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.
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 Southeast Asia (Fraussen 2008; Fraussen & Stahlischmidt 2012; Fraussen & Stahlischmidt 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 unresolved infrageneric 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*, i.e., *Manaria* Smith, 1906, *Eosiphon Thiele, 1929, Gailllea Kantor, Puillandre, Fraussen, Fedosov & Bouchet, 2013* (all three genera generate 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 Bucconulidae. 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, *Berylisma* Iredale, 1924), *Aeneator* (=*Ellicea* Finlay in Marwick 1928, †*Pitella* 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 Buccinoida, 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 Mu-
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 buccinoidae 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 Siphonalinidae. 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 Trace 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
- 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
- el: 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

| Specimen code | Genus | species | Collection data | BOLD | Genbank (COI) | Genbank (28S) | Source |
|---------------|-------|---------|-----------------|------|--------------|--------------|--------|
| IM-2007-32673 | Siphonalia | spadicea | TAIWAN 2004, st. CP264 | NEOGA544-10 | MK67642 | – | Present study |
| IM-2007-32674 | Siphonalia | spadicea | TAIWAN 2004, st. CP264 | NEOGA545-10 | MK67658 | – | Present study |
| IM-2007-32762 | | spadicea | TAIWAN 2001, st. CP79 | NEOGA589-10 | MK67634 | – | Present study |
| IM-2007-32856 | | spadicea | TAIWAN 2004, st. CP244 | NEOGA601-10 | MK67646 | – | Present study |
| IM-2007-32995 | | spadicea | TAIWAN 2001, st. CP109 | NEOGA666-10 | MK67652 | – | Present study |
| IM-2007-32997 | | spadicea | TAIWAN 2001, st. CP109 | NEOGA668-10 | MK67664 | – | Present study |
| IM-2007-32996 | | spadicea | TAIWAN 2001, st. CP109 | NEOGA667-10 | MK67656 | MK67635 | Present study |
| IM-2009-11271 | | spadicea | TAIWAN 2004 st. CH257 | BUCC001-19 | MK67649 | – | Present study |
| IM-2013-41068 | Phaenomenella | cf thachi | TAIWAN 2013 st. CP4090 | BUCC007-19 | MK67653 | – | Present study |
| IM-2013-41072 | | inflata | TAIWAN 2013 st. CP4080 | BUCC008-19 | MK67650 | – | Present study |
| IM-2013-41073 | | inflata | TAIWAN 2013 st. CP4090 | BUCC009-19 | MK67660 | – | Present study |
| IM-2013-50012 | | cf thachi | DONGSHA 2014 st. CP4120 | BUCC006-19 | MK67654 | MK67634 | Present study |
| IM-2013-50023 | | insulaprataensis | DONGSHA 2014 st. CP4129 | BUCC002-19 | MK67648 | MK67631 | Present study |
| IM-2013-50024 | | insulaprataensis | DONGSHA 2014 st. CP4129 | BUCC003-19 | MK67661 | – | Present study |
| IM-2013-50025 | | insulaprataensis | DONGSHA 2014 st. CP4129 | BUCC004-19 | MK67655 | – | Present study |
| IM-2013-50260 | | cf callophorella | DONGSHA 2014 st. CP1430 | BUCC005-19 | MK67665 | MK67639 | Present study |
| IM-2013-61674 | | samadiae n. sp. | ZHONGSHA 2015 st. CP4131 | BUCC013-19 | MK67662 | MK67638 | Present study |
| IM-2013-61617 | | samadiae n. sp. | ZHONGSHA 2015 st. CP4133 | BUCC015-19 | MK67644 | MK67628 | Present study |
| IM-2013-34644 | | nicoi n. sp. | AURORA 2007 st. CP2685 | NEOGA783-10 | MK67659 | – | Present study |
| IM-2013-59398 | | nicoi n. sp. | ZHONGSHA 2015 st. CP4157 | BUCC016-19 | MK67645 | MK67629 | Present study |
| IM-2013-61585 | | nicoi n. sp. | ZHONGSHA 2015 st. CP4132 | BUCC014-19 | MK67641 | MK67627 | Present study |
| IM-2013-61637 | | nicoi n. sp. | ZHONGSHA 2015 st. CP4133 | BUCC010-19 | MK67647 | MK67630 | Present study |
| IM-2013-61639 | | nicoi n. sp. | ZHONGSHA 2015 st. CP4133 | BUCC011-19 | MK67651 | MK67633 | Present study |
| IM-2013-61673 | | nicoi n. sp. | ZHONGSHA 2015 st. CP4134 | BUCC012-19 | MK67659 | MK67637 | Present study |
| IM-2007-34369 | Calagrassor | aldermenensis | AURORA 2007 st. CP2673 | – | – | – | – |
| IM-2007-32864 | Manaria | clandestina | PANGLAO 2005 st. CP2389 | – | – | – | – |
| IM-2007-32952 | brevicauda | – | SALOMON 2 st. CP2219 | – | – | – | – |
| IM-2009-7079 | Enigmaticolus | monnieri | MIRIKY st. CP3279 | – | – | – | – |
| 20140783 | Buccinum | undatum | Reykyavanaski, Iceland | – | – | – | – |
| KK12 | Kelletia | kelleti | Santa Barbara, California, USA | – | – | – | – |
| KL2 | lischkei | Kansai, Mie Prefecture, Japan | – | – | – | – | – |
| SFKH-TMP005 | Pararetifusus | carinatus | Chatham Rise, NZ | – | – | – | – |
| M.190082/2 | Penion | chatharmensis | Chatham Rise, NZ | – | – | – | – |
| M.190085 | chatharmensis | – | Chatham Rise, NZ | – | – | – | – |
| M.183792/1 | cuvierianus | – | Red Mercury Island, NZ | – | – | – | – |
| M.183927 | cuvierianus | – | Coromandel, NZ | – | – | – | – |
| C.456980 | mandanarius | – | Gabo Island, Victoria, Australia | – | – | – | – |
| C.487648 | maximus | – | Terrigal, NSW, Australia | – | – | – | – |
| Phoenix1 | Kellettalia | faedifolium | Otago Peninsula, NZ | – | – | – | – |
| Phoenix9 | sulcatus | Auckland, NZ | – | – | – | – | – |
| M.274111 | Aeneator | benthicola | Cape Palliser, NZ | – | – | – | – |
| SFKH-TMP015 | elegans | – | Chatham Rise, NZ | – | – | – | – |
| M.279437 | otaogensis | – | Tasman Bay, NZ | – | – | – | – |
| M.190119 | recens | – | Cape Turnagain, NZ | – | – | – | – |
| SFKH-TMP013 | valeauctus | – | TEN 616/83, NZ | – | – | – | – |
| M.183832 | Antarcitoneatna benthicola | Chatham Rise, NZ | – | – | – | – | – |
| SFKH-TMP014 | Austrosusus | glans | Island Bay, Wellington, NZ | – | – | – | – |
| M.302907/2 | Buccinulum | fuscozonatum | Ariel Bank, Gisborne, NZ | – | – | – | – |
| M.25827/6 | pallidum | – | Stewart Island, NZ | – | – | – | – |
| M.302870/2 | peritaxa finlayi | – | Point Gibson, NZ | – | – | – | – |
| M.31475/4 | robustum | – | Onora Bay, Bay of Islands, NZ | – | – | – | – |
| SFKH-TMP012 | vittatum vittatum | – | Mahia Peninsula, NZ | – | – | – | – |
| SFKH-TMP009 | Cominella | apsodesa | Urupukapuka Bay, NZ | – | – | – | – |
| SFKH-TMP010 | virgata | – | Spirits Bay, NZ | – | – | – | – |
| SFKH-TMP004 | Glaphyrina | caudata | Farwell Spit, Golden Bay, NZ | – | – | – | – |
Phaenomenella callophorella (Fraussen, 2004), 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. callophorella 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 cassidariaformis, 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 Phaenomenella with Siphonalia.

The two major clades of the Southern hemisphere buccinids included in the present study formed a weakly 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 BUCGINIDAE 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 forcar 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 | 000 |
| IM-2013-50203 | Ph. insulapratensis | 133 133 |
| IM-2013-50204 | Ph. insulapratensis | 133 133 000 |
| IM-2013-50205 | Ph. insulapratensis | 139 139 006 006 |
| IM-2013-41068 | Ph. cf thachi | 127 127 127 127 002 |
| IM-2013-50012 | Ph. cf thachi | 130 130 120 120 123 077 080 |
| IM-2013-50260 | Ph. cf thachi | 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. | 143 143 133 133 139 079 079 077 009 009 002 002 004 004 |
| IM-2013-61673 | Ph. nicoi n. sp. | 143 143 133 133 139 079 079 077 009 009 002 002 004 004 000 |
| 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 |
| IM-2007-32856 | S. spadicea | 185 185 185 185 182 168 168 171 162 162 169 169 166 166 166 166 169 169 006 006 006 006 |
| IM-2007-32995 | S. spadicea | 198 198 198 198 194 194 174 174 178 178 168 176 176 173 173 173 176 176 002 002 002 002 009 |
| IM-2007-32996 | S. spadicea | 192 192 191 191 188 188 168 171 162 162 169 169 167 167 166 167 160 170 002 002 004 004 004 004 |
| IM-2009-11271 | S. spadicea | 195 195 194 194 191 171 174 165 172 172 170 170 169 173 173 000 000 000 000 006 002 002 002 |
| IM-2007-32997 | S. spadicea | 192 192 191 191 188 188 168 171 162 162 169 169 167 167 166 167 160 170 002 002 004 004 004 004 000 002 |
| IM-2013-61674 | Ph. samadiae n. sp. | 157 157 157 157 163 172 171 156 176 176 173 173 179 176 176 186 186 186 186 182 183 186 183 |
| IM-2013-61617 | Ph. samadiae n. sp. | 160 160 159 159 166 169 168 152 167 164 164 164 170 167 167 179 179 179 179 170 183 183 176 179 176 006 |
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.
**Phaenomenella samadiae** n. sp.  
(Figs 4; 5A, B; 6)

**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. CP4134; 19°50’N, 116°27’E; 1128-1278 m • 2 lv; MNHN-IM-2013-50260 (Fig. 4D), MNHN-IM-2013-59393 (Fig. 4G); ZHONGSHA; st. CP4157; 19°48’N, 116°29’E; 1205-1389 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

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**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.
Taxonomic position of Phaenomenella

**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 inclined 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
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 tricusperate with weakly curved basal side, attached to membrane. Outermost cusp recurved, medium long, inner cup weakly recurved, about ½ of outer cup length. Intermediate cusp shortest, situated slightly closer to inner cup.

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 ½ of mantle width; bipectinate symmetric on top spiral cords, about 55 on last whorl. Radula with tricusperate central teeth with rectangular basal part and tricusperate lateral teeth with longest outermost cusp. 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 circular 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, pr). 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 of Leiblein medium large, S-twisted, situated beneath salivary glands 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. insulapataensei (Okutani & Lan, 1994), which possesses smaller, more ovoid shell with faster incrementing teleoconch whors and a longer and more distinct canal.
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. 4E, 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. 7F). Scale bars: 100 μm.
Fig. 6. — Anatomy of Phaenomenella samadai 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-2013-81639, 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 1/5–1/6 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 tricuspidate with weakly curved basal side, attached to membrane. Outermost cusp recurved, medium long, inner cusp weakly recurved, about 2/3 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 rhynchodaeme (Fig. 8D, pr). Several bands of proboscis retractors muscles attached to middle part on both sides of rhynchodaeme (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 Leibl (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 Leibl 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 conspecificity 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 telecoconch whors 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 tricuspidate with weakly curved, nearly straight basal side, attached to membrane. Outermost cusp recurved, medium long, inner cusp weakly recurved, about 2/3 of outer cusp length. Intermediate cusp shortest, situated closer to inner cusp.
Fig. 9. — Shells of studied Siphonala 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
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 rhynchodaum, thick, contracted (Fig. 10E, F, pr). Proboscis retractors (prr) attached to rhynchodaum along both sides of anterior oesophagus (mostly on its right side), connecting rhynchodaum 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, llf), 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.

**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 tricuspidate 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. Large 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.

**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 insulapratensis*) 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 intragenic 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. murrayi* 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. samadai* 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. samadai* 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 Siphonalia in its original scope. None of the Recent genera, originally included by Finlay (1928) in the subfamily, that are *Penion*, *Aenator* 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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