Phylogenetic ecology of octocoral - gastropod associations

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Chapter 5

A new perspective on Ovulidae phylogenetics and systematics with special reference to the subfamily Aclyvolvinae

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Abstract

Molecular phylogenetic research on species of the octocoral-associated family Ovulidae is still very limited. Phylogenetic relationships between subfamilies and genera are unclear and morphological characters can be confusing when dealing with species delimitations. Here four molecular markers (COI, 16S, 28S, and H3) and morphometrics are used to reconstruct the phylogeny and asses the systematics of the Aclyvolvinae, one of four subfamilies within the Ovulidae. These data are also analysed with 16S and COI sequences for other Ovulidae species from the remaining three subfamilies to identify the phylogenetic relationship of the subfamily Aclyvolvinae among the other ovulid subfamilies. The results show that two out of four subfamilies (viz. Aclyvolvinae and Simniinae) are polyphyletic. Within the subfamily Aclyvolvinae, the type species of *Hiatavolva*, *H. depressa*, does not cluster with the other *Hiatavolva* spp. Instead, the other species, *H. rugosa* and *H. coarctata,* cluster with the type and other species of the genus *Aclyvolva* and are therefore moved to that genus. Molecular and morphometric results show that *A. lamyi* and *A. nicolamassierae* are synonyms of *A. lanceolata* and that *A. rugosa* (n. comb.) is a synonym of *A. coarctata* (n. comb.). The genus *Kuroshiovolva* could not be retrieved in a fixed phylogenetic position within the Aclyvolvinae, but did not cluster with *Hiatavolva depressa* or *Aclyvolva* spp. Its taxonomic position remains therefore uncertain. In addition, photographs of type species are provided, as well as new information on the geographical distribution and host species of Aclyvolvinae.

Introduction

Species of the family Ovulidae occur in tropical, subtropical and temperate waters, but their diversity is highest in tropical waters of the Indo-Pacific (Lorenz and Fehse, 2009). Most of them are obligate symbionts of octocoral species. To provide camouflage against visual predation, their mantle colour is usually similar to that of their host octo-

Fig. 1. *In situ* images of Aclyvolvinae snails and their corals hosts. a) *Aclyvolva lanceolata* (RMNH.Mol.164192) on *Viminella* sp. at Kudat, Malaysia. b) *A. lamyi* (RMNH.Mol.164181) on *Junceella* sp. at Kudat, Malaysia. c) *Hiatavolva coarctata* (RMNH.Mol.164234) on *Ellisella* sp. at Lembeh Strait, Indonesia. d) *H. rugosa* (RMNH.Mol.164197) on *Ctenocella* sp. at Pulau Banggi, Malaysia. e) *H. depressa* (RMNH.Mol.164147) on *Alertigorgia orientalis* (Ridley, 1884) at Pulau Banggi, Malaysia. f) *Kuroshiovolva shingoi* at Bohol, Philippines. Photographs a-e by the author. f by E. Guillot de Suduiraut.

corals (Schiaparelli *et al*., 2005). Moreover, some ovulid species even mimic typical morphological octocoral host structures, such as their polyps (Fig. 1).

The family Ovulidae Fleming, 1882, has recently been revised (Fehse, 2007), which resulted in the recognition of four subfamilies, namely Ovulinae Fleming, 1822, Simniinae Schilder, 1925, Aclyvolvinae Fehse, 2007 and Prionovolvinae Fehse, 2007. The division into four separate subfamilies was partly based on a paper by Schiaparelli *et al*. (2005), in which the first molecular phylogeny reconstruction of the family Ovulidae was presented based on the mitochondrial 16S rRNA sequences. This phylogenetic reconstruction showed five groups in a polytomy (clades A-E after Schiaparelli *et al*., 2005). These clades were moderately to well-supported and could each represent a subfamily. Fehse (2007) combined the molecular 16S rRNA results of Schiaparelli *et al*. (2005) together with morphological characters as distinguished by Simone (2004) to erect the subfamilies Prionovolvinae and Aclyvolvinae. Of all four subfamilies, the Aclyvolvinae are morphologically well defined, easily recognisable as a subfamily, and holds the least number of species. Currently the Aclyvolvinae comprises eight recognised species (Lorenz and Fehse, 2009), divided over three genera (*Aclyvolva*, *Hiatavolva* and *Kuroshiovolva*). All are restricted to the central Indo-Pacific, except for *Aclyvolva nicolamassierae* Fehse, 1999, which occurs in the western Indian Ocean and the Red Sea (Fehse, 1999; Lorenz and Fehse, 2009). Species of *Aclyvolva* and *Hiatavolva* are hosted by gorgonians of the family Ellisellidae (Schiaparelli *et al*., 2005; Lorenz and Fehse, 2009; Reijnen, 2010), whereas members of *Kuroshiovolva* are found associated with primnoid corals of the genus *Plumarella* (Lorenz, 2009). Unfortunately, most ovulid material deposited in museum collections is not accompanied by data on the host species. The shells of Aclyvolvinae can easily be distinguished from those of other ovulids by their lanceolate form and the absence of a well-developed funiculum. Species-specific differences in the Aclyvolvinae are based on conchological characters such as the density and coarseness of the striae, or the presence or absence of longitudinal growth lines, or colour. Although these characters seem to be clear, large shell collections show much interspecific overlap in morphology, obscuring species differences. In juvenile shells the conchological characters are lacking or are expressed differently. As a consequence, many names have become available for similar lanceolate shells and there is disagreement among taxonomists. For example, Cate (1973) described two new genera and synonymized some species, while also describing or resurrecting others. Later, Lorenz and Fehse (2009) synonymized most of Cate’s new species and many other available names, leaving only eight recognized species in the Aclyvolvinae. In the first molecular phylogenetic analysis of ovulids, Schiaparelli *et al*. (2005) included two species of Aclyvolvinae: *Aclyvolva lanceolata* (Sowerby II, 1848) and *A*. cf. *lamyi* (Schilder, 1932). These species clustered together in a monophyletic clade. The relationships between this clade of Aclyvolvinae and the other three subfamilies remained unresolved. These taxonomic uncertainties indicate the need for an integrated molecular and morphological approach to clarify the interspecific relationships in the Aclyvolvinae, which is the aim of the present study. To reconstruct the phylogenetic relationships between the Aclyvolvinae and the other ovulid subfamilies, to test generic assignments and to clarify the taxonomic status of the available species, material of seven nominal

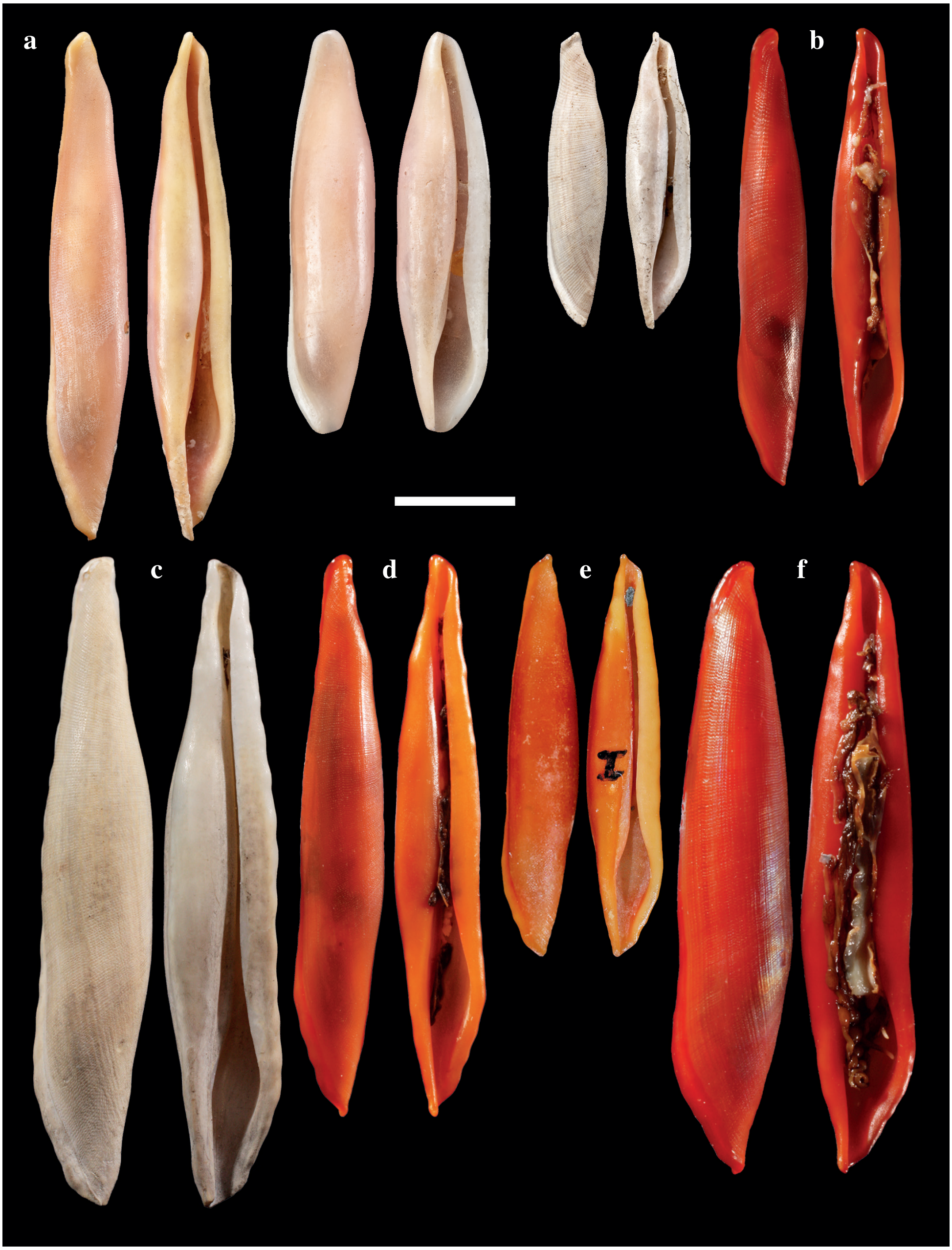

Fig. 2. Dorsal and ventral views of *Aclyvolva* (type)specimens. a) lectotype (left) and paralectotypes of *Ovulum lanceolatum* (=*Aclyvolva lanceolata*). b) *Aclyvolva lanceolata* (RMNH.Mol.164179). c) Holotype of *Neosimnia lamyi* (= *Aclyvolva lamyi*) (MNHN IM 2000-27664). d) *Aclyvolva lamyi* (RMNH.Mol.164165). e) Holotype of *Aclyvolva nicolamassierae*. f) *Aclyvolva nicolamassierae* (RMNH.Mol.337794). Photographs by author except for a) Andreia Salvador (BMNH) e) Dr. Vollrath Wiesse (Haus der Natur – Cismar). The scale bar represents 5 mm.

Aclyvolvinae species was sequenced. Morphological characters were evaluated to clarify species delimitations.

Material and methods

Abbreviations institutions

ANSP	The Academy of Natural Sciences of Drexel University, Philadelphia, USA
BMNH	Natural History Museum, London, UK
MNHN	Muséum national d'Histoire naturelle, Paris, France
Naturalis	Naturalis Biodiversity Center, Leiden, The Netherlands
SI	Smithsonian Institution, Washington D.C., USA

Sampling and identification

A total of 83 snail specimens and their cnidarian hosts were collected representing Ovulidae (n=79), Pediculariidae (n=3) and Cypraeidae (n=1). The latter two were used as outgroups. Snails belonging to the subfamily Aclyvolvinae represented seven nominal species: *Aclyvolva lamyi* (n=3), *A. lanceolata* (n=9), *A. nicolamassierae* (n=1), *Hiatavolva coarctata* (Sowerby II in Adams & Reeve, 1848) (n=13), *H. depressa* (Sowerby III, 1875) (n=2), *H. rugosa* (Cate & Azuma in Cate, 1973) (n=17) and *Kuroshiovolva shingoi* (Azuma & Cate, 1971) (n=1) (Fig. 2, 3). Two specimens included in the dataset represent type species of the genus, which are the type genera of their respective subfamilies; *Aclyvolva lanceolata* (Aclyvolvinae) and *Ovula ovum* (Linnaeus, 1758) (Ovulinae). For two other subfamilies, the Prionovolvinae and Simniinae, the type species are *Prionovolva brevis* (Sowerby I, 1828) and *Simnia nicaeensis* Risso, 1826, respectively, but unfortunately these are not represented due to the unavailability of suitable material.

The ovulid specimens were collected in Indonesia, Malaysia, Saudi Arabia and Thailand (see supplementary material S1 for more information). Voucher specimens were fixed in 70% ethanol and deposited in the mollusc collection of Naturalis (coded as RMNH.Mol) except for *Kuroshiovolva shingoi* Azuma and Cate, 1971. The voucher specimen for *K. shingoi* is curated by the SI and the sequences were provided by Dr. C.P. Meyer (SI). To identify the collected specimens a stereomicroscope (Leica MZ16) was used and specimens were compared with photographs of the Aclyvolvinae type specimens of *Aclyvolva nicolamassierae*, *Hiata rugosa*, *Neosimnia lamyi*, *Ovulum lanceolatum* and *O. coarctatum*) (Fig. 2, 3) and the ovulid monographs by Cate (1973) and Lorenz and Fehse (2009) amongst other Ovulidae literature.

DNA extraction and sequencing

Tissue for DNA extraction was obtained from the foot and/or mantle of the snails. The DNeasy Kit (QIAGEN) was used according to the corresponding protocol for animal tissue (v. 07/2006). Digestions were performed overnight for approximately 16 h and DNA elution was performed with 100 μl of buffer AE. DNA extracts were diluted (1:100 or 1:300) before PCR amplification. The PCR mixture contained: 2.5 μl PCR CoralLoad Buffer (containing 15 mM MgCl2) (QIAGEN), 0.5 μl dNTP's (2.5 mM), 1.0 μl per

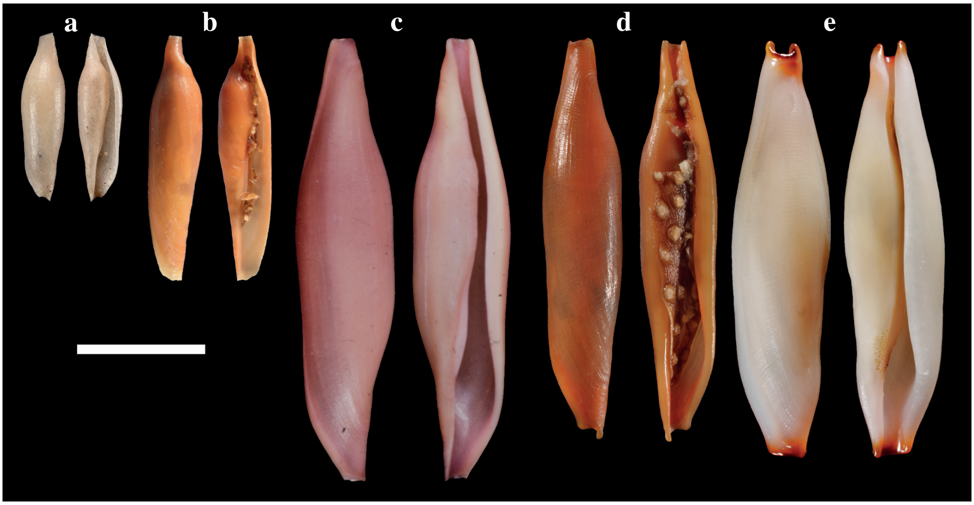

Fig. 3. Dorsal and ventral views of *Hiatavolva* (type)specimens. a) Holotype of *Ovulum coarctatum* (=*Hiatavolva coarctata*). b) *Hiatavolva coarctata* (RMNH.Mol.164185). c) Holotype of *Hiata rugosa* (= *Hiatavolva rugosa*). d) *Hiatavolva rugosa* (RMNH.Mol.164234). e) *Hiatavolva depressa* (RMNH.Mol. 164182). Photographs by author except for a) Andreia Salvador (BMNH). c) Prof. Gary Rosenberg (ANSP). The scale bar represents 5 mm.

primer (10 μM), 0.3 μl Taq polymerase (15 units/μl) (QIAGEN) and 18.7 μl of extra pure water and 1.0 μl (diluted) DNA extract. For amplification of the 28S marker 5.0 μl of water was replaced by 5.0 μl QSolution (QIAGEN). All PCR cycles consisted of an initial denaturing step of 95 °C for 1 min. followed by 39 cycles of 95°C for 10 s., preferred annealing temperature (see Table 1) for 1 min and an extension step of 72°C for 1 min. The final PCR cycle was followed by an elongated extension step of 72°C for 5 min. Successfully amplified samples were sent to Macrogen Europe for PCR cleaning and sequencing on an ABI Automated Sequencer 3730xl. Besides the Aclyvolvinae specimens, 41 specimens of 15 nominal ovulid species were sequenced for 16S and cytochrome c oxidase subunit I (COI). Not all markers were successfully amplified for all specimens, an overview of the sequence and provenance data is provided in Table S1. Sequence data for seven ovulid species (viz. *Crenavolva aureola* (4), *C. striatula* (1), *C. trailli* (2), *Cymbovula acicularis* (3), *Cyphoma gibbosum* (6), *Primovula rosewateri* (1) and *Simnia patula* (1)) was obtained from GenBank (see also Supplementary Material Table S1). All novel sequences are uploaded to GenBank (accession numbers: KP259314-KP259547 and KP271159-KP271161)

Molecular analyses

Sequences were edited using either Geneious Pro 5.6.4 or Sequencher 4.10.1 and aligned with ClustalW implemented in Bioedit (Hall, 1999) or the MAFFT algorithm used on the GUIDANCE server (Penn *et al*., 2010). All newly acquired sequences were checked against GenBank to check for resemblance with sequence data previously submitted by

Table 1. Information on primers, specific conditions and their references.

Primer names	Primer sequences	Region	Annealing T	Fragment size	Reference(s)
H3F & H3R	ATGGCTCGTACCAAGCAGACVGC & ATATCCTTRGGCATRATRGTGAC	Histone 3 (nuclear)	50	~ 380	Colgan *et al*., 2000
LSU5 & LSU800rc	TAGGTCGACCCGCTGAAYTTAAGCA & GACTCCTTGGTCCGTGTTTC	28S (nuclear)	50	~ 800	Littlewood *et al*., 2000; this publication
16Sar & 16Sbr	CGCCTGTTTATCAAAAACAT & CCGGTCTGAACTCAGATCACGT	16S (mitochondrial)	52	~ 540	Palumbi *et al*., 1996
LCO-1490 & HCO-2198	GGTCAACAAATCATAAAGATATTGG & TAAACTTCAGGGTGACCAAAAAATCA	COI (mitochondrial)	40-44	~ 660	Folmer *et al*., 1994

Meyer (2003) and Schiaparelli *et al*. (2005). Eventually sequences were concatenated with the help of SequenceMatrix (Vaidya *et al*., 2011) to create two datasets, one containing ovulid species representing all subfamilies (based on the 16S and COI markers) and a second dataset containing data of solely Aclyvolvinae (based on 16S, COI, histone H3 and 28S rRNA). The dataset containing all Ovulidae is 1,191 base pairs in length, including insertions and deletions (indels), and the Aclyvolvinae dataset is 2,296 base pairs long including indels. Each dataset was subjected to two model-testing algorithms, one implemented in MEGA 6.0.6 (Tamura *et al*., 2013) and to jModeltest2 (Darriba *et al*., 2012) (all AIC calculations). Subsequently the most optimal evolutionary model was selected for the various phylogeny reconstructions that were performed: Maximum Likelihood (ML) analyses (500 bootstrap iterations) in MEGA 6.06 and Bayesian inferences (BI) were calculated in MrBayes 3.2.2 (Ronquist and Huelsenbeck, 2003). Bayesian inferences were calculated over 10 million replicates using the dirichlet method. A tree was sampled every 100 iterations. The burnin was set to 50.000. The standard deviation of split frequencies was < 0.01. Support values for a MP analysis were determined over 500 bootstrap iterations using nearest neighbor interchange and the Tree-Bisection-Reconnection (TBR) branch swapping algorithm was used with ten initial trees. To check for non-arbitrary species delimitation, the molecular concatenated dataset for the four molecular markers was submitted to the online program ABGD (Automatic Barcode Gap Discovery) (Puillandre *et al*., 2012). Default settings with the Kimura (K80) TS/TV algorithm were used.

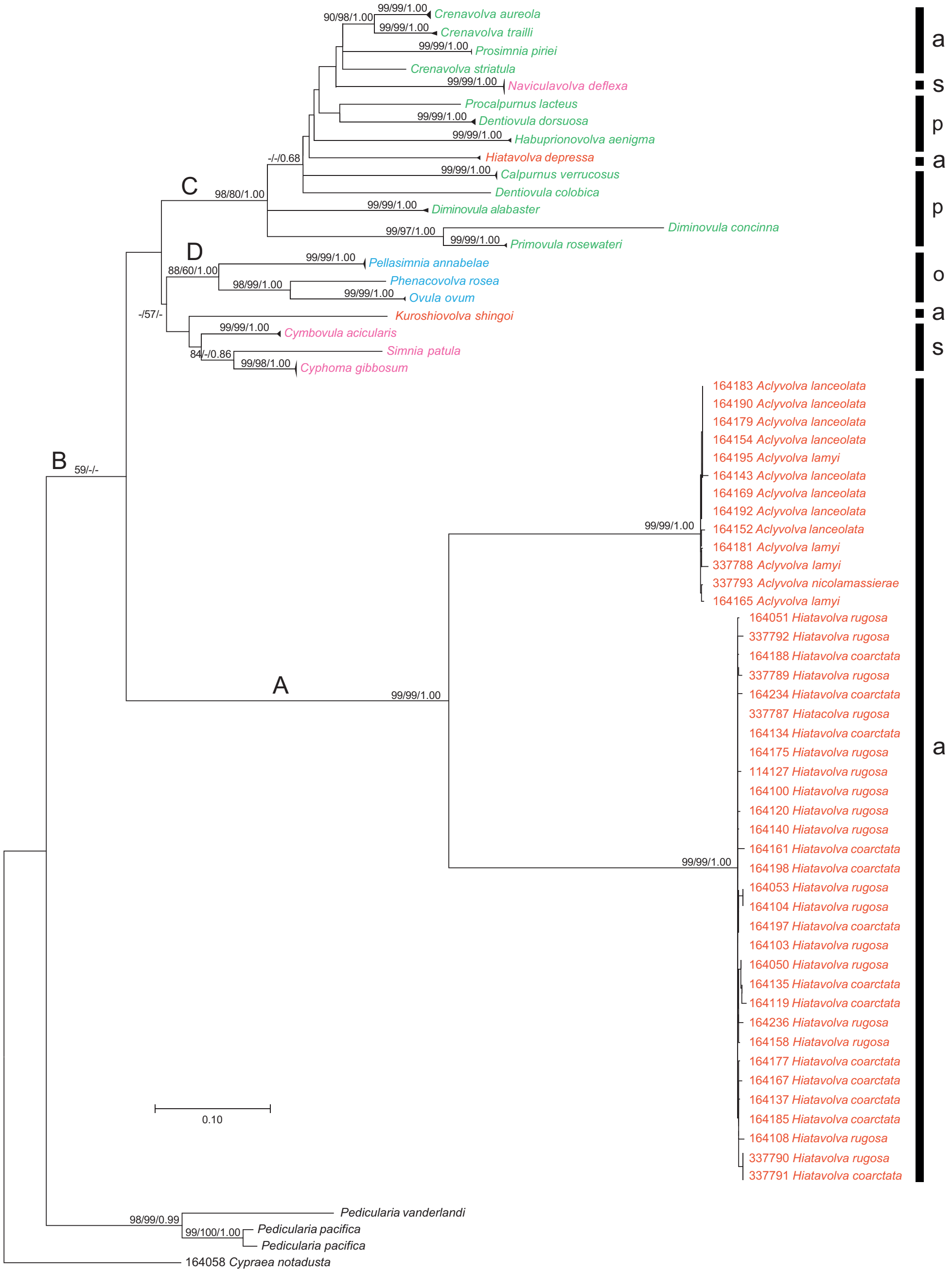

Fig. 4. Phylogeny reconstruction consisting of species representing each of the four subfamilies (Aclyvolvinae (= a), Ovulinae (= o), Prionovolvinae (= p) and Simniinae (= s)) within the Ovulidae. The phylogeny is based on 16S and COI. Support values are respectively bootstrap support values for MP and ML analyses, and posterior probabilities for BI. A-D refer to specific clades.

Morphological measurements and analyses

Shell morphological features were analysed by plotting 151 landmarks on photographs of the dorsal side of the sequenced specimens (in standard orientation as in Figs 2, 3), describing the entire shell outline. The Tps software package (tpsUtil, tpsDig2 and tpsRelw) (Rohlf, 2006) was used to create the morphological dataset and to calculate relative warps. The resulting relative warp data was exported to PAST (Palaeontological Statistics; Hammer *et al*., 2001) and was subjected to a principal component analysis (PCA). The length of all Aclyvolvinae specimens was measured with a calibrated digital calliper (Mitutoyo 500) as in Rosenberg (2010).

Results

Molecular analyses

In total 237 novel sequences for four molecular markers were generated including those from outgroup taxa. Sequences were combined into two datasets 1) All Ovulidae and 2) All Aclyvolvinae. The results from the different modeltest approaches were as follows: GTR+I+G by MEGA and TVM+I+G by jModeltest as most optimal evolutionary model. For the Aclyvolvinae dataset the GTR+I+G model was selected by both MEGA and jModeltest. Since the second best option in jModeltest Ovulidae dataset was the GTR+I+G model with only a small decimal difference in the likelihood calculations between the TVM+I+G and GTR+I+G model, the GTR+I+G model was selected for all analyses. The phylogeny reconstructions based on the Ovulidae dataset with representatives of all subfamilies showed that the relationships between the subfamilies, Simniinae, Prionovolvinae and Aclyvolvinae are unresolved (Fig. 4) only the Ovulinae are retrieved as a monophyletic group. Species of the subfamily Aclyvolvinae were retrieved at three different positions in the phylogeny reconstruction, which indicates that this subfamily is polyphyletic according to the definition of the subfamily Aclycolvinae of Fehse (2007). The Aclyvolvinae group that consists of *Aclyvolva lamyi*, *A. lanceolata*, *A. nicolamassierae*, *Hiatavolva coarctata* and *H. rugosa* (clade A in Fig. 4) is retrieved as a highly supported clade (99/99/100) to the clade containing members from all ovulid subfamilies. Phylogenetic relationships between these two clades are not supported (B in Fig. 4; 59/-/-). The type species of the genus *Hiatavolva*, *H. depressa*, is found among the Prionovolvinae. Phylogenetic relationships between the species in the group that contains *H. depressa* are unresolved, but all together this clade (clade C in Fig. 4), is well-supported (98/80/100). The other representatives of the genus *Hiatavolva* (*H. coarctata* and *H. rugosa*) are not retrieved as a sister species to the type species *H. depressa*, but cluster strongly as a sister group of *Aclyvolva* (clade A in Fig. 4). The genus *Kuroshiovolva*, here represented by *K. shingoi*, does not have a fixed position in the phylogeny reconstructions based on the ML, MP, and BI analyses. This species is either found unsupported as a sister species to all subfamilies or is retrieved in the group containing the Atlantic Ovulidae representatives *Cyphoma gibbosum*, *Cymbovula acicularis* and *Simnia patula*.

The cladogram based on four markers, representing only Aclyvolvinae species (Fig. 5), shows that there is almost no genetic distance between the nominal species *H. coarctata*/*H. rugosa* and *A. lanceolata*/*A. nicolamassierae*/*A. lamyi*. The non-arbitrary approach

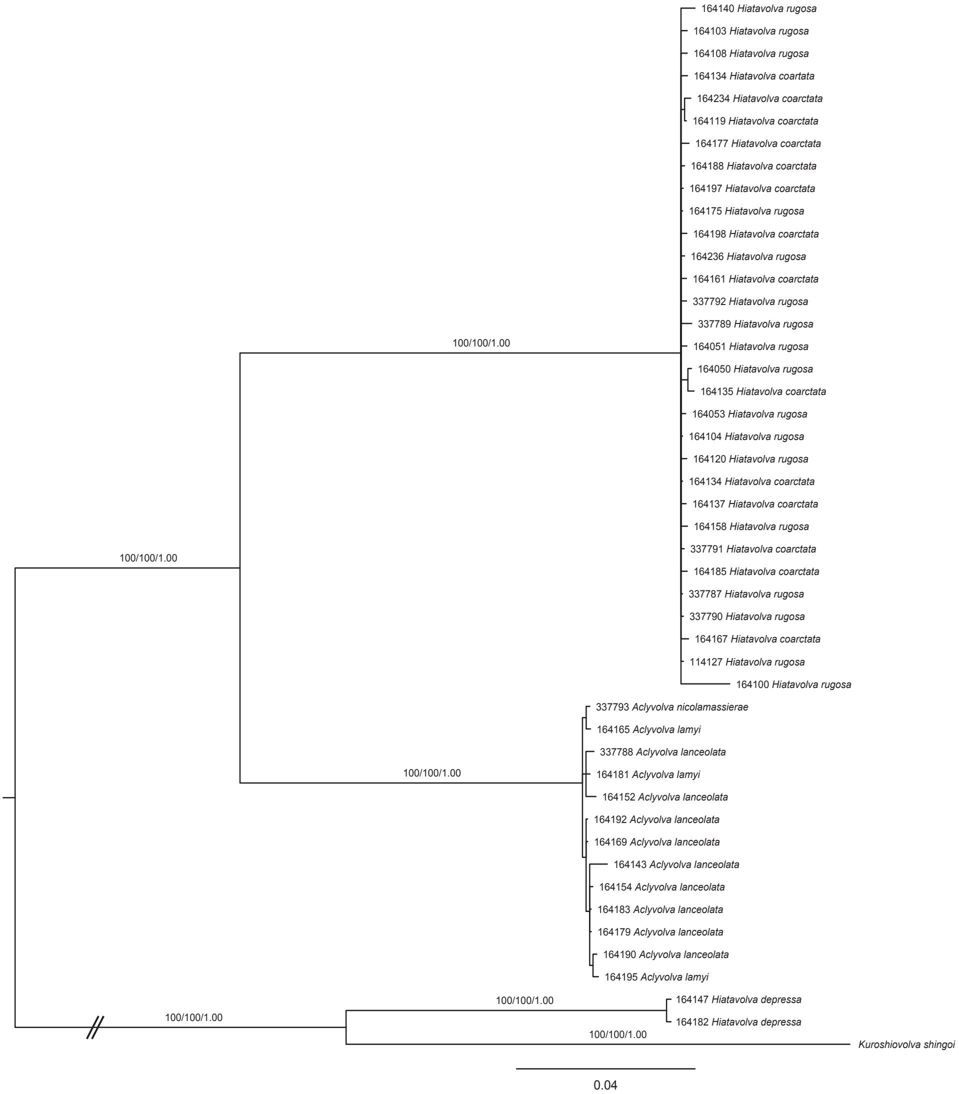

Fig. 5. Phylogeny reconstruction of the Aclyvolvinae based on 16S, COI, H3 and 28S. Support values are respectively bootstrap support values for MP and ML analyses, and posterior probabilities for BI.

for species delimitation in the ABGD analysis, supported these findings. Based on the differences in intra vs. interspecific sequence variation, the ABGD analysis resulted in four groups of species according to the clades in Figure 5, containing: 1) *A. lanceolata*/*A. nicolamassierae*/*A. lamyi*, 2) *H. coarctata*/*H. rugosa*, 3) *H. depressa* and 4) *K. shingoi*.

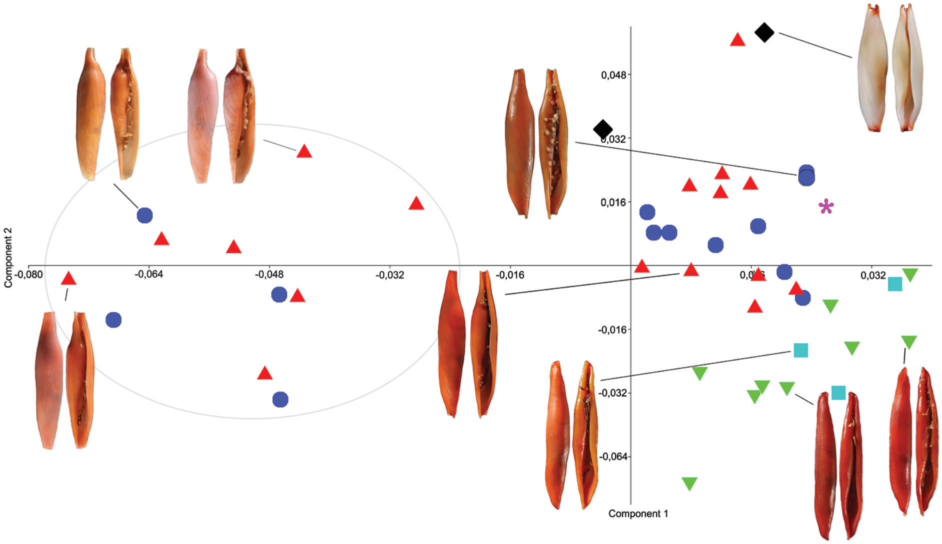

Fig. 6. Plot of the results of the principal component analysis (PC1 and PC2) on 44 relative warps and 151 landmarks. Square: *A. lamyi*; inverted triangle: *A. lanceolata*; asterix: *A. nicolamassierae*; circle: *H. coarctata*; diamond: *H. depressa*; triangle: *H. rugosa*. Images of the shells are not to scale.

Morphological analyses on Aclyvolvinae

The PCA was based on 44 relative warp coordinates of 151 landmarks. Principal component 1, 2, and 3 accounted for 88% of the variation amongst samples. *H. coarctata* and *H. rugosa* were scattered throughout the plot in two recognisable groups composed of each nominal species (Fig. 6).

Aclyvolva spp. also formed a group without further noticeable separation between species except for *A. nicolamassierae* which falls just outside the cluster near to the *Hiatavolva* spp. The two specimens of *H. depressa* did not cluster with the other *Hiatavolva* or *Aclyvolva* species. As a result of the separation into two groups, each containing specimens of *H. coarctata* and *H. rugosa*, shells were investigated more closely. The encircled specimens in the plot are all smaller in size (mean length = 12.14 mm, ± 2.56 mm, n=11) whereas the non-encircled specimens are longer (mean length = 15.81 mm ± 2.70 mm, n=19). Moreover, shells on the left have a less developed and less calloused shell, which is typical for juveniles or subadults, whilst specimens on the right side generally have a well-developed labrum and adapical and abapical canals.

Discussion

Molecular phylogeny and subfamily classification of Ovulidae

The deep phylogeny of the Ovulidae, as shown in the present phylogeny reconstruction (Fig. 4) is far from resolved. Many nodes are not or poorly supported, which hampers the higher taxonomic classification within the Ovulidae. Furthermore, the proposed higher systematic classification as proposed by Fehse (2007), is inconsistent with the present molecular results. This study only deals with a limited number of representatives from the subfamilies, but already shows that the Simniinae, Prionovolvinae and Aclyvolvinae are not monophyletic subfamilies. The only monophyletic subfamily is the Ovulinae. Both Schiaparelli *et al*. (2005) and Fehse (2007) also concluded that the Ovulinae are monophyletic. In order to guarantee monophyly for the other three subfamilies, taxonomic rearrangements have to be made. Whether such rearrangements can be supported with morphological data is uncertain and requires additional studies. What can be observed from the phylogeny reconstruction is that ovulid shell shapes (e.g. rhomboid, lanceolate, globose or pyriform) are not restricted to specific clades in the phylogeny reconstructions. For example species having the lanceolate shells (e.g. Aclyvolvinae *sensu lato*) are retrieved at three positions in the cladogram, and likely reflects convergent evolution in ovulid shell shape rather than common ancestry. Studies on homoplasy and convergent evolution in marine gastropods (e.g. Marko and Vermeij, 1999; Johannesson, 2003) show that ecological factors can influence shell morphological features. Especially since ovulids live in close association with certain octocoral families or genera, homoplasy in ovulid shell shapes could indicate there is a functional requirement to live and survive on specific host species. Traditional taxonomic arrangements based on shell shapes are therefore biased by possible convergent evolution in Ovulidae, possibly triggered by host species symbiosis which finally troubles the higher systematics in the family Ovulidae.

Classification of Aclyvolvinae sensu stricto*: molecular and morphological evidence*
For the Aclyvolvinae, seven of the eight nominal species are retrieved at three different positions in the cladogram. Two species (*H. depressa* and *K. shingoi*) do not cluster near the clade containing the type species of the Aclyvolvinae. It is therefore clear that *H. depressa* does not belong in the subfamily Aclyvolvinae. *H. depressa* is morphologically also very distinct from all other Aclyvolvinae because of indented terminals creating two teeth-like projections at either terminal end. The phylogenetic position of *K. shingoi* is harder to justify due to unresolved grouping with other species from different subfamilies e.g. Simniinae. From a morphological perspective the placement of *K. shingoi* within the Simniinae is not in contrast with the shell-based diagnosis for this family, except for lacking a prominent transverse cord-like funiculum, which is lacking in all *Kuroshiovolva* species (Lorenz & Fehse, 2009). Besides the Simniinae, *K. shingoi* also clustered with members of the subfamily Ovulinae, although support values are low. The diagnosis for the subfamily Ovulinae states that shells can be ovate to spindle-shaped and that the funiculum is usually absent or indistinct and that the anal canal of their shells is slightly twisted. When *Kuroshiovolva* species are compared with this diagnosis, the shell shape and twisted anal canal cannot be matched. The position of this genus within the Ovulidae is therefore still unclear and requires additional research. The type specimen of *Hiatavolva coarctata* is a subadult shell and is therefore lacking most of the characters used in adult shells to distinguish species. Actually, the last sentence of the species description of *H. coarctata* by Sowerby II (1848) states: “It may, however, very possibly be a young shell”. Liltved (1989) agrees that the type of

H. coarctata is most probably a subadult shell, which does not fully resemble the characteristics in the adult shell morphology. Additionally, Liltved (1989: p. 132) also questioned the difference between *Phenacovolva coarctata* and *P. rugosa* (= *H. coarctata* and *H. rugosa*) based on their shell morphology. Nevertheless, Fehse (1999) disagreed with Liltved based on three shell characters: (1) small size, (2) shorter terminals, and (3) colour. Two of these characters are related to the subadult stage of the shell, e.g. the small size and shorter terminals. Colour was later disregarded by Lorenz and Fehse (2009) since they only identified two morphological differences to identify these species: (1) terminal length and (2) longitudinal sculpturing. Newly collected specimens in this study, from subadult and adult stages were morphologically assigned to either *H. coarctata* or *H. rugosa* based on these two characteristics. The morphometric analysis of these specimens shows that the juveniles are indeed morphologically distinct from adults (apart from just their size) whilst the molecular results do not show any support to separate these morphospecies into different species groups (Fig. 4, 6). This supports the assumption that juvenile shells are morphologically significantly different in comparison to their adult conspecifics. As can been observed in the successive growth stages of *Cyphoma gibossum*, juveniles in the family Ovulidae can differ morphologically very much from conspecific adults (Reijnen *et al*., 2010). This variable shape has probably caused problems in the identification of Aclyvolvinae specimens in earlier studies (e.g. Schiaparelli *et al*., 2005). Molecular data is one of the tools that could help to overcome difficulties in morphological species identifications. Molecular data for 16S, presented here, was checked against molecular data of Schiaparelli *et al*. (2005) deposited on GenBank. Specimens identified by the author as *H. coarctata*/*rugosa* match convincingly with *A. lanceolata* of Schiaparelli *et al*., 2005. Consequently, material herein identified as *A. lanceolata,* matched with *A. cf. lamyi* sequences from GenBank (Schiaparelli *et al*., 2005). Comparison of the photographs of the living animals and their respective shells (Suppl. Mat. Fig 3H, I, L, M and 4F-I, L) provided by Schiaparelli *et al*. (2005) with specimens figured in Cate (1973), Lorenz and Fehse (2009) and the images of the holotypes shown here, indicate that the GenBank specimens most probably have been misidentified (see also: Fehse, 2006, p. 19). However, in case of the Aclyvolvinae, shell morphological features are often indistinct but mantle patterns and structures provide an additional tool for identifying these species. *In situ* images show that *H. coartata* specimens have retractile mimetic gorgonian polyps whilst specimens representing *A. lanceolata* lack these mimetic polyps but have papillae on their mantle that might be of a different colour when compared to the rest of the mantle colour (Reijnen, 2011: Fig. 3 A,B; Lorenz and Fehse 2009: Fig A350-A365).

Remarks on distribution and host species of Aclyvolvinae

The distribution of ovulid species is highly dependent on the abundance of their host species. For example the coral hosts of the ovulid group containing *A. lanceolata* and its direct sister group containing some *Hiatavolva* spp. (clade A in Fig. 4), are different than those of *H. depressa* and *Kuroshiovolva* spp. *Hiatavolva depressa* is only known from *Alertigorgia orientalis* (Ridley, 1884) and *A. hoeksemai* van Ofwegen & Alderslade, 2007 from the octocoral family Anthothelidae. Species from the genus *Kuroshiovolva* are only found in association with *Plumarella* spp. (family Primnoidae) and possibly *Astrogorgia* sp. (family Plexauridae). In comparison, all other Aclyvolvinae are found on octocorals of the family Ellisellidae (primarily *Ctenocella*, *Dichotella, Ellisella* and *Junceella*). As a consequence of these intricate associations, the absence of *H. depressa* in the Indian Ocean and Red Sea can be directly related to the absence of host corals of its host genus *Alertigorgia*. In contrast, *Aclyvolva* species are associated with Ellisellidae. Members of this family are found at the Indo-Pacific in shallow and deep water thereby fostering the distribution of *Aclyvolva* spp. In the collections of Naturalis there is also a specimen of *A. lanceolata* from the Persian Gulf (RMNH.Mol.187230). Like *A. nicolamassierae*, specimens from almost enclosed water bodies, such as the Red Sea and the Persian Gulf, are often considered endemic and/or new to science. Nevertheless, newly acquired molecular data for *A. nicolamassierae* from the Red Sea showed no

Table 2. Aclyvolvinae species, host species and ovulid distribution including their reference for *Aclyvolva*, *Hiatavolva* and *Kuroshiovolva* species.

Ovulid species (this study)	Original identification	Known octocoral host species	Geographical location	Reference
Aclyvolva coarctata	*Aclyvolva lanceolata*	*Ellisella* sp.; ?*Muricella* sp.	Sulawesi, Indonesia	Schiaparelli *et al.*, 2005
Aclyvolva coarctata	*Hiata coarctata*	?*Echinogorgia rigida*	Kanagawa Prefecture, Japan	Mase, 1989
Aclyvolva coarctata	*Hiatavolva coarctata*	?*Echinogorgia* sp.; ?*Melithaea* sp.; ?*Muricella* sp.	Reunion to western Pacific	Lorenz and Fehse, 2009 (see also caption A356, A357 in Lorenz and Fehse, 2009)
Aclyvolva coarctata	*Hiatavolva coarctata*	*Dichotella* sp.; *Ellisella* sp.	Halmahera, Indonesia	Reijnen, 2010
Aclyvolva coarctata	*Hiatavolva coarctata*	*Ctenocella* sp.; *Ellisella* sp.; *Verrucella* sp.; *Viminella* sp.	Indonesia; Malaysia	This publication
Aclyvolva coarctata	*Hiatavolva rugosa*	?*Echinogorgia* sp.; *Ellisella* sp.; *Verrucella* sp.; *Viminella* sp.	Japan; Philippines; Indonesia; Queensland, Australia; E South Africa	Lorenz and Fehse, 2009
Aclyvolva lanceolata	*Aclyvolva* cf. *lamyi*	*Dichotella* sp.	Sulawesi, Indonesia	Schiaparelli *et al.*, 2005
Aclyvolva lanceolata	*Aclyvolva lamyi*	*Ellisella* sp.; *Junceella* sp.	Philippines; Australia; Indonesia	Lorenz and Fehse, 2009
Aclyvolva lanceolata	*Aclyvolva lamyi*	*Ctenocella* sp.; *Junceella* sp.	Malaysia	This publication
Aclyvolva lanceolata	*Aclyvolva lanceolata*	*Dichotella* sp.; *Ellisella* sp.; *Junceella* sp.	Central Indo-Pacific	Lorenz and Fehse, 2009

genetic difference with *A. lanceolata* specimens from Indonesia and Malaysia and this species is therefore hereafter synonymised with *A. lanceolata*. As a result it can be concluded that *A. lanceolata* is distributed throughout the entire Indo-Pacific. *Kuroshiovolva* specimens are scarcely available in natural history collections and as a result not much is known about its host species. Three publications provide host data for species belonging to this genus (see Table 2). All publications mention *Plumarella* as the primary host genus, except for Lorenz (2009) who also mentions *Astrogorgia*. According to Fabricius and Alderslade (2001) there is only one *Plumarella* species known from shallow water (*Plumarella penna*), which occurs in Australia, all other species are from deeper and colder water. *Plumarella* spp. are considered to have a very limited distribution and it is therefore unclear what the effect is on the distribution of *Kuroshiovolva* spp.

Table 2. Cont.

Aclyvolva lanceolata	*Aclyvolva lanceolata*	*Ellisella* sp.	Halmahera, Indonesia	Reijnen, 2010
Aclyvolva lanceolata	*Aclyvolva lanceolata*	*Verrucella* sp.; *Junceella* sp.; *Ctenocella* sp.; *Viminella* sp.; *Dichotella* sp.	Malaysia; Thailand	This publication
Aclyvolva lanceolata	*Aclyvolva nicolamassierae*	*Ellisella* sp.	Red Sea, Tanzania to S Mozambique, Reunion	Lorenz and Fehse, 2009
Hiatavolva depressa	*Hiatavolva depressa*	*Alertigorgia orientalis*; *A. hoeksemai*	Central Indo-Pacific (Australia, Indonesia, Malaysia, New Caledonia)	Lorenz and Fehse, 2009
Hiatavolva depressa	*Hiatavolva depressa*	*Alertigorgia orientalis*	Malaysia	This publication
Kuroshiovolva lacanientae	*Kuroshiovolva lacanientae*	*Plumarella* sp.; *Astrogorgia* sp.	Philippines	Lorenz, 2009
Kuroshiovolva shingoi	*Kuroshiovolva shingoi*	*Plumarella* sp.	Japan; Philippines; New Caledonia; Fiji; New South Wales, Australia	Lorenz and Fehse, 2009
Kuroshiovolva shingoi	*Kuroshiovolva shingoi*	*Plumarella cristata* (= *Acanthoprimnoa cristata*)	Wakayama Prefecture, Japan	Yamamoto, 1972
Prosimnia draconis	*Prosimnia (Prosimnia) coarctata*	?*Melithaea flabellifera* (= *M. japonica*)	Wakayama Prefecture, Japan	Yamamoto, 1972

Doubtful host records

For *A. coarctata* all host genera in Table 2, except for *Echinogorgia*, *Melithaea* and *Muricella*, are representatives of the family Ellisellidae. The other three genera belong to the families Plexauridae, Melithaeidae and Acanthogorgiidae respectively. The host record for *Melithaea flabellifera* (= *M. japonica*, Matsumoto and Ofwegen, 2015) comes from Yamamoto (1973). Fortunately there are photographs of the living specimen included which clearly show that the ovulid species is actually a *Prosimnia* cf. *draconis* Cate, 1973 on a melithaeid, which is the common host genus for this ovulid species (Reijnen, 2010). For *A. coarctata* this host species record should therefore be neglected. Also the identification of *Muricella* and *Echinogorgia* as host genera (see caption A356, A357 in Lorenz and Fehse 2009) seems questionable. *Muricella* species are notoriously hard to identify (Reijnen *et al*., 2011) but based on the photographs it can be concluded the host species most likely represents a *Verrucella* sp. from the family Ellisellidae. *Verucella* and *Muricella* both have a planar and reticulated growth form. The other doubtful host record is that of *Echinogorgia* (Mase, 1989; Lorenz and Fehse, 2009). *Echinogorgia* is easily confused with other gorgonian genera (e.g. *Paraplexaura*) and cannot be identified *in situ* based on its habitus. Moreover, this genus is very uncommon in the Indo-Pacific which makes it more questionable as a possible host species. This specific host record remains doubtful unless tissue samples of the host can be examined.

Systematics

Based on the aforementioned phylogenetic and morphological analyses, three species names should be synonymised (*A. lamyi*, *A. nicolamassierae* and *H. rugosa* and/or placed into a different genus (*H. coarctata*). Due to the position of *A. lanceolata* as type of the name-bearing genus of the respective subfamily, the species represented in this clade (Clade A in Fig. 4) can be referred to as 'true' Aclyvolvinae. As a result of their morphological resemblance and phylogenetic affinity, the species *Hiatavolva rugosa* and *H. coarctata* should for that reason be transferred to the genus *Aclyvolva*.
The systematic account of the ovulid species is therefore as follows:

Ovulidae Fleming, 1822
Prionovolvinae Fehse, 2007
Hiatavolva Cate, 1973

Hiatavolva depressa (Sowerby III, 1875)

Ovulum depressum Sowerby III, 1875: 128, pl. 24, fig. 1
Phenacovolva depressa.— Iredale, 1935: 105
Neosimnia (*Pellasimnia*) *depressa*.— Allan, 1956: 130
Hiata depressa.— Cate, 1973: 87, fig. 194
Hiatavolva depressa.— Lorenz and Fehse, 2009: 135, pl. 192, fig. 1-6

Aclyvolvinae Fehse, 2007
Aclyvolva Cate, 1973

Aclyvolva lanceolata (Sowerby II, 1848)

Ovulum lanceolatum Sowerby II, 1848: 135
Ovula lanceolata.— Weinkauff, 1881: 207, pl. 52, fig. 10-11
Neosimnia lamyi Schilder, 1932: 54, pl. 4, fig. 44
Neosimnia lanceolata.— Allan, 1956: 127
Aclyvolva nicolamassierae Fehse, 1999: 51, pl. 2, fig. 1-2
Aclyvolva lanceolata.— Lorenz and Fehse, 2009:
Hiatavolva cf. *lamyi*.— Lorenz and Fehse, 2009: 615, A352
Aclyvolva (cf.) *lamyi*.— Lorenz and Fehse, 2009: 134, pl. 190, fig. 1-10, A353-A355

Aclyvolva coarctata (Sowerby II, 1848 in Adams and Reeve, 1848) comb. nov.

Ovulum coarctatum Sowerby II, 1848 (in Adams and Reeve, 1848): 21, pl. 6, fig 2a,b
Ovula coarctata.— Weinkauff, 1881: 188 pl. 48, fig 9, 12
Prosimnia (*Prosimnia*) *coarctata*.— Kuroda, 1958: 169
Hiata rugosa Cate and Azuma, 1973 (in Cate, 1973): 87, fig. 197
Phenacovolva coarctata.— Liltved, 1989: 132
Hiatavolva coarctata.— Lorenz and Fehse, 2009: 135, pl. 191, figs. 1-10, 18, A356-A359, not A360-A361 (= *Aclyvolva lanceolata*)
Hiatavolva rugosa.— Lorenz and Fehse, 2009: 135, pl. 191, figs. 11-17, A362-A365

Due to the above taxonomic and systematic changes, the diagnosis for the genus *Aclyvolva* should be extended with characters used to distinguish *Aclyvolva* from *Hiatavolva*. The modified diagnosis of *Aclyvolva* is as follows: “Shells elongate, narrow, rather cylindrical. Posterior terminal narrow, anterior broader. Canals open. Tips of terminals usually pointed but can also be blunt or have indented terminal tips. Aperture narrow and wideness in the fossular section, abruptly constricting to form the siphonal canal. Funiculum absent.” (adapted from Lorenz and Fehse, 2009).

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Suppl. Mat. S1. Provenance data for Ovulidae used in this study.

Collection Code (RMNH.Mol.)	Genus	Species	Author	COI	16S	H3	28S
164165	*Aclyvolva*	*lamyi*	(Schilder, 1927)	KP259478	KP259362	KP259527	KP259408
164181	*Aclyvolva*	*lamyi*	(Schilder, 1927)	KP259486	KP259370	-	KP259414
164195	*Aclyvolva*	*lamyi*	(Schilder, 1927)	KP259494	KP259378	KP259537	KP259421
164143	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259466	KP259349	KP259522	-
164152	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259470	KP259354	KP259523	KP259404
164154	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259472	KP259356	KP259524	KP259405
164169	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259480	KP259364	-	KP259410
164179	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259485	KP259369	-	KP259413
164183	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259488	KP259372	KP259532	KP259416
164190	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259492	KP259376	KP259535	KP259419
164192	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259493	KP259377	KP259536	KP259420
337788	*Aclyvolva*	*lanceolata*	(Sowerby II, 1848)	KP259505	-	KP259543	KP259427
337793	*Aclyvolva*	*nicolamassierae*	Fehse, 1999	KP259510	KP259393	KP259547	KP259432
164077	*Calpurnus*	*verrucosus*	(Linnaeus, 1758)	KP259446	KP259327	-	-
164078	*Calpurnus*	*verrucosus*	(Linnaeus, 1758)	KP259447	KP259328	-	-
164079	*Calpurnus*	*verrucosus*	(Linnaeus, 1758)	KP259448	KP259329	-	-
164117	*Calpurnus*	*verrucosus*	(Linnaeus, 1758)	KP259455	KP259338	-	-
164072	*Crenavolva*	*aureola*	(Fehse, 2002)	KP033151	KP033143	-	-
164085	*Crenavolva*	*aureola*	(Fehse, 2002)	KP033152	KP033144	-	-
164209	*Crenavolva*	*aureola*	(Fehse, 2002)	KP033156	KP033148	-	-
164217	*Crenavolva*	*chiapponii*	Lorenz & Fehse, 2009	KP033158	KP033149	-	-
164186	*Crenavolva*	*striatula*	(Sowerby I, 1828)	KP033154	KP033146	-	-
164144	*Crenavolva*	*trailli*	(Adams, 1855)	KP033153	KP033145	-	-
164189	*Crenavolva*	*trailli*	(Adams, 1855)	KP033155	KP033147	-	-
100779	*Cymbovula*	*acicularis*	(Lamarck, 1810)	GU363447	GU363434	-	-
100792	*Cymbovula*	*acicularis*	(Lamarck, 1810)	GU363448	GU363436	-	-
100815	*Cymbovula*	*acicularis*	(Lamarck, 1810)	GU363449	GU363437	-	-
100744	*Cyphoma*	*gibbosum*	(Linnaeus, 1758)	GU363439	GU363427	-	-
100780	*Cyphoma*	*gibbosum*	(Linnaeus, 1758)	GU363440	GU363428	-	-
100781	*Cyphoma*	*gibbosum*	(Linnaeus, 1758)	GU363444	GU363432	-	-
100804	*Cyphoma*	*gibbosum*	(Linnaeus, 1758)	GU363443	GU363431	-	-
100809	*Cyphoma*	*gibbosum*	(Linnaeus, 1758)	GU363446	GU363433	-	-
100811	*Cyphoma*	*gibbosum*	(Linnaeus, 1758)	GU363441	GU363429	-	-
164058	*Notadusta*	*punctata*	(Linnaeus, 1771)	KP259441	KP259322	-	-
164099	*Dentiovula*	*colobica*	(Azuma & Cate, 1971)	KP259451	KP259333	-	-
164061	*Dentiovula*	cf. *dorsuosa*	(Hinds, 1844)	KP259442	KP259323	-	-
164095	*Dentiovula*	*dorsuosa*	(Hinds, 1844)	KP271160	KP259332	-	-
164150	*Dentiovula*	*dorsuosa*	(Hinds, 1844)	KP259469	KP259353	-	-

Locality	Date	Latitude (degrees)	Longitude (degrees)	Host species
Malaysia, Sabah, NE Pulau Banggi, NE Balundangan Besar Island, TMP.21	09/14/12	7°20’50.5” N	117°21’24.3” E	*Junceella* sp.
Malaysia, Sabah, Lubani Rock, TMP.03	09/07/12	6°53’45.0” N	117°23’15.8” E	*Junceella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Ctenocella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Verrucella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Junceella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Ctenocella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Ctenocella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Ctenocella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Junceella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Verrucella* sp.
Malaysia, Sabah, Lundayang, TMP.04	09/08/12	6°48’39.4” N	117°21’59.1” E	*Viminella* sp.
Thailand, Pattaya, Koh Thai Ta Mun	Feb-11	13°06’30.5” N	100°48’11.0” E	*Dichotella gemmacea*
Saudi Arabia (Red Sea), offshore of Farasan Banks, Shib Radib	08/03/13	16°46’ N	41°56’ E	?
Malaysia, Sabah, Ligitan Island 1 SW, SEM.13	12/03/10	4°11’13.4” N	118°47’29.6” E	*Sarcophyton* sp.
Indonesia, off Halmahera mainland, Teluk Dodinga; W Karang Ngeli, TER.40	11/15/09	0°46’25.3” N	127°32’22.0” E	*Sarcophyton trocheliophorum*
Malaysia, Sabah, Pasalat Reef, SEM.23	12/07/10	4°30’50.0” N	118°44’30.9” E	*Lobophytum pauciflorum*
Malaysia, Sabah, Selakan Island, SEM.42	12/12/10	4°34’23.6” N	118°43’02.5” E	*Sarcophyton* sp.
Malaysia, Sabah, Si Amil Island, SEM.16	12/04/10	4°19’02.1” N	118°52’30.7” E	*Acanthogorgia* sp.
Indonesia, Halmahera, Tidore, N of Desa Rum,TER.18	11/04/09	0°44’35.8” N	127°23’06.3” E	*Acanthogorgia* sp.
Indonesia, Halmahera mainland, Tanjung Ratemu (S of river), TER.21	11/05/09	0°54’24.7” N	127°29’17.7” E	*Acanthogorgia* sp.
Indonesia, N Sulawesi, Lembeh Strait, Tanjung Kusukusu, LEM.31	02/16/12	1°27’13.8” N	125°14’12.9” E	*Acanthogorgia* sp.
Malaysia, Sabah, S Pulau Banggi, E Molleangan Besar Island, TMP.37	09/19/12	7°05’07.2” N	117°03’33.8” E	*Echinogorgia* sp.
Malaysia, Sabah, Kalang, TMP.41	09/18/12	6°59’48.1” N	117°03’13.4” E	*Subergorgia* sp.
Malaysia, Sabah, Kalang, TMP.41	09/18/12	6°59’48.1” N	117°03’13.4” E	*Paraplexaura* sp.
Curaçao, Barank’i Karanito, CUR.15	05/19/05	12°02’13.5” N	068°48’14.2” E	*Antillogorgia acerosa*
Curaçao, Santa Martha, CUR.18	05/24/05	12°16’04.9” N	069°07’43.6” E	*Gorgonia ventalina*
Curaçao, Caracasbaai, CUR.17	06/03/05	12°03’01.6” N	068°52’01.2” E	*Antillogorgia bipinnata*
Curaçao, Marie Pampoen / Carpile, CUR.05	05/01/05	12°05’42.1” N	068°54’43.0” E	*Gorgonia flabellum*
Curaçao, Barank’i Karanito, CUR.15	05/19/05	12°02’13.5” N	068°48’14.2” E	*Gorgonia ventalina*
Curaçao, Barank’i Karanito, CUR.15	05/19/05	12°02’13.5” N	068°48’14.2” E	*Plexaurella nutans*
Curaçao, St. Michielsbaai, CUR.21	05/31/05	12°08’50.9” N	068°59’56.6” E	*Pseudoplexaura porosa*
Curaçao, Superior Producer (wreck), CUR.22	06/02/05	12°05’21.5” N	068°56’35.5” E	*Antillogorgia americana*
Curaçao, Superior Producer (wreck), CUR.22	06/02/05	12°05’21.5” N	068°56’35.5” E	*Muricea muricata*
Malaysia, Sabah, Kapikan Reef, SEM.33	12/09/10	4°39’04.9” N	118°49’18.2” E	-
Malaysia, Sabah, Ligitan Island 1 SW, SEM.13	12/03/10	4°11’13.4” N	118°47’29.6” E	*Acanthogorgia sp.*
Malaysia, Sabah, Timba Timba Island, SEM.27	12/08/10	4°33’39.2” N	118°55’29.3” E	*Chironephthya* sp.
Malaysia, Sabah, Darby Bank, SEM.04	11/30/10	4°08’23.0” N	118°10’14.6” E	*Siphonogorgia* sp.
Malaysia, Sabah, NE Pulau Banggi, NE Balundangan Besar Is., TMP.21	09/14/12	7°20’50.5” N	117°21’24.3” E	*Siphonogorgia* sp.

Suppl. Mat. S1. Cont.

Collection Code (RMNH.Mol.)	Genus	Species	Author	COI	16S	H3	28S
164174	*Diminovula*	*alabaster*	(Reeve, 1865)	KP259482	KP259366	-	-
164200	*Diminovula*	*alabaster*	(Reeve, 1865)	KP259497	KP259381	-	-
164163	*Diminovula*	*concinna*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259477	KP259361	-	-
164215	*Habuprionovolva*	*aenigma*	(Azuma & Cate, 1971)	KP259498	KP259382	-	-
164216	*Habuprionovolva*	*aenigma*	(Azuma & Cate, 1971)	KP259499	KP259383	-	-
164119	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259456	KP259339	KP259516	KP259399
164134	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259462	KP259345	KP259518	KP259401
164135	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259463	KP259346	KP259519	KP259402
164137	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259465	KP259348	KP259520	KP259403
164161	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259475	KP259359	KP259526	KP259407
164167	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259479	KP259363	KP259528	KP259409
164177	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259484	KP259368	KP259530	KP259412
164185	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259489	KP259373	KP259533	KP259417
164188	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259491	KP259375	KP259534	KP259418
164197	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259495	KP259379	KP259538	KP259422
164198	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259496	KP259380	KP259539	KP259423
164234	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259501	KP259385	KP259540	KP259424
337791	*Hiatavolva*	*coarctata*	(Sowerby II, *in* Adams & Reeve, 1848)	KP259508	KP259391	KP259545	KP259430
164147	*Hiatavolva*	*depressa*	(G.B. Sowerby III, 1875)	-	KP259351	-	-
164182	*Hiatavolva*	*depressa*	(G.B. Sowerby III, 1875)	KP259487	KP259371	KP259531	KP259415
114127	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259435	KP259316	-	-
164050	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259438	KP259319	KP259511	KP259394
164051	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259439	KP259320	KP259512	KP259395
164053	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259440	KP259321	KP259513	KP259396
164100	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259452	KP259334	KP259514	KP259397

Locality	Date	Latitude (degrees)	Longitude (degrees)	Host species
Malaysia, Sabah, S Pulau Banggi, Pancang Pukul, TMP.40	09/18/12	7°02’01.6” N	117°04’25.1” E	*Nephthea* sp.
Malaysia, Sabah, ENE Pulau Banggi, Latoan Patch, TMP.19	09/14/12	7°17’43.3” N	117°24’06.1” E	*Nephthea* sp.
Malaysia, Sabah, NE Pulau Banggi, NE Banggi Outer Reef, TMP.20	09/14/12	7°22’53.7” N	117°22’24.6” E	*Coelogorgia plumosa*
Indonesia, Halmahera mainland, Tanjung Ratemu (S of river), TER.27	11/08/09	0°54’44.5” N	127°29’09.9” E	*Dendronephthya* sp.
Indonesia, Raja Ampat Islands, W. Papua, Yeffam Isl., NW Pulau Keruo, RAJ.65	12/13/07	0°35’15.4” S	130°17’42.7” E	*Dendronephthya* sp.
Malaysia, Sabah, Bumbun Island W (channel), SEM.22	12/05/10	4°27’27.5” N	118°34’14.9” E	*Ctenocella* sp.
Indonesia, N Sulawesi, Bunaken Island, Raymond, MEN.11	12/02/08	1°37’44.6” N	124°44’07.0” E	*Ellisella ceratophyta*
Indonesia, N Sulawesi, Bunaken Island, Mandolin, MEN.16	12/04/08	1°36’43.8” N	124°43’56.7” E	*Ellisella ceratophyta*
Indonesia, N Sulawesi, Bunaken Island, Lekuan III, MEN.14	12/12/08	1°36’20,3” N	124°46’08,0” E	*Ellisella ceratophyta*
Malaysia, Sabah, NE Pulau Banggi, NE Balundangan Besar Is., TMP.21	09/14/12	7°20’50.5” N	117°21’24.3” E	*Ctenocella* sp.
Malaysia, Sabah, E Pulau Banggi, Purukan Sibaliu, TMP.15	09/11/12	7°12’41.5” N	117°28’13.7” E	*Verrucella* sp.
Malaysia, Sabah, NE Pulau Banggi, NE Balundangan Besar Is., TMP.21	09/14/12	7°20’50.5” N	117°21’24.3” E	*Ctenocella* sp.
Malaysia, Sabah, NE Pulau Banggi, NE Balundangan Besar Is., TMP.21	09/14/12	7°20’50.5” N	117°21’24.3” E	*Ctenocella* sp.
Malaysia, Sabah, Lubani Rock, TMP.03	09/07/12	6°53’45.0” N	117°23’15.8” E	*Viminella* sp.
Malaysia, Sabah, SE Pulau Banggi, SW Carrington Reef, TMP.38	09/20/12	7°07’49.4” N	117°13’41.9” E	*Ctenocella* sp.
Malaysia, Sabah, Kalang, TMP.41	09/18/12	6°59’48.1” N	117°03’13.4” E	*Verrucella* sp.
Indonesia, N Sulawesi, Lembeh Strait, Tanjung Nanas I, LEM.01	01/30/12	1°27’40.4” N	125°13’36.4” E	*Ellisella* sp.
Indonesia, N Sulawesi, Lembeh Strait, Tanjung Kusukusu, LEM.31	02/16/12	1°27’13.8” N	125°14’13.0” E	*Ellisella* sp.
Malaysia, Sabah, SE Pulau Banggi, SW Carrington Reef, TMP.38	09/20/12	7°07’49.4” N	117°13’41.9” E	*Alertigorgia orientalis*
Malaysia, Sabah, E Pulau Balambangan, SE Tanjung Siagut, TMP.30	09/23/12	7°20’10.5” N	117°01’24.3” E	*Alertigorgia orientalis*
Indonesia, W. Papua, Raja Ampat Islands, Jelly Point, RAJ.03	11/21/07	0°32’15.0” S	130°57’06.7” E	*Ellisella* sp.
Malaysia, Sabah, Bohayen Island, SEM.26	12/08/10	4°28’05.6” N	118°56’50.8” E	*Viminella* sp.
Malaysia, Sabah, Sipadan Island, Mid Reef, SEM.59	12/18/10	4°06’47.8” N	118°38’10.1” E	*Viminella* sp.
Malaysia, Sabah, Bohayen Island, SEM.26	12/08/10	4°28’05.6” N	118°56’50.8” E	*Ellisella* cf. *ceratophyta*
Malaysia, Sabah, Si Amil Island, SEM.16	12/04/10	4°19’02.1” N	118°52’30.7” E	*Viminella* sp.

Suppl. Mat. S1. Cont.

Collection Code (RMNH.Mol.)	Genus	Species	Author	COI	16S	H3	28S
164103	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	-	KP259335	-	-
164104	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259453	KP259336	KP259515	KP259398
164108	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	-	KP271159	-	-
164120	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259457	KP259340	KP259517	KP259400
164140	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP271161	-	KP259521	-
164158	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259474	KP259358	KP259525	KP259406
164175	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259483	KP259367	KP259529	KP259411
164236	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259502	KP259386	KP259541	KP259425
337787	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259504	KP259388	KP259542	KP259426
337789	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259506	KP259389	KP259544	KP259428
337790	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259507	KP259390	-	KP259429
337792	*Hiatavolva*	*rugosa*	(Cate & Azuma *in* Cate, 1973)	KP259509	KP259392	KP259546	KP259431
-	*Kuroshiovolva*	*shingoi*	Azuma & Cate, 1971	-	-	-	-
164066	*Naviculavolva*	*deflexa*	(Sowerby II, 1848)	KP259443	KP259324	-	-
164094	*Naviculavolva*	*deflexa*	(Sowerby II, 1848)	KP259450	KP259331	-	-
164130	*Naviculavolva*	*deflexa*	(Sowerby II, 1848)	KP259459	KP259342	-	-
164145	*Naviculavolva*	*deflexa*	(Sowerby II, 1848)	KP259467	KP259350	-	-
164149	*Naviculavolva*	*deflexa*	(Sowerby II, 1848)	KP259468	KP259352	-	-
164153	*Naviculavolva*	*deflexa*	(Sowerby II, 1848)	KP259471	KP259355	-	-
164155	*Naviculavolva*	*deflexa*	(Sowerby II, 1848)	KP259473	KP259357	-	-
164173	*Naviculavolva*	*deflexa*	(Sowerby II, 1848)	KP259481	KP259365	-	-
164069	*Ovula*	*ovum*	(Linnaeus, 1758)	KP259444	KP259325	-	-
164080	*Ovula*	*ovum*	(Linnaeus, 1758)	KP259449	KP259330	-	-
337786	*Pedicularia*	*pacifica*	Pease, 1865	KP259503	KP259387	-	-
099021B	*Pedicularia*	*pacifica*	Pease, 1865	KP259434	KP259315	-	-
099021A	*Pedicularia*	*vanderlandi*	Goud & Hoeksema, 2001	KP259433	KP259314	-	-
164047	*Pellasimnia*	*annabelae*	Lorenz & Fehse, 2009	KP259436	KP259317	-	-
164076	*Pellasimnia*	*annabelae*	Lorenz & Fehse, 2009	KP259445	KP259326	-	-

Locality	Date	Latitude (degrees)	Longitude (degrees)	Host species
Indonesia, off Halmahera mainland, Teluk Dodinga, Karang Ngeli W, TER.40	11/15/09	0°46’25,3” N	127°32’22,0” E	*Ellisella* sp.
Indonesia, Halmahera, off Tidore, Pulau Pilongga S, TER.35	11/12/09	0°42’44,1” N	127°28’47,3” E	*Dichotella gemmacea*
Indonesia, Halmahera, Maitara, Maitara W, TER.09	10/29/09	0°43’47,6” N	127°21’44,7” E	*Ellisella* sp.
Malaysia, Sabah, Ligitan Island 1 SW, SEM.13	12/03/10	4°11’13.4” N	118°47’29.6” E	*Viminella* sp.
Indonesia, Halmahera, Tidore, Tanjung Ebamadu, TER.08	10/28/09	0°45’23,4” N	127°24’26,5” E	*Ellisella* sp.
Malaysia, Sabah, Lubani Rock, TMP.03	09/07/12	6°53’45.0” N	117°23’15.8” E	*Ctenocella* sp.
Malaysia, Sabah, S Pulau Banggi, S Patanunan Island, TMP.36	09/19/12	7°05’59.7” N	117°05’21.1” E	*Ctenocella* sp.
Indonesia, N Sulawesi, Lembeh Strait, Tanjung Nanas I, LEM.33	02/17/12	1°27’39.5” N	125°13’35.8” E	*Ellisella* sp.
Indonesia, Pulau Pulau Gura Ici, Pulau Lelai S, TER.29	11/09/09	0°01’58.3” S	127°14’56.8” E	*Dichotella gemmacea*
Indonesia, N Sulawesi, Lembeh Strait, Teluk Makawide, LEM.19	02/09/12	1°29’05.1” N	125°14’26.1” E	*Ellisella* sp.
Indonesia, N Sulawesi, Lembeh Strait, N Pulau Dua, LEM.25	02/13/12	1°23’28.6” N	125°12’58.7” E	*Ellisella* sp.
Indonesia, N Sulawesi, Lembeh Strait, N Sarena Kecil, LEM.32	02/16/12	1°27’26.9” N	125°13’37.6” E	*Viminella* sp.
-	-	-	-	-
Malaysia, Sabah, S Boheydulang Island 1, SEM.37	12/11/10	4°35’00.4” N	118°46’40.5” E	*Hicksonella* sp.
Malaysia, Sabah, S Ligitan Reef 1, SEM.09	12/01/10	4°14’07.7” N	118°33’22.7” E	*Hicksonella* sp.
Malaysia, Sabah, Alert Patches 2, SEM.05	11/30/10	4°09’37.7” N	118°15’37.3” E	*Hicksonella* sp.
Malaysia, Sabah, NE Pulau Banggi, NE Banggi Outer Reef, TMP.20	09/14/12	7°22’53.7” N	117°22’24.6” E	*Rumphella*sp.
Malaysia, Sabah, NE Pulau Malawali, S Sibaliu, TMP.14	09/11/12	7°06’50.0” N	117°22’36.8” E	*Rumphella*sp.
Malaysia, Sabah, ENE Pulau Banggi, Latoan Patch, TMP.19	09/14/12	7°17’43.3” N	117°24’06.1” E	*Rumphella*sp.
Malaysia, Sabah, ENE Pulau Banggi, Latoan Patch, TMP.19	09/14/12	7°17’43.3” N	117°24’06.1” E	*Rumphella*sp.
Malaysia, Sabah, SWLigitan Island 1, SEM.13	12/03/10	4°11’13.4” N	118°47’29.6” E	*Hicksonella* sp.
Malaysia, Sabah, Kapalai Island, SEM.10	12/02/10	4°13’04.8” N	118°40’20.1” E	*Sarcophyton glaucum*
Indonesia, Halmahera, Ternate, Tanjung Pasir Putih, TER.16	11/02/09	0°51’50.4” N	127°20’36.7” E	*Sarcophyton trocheliophorum*
Indonesia, Halmahera, Ternate, Restaurant Floridas, TER.03	10/25/09	0°45’35.8” N	127°21’25.4” E	*Stylaster* sp.
Indonesia, Bali, N side of Nusa Lembongan, Tanjung Taal	04/22/01	8°39’33” S	115°26’37” E	*Distichopora vervoorti*
Indonesia, Bali, N side of Nusa Lembongan, Tanjung Taal	04/22/01	8°39’33” S	115°26’37” E	*Distichopora vervoorti*
Malaysia, Sabah, S Larapan Island 2, SEM.57	12/17/10	4°32’51.1” N	118°36’32.3” E	*Annella* sp.
Indonesia, Halmahera, Hiri, Tanjung Ngafauda, TER.14	10/31/09	0°54’38.3” N	127°19’02.7” E	*Annella* sp.

Suppl. Mat. S1. Cont.

Collection Code (RMNH.Mol.)	Genus	Species	Author	COI	16S	H3	28S
164114	*Pellasimnia*	*annabelae*	Lorenz & Fehse, 2009	KP259454	KP259337	-	-
164162	*Pellasimnia*	*annabelae*	Lorenz & Fehse, 2009	KP259476	KP259360	-	-
164187	*Pellasimnia*	*annabelae*	Lorenz & Fehse, 2009	KP259490	KP259374	-	-
164128	*Phenacovolva*	*rosea*	(Adams, 1854)	KP259458	KP259341	-	-
164049	*Primovula*	*rosewateri*	(Cate, 1973)	KP259437	KP259318	-	-
164062	*Primovula*	*rosewateri*	(Cate, 1973)	KP033150	KP033142	-	-
164221	*Procalpurnus*	*lacteus*	(Lamarck, 1810)	KP259500	KP259384	-	-
164132	*Prosimnia*	*piriei*	(Petuch, 1973)	KP259460	KP259343	-	-
164133	*Prosimnia*	*piriei*	(Petuch, 1973)	KP259461	KP259344	-	-
164136	*Prosimnia*	*piriei*	(Petuch, 1973)	KP259464	KP259347	-	-
110064	*Simnia*	*patula*	(Pennant, 1777)	GU363450	GU363438	-	-

Locality	Date	Latitude (degrees)	Longitude (degrees)	Host species
Malaysia, Sabah, Darby Bank, SEM.04	11/30/10	4°08’23.0” N	118°10’14.6” E	*Annella* sp.
Malaysia, Sabah, NE Pulau Banggi, NE Balundangan Besar Is., TMP.21	09/14/12	7°20’50.5” N	117°21’24.3” E	*Annella* sp.
Malaysia, Sabah, S Pulau Banggi, S Balak-Balak Island, TMP.39	09/19/12	7°20’22.6” N	117°08’36.0” E	*Annella* sp.
Malaysia, Sabah, Horn Reef, SEM.08	12/01/10	4°14’32.0” N	118°26’24.1” E	*Acanthogorgia* sp.
Malaysia, Sabah, Sipadan Island, Hanging Gardens, SEM.60	12/18/10	4°06’40.3” N	118°37’29.3” E	*Villogorgia* sp.
Malaysia, Sabah, N Kulapuan Island 2, SEM.31	12/09/10	4°32’07.4” N	118°50’18.2” E	*Paratelesto* sp.
Indonesia, N Sulawesi, Lembeh Strait, Batu Kapal, LEM.35	02/18/12	1°32’56.8” N	125°17’31.8” E	*Sinularia pavida*
Indonesia, N Sulawesi, Bunaken Island, Lekuan II, MEN.04	11/27/08	1°36’00.4” N	124°45’58.4” E	*Euplexaura* sp.
Indonesia, N Sulawesi, Bunaken Island, Sachiko’s Point, MEN.10	12/01/08	1°37’52.5” N	124°46’20.4” E	*Euplexaura* sp.
Indonesia, N Sulawesi, Manado Tua, Muka Gereja, MEN.17	12/05/08	1°36’57.4” N	124°41’40.0” E	*Euplexaura* sp.
North Sea, South side of Doggersbank	09/19/03	54°20’ N	02°20’ E	*Alcyonium digitatum*