted to left side and not surrounded by a circlular fold.

Digestive system. Proboscis almost completely inverted into rhynchodaeum (Fig. 6E, pr). Several bands of proboscis retractors attached at middle part of both sides of rhynchodaeum (Fig. 6E, prr). Anterior oesophagus straight, along ventral side of rhynchodaeum (Fig. 6E, aoe). Valve of Leiblein medium large, situated immediately before nerve ring (Fig. 6G, vl). Salivary glands large (about half proboscis length), fused ventrally (Fig. 6E, F, sg), with thin salivary ducts following along anterior oesophagus. Gland of Leiblein large, S-twisted, situated beneath salivary glands (Fig. 6E, gl) and following along posterior oesophagus and anterior aorta. Stomach small, occupying about 0.25 whorl (Fig. 6D). Posterior mixing area small, posterior oesophagus and intestine wide.

Remarks

The new species demonstrates some variability in shell shape with more inflated shell outline in smaller specimens.

The new species is most similar in the shell shape to *P. mokenorum* Fraussen, 2008 from the Andaman Sea, differing in better pronounced spiral cords. Another somewhat similar species is *P. insulapratasensis* (Okutani & Lan, 1994), which possesses smaller, more ovoid shell with faster incrementing teleoconch whorls and a longer and more distinct canal.

Phaenomenella nicoi n. sp.

(Figs 5C-F; 7; 8)

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Material examined. — **Holotype**. **South China Sea** • MNHN-IM-2013-61585 (sequenced, Fig. 7A-C); S.W. off Dong Sha, ZHONGSHA 2015; st. CP4132; 20°07'N, 116°22'E; 958-988 m.

Other sequenced material. — **South China Sea** • 3 lv; MNHN-IM-2013-61637 (Figs 7H; 8E-G), MNHN-IM-2013-61638, MNHN-IM-2013-61639 (Fig. 7E); S.W. off Dong Sha, ZHONGSHA 2015, st. CP4133; 19°59'N, 116°24'E; 999-1070 m • 1 lv.; MNHN-IM-2013-61673 (Fig. 7I); st. CP4134; 19°50'N, 116°27'E; 1128-1278 m • 1 lv; MNHN-IM-2013-59398 (Fig. 7D); st. CP4157; 19°48'N, 116°29'E; 1205-1389 m.
Philippines • 1 lv; MNHN-IM-2007-34639; AURORA 2007; st. CP2685; 15°00'N, 123°06'E; 1155-1302 m (Fig. 7 F).

Other studied material. — **South China Sea** • 2 lv; MNHN-IM-2013-61590, MNHN-IM-2013-61592 (Fig. 7K, L); S.W. off Dong Sha, ZHONGSHA 2015; st. CP4132; 20°07'N, 116°22'E; 958-988 m • 5 lv; MNHN-IM-2013-59661, MNHN-IM-2013-61636 (Figs 7J, 8A-D), MNHN-IM-2013-63029, MNHN-IM-2013-63025, MNHN-IM-2013-61638; st. CP4133; 19°59'N, 116°24'E; 999-1070 m • 2 lv, MNHN-IM-2013-61671, MNHN-IM-2013-61672; st. CP4134; 19°50'N, 116°27'E; 1128-1278 m • 1 lv; MNHN-IM-2013-59397; st. CP4157; 19°48'N, 116°29'E; 1205-1389 m, S off Helen Shoal • 2 lv; MNHN-IM-2013-61815, MNHN-IM-2013-59663; st. CP4141; 18°49'N, 113°58'E; 1151-1286 m.
Philippines • 1 lv; MNHN-IM-2007-34644 (Fig. 7); AURORA 2007; st. CP2685; 15°00'N, 123°06'E; 1155-1302 m, SL 38.7 mm.

Etymology. — Named in honour of Nicolas Puillandre, associate professor of MNHN, our long term co-author and participant of many expeditions with whom we had a pleasure to share the lab bench for long hours.

Diagnosis. — Shell medium sized for genus, up to 42 mm, fusiform with high spire and attenuated, medium long, and slightly inclined to left siphonal canal. Protoconch large, paucispiral, of about 2 whorls. Spiral sculpture of distinct flat on top spiral cords, about 55 on last whorl. Radula with tricuspate central teeth with rectangular basal part and tricuspate lateral teeth with longest outermost cusp.

Distribution. — The species is found so far in the South China Sea at 999-1389 m and Philippines (in Philippine Sea) at 1155-1302 m.

Description (holotype)

Shell

Shell fusiform with high spire and attenuated siphonal canal (Fig. 7A-C), fragile, white under periostracum. Siphonal canal medium long, slightly inclined to left and crossing coiling axis. Protoconch paucispiral, of about 2 whorls, partially eroded as well as upper teleoconch whorls, teleoconch whorls 6 ½ in number. [Better preserved protoconch found in specimen MNHN-IM-2013-61592 (Fig. 7L): bulbous, of nearly 2 whorls, diameter 2.05 mm, exposed height 2.1 mm. Protoconch surface eroded, sculpture not seen. Boundary with teleoconch marked by weak (about 5) orthocline ribs.] Teleoconch whorls convex, weakly angulated at shoulder. Suture distinct, shallowly impressed. Spiral sculpture of distinct flat on top spiral cords, covering entire shell surface. Number of cords increasing from 8 on first teleoconch whorl to 19 on

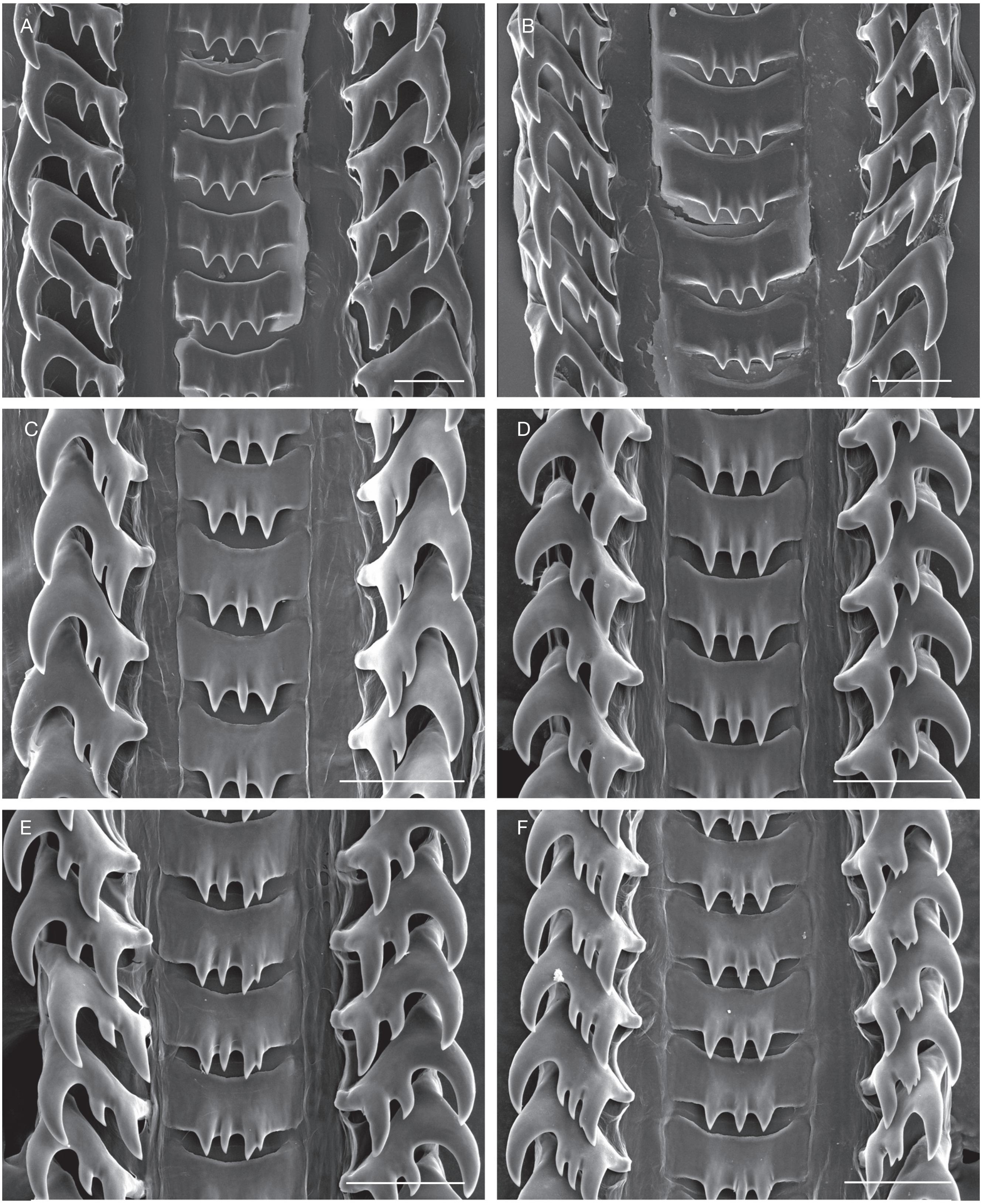

Fig. 5. — Radulae of *Phaenomenella* spp. **A**, **B**, *Phaenomenella samadiae* n. sp.; holotype, MNHN-IM-2013-61617 (shell on Fig. 4A-C) (**A**); MNHN-IM-2013-61674 (shell on Fig. 4 E, F) (**B**); **C**-**F**. *Phaenomenella nicoi* n. sp.; **C**, holotype, MNHN-IM-2013-61585 (shell on Fig. 7A-C); **D**, MNHN-IM-2013-59398 (shell on Fig. 7D); **E**, MNHN-IM-2013-61639 (shell on Fig. 7E); **F**, MNHN-IM-2013-61673 (shell on Fig. 7I). Scale bars: 100 µm.

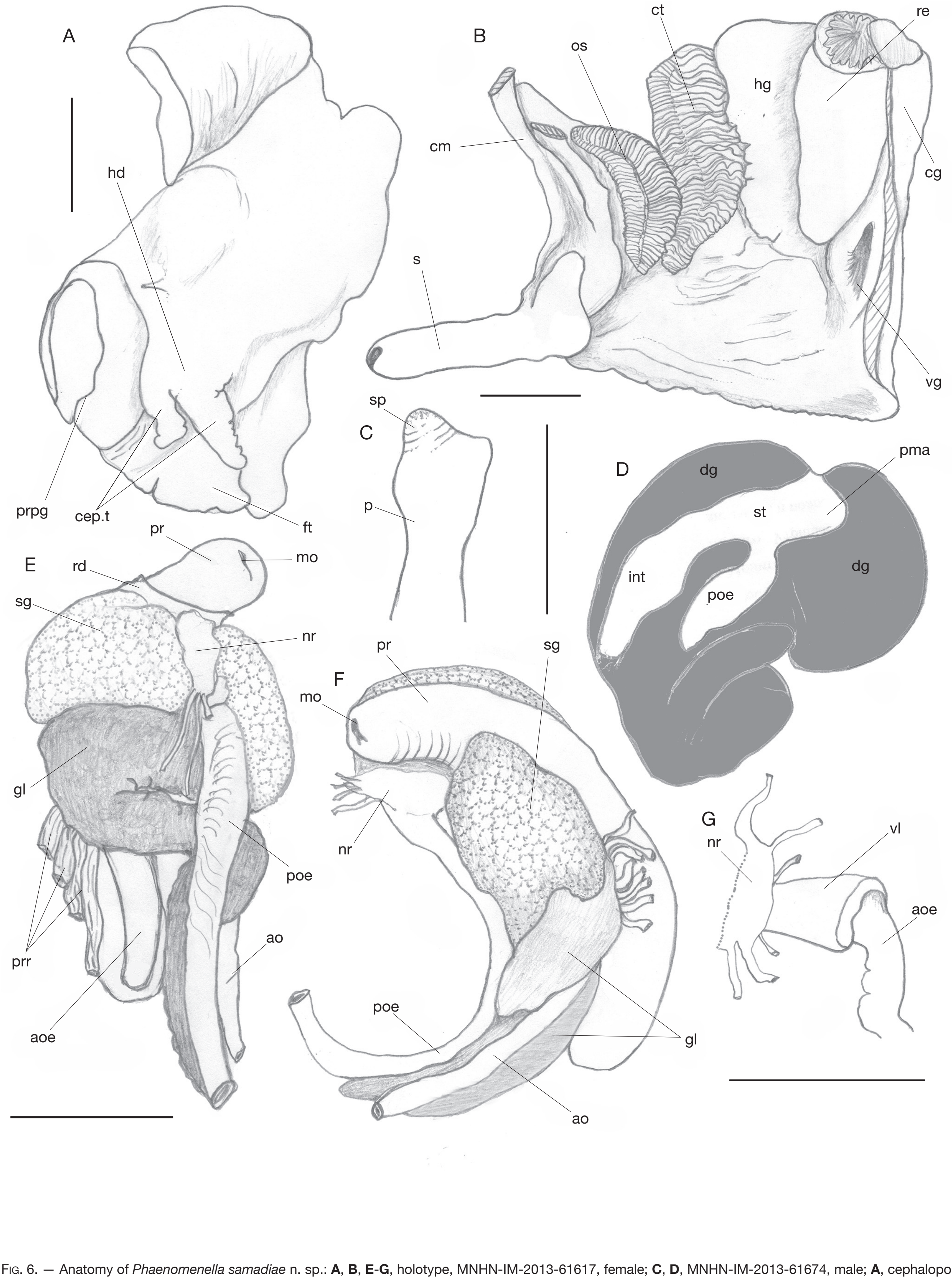

FIG. 6. — Anatomy of *Phaenomenella samadiae* n. sp.: **A**, **B**, **E**-**G**, holotype, MNHN-IM-2013-61617, female; **C**, **D**, MNHN-IM-2013-61674, male; **A**, cephalopodium, front view, mantle removed; **B**, mantle; **C**, uppermost part of penis; **D**, stomach, external view; **E**, foregut, ventral view; **F**, foregut, lateral view; **G**, valve of Leiblein. Abbreviations: see material and methods. Scale bars: 5 mm.

Fig. 7. — Shells of *Phaenomenella nicoi* n. sp.: **A**-**C**, holotype, MNHN-IM-2013-61585, SL 41.1 mm; **D**, ZHONGSHA 2015, st. CP4157, sequenced spm, MNHN-IM-2013-59398, SL 37.5 mm; **E**, ZHONGSHA 2015, st. CP4133, sequenced spm, MNHN-IM-2013-61639, SL 43.2 mm; **F**, AURORA 2007, st. CP2685, sequenced spm, MNHN-IM-2007-34639, SL 34.7 mm; **G**, AURORA 2007, st. CP2685, not-sequenced spm, MNHN-IM-2007-34644, SL 38.7 mm; **H**, ZHONGSHA 2015, st. CP4133, sequenced spm, MNHN-IM-2013-61637, SL 30.6 mm (anatomy studied); **I**, ZHONGSHA 2015, st. CP4134, sequenced spm, MNHN-IM-2013-61673, SL 42 mm; **J**, ZHONGSHA 2015, st. CP4133, not-sequenced spm, MNHN-IM-2013-61636, SL 40.2 mm (anatomy studied); **K**, **L**, ZHONGSHA 2015, st. CP4132, not-sequenced spm, MNHN-IM-2013-61592, 39.1 mm; **L**, enlarged protoconch. Scale bars: A-K, 20 cm; L, 1 mm.

FIG. 8. — Anatomy of *Phaenomenella nicoi* n. sp.: **A**-**D**, MNHN-IM-2013-61636, male; **E**-**G**, MNHN-IM-2013-61637, female: **A**, soft body removed from the shell; **B**, penis; **C**, proboscis, opened dorsally; **D**, foregut, right lateral view; **E**, foregut, right lateral view, right salivary gland displaced; **F**, foregut, right lateral view, right salivary gland in original position; **G**, stomach, outer view. Abbreviations: see material and methods. Scale bars: 5 mm.

penultimate whorl, on last whorl 55 cords, of which about 20 on canal. Cords differing slightly in width, with most narrow on subsutural ramp, interspaces between cords about ⅓-½ of cord's width. Strong axial ribs present on entire shell, suture to suture on uppermost teleoconch whorls, gradually becoming obsolete on subsutural ramp and absent on ramp of last and penultimate whorls. On last whorl ribs distinct only on shoulder, producing its angulated appearance. Number of ribs stable, i.e., 15-16 per whorl.

Aperture ovate, white inside, angulated posteriorly, outer lip thin, evenly convex, concave at transition to canal. Parietal wall and columella with narrow and thin glossy callus.

Shell covered with very light olive adhering periostracum, forming densely spaced low axial lamellae visible in interspaces between cords.

Operculum partially abraded, when intact (Fig. 7 D) spanning most of aperture with distinctly turned leftwards terminal nucleus and rounded upper part.

Radula (Fig. 5 C-F)

Examined in five specimens, including holotype. Rather similar in all specimens; central tooth with rectangular basal part with weakly arcuate anterior margin and three medium long triangular broad cusps, central one shorter and narrower than lateral ones. Lateral teeth normally tricuspate with weakly curved basal side, attached to membrane. Outermost cusp recurved, medium long, inner cusp weakly recurved, about ⅔ of outer cusp length. Intermediate cusp shortest, situated slightly closer to inner cusp. In one sequenced specimen (MNHN-IM-2013-61673, Fig. 5F) intermediate cusps of the left lateral teeth of the radula paired, nearly equal in size, while lateral teeth on right side have broader intermediate cusp subdivided on top.

Measurements (holotype)

Shell length 41.3 mm, last whorl length 26.9 mm, aperture length (without canal) 16.0 mm, diameter 16.5 mm. In the largest specimen studied, shell length reaching 43 mm.

Anatomy

Two specimens examined: MNHN-IM-2013-61636, male, and MNHN-IM-2013-61637, female, sequenced paratype (similar in both studied specimens). Soft body partly extracted from the shell. Head medium large, with two long tentacles and large black eyes on lobes at bases of tentacles. Mantle similar to that of *Phaenomenella samadiae* n. sp. Penis flattened, with seminal papilla situated on its top and surrounded by circle fold of skin (Fig. 8B).

Digestive system. Proboscis almost completely inverted into rhynchodaeum (Fig. 8D, pr). Several bands of proboscis retractors muscles attached to middle part on both sides of rhynchodaeum (Fig. 8D-F, prr). Buccal mass slightly shorter than retracted proboscis (Fig. 8C, bm), attached to its walls by multiple odontophoral retractors (Fig. 8C, odr). Radula lying in middle of buccal mass and attached to proboscis walls by median retractor (Fig. 8C, mrr).

Anterior oesophagus straight, following along ventral side of proboscis (Fig. 8E, aoe). Valve of Leiblein (Fig. 8D, E, vl) medium large, coniform, situated immediately before nerve ring (Fig. 8D, nr). Salivary glands medium-large (about 0.3 proboscis length), fused ventrally beneath nerve ring (Fig. 8E, F, sg), with very thin strongly convoluted salivary ducts following along anterior oesophagus. Gland of Leiblein medium in size (Fig. 8D, E, gl), following along posterior oesophagus and anterior aorta. Stomach rather large, spanning about 0.4 whorl (Fig. 8G). Posterior mixing area (pma) twice larger than in *Phaenomenella samadiae*, posterior oesophagus and intestine medium wide.

REMARKS

The new species is highly variable in shell shape. Some of the specimens are much more slender (Fig. 7D, I, G) and the axial ribs are either very weak or obsolete. The specimen with no axial ribs was collected at a maximal depth (1634-1683 m), but there is not clear correlation with depth, since syntopic specimens can have strong or weak axial ribs. Nevertheless the molecular data clearly indicates the conspecifity of "typical" angulated specimens with well-developed ribs and smooth ones. The specimens collected at greater depth have the protoconch and upper teleoconch whorls more eroded or missing.

In general shape the new species has some resemblance to *P. mokenorum* Fraussen, 2008 from the Andaman Sea, differing in better pronounced axial ribs in later teleoconch whorls and more attenuated narrow siphonal canal. Also *P. nicoi* n. sp. has smaller size (maximal shell length 42 mm versus 55.6 mm in *P. mokenorum*).

Genus *Siphonalia* A. Adams, 1863

TYPE SPECIES. — *Buccinum cassidariaeforme* Reeve, 1846 (Subsequent designation by Cossmann 1889).

Siphonalia cassidariaeformis (Reeve, 1846)

(Figs 9A-C; 10; 11A)

Buccinum cassidariaeformis Reeve, 1846: pl. 2, sp. 11..

MATERIAL EXAMINED. — **Japan** • 2 lots, 3 specimens; Off Hashima, Miyazaki Prefecture, Kyushu; 10.V.1996 (no. 1, Fig. 9A); Off Atsumi Peninsula, Aichi Prefecture; 30 m; 13.V.2001 (nos. 2, 3, Figs 9B, C).

COMPLEMENT TO DESCRIPTION

Radula

Radula studied in three specimens. Rather similar in all specimens (Fig. 11A, B); central tooth with rectangular basal part and weakly arcuate anterior margin and three medium long triangular broad cusps, central one equal in length but slightly narrower than lateral ones. Lateral teeth tricuspate with weakly curved, nearly straight basal side, attached to membrane. Outermost cusp recurved, medium long, inner cusp weakly recurved, about ⅔ of outer cusp length. Intermediate cusp shortest, situated closer to inner cusp.

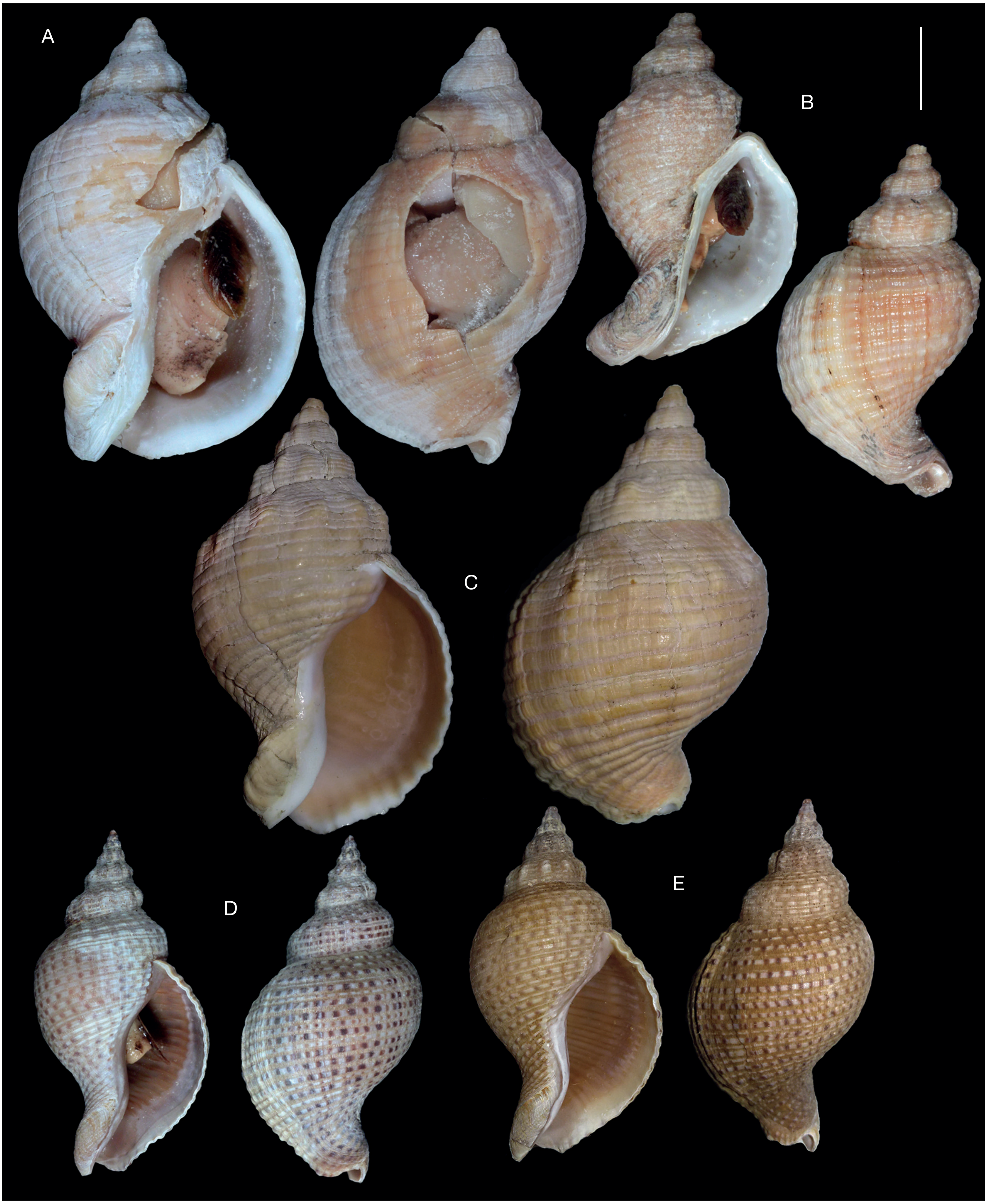

FIG. 9. — Shells of studied *Siphonalia* spp.: **A**-**C**, *S. cassidariaeformis* (Reeve, 1846): specimen no. 1 (**A**), specimen no. 2 (**B**), specimen no. 3 (**C**); **D**, **E**, *S. pfefferi* G. B. Sowerby III, 1900; **D**, specimen no. 1; **E**, specimen no. 2. Scale bar: 10 mm.

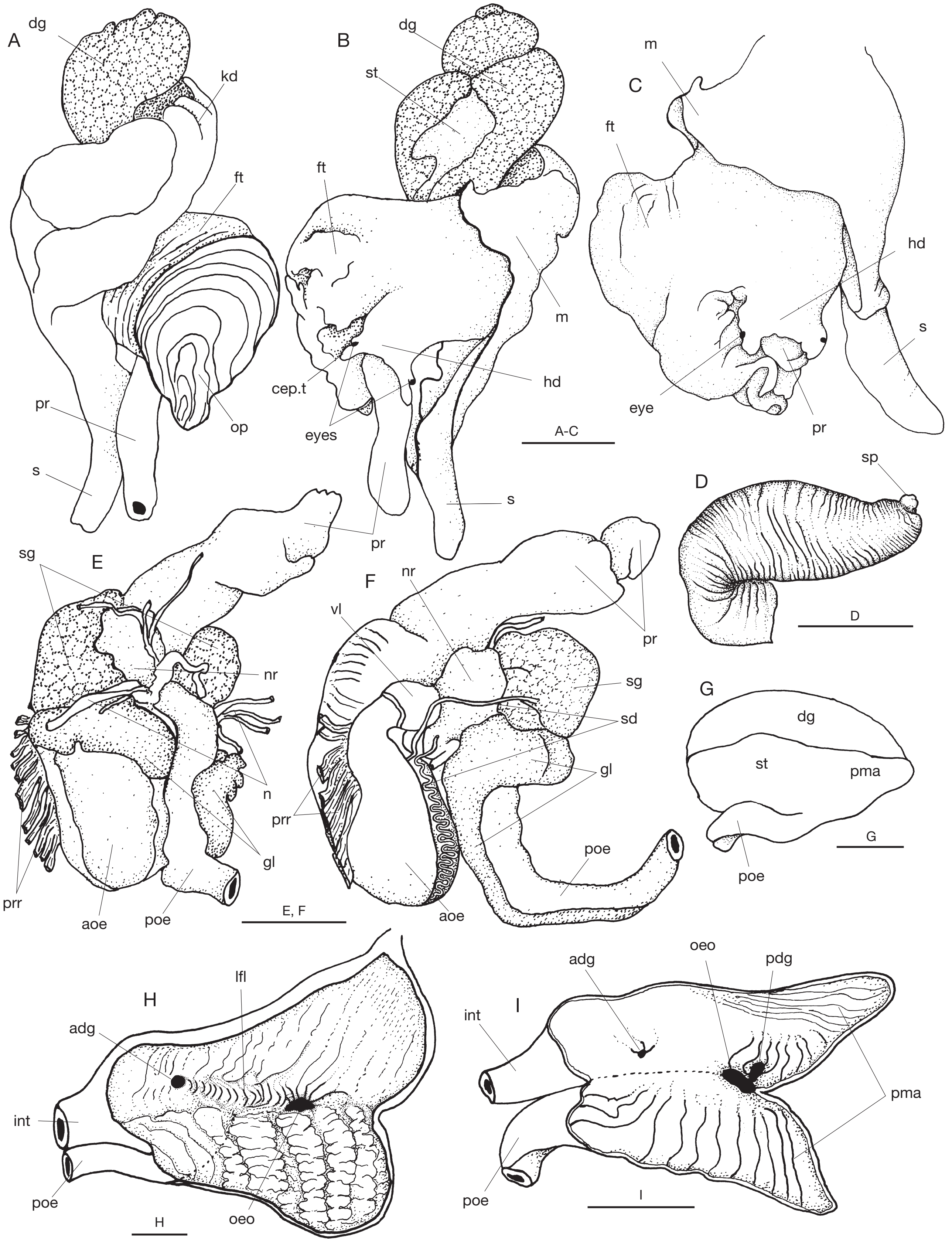

Fig. 10. — Anatomy of *Siphonalia cassidariaeformis* (Reeve, 1846): **A**, **B**; ventral (**A**) and dorsal (**B**) views of body of specimen no. 1, removed from the shell; **C**, cephalopodium of no. 2, front view; **D**, penis of no. 3; **E**, **F**, foregut of no. 1, with right salivary gland in original position (**E**) and removed (**F**); **G**, stomach of no. 2, external view; **H**, stomach of no. 1, opened dorsally; **I**, stomach of no. 2, opened dorsally. Abbreviations: see material and methods. Scale bars: A-F, 10 mm; G, I, 5 mm; H, 1 mm

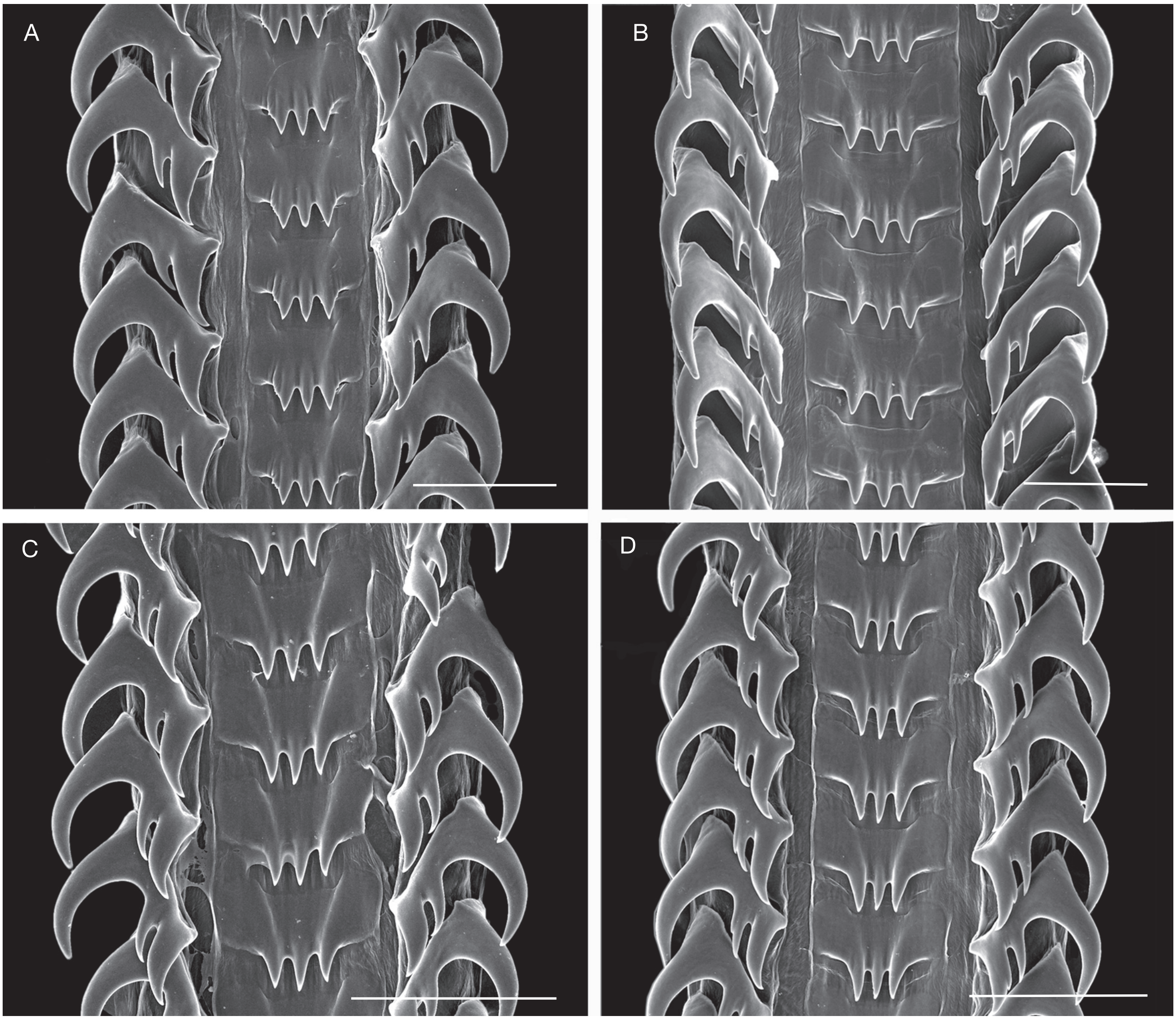

Fig. 11. — Radulae of *Siphonalia* spp. **A**, *S. cassidariaeformis* (Reeve, 1846) no. 1; **B**, *S. cassidariaeformis* no. 2; **C**, *S. pfefferi* G. B. Sowerby III, 1900 no. 1; **D**, *S. pfefferi* no. 2. Scale bars: 200 µm.

Anatomy

Soft body (no. 1, female, Fig. 10A, B, E, F, no. 2, female, Fig. 10C) with approximately 3 whorls. Head short and broad, with short contracted tentacles. Eyes small, situated at small lobes in the middle of tentacles (Fig. 10B, C, eyes). Foot contracted, with very narrow propodium and large operculum with terminal nucleus. Penis of spm. no. 3 (Fig. 10D) medium long, flattened, contracted, with small (contracted) rounded seminal papilla at the top, surrounded by circular fold of skin. Mantle with very long siphon in dissected specimens (longer than half mantle width).

Digestive system. Proboscis half everted out of rhynchodaeum, thick, contracted (Fig. 10E, F, pr). Proboscis retractors (prr) attached to rhynchodaeum along both sides of anterior oesophagus (mostly on its right side), connecting rhynchodaeum to lateral walls of body haemocoel. Anterior oesophagus short and wide, dorso-ventrally flattened, along ventral side of proboscis (Fig. 10E, F, aoe) into relatively small rounded valve of Leiblein (Fig. 10F, vl), situated immediately anterior to nerve ring (Fig. 10F, nr). Salivary glands medium small (about 0.25 proboscis length) (Fig. 10E, F, sg), with very thin strongly convoluted salivary ducts (Fig. 10F, sd) following along anterior oesophagus. Gland of Leiblein large (Fig. 10E, F, gl), following along thick, round in section posterior oesophagus (Fig. 10E, F, poe). Stomach spanning about 0.3 whorl (Fig. 10G). Posterior mixing area not large in spm. no. 1, large in spm. no. 2 (Fig. 10G, I, pma). Posterior oesophagus and intestine medium wide in both specimens. Opening of posterior duct of digestive gland (found in spm. no. 2) located near oesophageal opening (Fig. 10I, pdg), opening of anterior duct (found in spms. nos. 1 and 2) located near beginning of intestine. Inner stomach wall between two openings with longitudinal fold (Fig. 10H, lfl), lined with low oblique folds, remaining part of inner and outer stomach walls lined with moderately high transverse folds.

Siphonalia pfefferi G. B. Sowerby III, 1900
(Figs 9D, E; 11C, D; 12)

Siphonalia pfefferi G. B. Sowerby III, 1900: 440, pl. 11, fig. 3.

MATERIAL EXAMINED. — **Japan** • 1 lot, 2 specimens; Off Hashima, Miyazaki Prefecture, Kyushu; 10.V.1996 (nos. 1, 2, figs 8D, E).

COMPLEMENT TO DESCRIPTION

Radula

Radula rather similar in both specimens (Fig. 11C, D); central tooth with rectangular basal part and weakly arcuate anterior margin and three medium long triangular broad cusps, central one equal in length but slightly narrower than lateral ones. Lateral teeth tricuspate with weakly curved basal side, attached to membrane. Outermost cusp recurved, medium long, inner cusp weakly recurved, about ⅔ of outer cusp length; inner cusp in right longitudinal row of specimen spm. no. 2 partially subdivided (Fig. 11D). Intermediate cusp shortest, situated closer to inner cusp; inner cusp of spm. no. 2 partially subdivided in left longitudinal row.

Anatomy (spm. no. 1, male, Fig. 12)

Head very short and broad, tentacles short, contracted, with small eyes at lobes. Foot contracted, propodium moderately wide, operculum oval with terminal nucleus. Penis rather large (Fig. 12C), flattened, with long narrow seminal papilla in deepening at the top. Mantle with medium long siphon.

Digestive system. Proboscis partly everted out of rhynchodaeum, with contracted walls. Multiple proboscis retractors attaching mostly along right side of anterior oesophagus (Fig. 12D, E, prr), connecting rhynchodaeum and lateral walls of body haemocoel. Buccal mass slightly shorter than retracted proboscis (Fig. 12F, bm), attaching to its walls by multiple odontophoral retractors (odr). Radula lying in middle of buccal mass and attached to proboscis walls by median retractor (Fig. 12F, mrr). Salivary glands (Fig. 12D, E, sg) medium large (0.4 proboscis length), oval, with salivary ducts following on both sides of anterior oesophagus. Anterior oesophagus wide, dorso-ventrally flattened (Fig. 12E, aoe), valve of Leiblein rounded, medium large. Posterior oesophagus (poe) relatively narrow. Gland of Leiblein large, folded beneath nerve ring (Fig. 12E, gl). Stomach spanning about 0.3 whorl (Fig. 12G). Posterior mixing area not large (Fig. 12G, H, pma). Intestine medium wide. Opening of posterior duct of digestive gland located near oesophageal opening (Fig. 12I, pdg), opening of anterior duct located closer to beginning of intestine. Inner stomach wall between two openings contains longitudinal fold (Fig. 12H, lfl), lined with low oblique folds, rest part of inner and outer stomach wall lined with moderately high transverse folds.

DISCUSSION

Results of the phylogenetic analysis suggest close affinities of *Siphonalia* and *Phaenomenella* that remained unnoticed previously. Fraussen & Hadorn (2006), while describing *Phaenomenella*, compared it to *Manaria* and *Eosipho*, but not to *Siphonalia*. The shell outline of some *Phaenomenella* (e.g. *Phaenomenella insulapratasensis*) is rather similar to *Siphonalia*: the shell is stout, with strongly convex whorls and a recurved siphonal canal. Species of *Phaenomenella* though have a much larger (about twice) protoconch in comparison with *Siphonalia*. The intrageneric variability of shell shape in *Phaenomenella* in its current definition is very high (Fraussen & Stahlschmidt 2013) and in its extremes there is no resemblance between the two genera. It should also be born in mind that some of the most diverging species of *Phaenomenella* were not yet sequenced and may fall into other lineages.

Representatives of both genera are also anatomically similar, particularly in the digestive system characters. Both *Phaenomenella* and *Siphonalia* have a broad, medium long in the contracted state proboscis, medium large salivary glands and a large gland of Leiblein. It should be mentioned that despite these general similarities, there are no unique morphological characters uniting both genera. The radular morphology is very similar in both genera (radula of one more species, *S. marybethi* Parth, 1996 was illustrated in Zhang & Zhang 2018), however, as in the case with the body anatomy, it is of rather generalized buccinid appearance; similar radular morphology can be found in many unrelated genera – eg. *Latisipho* Dall, 1916 (Kosyan 2006), *Plicifusus* Dall, 1902 (Kosyan & Kantor 2012), *Aulacofusus* Dall, 1918 (Kosyan & Kantor 2013).

Our molecular analysis did not recover *Phaenomenella* as monophyletic. In both COI and combined COI+28S analyses the internal relationships within *Phaenomenella* – *Siphonalia* clade are not resolved. *Siphonalia spadicea* cluster without significant support with *P. samadiae* n. sp. We have only a single species of *Siphonalia* in our analyses so it is too preliminary to change the classification on the basis of the incomplete dataset. Therefore we presently retain the validity of *Phaenomenella*, although it is possible that *Phaenomenella* and *Siphonalia* can belong to a single genus. One of the distinctions between the genera is the depth range of known species. Generally, species of *Siphonalia* dwell at shallower depths – from 10 to 300 m (Okutani 2000), while *Phaenomenella* is recorded at 190-1389 m (Fraussen & Stahlschmidt 2013; herein). The new species are attributed to *Phaenomenella* based on stronger conchological similarity to other species of the genus rather than to species of *Siphonalia*. Unfortunately the protoconch of *P. samadiae* n. sp. was decollated in all available specimens, but the protoconch of *P. nicoi* n. sp. is large globose, similar to other species of *Phaenomenella*.

The analysis of a broader dataset of Buccinoidea rejected the monophyly of Siphonaliinae in its original scope. None of the Recent genera, originally included by Finlay (1928) in the subfamily, that are *Penion, Aeneator* and *Glaphyrina,* are closely related neither to each other, nor to *Siphonalia.* The system of Buccinidae and Buccinoidea in general is still far

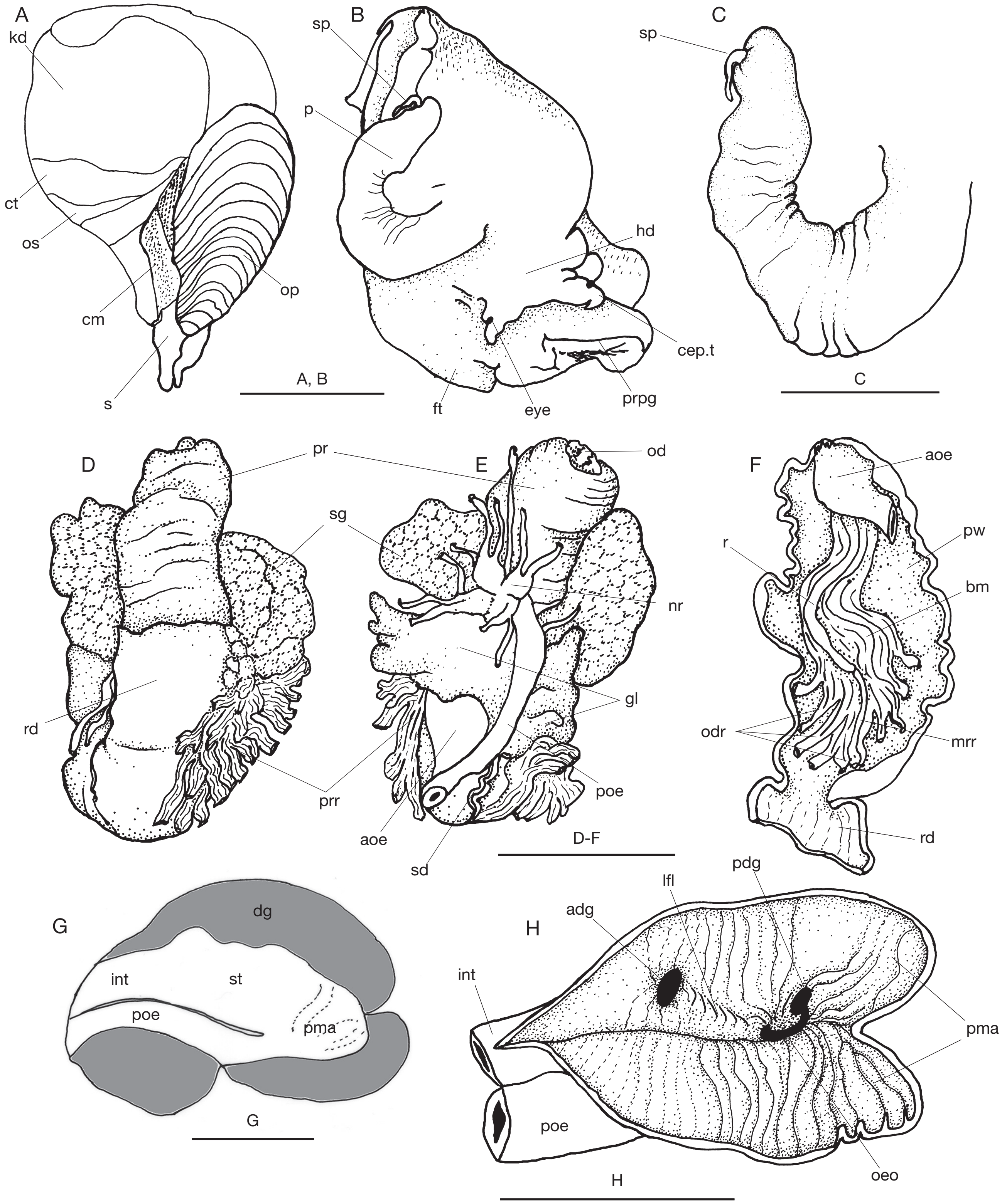

FIG. 12. — Anatomy of *Siphonalia pfefferi* G. B. Sowerby III, 1900, specimen no. 1: **A**, cephalopodium, ventral view; **B**, cephalopodium, dorsal view, mantle removed; **C**, penis; **D**, foregut, dorsal view; **E**, foregut, ventral view; **F**, proboscis opened dorsally; **G**, stomach, external view; **H**, stomach, opened dorsally. Abbreviations: see material and methods. Scale bars: A-F, 10 mm; G, H, 5 mm.

from being resolved, with many problematic buccinoidean lineages (see e.g. Couto *et al.* 2016; Harasewych 2018). Therefore the rank of the inferred clade *Siphonalia* + *Phaenomenella* can be resolved only after obtaining the robust phylogeny of the entire superfamily Buccinoidea.

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