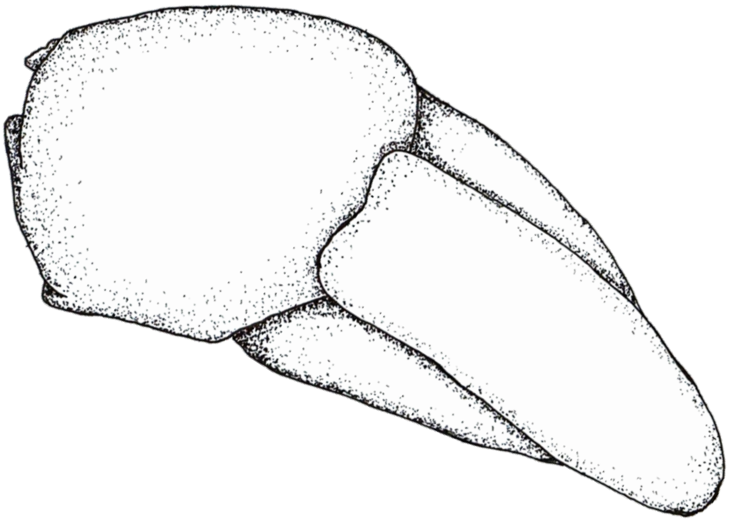
THE SYSTEMATICS OF CEPHALASPIDEA (MOLLUSCA: GASTROPODS) REVISITED, WITH A STUDY ON THE DIVERSITY OF DEEP SEA PHILINIDAE *SENSU LATO* FROM THE WEST PACIFIC



Master Thesis

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I was like a boy playing on the sea-shore, and diverting myself now and then finding a smoother pebble or a prettier shell than ordinary, whilst the great ocean of truth lay all undiscovered before me.

Isaac Newton

Contents

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Abstract:

The Cephalaspidea are the second most diverse marine clade of the Euthyneura gastropods, after the Nudipleura with many groups still known largely from shells or little anatomical data. These marine snails occur worldwide across all latitudes and depths. The definition of the group and the relationships between members has been hampered by the difficulty of establishing sound synapomorphies, but the advent of molecular phylogenetics in recent times has helped changed significantly this situation. Yet, because of reduced taxon sampling and few genetic markers employed in previous studies many questions about the sister relationships and monophyletic status of several families remained open.

In this study over 100 taxa were included covering 100% of the traditionally recognized valid families and about 50% of the genera. The goals were to (1) produce a new hypothesis of relationships for the Cephalaspidea gastropods including for the first time representatives from all families by means of multi-locus phylogenetic analyses (2) to infer relationships between families and test their monophyly, and (3) to study the diversity and systematics of the elusive deep sea West Pacific Philinidae *sensu lato* cephalaspids.

Bayesian molecular phylogenetics based on two mitochondrial (COI, 16S rRNA) and two nuclear gene markers (28S rRNA and Histone-3) was used to infer the relationships of Cephalaspidea and to aid on species delimitation within Philinidae *s. l.*. Additionally, species of the Philinidae *s. l.* were studied by fine anatomical dissection and scanning electron microscopy.

The monophyly of the Cephalaspidea without Runcinacea was confirmed. The families Cylichnidae, Diaphanidae, Haminoeidae, Philinidae, Retusidae, and Scaphandridae were found to be not monophyletic. This result suggests that the family level taxonomy of the Cephalaspidea warrants a profound revision and several new family and genera names are required to reflect the new phylogenetic hypothesis presented in this work.

Philinidae *s. l.* was polyphyletic with four independent main lineages (family level) and seven genera. The generic names *Hermania*, *Laona*, *Philinorbis*, and *Praephiline* are reinstated as valid. Sixteen species of deep sea West Pacific Philinidae *s. l* were recognized of which 13 are putatively new to Science, emphasising how little is still known about the biodiversity of the deep sea in the tropical Indo-Pacific.

1. Introduction

1.1. What is the Cephalaspidea?

The Cephalaspidea is a major group of euthyneuran gastropods with about 634 distributed worldwide across all latitudes. Within Euthyneura they belong to the clade Euopisthobranchia together with Umbraculoidea, Anaspidea, Runcinacea, and Pteropoda (Jörger et al., 2010). They can be found in the intertidal, in shallow depths, and in the deep sea, and are especially abundant in tropical and subtropical waters of the Indo-Pacific (Lin and Qi, 1985). The common name “bubble shells” refers to the shape most commonly found in the shells of the cephalaspids, where the last whorl is elongated and comprise most of the shell. The scientific name Cephalaspidea (Fischer, 1883) (Gr. *kephalē*, head Gr. *aspis,* shield; Jaeger, 1978) refers to the presence of a cephalic shield or lobe of the head foot that overlaps the shell anteriorly and protects the mantle cavity opening (Burn and Thompson, 1998).

They are of special evolutionary and phylogenetic interest since they have been considered the basal lineage of the traditional Opisthobranchia *sensu* Burn and Thompson (1998) (Rudman, 1972a;e; Mikkelsen, 1993; 1996). The cephalaspideans have been thought to be descended from early ophistobranchs with a burrowing lifestyle (Burn and Thompson, 1998), but this is today debatable because traditional cephalaspidean taxa like *Ringicula*, *Acteon* and *Pupa* were shown to belong to, Architectibranchia, a separate major evolutionary lineage of the Heterobranchia gastropods (e.g. “Lower Heterobranchia”, Architectibranchia (Acteonoidea), and Euthyneura including Nudipleura, Eupoisthobranchia and Panpulmonata) (Thollesson, 1999; Dayrat et al., 2001; Wägele et al., 2003; Vonnemann et al., 2005; Malaquias et al., 2009a; Jörger et al., 2010; Wägele et al., 2013) and Opisthobranchia is now regarded a non-monophyletic group (Jörger et al., 2010; Shrödl et al., 2011; Wägele et al., 2013). Stratigraphical and paleontological methods are hard to use for traditional opisthobranchs (Wägele, 2004), even though the Mollusca have one of the best known fossil records of the invertebrates (Mikkelsen, 1996). In comparison to the thick shells of other molluscs, the reduced and thin shells of traditional opisthobranchs do not preserve as well. This causes fossils of traditional opisthobranchs groups to be scant or non-existent for ca. 70% of the species, which lack a shell (Wägele, 2004). Yet, the absence in the fossil record of these molluscs does not mean that these lineages were not represented in paleo-ecossystems (Wägele, 2004; Mikkelsen, 1996). Due to the absence or fragility of the shells cephalaspidean fossils are rare (Mikkelsen, 1996), however some have been found allowing to estimate approximately the time of the families cladogenesis: Bullidae 180 mya (Tracey et al., 1993), Diaphanidae 160 mya (Wenz and Zilch, 1959), Cylichnidae and Scaphandridae 150 mya (Wenz and Zilch, 1959), Philinidae 90 mya (Wenz and Zilch, 1959), Retusidae 80 mya (Bandel, 1994) and Haminoeidae 70 mya (Tracey et al., 1993). Nevertheless, the age of the origin of Bullidae have been disputed by Malaquias and Reid (2008a) who concluded that these fossils belong to a different taxonomic group, the oldest fossils that can be safely attributed to Bullidae are from about 33.9–48.6 mya (MacNeil, 1964; Malaquias and Reid, 2008a; Nakamori et al., 1998). While for *Scaphander* the oldest fossils that can be safely attributed to this genus is about 55.8-58.7 mya (Eilertsen and Malaquias, 2013a,b) found in Poland (Krach, 1969) and California, USA (Schoellhamer et al., 1981, Weaver, 1949). The reason for the uncertainties around these dates are due to the difficulty of ascribing the fossils to the correct taxon (Wägele, 2004). Shells as the only systematic character hampers identification as intraspesiffic variation and morphological similarity is common between families and genera (Mikkelsen, 1996; 2002; Marin et al., 1999). In a molecular clock analysis of the Euthyneura Dinapoli and Klussmann-Kolb (2010) estimated the occurrence of Euthyneura to the Middle Carboniferous to Early Triassic (approximately 325-290 million years ago) with the first major diversification occurring between the Permian and the Triassic (300-200 mya). According to these estimates the Cephalaspidea likely first occurred 190-75 mya, the node age of the Cephalaspidean branch of 141 mya is close to the first occurrence in the fossil record of the families Diaphanidae and Cylichnidae. The divergence of the Haminoeidae form the line containing Diaphanidae was estimated to 125-25 mya, the node age of this split, 48.3 mya is not far of from the fossil estimate. However as Dinapoli and Klussmann-Kolb's (2010) analysis only included the species *Toledonia globosa* and *Haminoea hydatis,* it is not possible to compare with the fossil estimates of the other families. Jörger et al. (2010) included more genera in their molecular clock analysis estimating the occurrence of Cephalaspidea to approximately 175-75 mya with an node age of 162 mya, which is close to the first known fossils of Cylichnidae, however the line containing *Cylichna*, *Toledonia* and *Diaphana*, had a estimated node age of 85 mya. The node ages of Bulla, Scaphander and Hamonoiea were estimated to approximately 50 mya which is largely congruent with the fossil estimates and the results of Dinapoli and Klussmann-Kolb (2010). *Philine exigua* was the earliest to diverge with an estimated node age of 105 which is not far off from the fossil estimates of 90 mya.

1.1.2 Systematics and phylogeny of Cephalaspidea

1.1.2.1. The morphology based period

The relationships within the Cephalaspidea were for a long time vague and mostly based on morphology, which in most cases is unreliable to determine relationships within this group. At the species level those species that have been described were often largely based on shells alone, which is problematic due to intraspesiffic variation and morphological similarity between the various families and genera (Mikkelsen, 1996; 2002; Marin et al., 1999).

Morphological traits have long been used to infer relationships within the Cephalaspidea. One of these traits is the shell where the last whorl is elongated and compromise most of the teleoconch. The presence of a cephalic shield or lobe of the head foot that overlaps the shell anteriorly and protects the mantle cavity opening was viewed as a distinctive trait of the whole Cephalaspidea (Burn and Thompson, 1998). However, these characters are also found in taxa currently excluded from the group (Malaquias et al., 2009a) and are thought to be a example of convergent evolution (homoplasy) resulting from adaptations to a burrowing life style (Mikkelsen, 1996).

After Cephalaspidea was first proposed by Fischer (1883) a number of enigmatic families have been moved back and forth between the cephalaspids and other opisthobranch groups. Haszprunar (1985) proposed an entirely new taxon Architectibranchia for the families Acteonidae, Aplustridae, Bullinidae, Diaphanidae, Notodiaphanidae and Ringiculidae, which he excluded from the Cephalaspidea. The author recognized that the group was united based on plesiomorphies alone. Much of the difficulties with defining the Cephalaspidea is based on the selection of synapomorphies (Mikkelsen, 1993).

The first comprehensive cladistic analysis of the Cephalaspidea *sensu lato* was done by Mikkelsen (1996). The lack of synapomorphies for Architectibranchia led Mikkelsen (1996) to consider this group paraphyletic, and in her analysis Acteonoidea showed higher affinity with the "Lower Heterobranchia" together with *Gegania,* while *Hydatina* and *Ringicula* remained in Architectibranchia. However Mikkelsen (1996) suggested usage of the unresolved groups Architectibranchia and Lower Heterobranchia to avoid naming new higher taxa based on uncertain status, leaving the Architectibranchia to function as an archive for cephalaspids with basal traits that could not be placed within defined groups. Nonetheless, Mikkelsen (1996) using a phylogenetic framework confirmed Haszprunar's (1985) hypothesis in part, i.e., the exclusion of *Acteon, Ringicula* and *Hydatina* from the Cephalaspidea leaving her to consider the remaining Cephalaspidea monophyletic. Mikkelsen (1996) refered to this latter group as the Cephalaspidea *sensu stricto* including the super-families Bulloidea (*Bulla, Smaragdinella* and *Haminoea*) and Philinoidea (*Cylichna, Retusa, Acteocina, Scaphander* and *Philine*) and recognised four synapomorphies for the group: three solidified gizzard plates, circulatory ciliated strips in the mantel cavity that bend near the lateral opening, the cerebral nerve ring being placed anteriorly of the buccal bulb, and the genital ganglion being fused to the visceral nerve ring. In a following study Mikkelsen (2002) excluded the two last synapomorphies, but as noted by Malaquias et al. (2009a) both these studies did not include species with internal or absent shells such as Gastropteridae and Aglajidae or more enigmatic taxa such as Diaphanidae and Runicinidae.

1.1.2.2. The DNA based period

With the dawn of molecular phylogenetics another set of character became available to decode relationships between cephalaspids. However, molecular phylogenetics have also given a great diversity of results depending on which taxa or molecular characters were included in the analyses (Malaquias et al., 2009a).
Several molecular studies have found the Cephalaspidea *sensu stricto* to be monophyletic; however these studies retrieved different taxa at a basal position, which may be an effect of character choice but mostly a consequence of the different taxa sampling included in the analyses.

Thollesson (1999) analysed the relationships within the Euthyneura by means of 16S rRNA. This study included members of the Cephalaspidea *s. l.*: *Acteon tornatilis* Linnaeus 1758, *Diaphana minuta* Brown 1827, *Philine aperta* Linneaus 1767 and *Scaphander punctostriatus* (Mighels and Adams, 1842). *A. tornatilis* was shown to be ancestral to the clade containing the rest of Euthyneura. The three members of Cephalaspidea *s. s.* were monophyletic, and formed a sister clade to the Anaspidea.
Dayrat et al. (2001) produced a molecular phylogeny, resulting in a parsimony tree of Euthyneura based on 28S rRNA as the sole character. They confirmed Cephalaspidea *s. l.* to be not monophyletic and found Mikkelsen's (1996) Cephalaspidea *s. s.* to be monophyletic, but the latter clade received low support (Bootstrap = 62). Yet, the authors noted that it corresponded with the results of an earlier morphological analysis (Dayrat and Tillier, 2001) and the findings by Thollesson (1999). However *Haminoea* was viewed as problematic as the molecular analysis placed it within the Cephalaspidea *s. s.* while in their morphological analysis placed it and other "bullaceans" like *Smaragdinella* and *Bulla* closer to Anaspidea. For this reason they chose not to include *Haminoea* in Cephalaspidea *s. s.* in the Combinable Component Consensus analysis which included morphological and molecular data from both studies (Dayrat and Tillier, 2001; Dayrat et al., 2001).

Wollscheid-Lengeling (2001) studied the phylogeny of Nudibranchia but did not discuss their findings in the context of the phylogeny of the Opisthobranchia. However they retrieved monophyly of many other clades of the Euthyneura. This study only included two cephalaspids; *Haminoea cymbalum* (Quoy and Gaimard, 1832) and *Smaragdinella* sp., which were found monophyletic in most analyses. This study was the first to use three different gene markers in a phylogenetic study of opisthobranchs (18S rRNA, 16S rRNA and COI).

Based on the same molecular character choice and the availability of more sequences Wägele et al. (2003) produced a phylogeny of the traditional Opisthobranchia. This study used a considerably larger taxon sampling for Cephalaspidea *s. s.* including members of the families Bullidae, Haminoeidae, Aglajidae, Diaphanidae, Philinidae and Cylichnidae (*Scaphander punctostriatus*), however without complete gene coverage for all species. The Architectibranchia taxa (part of the Cephalaspidea *s. l.*) *Aceton tornatilis* and *Pupa strigosa* (Gould, 1859) were also included. The Cephalaspidea *s. s.* was found to be monophyletic in the 18S rRNA maximum parsimony and distance analysis (BS = 100), but poorly supported in the 16S rRNA maximum parsimony analysis (BS = 56) and Distance analysis (BS = 51). In the combined (18S rRNA + 16S rRNA) analyses the Cephalaspidea *s. s.* were retrived as monophyletic with high support (BS = 100) however included only the haminoid genera *Haminoea* and *Smaragdinella*. In the 18S, COI and combined analyses the Anaspidea was retrieved sister to Cephalaspidea *s. s.* In addition to the nucleotide analyses the authors also analysed COI amino acid characters (165 characters), in this analysis the Cephalaspidea *s. s.* was rendered monophyletic albeit with only two members of Haminoeidae and *Bulla gouldiana* Pilsbry 1895 included. As so few taxa were included Wägele et al. (2003) emphasised that the sampling of Cephalaspidea s. s. was not representative for the group.

Grande et al. (2004) reconstructed the phylogenetic relationships within the Opisthobranchia based on mitochondrial gene markers. The authors retrieved two main branches of opisthobranchs; one consisting of Cephalaspidea *s. s.*, Anaspidea and Tylodioidea (Umbraculoidea) and the other containing Nudipleura and Architectibranchia. Cephalaspidea *s. s.* was found monophyletic with high support and containing the taxa *Haminoea japonica* (Pilsbry, 1895) (as *H. callidegenita* Gibson and Chia 1989a , *Philine aperta* and *Chelidonura africana* Pruvot-Fol 1953 this clade was resolved as sister to *Runcina coronata* Quatrefages 1844 with high support, which presently is ascribed to its own high rank taxon**.**

Vonnemann et al. (2005) reconstructed the phylogeny of the Opisthobranchia based on the nuclear markers 18S rRNA and 28S rRNA. As representatives of the Cephalaspidea *s. s.* the authors included the taxa *Haminoea hydatis* Linnaeus 1758, *Phanerophthalmus smaragdinus* Ruppell and Leuckart 1828, *Atys semistriatus* Pease 1860, *Odontoglaja guamensis* Rudman 1978, *Navanax inermis* Cooper 1863, *Chelidonura inornata* Baba 1949, *Philinopsis pilsbryi* C. Eliot 1900, *Philinoglossa praelongata* Salvini-Plawen 1973, *Retusa* sp., *Bulla* cf. *striata* Bruguiere 1792, *Sagaminopteron psychedelicum* Carlson and Hoff 1974 and *Runcina adriatica* Thompson 1980, thus being the most comprehensive molecular analysis for the Cephalaspidea at the time. Anaspidea and Cephalaspidea *s. s.* were found to sister taxa with high support in the combined analysis of 18S and 28S, however was not well supported in the single gene analyses. In most analyses the major clades of the Opisthobranchia were supported, but interestingly *Runcina adriatica* was excluded from the Cephalaspidea *s. s.* in the 18S rRNA trees (both in maximum-likelyhood and distance analyses). In all analyses *Runcina* was found to have a basal position in the Cephalaspidea *s. s.*. *Runcina* has four gizzard plates whereas all other cephalaspids have three (Mikkelsen, 1996) and therefore, Vonnemann et al. (2005) suggested that the four gizzard plates condition may represent the pleisomorphic state.

Klussmann-Kolb & Dinapoli (2006) redefined the systematic placement of Thecostomata and Gymnostomata within Opisthobranchia based on COI, 18S rRNA and 28S rRNA molecular data. Representatives of the Cephalaspidea *s. s.* included in this study were *Haminoea hydatis, Bulla cf. striata, Chelidonura inornata* and *Gastropteron rubrum* Rafinesque 1814. Some genes were not possible to amplify for all taxa so the combined analysis including COI, 28S rRNA and 18S rRNA were preformed on fewer taxa. Cephalaspidea *s. s.* was found monophyletic with high support in this combined analysis although only *H. hydatis* and *B. striata* were included. This analysis supported the sister relationship between Anaspidea and Thecosomata+Gymnosomata. The authors claimed that Cephalaspidea *s. s.* could be the possible sister lineage to this larger clade, but none of their phylogenetic analyses supports this view (Klussmann-Kolb and Dinapoli, 2006).

The broadest phylogenetic study focusing on the relationship of the Cephalaspidea was published by Malaquias et al. (2009a). The authors included DNA sequences from the COI, 18S rRNA, and 28S rRNA gene markers. This study included the most comprehensive taxa sampling for the Cephalaspidea *s. s.* and Cephalaspidea *sensu lato*. The taxa included for the Cephalaspidea *s. s.* were: 7 species of Aglajidae, 4 species of Bullidae, 2 species of Cylichnidae, 3 species of Diaphanidae, 2 species of Gastropteridae, 15 species of Haminoeidae, and 3 species of Runcinidae *Philine aperta* was included for the Philinidae while *Philinoglossa praelongata* represented Philinoglossidae. Additionally 4 species of Acteonidae and 2 species of Aplustridae were included. Outgroups included members of the closely related taxa Anaspidea, Sacoglossa, Thecostomata and one Caenogastropod (Malaquias et al., 2009a). The most conservative molecular character among all species was 18S rRNA, which gave good resolution at deeper nodes, while 28S rRNA seemed to yield better resolution than 18S at family levels. As both genes were not represented for the all taxa, comparisons were hampered. The most variable character was COI. The best resolution at the family level was obtained in the combined analysis (Malaquias et al., 2009a). Malaquias et al. (2009a) found the Cephalaspidea *sensu lato* to be made up of three monophyletic groups:

- Runcinacea: Reinstated as a higher taxa due to the Runcinidae not nesting within Cephalaspidea but forming is own separated clade in all analyses.
- Architectibranchia: excluding Diaphanidae due to this taxa being found as part of the Cephalaspida *s. s.*.
- Cephalaspidea *sensu stricto* with Diaphanidae included but Runcinidae excluded. Diaphanidae was usually found to be basal to the other lineages of the Cephalaspidea *s. s.*.

The exclusion of Runcinacea is also supported by morphology as this group has unique traits, such as a undivided notum, lack of mantle cavity and presence of four gizzard plates (Burn and Thompson, 1998); (Malaquias et al., 2009a).

The Cephalaspidea *s. s.* was found to be polyphyletic in the 28S rRNA Bayesian analysis, but was retrieved as monophyletic in the 18S and COI single gene trees; 18S+28S combined analyses and combined analyses of all genes.

As for the phylogeny of the Cephalaspidea *s. s.* there were several interesting results differing from the most recent classifications proposed by Burn and Thompson (1998) and Bouchet and Rocroi (2005). Although few sister relationships were confirmed for families within the Cephalaspidea *s. s.* Bayesian analysis of 28S rRNA and the combined analysis indicated a sister relationship between Philinidae and Aglajidae with high support. Bayesian and distance analysis of nuclear 18S rRNA and 28S rRNA indicated a sister relationship between Philinoglossidae and Gastropteridae. Thus the traditional superfamily Philinoidea (sensu Mikkelsen, 1996: Cylichnidae (*Acteocina*, *Cylichna*, *Scaphander*), Philinidae (*Philine*), Retusidae (*Retusa*)) was not supported as only Philinidae and Aglajidae were part of the same clade, while the other "phinlinoideans" occurred scattered in other parts of the tree. Bayesian and distance analysis of all genes suggested that Bullidae and Retusidae (without *Volvuella*) could be sister lineages (albeit support was low). The family Scaphandridae was reinstated for *Scaphander* (previously in Cylichnidae) and the family Rhizoridae was also reinstated for *Volvuella* previously included in the Retusidae (Malaquias et al., 2009a).

Several families were retrieved polyphyletic and therefore, in need of redefinition to clarify their status (e.g. Cylichnidae, Diaphanidae, Retusidae, Haminoeidae). The superfamily Bulloidea (sensu Mikkelsen, 1996: Haminoeidae, Bullidae and Smaragdinellidae) was not monophyletic because Bullidae was not rendered sister to the clade including representatives of Haminoeidae and Smaragdinellidae. However, taxa from the latter two families clustered together (excluding *Ventomnestia*). Nevertheless, the tradicional definition of Haminoeidae (*Atys*, *Haminoea* and *Venomnestia*) and Smaragdinellidae (*Smaragdinella* and *Phanerothalamus*) was not supported because as mentioned above *Ventomnestia* was not retrieved within the Haminoeidae and *Atys* was sister to *Phanerothalamus* while *Haminoea* was sister to *Smaragdinella*. Therefore, the authors suggested a single family Haminoeidae, with *Ventomnestia* of uncertain taxonomic placement (Malaquias et al., 2009a; Bayesian all genes tree).

In a later study Malaquias (2010) investigated the systematics of *Bullacta exarata* (Philippi, 1849), a genus only previously investigated in their 18S rRNA gene analysis based on sequences generated by Wägele et al. (2003a). Malaquias (2010) found *Bullacta* with marginal support (PP = 0.9) basal to all other Haminoeidae taxa and considered the genus to belong in the family Haminoeidae.

Dinapoli and Klussmann-Kolb (2010) studied the phylogeny of the Heterobranchia by means of COI, 16S rRNA, 18S rRNA, and 28S rRNA gene markers. Only two cephalaspids were included in this study, *Haminoea hydatis* and *Toledonia globosa* Hedley 1916 and they were retrieved sister to each other within a paraphyletic Opisthobranchia.

Jörger et al. (2010) studied the origins of meiofaunal Euthyneura gastropods specifically the traditional Opisthobranchia order Acochlidia. Recent morphological analyses have connected them to other enigmatic Euthyneura like Rhodopemorpha (Salvini-Plawen and Steiner, 1996), Runcinacea and Cephalaspidea (Wägele and Klussmann Kolb, 2005; Schrödl and Neusser, 2010) like Diaphanidae (*Toledonia*) (Sommerfeldt and Schrödl, 2005). They results are largely congruent with Malaquias et al. (2009a): Cephalaspidea *s. s.* was found monophyletic with high support including Diaphanidae and excluding Runcinacea. The latter formed a sister relationship to Anaspidea and Pteropoda, which together formed a sister lineage to the Cephalaspidea *s. s.*. The two mesopsammic cephalaspideans, both earlier considered closely related phininids, were shown to have different origins. No sister relationship was found between *Philine exigua* Challis 1969 and *Philinoglossa praelongata*, the latter, showed a closer relationship with *Scaphander lignarius* Montfort 1810, (BS = 54, PP = 0.98) while *P. exigua* was related to *Bulla striata* Bruguiere 1792 and *Haminoea hydatis*, albeit with support lower than BS ≥ 50 and PP ≥ 0.95 . This results corroborate the paraphyletic status of the super-families Philinoidea and Bulloidea (sensu Mikkelsen, 1996).

Medina et al. (2011) investigated the phylogeny of Opisthobranchia, using mitochondrial genome phylogenies, based on sequences and gene arrangements. The. cephalaspideans included were *Smaragdinella calyculata*, *Bulla* sp., *Odontoglaja guamensis* and *Sagaminopteron nigropunctatum* (Carlson and Hoff, 1973). The authors retrieved both the Opisthobranchia (if the traditional pulmonate *Siphonaria* is included) and Cephalaspidea monophyletic with maximum support in their Bayesian analysis. A sister relationship between the Cephalaspidea and Anspidea received maximum support in both Bayesian and Maximum Likelihood analyses, which led the authors to erect the clade Placoesophaga for these gizzard bearing groups. This study was later criticized by Schrödl et al. (2011a) for citing previous studie as as supportive of their results, when these in reality showed higher support for alternative trees, leaving out some mitogenomes, and naming certain clades showed to be artificial due to poor taxon sampling in previous studies (e.g. Göbbler and Klussmann-Kolb., 2010; Jörger et al., 2010). The clade Placoesophaga had additionally already been defined as Euopisthobranchia by Jörger et al. (2010)

Göbbler and Klussmann-Kolb (2011) preformed the, until then, most comprehensive molecular phylogeny of the Euthyneura, including 58 species from all major clades. The Cephalaspidea were represented with *Bulla striata,* 2 species of Diaphanidae, 3 Haminoeidae (including *Smaragdinella* sp.), one species for each families Cylichnidae, Philinidae, Gastropteridae, and Philinoglossidae, and two species for the families Aglajidae and Retusidae. Euthyneura was retrieved as monophyletic, however Opisthobranchia was found to be polyphyletic with Sacoglossa and Acocholidacea clustering with Panpulmonata (sensu Jörger et al., 2010). The Cephalaspidea *s. s.* was rendered monophyletic including Diaphanidae in a basal position and with Runcinacea clustering elsewhere in the tree. Two clades were retrieved; one with *Bulla striata* sister to the Retusidae, and the other containing Haminoeidae and the paraphyletic Philinoidea with Retusidae excluded. The authors also included, for the first time, a species of the family Ilbiidae and showed it to be sister to Runcinidae within the clade Runcinacea. Previously, Malaquias et al.(2009a) considered Ilbiidae a group of uncertain taxonomic position.

The trends observed in the phylogenetic studies of Euthyneuran gastropods through the last 10 years are largely the same, pointing to that Opisthobranchia and Pulmonata are not natural groups. Schrödl et al. (2011b) summarized the results of these recent studies proposing a reclassification of the Euthyneura with Nudipleura as basal to the clade Tectipleura containing the sister taxon Panpulmonata and Euopisthobranchia, the latter including the Cephalaspidea *s. s.* (Thiele, 1931; Malaquias et al., 2009a; Dinapoli and Klussmann Kolb, 2010; Jörger et al., 2010; Medina et al., 2011; Schrödl et al., 2011b; Wägele et al., 2013).

Cephalaspidea has gone from basal “primitive” opisthobranchs to derived and specialized members of the clade Tectipleura (*sensu* Schrödl, 2011b and Wägele et al., 2013) within the monophyletic Euopisthobranchia (*sensu* Jörger et al., 2010, Brenzinger et al., 2013, and Wägele et al., 2013). However the phylogeny of the Cephalaspidea *sensu stricto* is not yet totally resolved. The most comprehensive taxon inclusion was done by Malaquias et al. (2009a), but this study only covered 63% of the families and 28% of the genera recognized to belong to the Cephalaspidea *sensu lato*. The superfamily Philinoidea was found not to be monophyletic as were several families who were retrieved polyphyletic and therefore, in need of redefinition to clarify their status (e.g. Cylichnidae, Diaphanidae, Retusidae, Haminoeidae). And though later studies have shed some light, they have not contributed much to clarify the internal phylogenetic relationships of the Cephalaspidea.

1.1.3 Morphology of Cephalaspidea

1.1.3.1 External morphology:

The anterior end or “head” is usually dorsally flattened and covered by a broad shield like lobe – the cephalic shield. The posterior part of the cephalic shield extends beyond the margin of the shell to protect the mantel cavity from accumulating substrate while burrowing (Burn and Thompson, 1998, Fischer, 1883). Previously thought to be a defining character of the group, it is however a homoplasy resulting from adaptation to the burrowing lifestyle and is also found in other groups (Mikkelsen, 1996). Paired sensory organs (Hancock’s organ) may be present under the antero-lateral edge of the cephalic shield. The shell can be partially covered posteriorly by a thin layer of tissue – the mantle lobe (Rudman, 1972), palial lobe (Burn and Thompson, 1998) or posterior shield (Price et al., 2011). Laterally on each side there are parapodial lobes, which are lateral extensions of the foot (Burn and Thompson, 1998).

1.1.3.2 Anatomy:

The anterior body cavity is dominated by the foregut and the male reproductive system. The mouth is connected to a buccal bulb that may contain a radula in some species/genera. The radula varies among cephalaspidean taxa, and some genera have lost it completely. The buccal bulb connects to an oesophagus that ends in a gizzard, often containing three gizzard plates used to crush food. Depending on the species and its feeding ecology the plates may be chitinous or calcified. In some species they are reduced or absent. The foregut anterior of the buccal bulb is encircled by the cerebral nerve ring. The genial aperture opens anteriorly on the right side and connects to the male reproductive system. This system in general consists of a penial atrium attached to the genial aperture and often contains a penial papilla. The male reproductive system may be simple only containing a small prostate in form of a sac or be highly complex like in some clades of the genus *Philine* which have highly intricate duct systems (Burn and Thompson, 1998, Rudman, 1971b, Rudman, 1972c, Rudman, 1972d, 1978) or as in the monotypic genus *Bullacta* (Malaquias, 2010). The prostate functions by pumping seminal fluid that is mixed with the spermatozoa prior to ejaculation (Thompson and Bebbington, 1969).

The reproductive system is hermaphroditic; the anterior part contains only male structures and it is often connected to the posterior part (the truly hermaphroditic part) by an external ciliated seminal grove (Burn and Thompson, 1998). Mating is always by means of transference of spermatophores with vaginal penetration (Burn and Thompson, 1998).

Cephalaspids are mostly monaulic, with eggs and spermantozoa being transported through the same genial duct or grooves, often only separated by tissue folds (Ghiselin, 1966; Hadfield and Switzer-Dunlap, 1984; Robles, 1975; Rudman, 1978; Gosliner, 1994; de Maintenon, 2001; Klussmann-Kolb, 2001; Malaquias and Reid, 2008b). This is in contrast to other hermaphroditic systems where eggs and spermatozoa are contained in separate ducts, as in Nudibranchia (Ghiselin, 1966; Klussmann-Kolb, 2001). Like in other Euthyneura, the mantle cavity of cephalaspids is usually found on the right side of the visceral mass, although some have it oriented anteriorly. Due to the presence of a single gill, auricle and excretory organ, the orientation of the mantle cavity is thought to be derived from ancestors that had full torsion, later to evolve partial detorsion (Purchon, 1977; Gosliner, 1991; Aktipis et al., 2008).

Shells in cephalaspids can be external, internal or absent. The shell when present has few whorls, with most of the shell comprised by the last elongated whorl encircling the teleoconch and often the protoconch as well. Most species have rounded or cylindrical shells with an egg/bubble shape and thus their common name “bubble shells”, while others have flattened plate-like shells.

In general, Diaphanidae have small opaque and fragile shells that accommodate the whole animal. The exception is the genus *Colpodaspis*, where the animal does not retract completely inside the shell (Burn and Thompson, 1998). Cylichnidae and Scaphandridae have strongly calcified shells, particularly the members of the latter family. While most members of Cylichnidae can totally retract within their shell, members of the Scaphandridae only retract partially into the shells. Philinidae have largely thin plate-like internal shells, but some do have external shells (e.g. *Philine denticulata* Adams 1800). Philinoglossidae are mostly shell-less, but may have vestigial remnants of internal shells, in *Pluscula cuica* the shell is reduced to the point that mostly shell building tissues are retained (Burn and Thompson, 1998; Brenzinger, 2013). Haminoeidae have fragile translucent shells that do not accommodate the whole animal. The shell and species diversity within this family is greater than in other families of the order; shells may be oval and external as in *Haminoea* or reduced and internal as in *Phanerothalamus* (Burn and Thompson, 1998; Marin et al., 1999; Malaquias et al., 2009b). Gastropteridae species may lack shells or have reduced internal transparent shells that can be coiled and smooth (Beeman and Williams, 1980; Burn and Thompson, 1998). Retusidae are usually small with largely similar but variable shells, with elevated to sunken apex and an aperture that lacks folds or projections. The shape may vary and there are examples of both oval and cylindrical shells, and most have little to no sculpture (Chaban, 2000). Bullidae have globose to oval solid shells and the animal can retract completely inside it. When the animal is active the mantle and cephalic shield may cover the shell (Beeman and Williams, 1980; Tryon et al., 1894; Marin et al., 1999; Malaquias and Reid, 2008a).

Due to the variability within genera (e.g. *Atys*) and families (e.g. Diaphanidae) and in many cases the similarities between them (e.g. *Diniatys* vs. *Haminoea*; Cylichnidae vs. Retusidae) shells are a difficult character to infer cephalaspidean relationships. However shells are definitely a useful character for initial recognition and separation between families and genera. In addition to the shell, the most relevant morphological traits used in species delimitation are the radula, gizzard plates, the male reproductive system, and in some cases the Hancock's organ (Thompson, 1973; Gosliner and Ghiselin, 1984; Talavera et al., 1987; Mikkelsen, 1993; Burn and Thompson, 1998; Malaquias and Reid, 2008a).

1.1.4 Ecology of Cephalaspidea

1.1.4.1 Habitat:

Most cephalaspids burrow in soft sediments aided by their shovel shaped cephalic shield and streamlined body (Burn and Thompson, 1998; Malaquias et al., 2009b), a lifestyle that is common among carnivores like Aglajidae, Philinidae, and Scaphandridae or herbivores like some Haminoeidae (Rudman, 1971a; Boulch Bleas, 1983; Garcia et al., 1991; Burn and Thompson, 1998). However exceptions exist, examples like intertidal Bullidae and Haminoeidae that can be found on sea grass, and algae, or some Gastropteridae that are associated with sponges and reefs, while miniscule Philinoglossidae live interstitially between sand grains (Vayssière, 1880; Berrill, 1931; Tchang, 1931; Marcus, 1967; Carlson and Hoff, 1973; Burn and Thompson, 1998; Malaquias et al., 2009b). Sediment associated taxa often burrow just under the surface of the substrate and they move by displacing sediment by aid of surface cilia covering the cephalic shield that transports particles posteriorly over the dorsal surface of the animal (Lemche, 1956; Hurst, 1965; Thompson, 1973; Villani and Martinez, 1993; Marin et al., 1999, Moreira et al., 2011).

1.1.4.2 Diet

Dietary specialization has been an important factor in the evolution and adaptive radiation of Cephalaspidea (Malaquias et al., 2009b). In opisthobranchs, herbivory has been thougth to be the most pleisomorphic state (Purchon, 1977) as has carnivory due the precived basal position of Architectibranchia within Opisthobranchia (Haszprunar, 1985). Later it was again suggested that herbivory was the pleisomorphic dietary trait of the opisthobranchs and the ancestral cephalaspids (Mikkelsen, 1996). The latter was seemingly confirmed by phylogenetic analysis where it was demonstrated that herbivory was indeed the pleisomorphic condition of Cephalaspidea, and carnivory evolved independently on three different lineages (Malaquias et al., 2009b). Few studies have been conducted that analyse the gut content of cephalaspideans; thus, accurate knowledge on their diet remains scant (Malaquias et al., 2009b). The carnivorous families are mostly infaunal predators in soft bottom environments of mud or sand where they feed on bivalves, polychaets, echinoids, crustaceans, gastropods, and foraminifera (Paine, 1963; Hurst, 1965; Shonman and Nybakken, 1978; Taylor, 1982; Kohn, 1983; Gosliner and Armes, 1984; Gosliner, 1989; Morton and Chiu, 1990; Taylor and Jensen, 1992; Chester, 1993; Burn and Thompson, 1998; Malaquias et al., 2004; 2009b; Eilertsen and Malaquias, 2013b). However some lineages of Aglajidae actively seek mobile prey like nemerteans and polychaets, plathyhelmites, and even other opisthobranchs, while some Gastropteridae feed on Porifera (Rudman, 1972b; Gosliner, 1978, 1980; Malaquias et al., 2009b).

Genera like Haminoeidae, Bullidae or Philinoglossidae are herbivores (Malaquias et al., 2004; 2009b). These mostly feed on filamentous algae and diatoms (e.g. Bacillariophyceae) (Guiart, 1901; Tchang, 1931; Rudman, 1971a; 1972b; Gibson and Chia, 1989a; Garcia et al., 1991; Sprung, 1994; Mikkelsen, 1996; Wägele and Klussmann Kolb, 2005; Malaquias et al., 2004; 2009b). It has been suggested that there is a correlation between shell reduction and dietary preferences in evolution of cephalaspids (Wägele, 2004; Malaquias et al., 2009b). Loss or reduction of the shell has been connected to the onset of foraging behaviour; many herbivorous groups have solid shells, while a number of carnivorous do not. This is however a faulty generalisation since the most heavily armoured member of this taxa is the carnivorous *Scaphander*, whereas the naked *Philinoglossa* prefers to graze on algae (Malaquias et al., 2009b).

1.1.4.3 Defence mechanisms

In the “Ophistobranchia” the reduction of the shell has usually been followed by the evolution of alternative protection mechanisms other than burrowing into the sediment. “Opisthobranchs” often use chemical substances for defence, in the Cephalaspidea it is reported that these substances usually originate as secondary metabolites obtained from their diet (Faulkner and Ghiselin, 1983, Marin et al., 1999). Some cephalaspids, among them *Philine quadripartita* (Ascanius, 1772) and *P. aperta* have been recorded to excrete strong acids like sulphuric acid (pH = 1–2) from sub-epidermal sacs when disturbed (Thompson, 1960; Thompson; 1986, Wägele et al., 2008). Other species like *Haminoea navicula* (Da Costa, 1778) have also evolved primitive camouflage similar to cephalopods, by using chromatophores in the dermis to adapt to the substrate (Edlinger, 1982).

1.1.4.4 Reproduction

Among cephalaspids the most common mating strategy is unilateral mating, where individuals assume either the male or female role (Anthes and Michiels, 2007a, Anthes and Michiels, 2007b). However some species also display a wider range of mating strategies ranging from exclusive unilateral (only one of the animals is inseminated), unilateral with alternating gender roles, to reciprocal inseminations (Anthes and Michiels, 2007b). Especially the families Aglajidae and Gastropteridae has been showed to have mating behaviours that cover the enire spectrum, even within species (Anthes and Michiels, 2007a, Anthes and Michiels, 2007b). Examples of species with a high occurrence of unilateral matings are *Chelidonura fulvipunctata*, *Siphopteron quadrispinosum* and *Philinopsis lineolata* (all approx. 50% of all matings) (Anthes and Michiels, 2007b). Examples of exclusively simultaneously reciprocal species are *Chelidonura vairans*, *Philinopsis gardineri* and *Gastropteron bicornutum* (Anthes and Michiels, 2007b). Examples of species with a high occurense of unilateral mating with alternating gender roles are *Chelidonura hirundinia*, *C. sandrana* (approx. 80-85% of all matings) and *Navanax inermis* (approx. 60% of all matings) (Anthes and Michiels, 2007b). Cephalaspids usually spawn ovoid, globular cylindrical, ribbon-like or string shaped egg masses, usually anchored to substrates or buried in sand (Hurst, 1967; Soliman, 1987; Schaefer, 1996; Mikkelsen, 2002; Anthes and Michiels, 2007b). *Bulla* usually have string like egg masses similar to *Aplysia* (Linneaus, 1767) (Bandel, 1976, Farfan and Buckle Ramirez, 1988, Schaefer, 1996) and is flexible in substrate choice but seems to prefer an algal substrate (Schaefer, 1996). Most species in *Haminoea* produce ribbon-like egg masses embedded in a transparent gel (Schaefer, 1996), however exceptions exist like *H. japonica* (Pilsbry, 1895) which have small sac-shaped egg masses (Usuki, 1966a;b), the latter type also occurs in *Retusa* (Rasmussen, 1944; Thorsen, 1946; Smith, 1967b; Thompson, 1967) and *Cylichna* (Lemche, 1956). *Philine* have a cylindrical or ovoid egg masses with a gel string that anchors it to the substrate (Thorsen, 1946; Lemche, 1956; Hamatani, 1961; Horikoshi, 1967;

Rudman, 1972b; Seager, 1978; Seager, 1979; Morton and Chiu, 1990; Schaefer, 1996). This latter type is common and have also been recorded in *H. solitaria* (Say, 1822) (Smallwood, 1904; Harrigan and Alkon, 1978), *Acteocina canaliculata* (Say, 1826) (Franz, 1971; Mikkelsen and Mikkelsen, 1984), *Gastropteron* and Aglajidae (Hamatani, 1961; Hurst, 1967; Rose, 1985; Strathmann, 1987).

1.1.5. Deep-Sea Cephalaspidea of the West Pacific

Through time many scientific studies have been conducted throughout the the Indo-West Pacific biogeographic region, but still many areas remain insufficiently sampled, this especially concerns the deep sea where new species are collected with every sampling expedition (Bouchet et al., 2008). Cephalaspidea is particularly abundant in tropical and sub-tropical waters of the Indo-Pacific (Lin and Qi, 1985), however the diversity and taxonomy of cephalaspideans from the deeper waters of these regions are little known, as most species have been described from shells and in most cases their anatomy were un-described (Valdés, 2008). In some cases the shell can be sufficient to differentiate between species but often only the combination of this character with soft anatomy enables a correct assignment. This is particularly important in the Cephalaspidea, where shells can be very similar between species and genera (Valdés, 2008). An additional problem confounding the systematic and taxonomy is the lack of proper descriptions, illustrations and difficulty to locate type specimens for many of the species, this leads to problems and difficulties to identify species and describe new ones.

Some of the first Deep Sea samplings in the Indo-West Pacific can be attributed to Hugh Cummings (1791-1865) a sail maker who became a noted collector and dealer of shells (Dance, 1966). Aboard his yacht constructed for sampling and storing specimens, the *Discoverer*, he built a large collection of gastropods from across the Pacific, on localities like Tahiti and other Polynesian islands, and later the Philippines, Singapore and Borneo (Reeve, 1862; Dance, 1966). He was also the first to collect shells from off-shore using a dredge, a tool that at that time was rarely used by other explorers (Reeve, 1862, Dance, 1966). Even though Hugh Cummings never described any species himself, his large collection was the foundation of many important works in the following years. Examples are *the Conchiological illustrations* (1832) and *Thesarus Conchyliorum* (1842–1887) by the Sowerbys (Sowerby, 1832; Sowerby et al., 1842–1887) and *Concologica Systematica* (1841) and *Conchologia Ioconica* (1843–1878) by Reeve (1841; 1843–1878).

Some of the earliest descriptions of Cephalaspidea from these regions are credited to Arthur Adams

(1820–1878), which were mostly based on the Cummings collection. During his time as a surgeon aboard *HMS Samarang* (Adams and Reeve, 1850) and *HMS Actæon* (Adams, 1862) and later years, A. Adams described many species of cephalaspids but often using very short diagnoses and based solely on shells (Dance, 1966). Adams's works mostly focused on shallow water species, but he also studied deep-sea faunas (Adams, 1862).

In the following years "deep sea" explorations found a great diversity of species; including cephalaspids. The so called "great expeditions" of the 19th and early 20th centuries led to the discovery of numerous new species. The first expedition sampling across the Indo-West Pacific was *The Challenger* (1873–76). The opisthobranchs were studied by Watson (1884a; b; c; 1886). Other milestone expeditions were *The USS Albatross* expeditions in Hawaii, Guam and the Philippines (1907–10) (Bouchet et al., 2008) the *Siboga* (1899–1900) expedition which sampled the waters around Indonesia (Bergh, 1905; Schepman, 1908) The last of the "great classical" expeditions in the area was the Danish *Galathea II* (1950–1952) (Bruun, 1959).

During several decades the study of the deep sea benthos in the Indo-West Pacific was largely overlooked. This started to change when the L'Institut de Recherche pour le Développement (IRD, previously known as ORSTOM) and the Muséum national d'Histoire naturelle (MNHN) came on the scene during the 80'ties, with the MUORSTOM expeditions, aiming to sample the deep-sea of the South and West Pacific, focusing on the bathymetric range between 100–1500 meters (Bouchet et al., 2008).

As a result of the MUORSTOM expeditions Valdés (2008) published a large monograph on the Cephalaspidea *s. l.* of the tropical south west Pacific, One hundred and twenty one species were studied and 39 new species were described. Of the total 121 species 53 belonged to the Cephalaspidea *sensu stricto,* including 21 new species to Sience. The most heavily sampled areas by the MUORSTOM expeditions were the South West Pacific around the Coral Sea and the adjacent islands of New Caledonia, Vanuatu, Fiji, Tonga, and Wallis & Futuna, which concealed 97 previously undocumented species of Cephalaspidea *s. l.*. while the waters around Indonesia and the Philippines produced 66 species. The difference in new records may be related to the higher sampling effort in the area around the Coral Sea and adjacent islands, Sixty seven of the 97 species of Cephalaspidea *s.l.* were endemic to this region compared to only 10 of the 66 species found in the waters around The Philippines and Indonesia (Valdés, 2008). On comparing lists of species found in other regions Valdés (2008) found that one hundred and sixteen species seem to be endemic to the South-West Pacific and that only five species were also found in Japanese waters. The shared presence of few species (18) between the Coral Sea and the adjacent region of Indonesia and the Philippines, led Valdés (2008) to suggest the presence of a barrier isolating these two major areas.

During the MUSORSTOM expeditions 121 Cephalaspidea *s.l.* (excluding Ringiculidae) were collected in deeper waters, compared to only 34 species of dorid nudibranchs (Valdés, 2008). This is in contrast with the shallow water fauna of the Indo-West Pacific where dorid nudibranchs usually outnumber the species of Cephalaspidea *s.l.* (Gosliner, 1987; Marshall and Willan, 1999; Bouchet et al., 2002). According to Valdés (2008) this pattern may suggest that Cephalaspidea *s.l.* are more successful in deep sea habitats. Nevertheless, he also notes that this pattern could be a bias resulting from the fact that most "cephalaspideans" have shells which tolerate dredging operations better than soft bodied "opisthobranchs". However, as carnivorous Cephalaspidea *s.l.* feed upon a wider range of prey that is abundant at higher depths they may be more successful across a wider bathymetric range compared to dorid nudibranchs which are more specialized predators (Valdés, 2001a, b; 2008)

1.1.6 The Philinidae *sensu lato*

1.1.6.1 External morphology

The results of the present study (discussed later) strongly indicate that the Philinidae is polyphyletic, but as this group generally has been regarded as monophyletic due to quite similar general morphology, thus the term Philinidae *sensu lato* will be adopted. The typical anatomy of members of the Philinidae *s. l.* are characterized by a broad flat cephalic shield that makes out half to two thirds of the dorsal surface, while the remaining is covered by the posterior shield. The foot usually have parapodial lobes that extend upwards along the lateral sides of the body (Rudman, 1972a; Burn and Thompson, 1998). The cephalic shield usually have cilia that aid in burrowing (Rudman, 1972a; Hurst, 1965), but may have a cilia free median line that usually runs the length of the shield when present (Rudman, 1972a). The cephalic shield may be elongate, square-like to oval, or rhomboid (this study); may also have a posterior indentation forming two lobes (Rudman, 1972a).

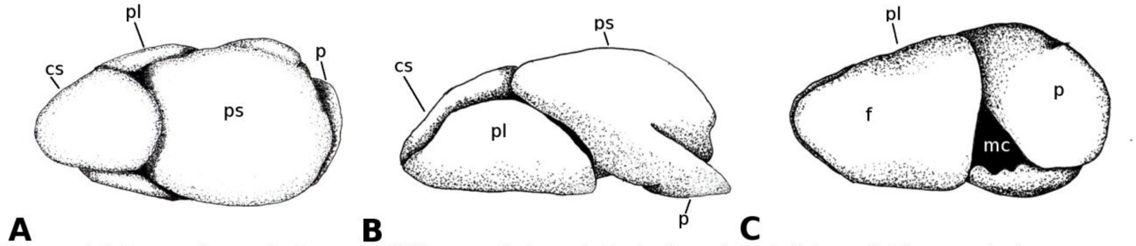


Figure 1.1 External morphology of *Philine* sp., left to rigth: A, dorsal. B, left lateral. C, ventral view. Abbreviations: cs, cephalic shield; pl, parapodial lobe; ps, posterior shield; p, pallial lobe; mc, mantle cavity.

The posterior shield is partially covered by the cephalic shield and may extend beyond the posterior margin of the foot; it may also have a posterior notch in some species (Rudman, 1972a). Most species are whitish in colour, but some species may have marks or coloured fields like the reddish *Philine rubrata* (Gosliner, 1988), *P. rubra* (Bergh, 1905), and *P. caballeri* (Ortea et al., 2001) and the black and white *P. orca* (Gosliner, 1988) are notable examples (Gosliner, 1988; Burn and Thompson, 1998).

1.1.6.2 Internal Morphology

The shell is most often internal, thin and brittle, usually flat and plate-like, but may also be oval or elongated in shape (Burn and Thompson, 1998). The aperture of the shell is wide and usually make up 2/3 of the entire shell (Ohnheiser and Malaquias, 2013). The shell is often smooth but may have a sculpture consisting of indentations and usually axial growth lines are present; the indentations may be punctuate forming dotted lines, but may also be fused leading to a chainlike sculpture, or totally fused forming more or less straight grooves (Ohnheiser and Malaquias, 2013).

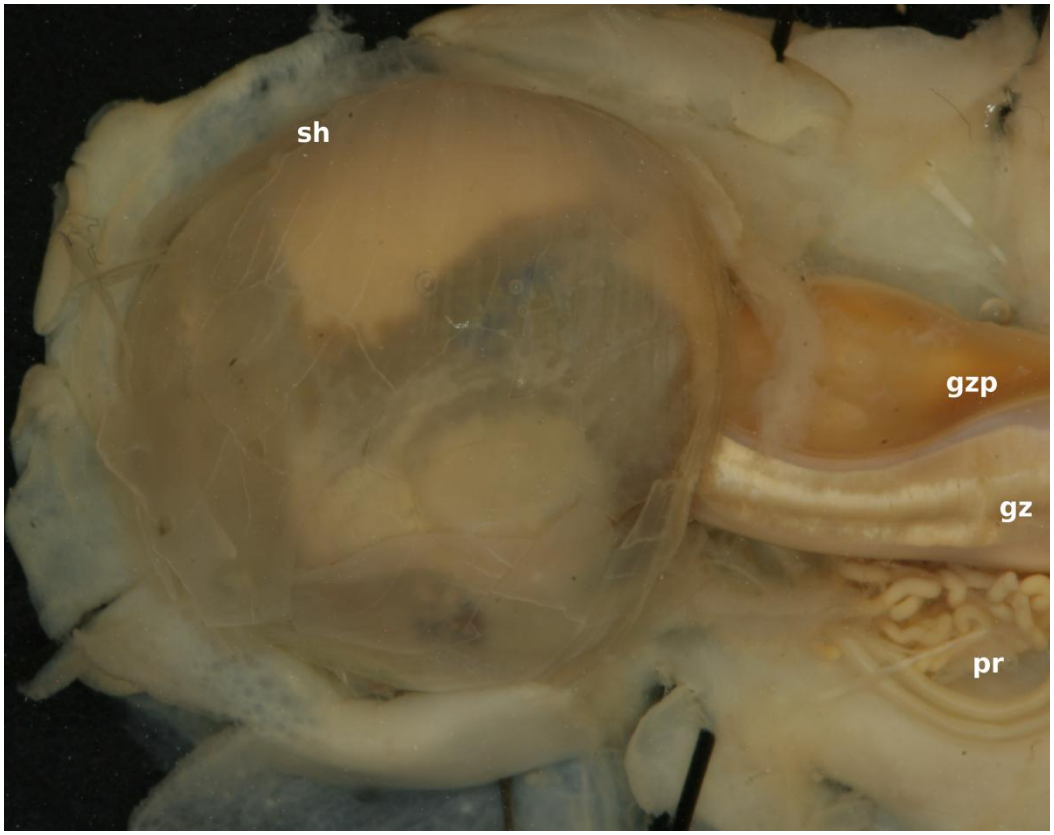


Figure 1.2 Internal moprphology of *Philine* sp. 3 MNHN, Paris-IM-2009-4333 Abbreviations: sh, thin internal shell. gzp, gizzard plate. gz, gizzard. pr. prostate. Gizzard partially muscularised inactive surface of gizzard plate naked, not covered by muscle.

The male reproductive system may have a simple prostate in the form of a single cavity as in *P. alba* and similar species, or consist of many intricate ducts as in the *P. aperta* species complex (Price et al., 2011). The shape of the penial papilla often varies between species, and is a good systematic character (Rudman, 1972a; Price et al., 2011; Ohnheiser and Malaquias, 2013). The hermaphroditic reproductive system is monaulic like in most cephalaspideans (Rudman, 1978; Hadfield and Switzer-Dunlap, 1984). Philinidae *s. l.* lack jaws, but the radula usually consist of a large inner lateral teeth that may be denticulated, and if present one to six outer lateral teeth. The radula may have a reduced simple rachidian tooth, but usually it is absent (Rudman, 1972a; Rudman, 1978; Price et al., 2011; Ohnheiser and Malaquias, 2013). Gizzard plates may be chitinous as in *P. alba* Mattox 1958 and *P. alboides* Price et al 2011, or calcareous as in *P. quadripartita* Ascanius 1772 and *P. orientalis* A. Adams (1854), usually the plates are of different shape with one small central plate and two larger lateral plates, but plates may also be equal like in *P. gibba*

Strebel 1908 and *P. finamarchia* M. Sars 1859 (Price et al., 2011; Ohnheiser and Malaquias, 2013); while some species like *P. lima* Brown 1827 lack gizzard plates (Ohnheiser and Malaquias, 2013).

1.1.6.3 Ecology

Philinidae *s. l.* are found worldwide living sublittorally in soft substrates like sand and mud where they burrow and forage for food in the upper layer of sediment (Lancaster, 1983; Burn and Thompson, 1998). They can be found in shallow waters as well as the deep sea, an example of the latter is *P. finmarchia* (M.Sars, 1859) that has been recorded alive at depths of 2304 m on the Norwegian slope (Høisæter, 2010). Most members of the family are carnivores that usually feed on infaunal molluscs, polychaetes, crustaceans, echinoids, and foraminifera. they may also display a scavenging behaviour (Brown, 1934; Hurst, 1965; Lancaster, 1983; Cedhagen, 1996; Burn and Thompson, 1998). There are also some reports of cannibalism in *P. orientalis* (as *P. japonica*) (Hamatani, 1961; Burn and Thompson, 1998). Horikoshi (1967) found the gut of several specimens of *P. denticulata* (Adams, 1800) filled with plant matter and suggested that this species could be herbivorous; moreover it lacks gizzard plates. Philinidae *s. l.* may be predated by fish, ophiuroids, asteroideans, polychaetes and various gastropods, which they try to avoid by burrowing and excreting deterrent acids (Stimpson, 1850; Thompson, 1960; Seager, 1982; Thompson, 1986; Wägele et al., 2008).

1.1.6.4 Reproduction*:*

Members of Philinidae *s. l.* spawn elongate, spherical or ovoid egg-masses that are usually anchored to the substrate by a mucous strand (Thorsen, 1946; Lemche, 1956; Hamatani, 1961; Horikoshi, 1967; Rudman, 1972b; Seager, 1978; 1979; Morton and Chiu, 1990; Schaefer, 1996). Several different development strategies have been documented; examples are: *P. quadripartita* (as *P. aperta*), *P. denticulata* and *P. scabra* where egg capsules hatch to release pelagic planktotrophic veliger larva (Tchang, 1931; Brown, 1934; Thorsen, 1946; Lemche, 1956; Horikoshi, 1967; Rasmussen, 1973; Lancaster, 1983; Schaefer, 1996; Burn and Thompson, 1998). *P. gibba* spawn around May, and have direct development hatching as benthic juveniles after *ca*. 120 days and still carrying some yolk in their visceral mass (Seager, 1978; 1979). Species can have apparently different life spans; for example *P. gibba* has been recorded to live approximately 5 years reaching sexual maturity around 3 years of age (Seager, 1979), whereas *P. paucipapillata* (as *P.orientalis*) lives approximately one year and are known to spawn on beaches on the West Pacific (e.g. Hong Kong) around May/June before dying (Morton and Chui, 1990a).

1.1.6.5 Taxonomy:

The Philinidae *s. l.* is currently comprised of four valid genera (e.g. *Globophiline* Habe, 1958, *Philine* Ascanius, 1772, *Philinorbis* Habe, 1950 and *Spiniphiline* Gosliner, 1988) and 90 species (Bouchet, 2013). The genus *Philine* is the most numerous and according to the World Register of Marine Species (Bouchet, 2013) there are currently 85 species of *Philine*. The most confounding factor on the taxonomy of the Philinidae is that most species have been described based only on shell morphology, and even today species continue to be described on this single character (Price et al., 2011). Morphologically similar species may have quite different internal anatomies, which is especially troublesome since for many species the internal anatomy is still unknown leading to taxonomic confusion (Price et al., 2011; Ohnheiser and Malaquias, 2013).

Several genera have been proposed based solely on shells or small anatomical variations (Lemche, 1948; Habe, 1950; Marcus, 1974; Price et al., 2011). Examples of genera erected based on shell characters alone are: *Laona* A. Adams 1865 (type: *L. zonata* A. Adams 1865 from O-Sima; Yohuko, Japan) and *Johania* Di Monterosato, 1884 (type: *J. retifera* Forbes 1844 from the Aegean Sea (Serpho)) (Ohnheiser and Malaquias, 2013). *Rhinodiaphana* Lemche 1967 (type: *R. ventricosa* Jeffreys 1865 from Isle of Skye, west Scotland, UK.) based on several shell and anatomical traits (Ohnheiser and Malaquias, 2013), *Retusophiline* Nordsieck 1972 (type: *R. lima* Brown 1827 from Greenock, west Scotland, UK.) was erected based on characters of the shell and cephalic shield (Ohnheiser and Malaquias, 2013). Some genera were however based on differences of their internal anatomy such as *Praephiline* Chaban and Soldatenko 2009 (type: *P.finmarchia* M. Sars 1859 from Finnmark, Norway, likely Vadsø) was erected based on putative differences of the prostate, penial papilla and gizzard (Chaban and Soldatenko, 2009a). While taxa like *Spiniphiline* Gosliner 1988 (type: *S. kensleyi* Gosliner 1988 from Aldabra Atoll, Seychelles) was erected to contain species with many autapomorhic features as the posterior termination of the visceral nerve loop near the midline of the animal, philinid shell with long lateral spines and a disc-like unpaired gizzard plate (Gosliner, 1988: Price et al., 2011).

Several of these generic names have later been synonymised with *Philine* as a result of anatomical and molecular studies (Rudman, 1972a; Marcus, 1974; Bouchet, 1975; Gosliner, 1980; 1988; Price et al., 2011; Ohnheiser and Malaquias, 2013).

For example *Laona* was erected by A. Adams (1865) based solely on the shell of *Lanoa zonata* Adams 1865 from Japan, which still have an unknown anatomy. This species was regarded as unique by Adams (1865) due to *'roughened by lamellose growth striae'*, and he motioned that *Philine pruinosa* Clark 1872 should be included in *Laona* due to similarities in the shell. Later Pruvot-Fol (1954) included several species without gizzard plates in this genus leading to extensive taxonomic confusion (Rudman, 2007 (Mar 16); Price et al., 2011). Price et al. (2011) included the gizzard plate-less species of *Laona* and *Spiniphiline* in their cladistic analysis and concluded that these genera should be regarded as synonyms of *Philine*. Moreover, a recent systematic review including a molecular phylogeny by Ohnheiser & Malaquias (2013) suggested the synonymization of the genera *Johania, Laona, Retusophilne* and *Praephiline* with *Philine*. The validity of the other genera is uncertain as fewer studies with phylogenetic frameworks have been conducted.

Two confounding Indo-West Pacific taxa that have been moved back and forth between Aglajidae and Philinidae are *Pseudophiline* Habe 1976 (Type: *P. hayashii* Habe 1976 from Esuzaki, Wakayama Pref., Honshu, Japan) and *Philinorbis* Habe 1950 (type: *P. teramachii* Habe, 1950 Tosa Bay, southern Shikoku, Japan), and even today there is still uncertainty about their family affinity. Okutani (2000) placed *Pseudophiline* in the Philinidae while *Philinorbis* was placed with Aglajidae, while the opposite is found in WoRMS (Bouchet, 2012; Rosenberg, 2012). In the OBIS IPMD database both are placed in Aglajidae (OBIS, 2006a; 2006b). *Philinorbis* was originally placed in the Philinidae by Habe (1950). Habe (1950) noted that *Pseudophiline* closely resembled *Philinorbis*, and that both were similar to other Philinidae, however as *Pseudophiline* seemingly had no radula or gizzard plates he reassigned them to Aglajidae (Habe, 1976; Chaban, 2011a). Gosliner (1980) mentioned that the morphology of these taxa was largely unknown, and regarded their shells to be similar to those of the Philinidae; moreover he emphasised that many *Philine* also have reduced radula and can lack gizzard plates, and Gosliner (1980) considered that most likely *Philinorbis* and *Pseudophiline* belong to the Philinidae (Gosliner, 1980). Kitao and Habe (1982), re-described *Pseudophiline hayashii* and found a philinid vestigial radula with two large lateral teeth and two outer lateral teeth in the buccal cavity and the authors thus suggested placing *Pseudophiline* in the Philinidae. Chaban (2011a) investigated the anatomy of one specimen of *Philinorbis* *teramachii* from Vietnamese waters, and based on known characters of the digestive system, shell and external morphology of *P. hayashii,* she suggested that *Pseudohiline* should be regarded as a junior synonym of *Philinorbis,* and both species should be assign to this genus and remain in the Philinidae. The taxonomic status of these two genera will be discussed later this thesis.

1.1.6.6 Phylogeny and evolution

Most studies directly concerning Philinidae *s. l.* focus on species descriptions and general biology or its placement within the Cephalaspidea. However three recent studies have addressed questions about the internal phylogeny of the family.

Price et al. (2011) did a detailed study of 16 species of *Philine* and produced a phylogenetic hypothesis based on morphological characters. The monophyly of *Philine* was confirmed, as well as the so called "*P. aperta* clade", including the type species *P. aperta* and closely related species. They also established new phylogenetically important morphological characters for species delimitation and systematics, like the microstructure of the gizzard plates, the branching pattern of the ducts of the prostate and details of the penial papilla. The authors also concluded that the division of *Philine* into different generic assignments like *Laona* or *Spiniphiline* was not supported and stressed that a broader revision of the classification of the family is needed.

Krug et al. (2012) based on a molecular study (16S rRNA) including native and invasive species of *Philine* collected along the East Pacific coast of North America confirmed that *P. paucipapillata* from Hong Kong and *P. quadripartita* from Europe are genetically distinct from similar species within the "*P. aperta*" clade (as suggested by Price et al., 2011) including from the morphologically sibling species *P. aperta* from South African (Price et al., 2011). *P. orientalis,* was found to be less related to the "*P. aperta*" clade than previously suggested by Price et al. (2011) based on morphological traits.

Ohnheiser and Malaquias (2013) in a recent study on Scandinavian *Philine* combining molecular characters (COI) and morphological characters (shell, radulae, gizzard plates, and male reproductive systems) concluded that there was no support for a generic division of the Atlantic species of *Philine,* and suggested that NE Atlantic species previously attributed to the genera *Praephiline, Laona,* and *Johania* should be ascribed to *Philine*.

As mentioned in previous sections several molecular phylogenetic studies have suggested a sister relationship between the Philinidae and Aglajidae and the paraphyly of Philinoidea (e.g. Grande et al., 2004; Malaquias et al., 2009a), but until the latter works become available the evolution of Philinoidea was a topic of heated debate (e.g. Rudman, 1978; Gosliner, 1980). Guiart (1901) and Boettger (1954) earlier suggested that Philinidae were direct ancestors of Aglajdae, while Ghiselin (1966) argued that Aglajidae, Gastropteridae, Scaphandridae (Cylichnidae) and Philinidae likely were closely related due to similarities in the reproductive system. Rudman (1972a; 1978) hypothesised that members of Philinoidea (as Philinaceae including Philinidae, Cylichnidae, Scaphandridae, Gastropteridae, and Aglajidae) shared common ancestry and evolved from a less derived Cylichnidae-like lineage, because Cylichnidae taxa retain less derived features like presence of jaws, radula with elaborated rachidian teeth, and numerous outer lateral teeth, while the rachidian tooth is reduced in Scaphandridae and present in a few less derived *Philine* and lost in the remaining families. He also recognized similarities between the nearly equal chitinous gizzard plates of Cylichnidae (e.g. *Cylichna thetidis* (Hedley, 1903)) and of those of less derived philinids like *Philine gibba* (Strebel, 1908). A branched hermaphroditic duct consist of a spermoviduct where the male part with a exogenous sperm sac is still connected to a glandular oviduct, a ooaulic system where gametes are transported along different ducts, the complexity of branching the branching may vary (Rudman, 1978). An unbranched hermaphroditic system is characterised by a monaulic organisation where a common duct is used for incoming and outgoing gametes, usually what remains of the male tesits branch. (Rudman, 1978). Rudman (1978) regarded a branched intricate hermaphroditic duct as the ancestral condition of the Philinoidea, while an unbranched system was viewed as a derived simplification, but as the unbranched system is found in all known Philinidae, and many Gastropteridae and Scaphandridae they may have evolved from a common ancestor cylichnid with a similar unbranched system. Rudman (1978) did not support the view of a close relationship between Philinidae and Aglajidae, despite the similarities especially between *Odontoglaja* and Philinidae, because on the unique aglajid traits such as presence of the “yellow gland”, sensory bristles, and of a branched hermaphroditic system. However, Rudman (1978) stressed that his hypothesis could be undermined by the possibility of parallel evolution of traits in the philinoidean.

Gosliner (1980) corroborated Rudman’s suggestion that tree nearly equal chitinous plates represented the ancestral state for the Philinoidea but Gosliner (1980) regarded the simpler unbranched reproductive system, where the hermaphroditic ducts open directly into the genital atrium, as the ancestral state, as it is found within several taxa in Cylichnidae, Philinidae, Gastropteridae and Aglajidae (Guiart, 1901; Rudman, 1972a; 1974; 1978; Gosliner, 1979; 1980). Gosliner (1980) hypothesised that Aglajidae evolved from a philinid ancestor, but that parallel evolution, causing independent loss of radula and gizzard plates, reduction of shell and elaboration of reproductive system, have occurred since the two lineages split. Rudman (1978) did not considered a relationship between Philinidae and Aglajidae as likely, because all known Philinidae had unbranched hermaphroditic systems as opposed to the more branched system of Aglajidae. However Gosliner (1980) found small branches in *Philine alba* Mattox 1958 and *P. falklandica* Powell 1951, showing that an elaboration of the hermaphroditic ducts have occurred in both Philinidae and Aglajidae.

Despite this past discussion on the relationships of the Philinoidea, recent molecular phylogenetic evidence suggests polyphyly of this clade with Cylichnidae, Scaphandridae and Philinidae + Aglajidae + Gastropteridae evolving from different ancestral lineages within the Cephalaspidea. This supports the view that morphological similarities may result from parallel evolution and not from common descendent. Nevertheless, a close relationship between the families Philinidae and Aglajidae, and between those and Gastropteridae, have been suggested by molecular phylogenetics including a broad sampling of Cephalaspidea (e. g. Malaquias et al., 2009a; Göbbler and Klussmann-Kolb, 2011; this study)

2. Objectives

This project aims to (1) produce a new hypothesis of relationships for the Cephalaspidea gastropods including for the first time representatives from all families by means of multi-locus phylogenetic analyses (2) to infer relationships between families and test the taxonomic classification proposed by Malaquias et al (2009a), and (3) to study the diversity and systematics of deep sea West Pacific Philinidae cephalaspids.

3. Materials and methods

3.1.1 Sampling: systematics review of deep-sea IWP Philinidae *sensu lato*

Philinidae specimens for morphological, anatomical, and phylogenetics study were obtained from the collections of the Muséum national d’Histoire naturelle, Paris (MNHN). These specimens were originally collected during several scientific expeditions in the Indo-West Pacific and have been fixed in absolute ethanol. Additional samples to complement the molecular phylogenetic analysis were obtained from the collections of the University Museum of Bergen (ZMBN) and mined from Genebank.

3.1.2 Sampling: Molecular phylogeny of Cephalaspidea

Samples were obtained mostly from the ZMBN and MNHN collections. DNA extractions of the rare species *Philinoglossa praelongata* and *Pluscula cuica* were obtained from the Zoologische Staatssammlung München (ZSM). Additional sequences were mined from the GenBank database. All gene markers concatenations were amplified form the same specimen*.
This sampling covers 100% of recognised valid families of Cephalaspidea and approximately 50% (excluding the problematic family Notodiaphanidae) of all recognised valid genera (Gofas, 2013a) (see table 3.1) compared to 60% of families and 17% of genera of Cephalaspidea included by Malaquias et al. (2009). Nine outgroups from higher different taxa consisting of 31 samples from 24 genera (see table 3.1) were included and the tree was rooted with the caenogastropod *Littorina littorea*. When possible at least four species per genera were included in the analyses. All specimens with less than two gene markers available were excluded from concatenated alignments, except in the case of 16S rRNA sequences of *Philine* species considered essential for the discussion about the systematics of Philinidae *sensu lato*.

* Regarding *Philine quadripartita* it was not possible to obtain the four gene markers from the same specimen; the COI sequence comes from one specimen whereas the remaining sequences come from another specimen, and the four sequences were concatenated for the final alignments. This was done because both specimens were collected at the same time from the same population in Tjärnö, Sweden (Aktipis and Giribet, 2012).

Table 3.1 List of specimens used in this study, with sampling localities, voucher numbers, and GenBank accession numbers.

Higher taxa	**Family**	***Species***	**Locality**	**Voucher No.**	**COI**	**16S**	**28S**	**H3**
Cephalaspidea	Diaphanidae	*Colpodaspis thompsoni*	Panglao, Philippines	MNHN42241	yes	yes	DQ927222	yes
Cephalaspidea	Diaphanidae	*Colobocephalus constellatus*	Sognefjorden, Norway		yes	yes	Yes	yes
Cephalaspidea	Diaphanidae	*Diaphana globosa*	Hauglandsosen, Norway	Unnumbered	yes	yes	yes	yes
Cephalaspidea	Diaphanidae	*Diaphana* sp.	Panglao, Philippines	MNHN42244	DQ974665	yes	DQ927223	yes
Cephalaspidea	Diaphanidae	*Diaphana* sp.	Panglao, Philippines	MNHN42254	DQ974666	yes	DQ927224	yes
Cephalaspidea	Diaphanidae	*Toledonia globosa*	Scotia Arc	EED-Phy-475	EF489395	EF489327	EF489375	
Cephalaspidea	Cylichnidae	*Acteocina lepta*	Tom Moore's Pond, Bermuda	ZMBN82986	yes	yes	yes	yes
Cephalaspidea	Cylichnidae	*Acteocina lepta*	Tom Moore's Pond, Bermuda	ZMBN82996	yes	yes	yes	yes
Cephalaspidea	Cylichnidae	*Cylichna cylindracea*	Wales. UK	BMNH20060323	yes	yes	yes	yes
Cephalaspidea	Cylichnidae	*Cylichna gelida*	Scotia Arc	EED-Phy-473		EF489326	EF489374	
Cephalaspidea	Scaphandridae	*Scaphander punctostriatus*	Norway	ZMBN 88006	Genbank	Genbank	Genbank	yes
Cephalaspidea	Scaphandridae	*Scaphander lignarius*	Bergen, Norway	ZMBN 88000	Genbank	Genbank	Genbank	yes
Cephalaspidea	Scaphandridae	*Scaphander* sp.	Between Surprise and Pott Island, New Caledonia	IM-2009-4317	Genbank	Genbank	Genbank	yes
Cephalaspidea	Scaphandridae	*Scaphander mundus*	East of Lamon Bay, Phillipines	IM-2009-4319	Genbank	Genbank	Genbank	yes
Cephalaspidea	Scaphandridae	*Roxania* sp.	Baler Bay, Philippines	IM-2009-4572	yes	yes	yes	yes
Cephalaspidea	Scaphandrdae	*Roxania* sp.	Panglao, Philippines	IM-2009-4382	yes			yes
Cephalaspidea	Scaphandridae	*Roxania* sp.	Baler Bay, Philippines	IM-2009-4323	yes	yes		yes
Cephalaspidea	Retusidae	*Retusa* sp.	North of Lamon Bay, Philippines	IM-2009-4364	yes	yes	yes	yes
Cephalaspidea	Retusidae	*Retusa* sp.	Panglao, Philippines	IM-2009-4346	yes	yes	yes	yes
Cephalaspidea	Retusidae	*Retusa* sp.	Panglao, Philippines	MNHN42243	DQ974679	yes	DQ927238	yes
Cephalaspidea	Retusidae	*Retusa* sp.	Hong Kong, China	ZMBN 81712	yes	yes	yes	yes
Cephalaspidea	Retusidae	*Retusa umbilicata*	Hauglandsosen, Norway	Unnumbered	yes	yes	yes	yes
Cephalaspidea	Retusidae	*Pyrunculus* sp.	Maui, Hawaii	IM-2009-4322	Yes		yes	yes
Cephalaspidea	Retusidae	*Pyrunculus* sp.	Panglao, Philippines	MNHN42243	yes	yes	yes	yes
Cephalaspidea	Rhizoridae	*Volvulella* sp.	Panglao, Philippines	MNHN 42256	DQ974684	yes	DQ927244	yes
Cephalaspidea	Philinidae	*Philine* sp.1	Sulu Sea, Philippines	IM-2009-4380			yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 5	Surprise Island, New Caledonia	IM-2009-4375	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 5	Surprise Island, New Caledonia	IM-2009-4374	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 5	Between Suprise and Pott Is. New Caledonia	IM-2009-4373	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 10	Surprise Island, New Caledonia	IM-2009-4372	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 13	East of Lamon Bay, Philippines	IM-2009-4369	yes	yes	yes	yes

Cephalaspidea	Philinidae	*Philine* sp. 3	Baler Bay, Philippines	IM-2009-4368	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 6	East of Lamon Bay, Philippines	IM-2009-4367	yes	yes		yes
Cephalaspidea	Philinidae	*Philine* sp. 6	East of Lamon Bay, Philippines	Im-2009-4366	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 6	East of Lamon Bay, Philippines	IM-2009-4365	yes	yes		yes
Cephalaspidea	Philinidae	*Philine* sp. 11	East of Lamon Bay, Philippines	IM-2009-4363	yes	yes	yes	Yes
Cephalaspidea	Philinidae	*Philine* sp. 9	East of Lamon Bay, Philippines	IM-2009-4362	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp.8	North of Lamon Bay, Philippines	IM-2009-4361	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 2	Between Suprise and Pott Is. New Caledonia	IM-2009-4360	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 2	Between Suprise and Pott Is. New Caledonia	IM-2009-4359		yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 3	Between Suprise and Pott Is. New Caledonia	IM-2009-4358	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 3	Between Suprise and Pott Is. New Caledonia	IM-2009-4357	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 3	Between Suprise and Pott Is. New Caledonia	IM-2009-4356	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 3	Between Suprise and Pott Is. New Caledonia	IM-2009-4355	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 3	Between Suprise and Pott Is. New Caledonia	IM-2009-4354	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 14	Bohol Sea, Philippines	IM-2009-4353	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine babai*	Bohol Sea, Philippines	IM-2009-4352	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine babai*	Panglao, Philippines	IM-2009-4344	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 7	Bohol Sea, Philippines	IM-2009-4341	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 15	Savu, Indonesia	IM-2009-4340		yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 4	Timor, Indonesia	IM-2009-4338	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 4	Timor, Indonesia	IM-2009-4337	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 4	Timor, Indonesia	IM-2009-4336	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 3	Pavuvu, Solomon Islands	IM-2009-4335	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 3	Pavuvu, Solomon Islands	IM-2009-4334	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 3	Pavuvu, Solomon Islands	IM-2009-4333	yes	yes	yes	yes
Cephalaspidea	Philinidae	*Philine* sp. 4	TAIWAN	IM-2009-4328	yes			yes
Cephalaspidea	Philinidae	*Philine* sp. 12	Surprise Island, New Caledonia	IM-2009-4316		yes	yes	yes
Cephalaspidea	Philinidae	*Philine ventricosa*	Bergen, Norway	ZMBN 87080.1	JX944803	yes	yes	yes
Cephalaspidea	Philinidae	*Philine indistincta*	Silavågen, Norway	ZMBN 82108	JX944798	yes		yes
Cephalaspidea	Philinidae	*Philine quadrata*	MAREANO, Norway Shelf	zmbn88012.1	JX944809	yes	yes	yes
Cephalaspidea	Philinidae	*Philine scabra*	Hauglandsosen, Norway	ZMBN 81821	JX944796	yes	yes	yes
Cephalaspidea	Philinidae	*Philine pruinosa*	Tjärnö. Sweden	ZMBN 87076	JX944808	yes	yes	yes

Cephalaspidea	Philinidae	*Philine confusa*	Hauglandsosen, Norway	ZMBN 87081	JX944804	yes	yes	yes
Cephalaspidea	Philinidae	*Philine quadripartita*	Spain		AY345016			
Cephalaspidea	Philinidae	*Philine grandioculi*	Off Lofoten, Norway	ZMBN_88009	JX944805	yes	yes	
Cephalaspidea	Philinidae	*Philine paucipapillata*	TAIWAN			JQ691691		
Cephalaspidea	Philinidae	*Philine aperta (quadripartita)*	Tjärnö. Sweden	MCZ DNA101778	GQ160767			
Cephalaspidea	Philinidae	*Philine aperta (quadripartita)*	Tjärnö. Sweden	MCZ DNA101268		DQ093482	DQ279988	DQ093508
Cephalaspidea	Philinidae	*Philine aperta*	South Africa			JQ691679		
Cephalaspidea	Philinidae	*Philine exigua*	?		HQ168450	HQ168412	HQ168438	
Cephalaspidea	Philinidae	*Philine angasi*	New Zealand			JQ691675		
Cephalaspidea	Philinidae	*Philine angasi*	Australia			JQ691677		
Cephalaspidea	Philinidae	*Philine auriformis*	New Zealand			JQ691680		
Cephalaspidea	Philinidae	*Philine aurifomis*	USA			JQ691681		
Cephalaspidea	Philinidae	*Philine orientalis*	Japan			JQ691684		
Cephalaspidea	Philinidae	*Philine orientalis*	USA			JQ691686		
Cephalaspidea	Philinoglossidae	*Philinoglossa praerlongata*	?	ZSM 2008917		HQ168411	yes	
Cephalaspidea	Philinoglossidae	*Philinoglossa praerlongata*	?	ZSM20080918				yes
Cephalaspidea	Philinoglossidae	*Pluscula cuica*	?		yes	yes	yes	yes
Cephalaspidea	Aglajidae	*Aglaja tricolorata*	Algave Portugal	BMNH20060327			DQ927215	yes
Cephalaspidea	Aglajidae	*Aglaja tricolorata*	?	Ag. iso e19	AM421902	AM421854	AM421950	
Cephalaspidea	Aglajidae	*Chelidonura africana*	Portugal	BMNH20030343	DQ974654	yes	DQ927216	yes
Cephalaspidea	Aglajidae	*Chelidonura electra*	?	Chel. iso149	AM421899	AM421843	AM421964	
Cephalaspidea	Aglajidae	*Chelidonura amoena*	?	Chel. iso e1	AM421901	AM421841	AM421962	
Cephalaspidea	Aglajidae	*Chelidonura berolina*	Bergen	Chel. iso 275	HQ011872	HQ011858		HQ011898
Cephalaspidea	Aglajidae	*Chelidonura flavobata*	?	Chel. iso RM17	AM421897	AM421845	AM421967	
Cephalaspidea	Aglajidae	*Chelidonura fluvipunctata*	?	Chel. iso 120	AM421896	AM421849	AM421971	
Cephalaspidea	Aglajidae	*Chelidonura hirundinia*	Bergen	Chel. Iso 76	HQ011877	HQ011862		HQ011905
Cephalaspidea	Aglajidae	*Chelidonura hirundinia*	?	Chel. iso 180	AM421881		AM421969	
Cephalaspidea	Aglajidae	*Chelidonura inorata*	?	Chel. iso 45	AM421898	AM421842	AM421965	
Cephalaspidea	Aglajidae	*Melanochlamys lorrainae*	Auckland, New Zealand	Melan. Iso 06NZ4	EU604710	EU604728	EU604737	
Cephalaspidea	Aglajidae	*Melanochlamys diomedea*	Friday Harbour, Washington State, USA	Melan. iso 06SJI3	EU604713	EU604731	EU604734	
Cephalaspidea	Aglajidae	*Melanochlamys cylindrica*	Auckland, New Zealand	Melan. iso 06NZ2	EU604700	EU604718	EU604736	
Cephalaspidea	Aglajidae	*Navanax nyanyanus*	Ilha Boavista, Cape Verde	LACM:153125	JN402066	JN402138		JN402090
Cephalaspidea	Aglajidae	*Navanax inermis*	Long Beach, California, USA	LACM:176388	JN402045	JN402154		JN402119
Cephalaspidea	Aglajidae	*Navanax gemmatus*	Pta Cahuita, Limón, Costa Rica	CASIZ 175767	JN402046	JN402151		JN402107
Cephalaspidea	Aglajidae	*Navanax aenigmaticus*	La Audiencia, Colima, Mexico	LACM:176392	JN402059	JN402144		JN402117

Cephalaspidea	Aglajidae	*Odontoglaja* sp.	Madagascar, Lalakajoro	Cas-Cephas 2	DQ974655		DQ927218	yes
Cephalaspidea	Aglajidae	*Odontoglaja guamensis*	?	Odo. iso E23	AM421869	AM421830		
Cephalaspidea	Gastropteridae	*Philinopsis pilsbryi*	?	Phil. iso 167	AM421888	AM421840	AM421956	
Cephalaspidea	Gastropteridae	*Philinopsis cyanea*	?	Phil. iso 239	AM421890	AM421832	AM421951	
Cephalaspidea	Gastropteridae	*Philinopsis depicta*	?	Phil. Iso e17	AM421892	AM421831	AM421954	
Cephalaspidea	Gastropteridae	*Philinopsis gardineri*	?	Phil. iso 168	AM421887	AM421837	AM421957	
Cephalaspidea	Gastropteridae	*Philinopsis lineolata*	?	Phil. iso 165	AM421884	AM421839	AM421958	
Cephalaspidea	Gastropteridae	*Gastropteridae* sp.	Surprise Island, New Caledonia	IM-2009-4370	yes	yes	Yes	yes
Cephalaspidea	Gastropteridae	*Sagaminopteron psechedelicum*	Madagascar, Kalakajoro	Cas-Cephas3	yes	yes	DQ927225	yes
Cephalaspidea	Gastropteridae	*Sagaminopteron ornatum*	?	Sag. iso. 240	AM421857	AM421814	AM421937	
Cephalaspidea	Gastropteridae	*Siphopteron tigrinum*	Madagascar, Kalakajoro	Cas-Cephas4	yes	yes	DQ927226	yes
Cephalaspidea	Gastropteridae	*Siphopteron brunneomarginatum*	?	Siph.b. iso. e4	AM421864	AM421816	AM421939	
Cephalaspidea	Gastropteridae	*Siphopteron qadrispinosum*	?	Sip. iso.179	AM421860	AM421819		
Cephalaspidea	Gastropteridae	*Siphopteron qadrispinosum*	?	Siph. Iso. 189			AM421941	
Cephalaspidea	Haminoeidae	*Atys naucum*	Palau, Hawaii	UF301586	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Atys semistriata*	Maui, Hawaii	ZMBN 81656	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Atys debilis*	Maui, Hawaii	ZMBN 81658	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Atys kuhnsi*	Maui, Hawaii	ZMBN 81660	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Liloa porcellana*	Maui, Hawaii		yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Liloa curta*	Tepung channel, Marianas islands, Guam.	UF374131	yes		Yes	yes
Cephalaspidea	Haminoeidae	*Liloa* sp.	Guam	ZMBN 81663	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Aliculastrum paralella*	Bile Bay, Marianas islands, Guam	UF 374138	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Aliculastrum paralella*	Guam	ZMBN 81670	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Aliculastrum* sp.	Bile Bay, Marianas islands, Guam	UF 374152	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Diniatys dubia*	Bile Bay, Marianas islands, Guam	UF 374148	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Diniatys dentifer*	Maui, Hawaii	ZMBN 81706	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Diniatys costulosa*	Maui, Hawaii	ZMBN 81802	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Diniatys monodonta*	Cocos, Marianas, Guam	UF 376788	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Haminoea cymbalum*	Magliao, Guam	ZMBN 81711	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Haminoea ovalis*	Maui, Hawaii	ZMBN81689	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Haminoea orbignyana*	Faro, Portugal	BMNH 20030296	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Haminoea hydatis*	Mediterranean France		yes	yes	Yes	yes

Cephalaspidea	Haminoeidae	*Limulatys semistriata*	Tepung channel, Marianas islands, Guam.	UF374125	yes	yes	Yes	yes
Cephalaspidea	Incertae sedis	*Ventomnestia villica*	Panglao, Philippines	MNHN 42239	yes	yes	DQ927236	yes
Cephalaspidea	Incertae sedis	*Ventomnestia vilica*	Maui, Hawaii	ZMBN 81716	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Bullacta exarata*	Korea	BMNH20070444	GQ332576	yes	HM100714	yes
Cephalaspidea	Haminoeidae	*Bullacta exarata*	Wenzhhou, China	LSGB25302	HQ834118	HQ833986		HQ834193
Cephalaspidea	Haminoeidae	*Phanerophthalamus smaragdinus*	Mangrove Bay, Egypt, Red Sea	BMNH20070584	yes		Yes	yes
Cephalaspidea	Haminoeidae	*Phanerophthalamus cylindricus*	Maui, Hawaii	ZMBN 81693	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Phanerophthalamus* sp.	Sulu Indonesia	BMHN20050661	yes	yes	DQ927241	yes
Cephalaspidea	Haminoeidae	*Smaragdinella* cf. *Calycuata*	Panglao, Philippines	MNHN 42257	DQ974682	yes	DQ927242	yes
Cephalaspidea	Haminoeidae	*Smaragdinella* sp.	Pulau Jung, Singapore Strait, Singapore	BMHN 20070586	yes		Yes	yes
Cephalaspidea	Haminoeidae	*Smaragdinella* sp.	Pulau Jung, Singapore Strait, Singapore	BMHN 20070586	yes	yes	Yes	yes
Cephalaspidea	Haminoeidae	*Smaragdinella calyculata*	Maui, Hawaii	ZMBN81646	yes	yes	Yes	yes
Cephalaspidea	Bullidae	*Bulla vernicosa*	Panglao, Philippines	MNHN42245	DQ974661	yes	DQ927219	yes
Cephalaspidea	Bullidae	*Bulla* cf. *peasena*	WV.Haw	ZMBN81715	yes	yes	Yes	yes
Cephalaspidea	Bullidae	*Bulla striata*	Senegal	BMNH 20030784/2	DQ986565	DQ986630	DQ986692	yes
Cephalaspidea	Bullidae	*Bulla ampulla*	VTM	BMNH 20041004	DQ986524	DQ986584	DQ986647	293
Outgroups								
Anaspidea	Akeridae	*Akera bullata*	Avgave Portugal		yes	yes	yes	yes
Anaspidea	Aplysiidae	*Aplysia californica*	California		AF077759	AF192295	AY026366	
Anaspidea	Aplysiidae	*Aplysia dactylomela*	Cape Verde		yes	yes	yes	yes
Sacoglossa	Volvattellidae	*Ascobulla* sp.	Panglao, Philippines	MNHN 42250	DQ974683	t355	DQ927243	yes
Sacoglossa	Volvattellidae	*Ascobulla* sp.	SUGARLOAF CANAL, SUGARLOAF KEY, FLORIDA, USA	BMNH20070601	yes	yes	yes	yes
Sacoglossa	Plakobranchidae	*Elysia timida*	Cuba	MNCN 15.05/53680	HQ616847	HQ616818		HQ616872
Sacoglossa	Plakobranchidae	*elysia papillosa*	Cuba	MNCN 24.922	HQ616844	HQ616815		HQ616869
Sacoglossa	Plakobranchidae	*Elysia pusilla*	Pago Bay, Guam	Ely. iso 09	JQ914601	JQ914630		JQ914646
Runcinacea	Runcinidae	*Runcina africana*	Tenerife, Canary Islands	BMNH 20030791/1	DQ974680	yes	DQ927240	yes
Runcinacea	Runcinidae	*Runcina divae*	FR.Ber	ZMBN 82997	yes	yes	yes	yes
Pteropoda	Cavoliniidae	*Clio pyramidata*	Canary Islands		DQ238000		DQ237986	EF133477
Pteropoda	Cavoliniidae	*Creseis* sp.	?	Creseis sp. GG-2005	DQ280021		DQ279989	DQ280012

Pteropoda	Pneumodermatidae	*Spongiobranchaea australis*	Scotia Arc		DQ238002		DQ237988	
Pteropoda	Pneumodermatidae	*Pneumoderma* cf. *Atlantica*	At.USA		DQ238003		DQ237989	EF133478
Acteonoidea	Acteonidae	*Acteon* sp.	Panglao, Philippines	MNHN 42253	DQ974648	yes	DQ927213	yes
Acteonoidea	Acteonidae	*Pupa solidula*	Dingo Beach, Australia		DQ238006	EF489319	AY427481	EF133483
Acteonoidea	Aplustridae	*Hydatina physis*	Madagascar	BMNH 20060098	DQ986572	DQ986637	DQ986699	
Acteonoidea	Aplustridae	*Hydatina physis*	Madagascar		DQ974651			yes
Acteonoidea	Aplustridae	*Micromelo undatus*	Tenerife, Canary Islands	BMNH 20030800	DQ974653	yes	DQ927214	yes
Umbraculoidea	Tylodinidae	*Tylodina perversa*	Canary Islands		yes	yes	yes	yes
Umbraculoidea	Umbraculidae	*Umbraculum* sp.	?	EED-Phy-661	GU213058	GU213044	GU213053	
Nudipleura	Pleurobranachidae	*Berthella martenis*	Panama, Las Secas, Islas sin nombre	MZUCR6982	HM162683	HM162592		HM162498
Nudipleura	Pleurobranachidae	*Berthella medietas*	Vic.Aus		FJ917491	FJ917433	FJ917473	
Nudipleura	Pleurobranachidae	*Berthellina edwardsi*	Cape Verde		yes		yes	yes
Nudipleura	Pleurobranachidae	*Pleurobranchus membranaceus*	Mediterranean France		FJ917496	FJ917437	FJ917478	
Nudipleura	Chromodorididae	*Hypseldoris picta*	Sennegal		yes	yes	?	yes
Nudipleura	Cadlinidae	*Aldisa smaragdina*	Canary Islands		yes	yes	yes	yes
Acochlida	Acochlidiidae	*Acochlidium fijiense*	?		HQ168458	HQ168420	HQ168446	
Acochlida	Acochlidiidae	*Strubellia paradoxa*	?		HQ168457	HQ168419	HQ168445	
L.Heterobranchia	Pyramidellidae	*Turbonilla* sp.	New Zealand	EED-Phy-572	FJ917276	FJ917257	FJ917236	EF133489
L.Heterobranchia	Pyramidellidae	*Eulimella ventricosa*	Gnejna Bay, Malta.	EED-Phy-5	FJ917274	FJ917255	FJ917235	
Caenogastropda	Litorinidae	*Littorina littorea*		MCZ DNA101389	DQ093525	DQ093481	FJ977692	DQ093507

3.2 Species identification and literature

Species were identified by comparison with original descriptions and general and regional publications about Philinidae. Difficult cases benefited from discussions with renowned malacologists like Terrence Gosliner and Ángel Valdés.

3.3 Anatomical work and scanning electron microscopy (SEM)

All specimens were preserved in ethanol rendering them useful for morphological and molecular analysis. Because of high level of convergence within the Philinidae, classification based on external features is difficult. Therefore, a preliminary sorting of specimens was done to group them in preliminary morpho-species and COI neighbour joining trees (barcoding tree) were inferred (see heading 3.4 for methodology) to test the preliminary morphological grouping and aid selecting specimens for anatomical study.

Whole specimens and intact shells were imaged by macrophotography. Morphological characters (e.g. radula, male reproductive system, gizzard plates) have been examined through fine dissection work using a dissecting microscope equipped with *camera lucida*. The male reproductive system was removed and drawn for comparison between specimens, penial papilla was critically point dried and investigated by SEM. The buccal bulb was extracted and dissolved with 10% commercial bleach to clean the radula. Gizzards were cut from the digestive tract, opened, plates removed and cleaned lightly with bleach until surrounding tissue could be removed. Radulae, gizzard plates, penial papillae and shell fragments were mounted for scanning electron microscopy (SEM) on metallic stubs and coated with gold-paladium. The anatomical work was done at the Invertebrate Collections Lab, Natural History Collections at the University Museum of Bergen, while SEMs were prepared and captured at the Laboratory for Electron Microscopy at the University of Bergen.

3.3.1 DNA extraction, amplification, and sequencing

DNA was extracted using the Qiagen DNeasy® Blood and Tissue Kit following the protocol recommended by the manufacturer. Clips of tissue of about 1-2 mm^2 were cut from mainly the foot or parapodial lobes for DNA extraction. Partial sequences of the mitochondrial genes cytochrome *c* oxidase subunit I (COI) and 16S rRNA and nuclear gens Histone-3 (H3) and 28S rRNA were amplified (see Table 3.2 for primers). Amplification was done through polymerase chain reaction (PCR) in a 50-μL final volume using Qiagen Taq DNA Polymerase (1000 U) (Cat.number: 201205). For markers that were more difficult to amplify, 25 μL reactions were run with TaKaRa Ex Taq Polymerase HS (250 U) (Cat. number: RR006A). All molecular work was conducted at the Biodiversity Laboratories, University of Bergen.

Protocol 1 (used for Qiagen Taq):

PCR reaction volumes were 50 μl. For COI and 16S rRNA the total volume consisted of 17.5 μl sigma water, 5 μl CoraLLoad buffer, 5 μl dNTP, 10 l Q-solution, 7 μl MgCl, 2 μl of each of the primers, 0.5 μl TAQ and 1 μl DNA. For H3 only 4 μl of MgCl was required and the volume of sigma water was adjusted to 20.5 2 μl. For 28S rRNA only 2 μl of MgCl was required and the volume of sigma water was adjusted to 22.5 μl.

Annealing temperature for COI was 45°C, for 16S was 51.5°C, for 28S was 52°C, and for H3 was 50°C.. The initial denaturation was achieved with 95 °C for 3 min followed by 39 cycles with denaturation at 94 °C for 45 s, annealing at a gene specific temperature for 45 s and extension at 72 °C for 2 min. Final extension was achieved at 72 °C for 10 min.

Protocol 2 (used for TaKaRa Taq):

For all gene markers the total reaction volume was 25 μl. The total volume consisted of 17.35 μl sigma water, 2.5 μl buffer, 2 μl dNTP, 1 μl of each primer, 0.15 μl TaKaRa Taq and 1 μl DNA.

A standard Barcode protocol was used for or all markers. Annealing temperature were the same as in Protocol 1. A hot start step was included with 94°C for 5 min, with 5 repetitions of initial denaturation at 94°C for 45s, initial annealing at 45°C for 30s and extension at 72°C for 1min, followed by 30 repetitions of denaturation at 94°C for 45 s, gene specific annealing temperature for 30s, extension at 72 °C for 1min and one final extension at 72°C for 10min.

Notes: For the most difficult samples an alternative method was tested, where successful PCRs were achieved by utilising TaKaRa Taq together with 5 μl of Qiagen Q solv, and Protocol 1 with a hot start step. Additionally, a time saving step included using 2.5 μl Qiagen coraLLoad with 1 µl MgCl instead of the TaKaRa buffer (which contains MgCl), was equally successful in all TaKaRa reactions.

All runs were preformed on Bio-Rad S2000 or Bio-Rad C1000 thermal cyclers with equal success rate. Each run included one positive and one negative control to test for contamination. DNA quantification and assessment of PCR product quality was done by gel-electrophoresis imaging. Depending on the final reaction volume of the PCR product, 3 (25 µl reactions) or 4 µl (50 µl reactions) was used in imaging. The PCR product was mixed with 1 µl loading buffer or used directly when Qiagen CoraLLoad buffer have been used in the PCR reactions. Additionally, 5 µl pGEM marker (Promega, Madison, WI, USA) was used to quantify and estimate the length of DNA fragments. Gels were 1.2 % agarose based on 0.5x TAE buffer with the staining agent GelRed (Biotium, Hayward, CA, USA). The gels were consistently run at 90V for 30 minutes and analysed in an UV-light chamber, the images were taken by GeneSnap (SynGene) and quantified by Manual Band Quantification in GeneTools (SynGene).

Table 3.2 Primers used for gene amplification and sequencing

Name	Sequence 5´- 3´	Source
COI		
LCO1490 (F)	GGTCAACAAATCATAAAGATATTGG	(Folmer et al., 1994)
HCO2198 (R)	TAAACTTCAGGGTGACCAAAAAATCA	(Folmer et al., 1994)
16S		
16S ar-L	CGCCTGTTTATCAAAAACAT	(Palumbi et al., 1991)
16S br-H	CCGGTCTGAACTCAGATCACGT	(Palumbi et al., 1991)
28S		
LSU5-F	TAGGTCGACCCGCTGAAYTTAAGCA	(Littlewood et al., 2000)
900-F	CCGTCTTGAAACACGGACCAAG	(Olson et al., 2003)
LSU1600-R	AGCGCCATCCATTTTCAGG	(Williams et al., 2003)
ECD2S-R	CTTGGTCCGTGTTTCAAGACGG	Modified from Littlewood *et al.* (2000)
Histone-3		
H3AD5’3’ (F)	ATG-GCT-CGT-ACC-AAG-CAG-ACV-GC	(Colgan et al., 1998)
H3BD5’3’ (R)	ATA-TCC-TTR-GGC-ATR-ATR-GTG-AC	(Colgan et al., 1998)

3.3.2 Purification and Sequencing

Purification of PCR product followed standard EXO-SAP method, using Exonuclease I (10 units/µl, product nr:70073z) and Shrimp Alkaline Phosphatase (1 unit/µl, product nr:70092z) produced by USB corporation, Cleveland, Ohio, USA (Affymetrix). Purification was run on Eppendorf Mastercycler ProS, with an incubation step at 37 ° C for 30 min and an enzyme inactivation step at 80 ° C for 15 min.

For the majority of the samples sequencing was performed by Macrogen Inc. on 10 µl purified reactions (Macrogen Europe, Amsterdam, the Netherlands). Few samples were sequenced using the University of Bergen sequencing facility following a Big Dye v. 3.1 enzyme purification protcoll. The total reaction volume consisted of: 10 µl reaction solution consisting of 10 ng purified PCR product, 1 µl BD, 1 µl 3.2 µmol foward primer, 1 µl 3.2 µmol reverse primer, 1 µl sequencing buffer and sigma water was added to get the total 10 µl solution. The reactions were run on a PCR thermal cycler, Using acycling protocol with a first step of 5 min at 96° C, followed by 25 cycles at 96° C for 10 seconds, 50° C for 5 seconds and 60° C for 4 minutes. Finished reaction was added 10 µl of ionized sigma water before delivery to the local sequencing laboratory. The sequencing reactions were run on ABI 3730XL DNA Analyzer (Applied Biosystems) at both facilities.

3.4 Molecular phylogenetic analysis

3.4.1 Sequences assembly and alignment

Initially Sequencher (version 4.10.1, Gene Codes Corp.) and later Geneious (version 6.1.4 Biomatters Ltd.) were used to assemble the chromatograms of the forward and reverse DNA strands, to assess the quality of the sequences and to edit the sequences. All sequences were meticulously revised and edited, and later blasted in Genbank (BLAST – National Library of Medicine, The National Center for Biotechnology) to check for contamination. Contigs of single genes and concatenated multiple genes were aligned with Muscle (Edgar, 2004a; 2004b) implemented in Geneious. Alignments were trimmed at both ends to a position where at least 50% of the sequences had data and remaining gaps were filled with missing data (N). Alignments are available from the author and will be made available through TreeBase after the results are formally published.

Saturation was tested for the first, second, and third codon positions of the protein coding genes COI and H3 using MEGA5 (Tamura et al., 2011). The non protein coding gene markers 16S rRNA and 28S rRNA were masked with Gblocks 0.91b (Castresana, 2000), to exclude regions full of gaps or overtly divergent regions, as this may diffuse the phylogenetic information (Castresana, 2000). Alignments of both gene markers were subjected to stringent and relaxed parameters.

Parameters used for a stringent masking: Minimum number of sequences for a conserved position: 50% of all sequences + 1. Minimum number of sequences for a flanking position: 85% of all sequences. Maximum number of contiguous non-conserved positions: 12. Minimum length of a block: for 16S: 5, for 28S: 2 (as there was many short blocks separated by gaps). Allowed gap positions: With half. For 16S rRNA 335 bp remained for the analysis (56% of the original 598 positions). For 28S rRNA 855 bp remained for the analysis (56% of the original 1506 positions).

Parameters used for a relaxed masking: Minimum number of sequences for a conserved position: 50% of all sequences + 1. Minimum number of sequences for a flanking position: 85% of all sequences. Maximum number of contiguous non-conserved positions: 12. Minimum length of a block: 5 (No need for less as all gaps allowed). Allowed gap positions: All. For 16S rRNA 469 bp remained for the analysis (92% of the original 506 positions). For 28S rRNA 1116 bp remained for the analysis (94% of the original 1178 positions). **Note:** The reduced number of positions in the relaxed datasets compared to the stringent is due to the datasets being realigned and re-trimmed after removing problematic sequences, after the initial masking. As the initial masking showed that the relaxed settings were the best settings for the datasets, the new alignments were rerun in Gblocks under the same parameters as the initial masking.

3.4.2 Phylogenetic analyses

JModeltest (Darriba et al., 2012) was used to find the best-fit models for the optimal single gene datasets under the Akaike information criterion (Akaike, 1974).

Table 3.3 Best-fit models for optimal datasets calculated in JModeltest under the Akaike criterion.

Parameters	COI	16S rRNA	28S rRNA	Histone 3
Dataset	3rd codon included	Relaxed masking	Relaxed masking	3rd codon included
No. of specimens used in this study	160	168	145	133
No. of included characters	644	469	1116	330
Best-fit modell	TVM+I+G	GTR+I+G	GTR+I+G	TVM+I+G

Frequency A	0.4976	0.3724	0.1465	0.2116
Frequency C	0.1137	0.0973	0.3225	0.3892
Frequency G	0.1122	0.1532	0.3541	0.1789
Frequency T	0.2765	0.3771	0.1769	0.2203
Γ shape (G)	0.3540	0.4770	0.5960	0.9840
Proportion of invariant sites (I)	0.3210	0.2260	0.2550	0.5330
R-matrix [A–C]	6.2048	1.0960	0.6708	1.8747
R-matrix [A–G]	74.7204	5.2805	1.7750	5.3739
R-matrix [A–T]	4.5018	2.2867	1.7551	2.2576
R-matrix [C–G]	13.8178	0.4358	0.3803	1.4908
R-matrix [C–T]	74.7204	7.6525	4.9105	5.3739
R-matrix [G–T]	1.0000	1.0000	1.0000	1.0000

The phylogenetic relationships of the Cephalaspidea families were inferred by Bayesian analysis. Eight initial individual gene analyses were preformed: COI, COI (3rd codon excluded), 16S Gblocks strict masking, 16S Gblocks relaxed masking, 28S Gblocks strict masking, 28S Gblocks relaxed masking, H3, and H3 (3rd codon excluded). The resulting trees were inspected by eye and the four trees with better resolved topolologies and best node support were chosen as optimal datasets for further analyses. COI and H3 with 3rd codon included and 16S and 28S with relaxed masking gave the best results and were implemented in concatenated datasets. The COI yied 160 sequences, the 16S rRNA yield 168 the 28S rRNA yield 145 and the Histone 3 yield 133 sequences. Three concatenated datasets were analysed: combined mitochondrial genes COI + 16S rRNA (174 sequences), combined nuclear genes 28S rRNA + H3 (164 sequences), and all gene markers combined (175 sequences).

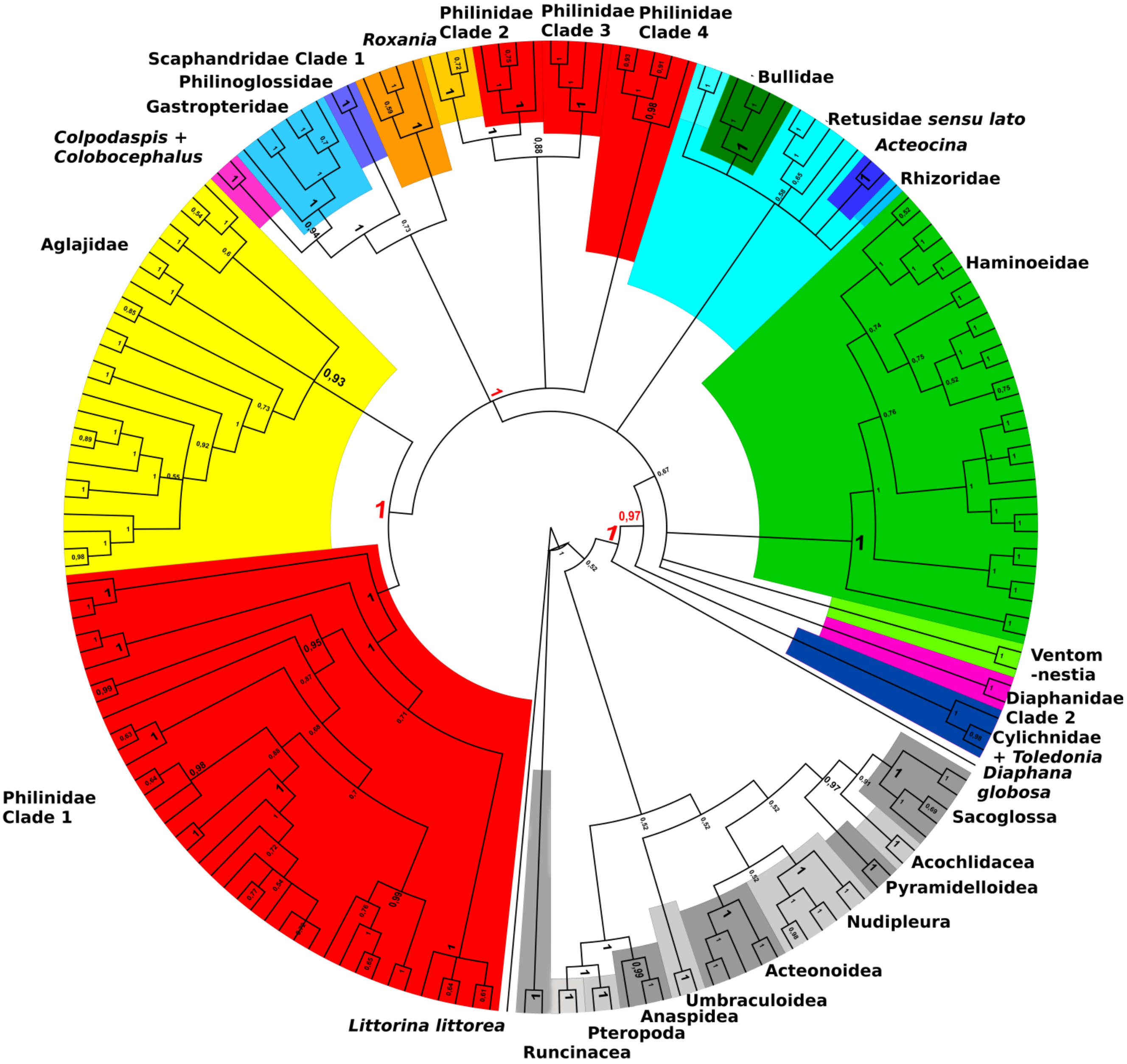
All datasets were analysed with MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) using 3 parallel runs of 15 million generations for single gene analyses and 25 million generations for concatenated datasets, with sampling every 100 generations. Concatenated datasets were partitioned by gene and each partition was run under the best fit model. Convergence of runs was inspected using Tracer v1.5 (Rambaut and Drummond 2007) with a burn-in set to 25%. Consensus phylograms were created in MrBayes, and FigTree v1.3.1 (Morariu et al., 2008) was used to create graphic representations of the trees and annotate them. The majority of the Bayesian analysis were run through the Bioportal and Lifeportal data clusters based at the University of Oslo (Kumar et al., 2009; Bioportal, 2013).

4. Results

4.1 Phylogeny of Cephalaspidea

4.1.1 Monophyly of Cephalaspidea

The monophyly of Cephalaspidea received maximum support in the Bayesian analysis of all genes combined (PP = 1; Tree 4.1), with *Diaphana globosa* sister to a monophyletic clade with the remaining Cephalaspidea (PP = 0. 97, Tree 4.1).

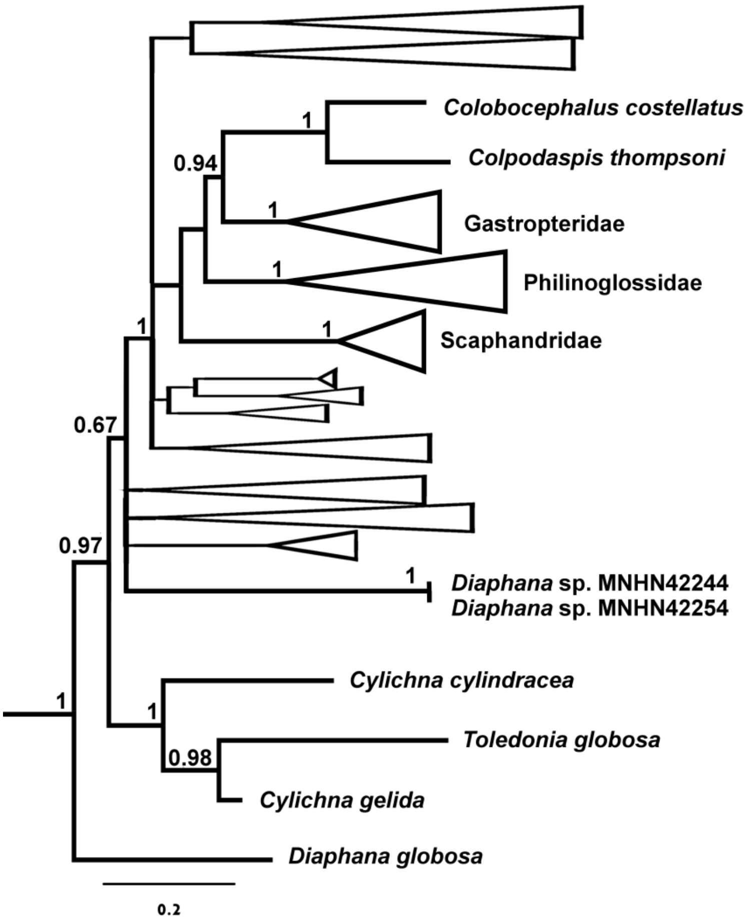


Tree 4.1 Bayesian phylogeny of the Cephalaspidea based on the combined analysis of the mitochondrial COI and 16S rRNA and nuclear 28S rRNA and Histone-3 genes. Figures on nodes are posterior probabilities. Coloured clades refer to Cephalaspidea families/groups; Grey clades refer to outgroups taxa used in the analysis. The tree was rooted with the Caenogastropod species *Littorina littorea*.

None of the single gene analyses supported the monophyly of Cephalaspidea. In the 16S rRNA and 28S rRNA all cephalaspidean taxa clustered together but with low support (16S, PP = 0.72; Tree 7.1.2 and 28S, PP= 0.87; Tree 7.2.1). While in the COI analysis the majority of Cephalaspidea taxa clustered together with maximum support (PP = 1; Fig. 7.1.1), however taxa like *Cylichna cylindracea* clustered with the Acteonoidea (PP = 0.94), and *Toledonia globosa* and *Diaphana globosa* were rendered sister to the Umbraculoidea (PP = 0.93). In the combined analysis of the nuclear genes 28S and H3, the Cephalaspidea was rendered paraphyletic (Tree 7.4) because *Elysia timida* (only H3) clustered with Bullidae (PP = 0.87). In the combined analysis of the mitochondrial genes COI and 16S the Cephalaspidea was found polyphyletic, the majority formed a marginally supported clade (PP = 0.93; Tree 7.3), however *Diaphana globosa*, *Toledonia globosa*, *Cylichna gelida* and *C. cylindracea* clustered basally in unsupported sister relationships to clade containing the Cephalaspidea and the majority of the outgroups.

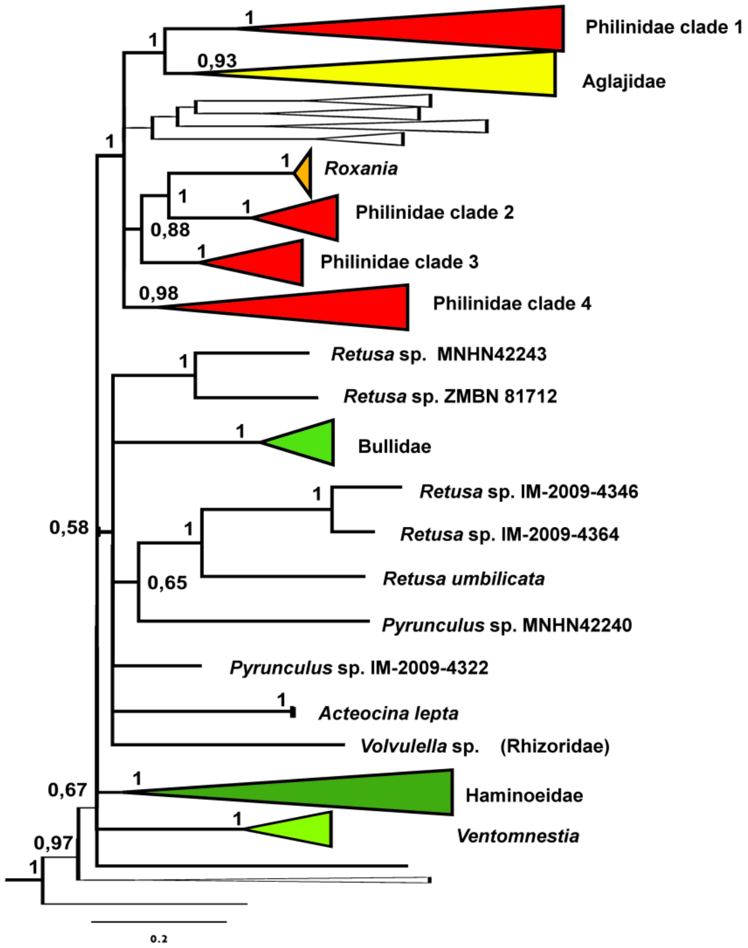
4.1.2 Family level phylogeny of Cephalaspidea

In the Bayesian analysis of all genes combined the family Diaphanidae in part (represented by *Diaphana globosa*) was the most basal branch. Cylichnidae in part (with representatives of the genus *Cylichna* and the “diaphanid” *Toledonia*) was retrieved basally within the Cephalaspidea and formed a clade with high support (PP = 1; Tree 4.2) but *Acteocina* (a traditional member of the Cylichnidae) branched off elsewhere in the tree. This was also found in the 16S single gene analysis albeit with low support (PP = 0.61). *Toledonia globosa* and *Cylichna gelida* were retrived as sister lineages with high support (PP = 0.98; Tree 4.2). This was also the case for the 16S (PP= 1; Tree 7.1.2), 28S (PP= 1; Tree 7.2.1) and combined COI + 16S (PP= 1; Tree 6.3) gene analyses. Scaphandridae (with *Scaphander*) and *Roxania* (taxa traditionally ascribed to the Cylichnidae) never clustered with Cylichnidae.



Tree 4.2 Part of tree depicted in figure Tree 4.1: Cylichnidae & Diaphanidae *sensu lato*

Diaphanidae was found to be polyphyletic in all analyses with *Diaphana*, *Toledonia*, *Colpodaspis* + *Colobocephalus* branching in different parts of the tree (Tree 4.2). The genus *Diaphana* was also rendered polyphyletic with West Pacific and Atlantic species branching in different parts of the tree (Tree 4.2). In the COI analysis *D. globosa* was retrieved sister to *Toledonia globosa* (PP = 1; Tree 7.1.1) but outside the main cluster of Cephalaspidea species, and *Cylichna cylindracea* clustered with Acteonoidea (PP = 0.94). The group with *Colpodaspis* + *Colobocephalus* was monophyletic in nearly all analyses (e.g. 16S, COI +16S, 28S, 28S + H3, and all genes combined) with maximum support (PP = 1; Tree 4.2) and was nearly supported in the H3 analysis (PP = 0.86; Tree 7.2.2). This clade was rendered sister to Gastropteridae in the combined analysis with marginal support (PP = 0. 94; Tree 4.2) and with maximum support in COI + 16S (PP = 0.99; Tree 7.3). However, the clade consisting of Gastropteridae + *Colpodaspis* + *Colobocephalus* was sister to Philinoglossidae with maximum support in the all genes analysis (PP = 1; Tree 4.2), and 28S analysis. (PP = 1; Tree 7.2.1)



Tree 4.3 Part of tree depicted in figure Tree 4.1: Philinidae *s. l.*, Bullidae, Retusidae *s. l.* and Haminoeidae

Haminoeidae was found monophyletic (PP = 1; Tree 4.3) and the genus *Ventomnestia* branched separated from other Haminoeidae species. The monophyly of Haminoeidae was also supported in the 28S analysis however with low support for the inclusion of *Bullacta* (28S; PP = 0.75, Tree 7.2.1) but the remaining Haminoeidae received maximum support (PP = 1). In the 28S + H3 analysis Haminoeidae was not monophyletic as *Bullacta* clustered elsewhere in the tree, but the remaining Haminoeidae (excluding *Ventomnestia*) was resolved as monophyletic (PP = 1; Tree 7.4).

Philinidae was found to be polyphyletic with species clustering in four different clades. The Philinidae s*ensu stricto* (Clade 1; Tree 4.3), received maximum support in the all genes combined analysis, 28S analyses and COI + 16S (albeit with lower support (PP = 0.84: Tree 6.3)) and was sister to the monophyletic Aglajidae with maximum support (PP = 1) in the combined analysis of all genes, 28S analysis (All genes: Tree 4.3; 28S: Tree 7.2.1) and marginal support in 28S + H3 (PP = 0.94; Tree 7.4). The family Aglajidae itself was monophyletic and marginally supported in the all genes combined analysis and 28S (All genes: PP = 0.93; Tree 4.3; 28S: PP = 0.94; Tree 7.2.1) and lower support in the 28S + H3 analysis (PP = 0.88; Tree 7.4). In the 16S analysis the Aglajidae was not monophyletic as one sequence of *Odontoglaja guamensis* did not cluster within Aglajidae, however the remaining members were supported (PP = 0.98; Tree 7.1.2) . Philinidae Clade 2 includes species that share a large muscular buccal bulb, a radula with powerful broad inner lateral teeth, a reduced gizzard with small chitinous gizzard plates, the male reproductive system is usually small, the prostate is short and tubular, and the conical penial atrium is always imbedded in the body tissue and not free in the body cavity and a flat, round and disc-like internal shell with spiral striae in the form solid sunken lines or no striae. This clade received maximum support in all single gene and all combined gene analyses, and was sister to a clade containing all species of the genus *Roxania* (PP = 1; Tree 4.3). This sister relationship was also recovered in the COI, and COI + 16S analyses with maximum support (PP = 1; COI: Tree 6.5.1 , COI + 16S: Tree 6.3) and with marginal support in 28S (PP = 0.94; Tree 7.2.1). In the 28S + H3 analysis this clade was found as sister to Haminoeidae with high support (PP = 0.97; Tree 7.4) Philinidae Clade 3 (PP = 1; Tree 4.3) includes species which share a thick, solid shell with chain-like spiral striae, a large prominent crop is usually present, the gizzard is reduced, but the chitinous gizzard plates are large compared to the foregut, the radula and buccal bulb may be reduced but when present have prominent muscles and a powerful radula with prominent cusps and robust denticles, a reduced rachidian tooth is usually present, the male reproductive system is simple and contained within the body cavity. . This clade received maximum support in all genes combined, 16S, 28S, 28S + H3 and COI +16S analyses (PP = 0.98-1; Combined: Tree 4.3, 16S: Tree 7.5.2, 28S: Tree 7.2.1, 28S + H3: Tree 7.4, COI + 16S: Tree 7.2.2) and lower support in the COI gene analysis (PP= 0.82; Tree 6.5.1) and H3 gene analysis (PP = 0.89; Tree 7.2.2). In the all genes combined analysis Philinidae Clade 3 was nearly supported as sister to the Philinidae Clade 2 + Roxania (PP = 0.88; Tree 4.3) In the 16S analysis Philinidae Clade 3 was found as sister to Philinidae Clade

2 with maximum support (PP = 1; Tree 7.5.2) and Philinidae Clade 4 as sister to this clade (PP = 0.99) .In the COI gene analysis the Philinoglossidae *Pluscula* was sister to the Philinidae Clade 3 with low support (PP = 0.56; Tree 6.5.1) . In the 28s + H3 analysis Philinidae Clade 3 was retrieved as sister to two members of *Roxania* with low support (PP = 0.78; Tree 7.4) A last clade (Philinidae Clade 4; PP = 0.98; Tree 4.3) includes Atlantic philinids with thicker, globose, internal shells, robust radula, and no gizzard plates, these species were recently revised by Ohnheiser and Malaquias (2013), and have a complicated taxonomic history including the erection of genera like *Laona.* This clade was found monophyletic in the combined gene analysis (PP = 0.98) and 28S (PP = 1; Tree 7.2.1) 16S (PP = 0.82; Tree 7.5.2) however in the COI, COI + 16S, 28S + H3 and H3 gene analysis only the species excluding *Philine quadrata* were found monophyletic with high support (PP = 1; COI: Tree 6.5.1, COI + 16S; Tree 6.3, 28S + H3; Tree 7.4, H3; Tree 7.2.2) *P. quadrata* was usually found in a poorly supported basal position or clustered elsewhere in the tree.

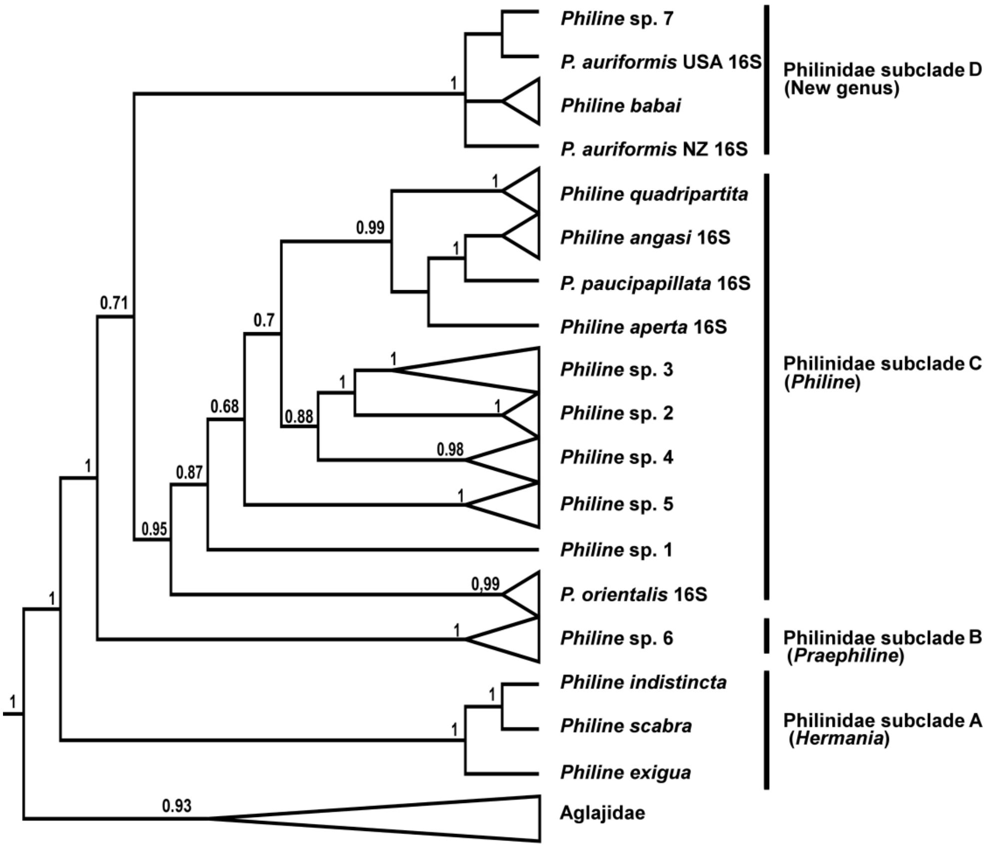
In the combined analysis of all genes Philinoglossidae, Gastropteridae and Diaphanidae clade 1 formed a well supported clade (PP = 1; Tree 4.3) with Scaphandridae in a less supported (PP = 0.73) sister relationship to this clade. Philinoglossidae was rendered monophyletic with maximum support in the analysis of all genes combined (PP = 1; Tree 4.1), , and lower support in the 28S (PP = 0.85; Tree 7.2.1) COI + 16S (PP = 0.71; Tree 6.3) and H3 (PP = 0.68; Tree 7.2.2) analyses. In the all genes combined analysis Philinoglossidae was retrieved as sister to a clade consisting of Gastropteridae and Diaphanidae Clade 1 with maximum support (PP = 1; Tree 4.3) and with lower support in 28S (PP = 0.77; Tree 7.2.1). In the combined analysis of 28S + H3 Philinoglossidae was found as sister to Gastropteridae with marginal support (PP= 0.9; Tree 7.4). Gastropteridae was monophyletic with maximum support in the all genes combined analysis, H3, 28S, 28S + H3 and COI +16S analyses (PP = 0.99-1; H3; Tree 7.2.2, 28S; Tree 7.2.1, 28S + H3: Tree 7.4, COI+16S: Tree), and with lower support in COI (PP = 0.93; Tree 6.5.1). In the all genes combined analysis the Gastropteridae was resolved as sister to Diaphanidae clade 1 with marginal support (PP = 0.94; Tree) in the COI analysis the Gastropteridae clustered with a non monophyletic Diaphanidae clade 1 with maximum support (PP = 1; Tree 7.1.1). Scaphandridae, with *Scaphander* and *Roxania*, was found to be polyphyletic since the latter two genera did not clustered together in any analyses. *Scaphander* was monophyletic with maximum support in all analyses and *Roxania* was monophyletic with maximum support in all analyses but the 16S and H3.

Retusidae was found to be polyphyletic as the species did not cluster together but instead in four different branches; two containing species of "*Retusa*" (both PP = 1; Tree 4.3) plus two independent lineages of *Pyrunculus* (Tree 4.3). Retusidae was not monophyletic in any of the analyses, but formed a clade with high support in COI (PP = 1; Tree 6.5.1) and COI + 16S (PP = 0.98; Tree 6.3) together with Bullidae, Rhizoridae and Cylichnidae *Acteocina*. Bullidae was rendered monophyletic with maximum support in the combined analysis of all genes (PP = 1; Tree 4.3) and in the COI, COI + 16S and 28S (PP = 0.99-1; COI; Tree, COI + 16S; Tree 6.3, 28S; Tree 7.2.1) in all analyses and with varying support in remaining analyses, (16S: PP = 0.97; Tree 7.1.2, 28 + H3: PP = 0.93; Tree 7.4 and H3: PP = 0.63; Tree 7.2.2).

The Rhizoridae was represented by a single species *Volvulella*, and therefore, its monophyly could not be tested.

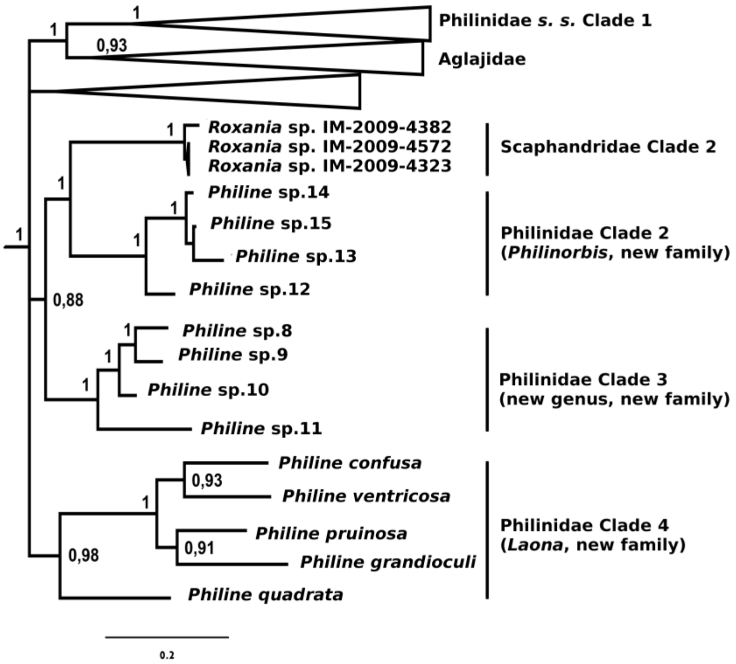
4.1.3 Relationships in the Philinidae *sensu lato* clades

Four sub-clades can be recognized within Philinidae Clade 1; these sub-clades can be differentiated by differences in the gizzard plates, male reproductive system, and shells (see Results section 4.1.4 and Discussion) as well as genetically.



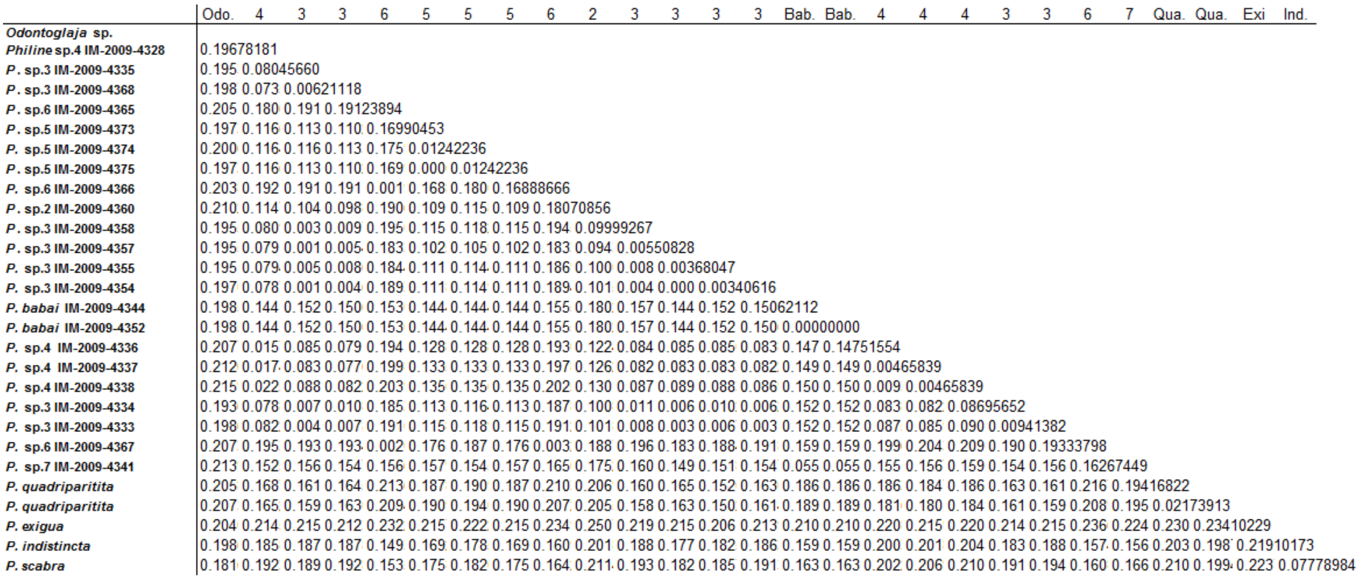
Tree 4.4 Part of tree depicted in figure Tree 4.2 represented as a cladogram: Philinidae *s. s.*. Species labelled with “16S” refer to samples where only characters from the 16S rRNA gene marker were available.

Minimum and maximum COI *p*-distance between clades is 14.9% and 25%, respectively. Sub-clade A (PP = 1) includes the species *Philine exigua*, *P. indistincta* and *P. scabra*. In this sub-clade COI *p*-distances vary 7.8%–21.9% between species. Sub-clade B with the single species *Philine* sp. 6, which is morphologically similar to the Atlantic species *P. finmarchica* (not included in the analyses; Ohnheiser and Malaquias, 2013). Sub-clade C (PP = 0.95), the *Philine sensu stricto* with the type species *P. aperta*. In this sub-clade COI *p*-distances vary between 0–2.2% within species and 7.3%–20.6% between species. And sub-clade D (PP = 1) with species *P. aurifromis*, *Philine babai*, and *Philine* sp.7. *Philine auriformis* from USA and New Zealand did not clustered together, which may indicate a case of misidentification. For these two samples only 16S data was available and they were both retrieved from GenBank. In sub-clade D, COI *p*-distances vary between 0%–0.3% within species and 5.5% between the species *P. babai* and *P.* sp. 7



Tree 4.5 Part of tree depicted in figure Tree 4.2: Philinidae *s. l.* clades 2, 3, and 4.

Philinidae clade 2-4 consists of species with only one representative each, Philinidae clade 2 (PP = 1) consist of *Philine* sp. 12-15, this clade had low success rate in amplification of COI gene marker (only two) thus p-distance estimates of 16S rRNA was used, 16S rRNA *p*-distances vary 1.9%–4.7% between species, which is congruent with the distance between separate species of *Scaphander* (1%-5%) analyzed in Eilertsen and Malaquias (2013). Philinidae clade 3 (PP = 1) consist of *Philine* sp. 8-11 COI *p*-distances vary 13.9%–22% between species. The separation of the species in Philinidae clade 4 (PP = 0.98) has been defined previously in Ohnheiser and Malaquias (2013), COI *p*-distances vary 19.5%–24.3% between species.



	Odo.	4	3	3	6	5	5	5	6	2	3	3	3	Bab.	Bab.	4	4	4	3	3	6	7	Qua.	Qua.	Exi	Ind.	
***Odontoglaja* sp.**																											
***Philine* sp.4 IM-2009-4328**	0.19678181																										
***P*. sp.3 IM-2009-4335**	0.195	0.08045660																									
***P*. sp.3 IM-2009-4368**	0.198	0.073	0.00621118																								
***P*. sp.6 IM-2009-4365**	0.205	0.180	0.191	0.19123894																							
***P*. sp.5 IM-2009-4373**	0.197	0.116	0.113	0.110	0.16990453																						
***P*. sp.5 IM-2009-4374**	0.200	0.116	0.116	0.113	0.175	0.01242236																					
***P*. sp.5 IM-2009-4375**	0.197	0.116	0.113	0.110	0.169	0.000	0.01242236																				
***P*. sp.6 IM-2009-4366**	0.203	0.192	0.191	0.191	0.001	0.168	0.180	0.16888666																			
***P*. sp.2 IM-2009-4360**	0.210	0.114	0.104	0.098	0.190	0.109	0.115	0.109	0.18070856																		
***P*. sp.3 IM-2009-4358**	0.195	0.080	0.003	0.009	0.195	0.115	0.118	0.115	0.194	0.09999267																	
***P*. sp.3 IM-2009-4357**	0.195	0.079	0.001	0.005	0.183	0.102	0.105	0.102	0.183	0.094	0.00550828																
***P*. sp.3 IM-2009-4355**	0.195	0.079	0.005	0.008	0.184	0.111	0.114	0.111	0.186	0.100	0.008	0.00368047															
***P*. sp.3 IM-2009-4354**	0.197	0.078	0.001	0.004	0.189	0.111	0.114	0.111	0.189	0.101	0.004	0.000	0.00340616														
***P. babai* IM-2009-4344**	0.198	0.144	0.152	0.150	0.153	0.144	0.144	0.144	0.155	0.180	0.157	0.144	0.152	0.15062112													
***P. babai* IM-2009-4352**	0.198	0.144	0.152	0.150	0.153	0.144	0.144	0.144	0.155	0.180	0.157	0.144	0.152	0.150	0.00000000												
***P*. sp.4 IM-2009-4336**	0.207	0.015	0.085	0.079	0.194	0.128	0.128	0.128	0.193	0.122	0.084	0.085	0.085	0.083	0.147	0.14751554											
***P*. sp.4 IM-2009-4337**	0.212	0.017	0.083	0.077	0.199	0.133	0.133	0.133	0.197	0.126	0.082	0.083	0.083	0.082	0.149	0.149	0.00465839										
***P*. sp.4 IM-2009-4338**	0.215	0.022	0.088	0.082	0.203	0.135	0.135	0.135	0.202	0.130	0.087	0.089	0.088	0.086	0.150	0.150	0.009	0.00465839									
***P*. sp.3 IM-2009-4334**	0.193	0.078	0.007	0.010	0.185	0.113	0.116	0.113	0.187	0.100	0.011	0.006	0.010	0.006	0.152	0.152	0.083	0.082	0.08695652								
***P*. sp.3 IM-2009-4333**	0.198	0.082	0.004	0.007	0.191	0.115	0.118	0.115	0.191	0.101	0.008	0.003	0.006	0.003	0.152	0.152	0.087	0.085	0.090	0.00941382							
***P*. sp.6 IM-2009-4367**	0.207	0.195	0.193	0.193	0.002	0.176	0.187	0.176	0.003	0.188	0.196	0.183	0.188	0.191	0.159	0.159	0.199	0.204	0.209	0.190	0.19333798						
***P*. sp.7 IM-2009-4341**	0.213	0.152	0.156	0.154	0.156	0.157	0.154	0.157	0.165	0.175	0.160	0.149	0.151	0.154	0.055	0.055	0.155	0.156	0.159	0.154	0.156	0.16267449					
P. quadriparitita	0.205	0.168	0.161	0.164	0.213	0.187	0.190	0.187	0.210	0.206	0.160	0.165	0.152	0.163	0.186	0.186	0.186	0.184	0.186	0.163	0.161	0.216	0.19416822				
P. quadriparitita	0.207	0.165	0.159	0.163	0.209	0.190	0.194	0.190	0.207	0.205	0.158	0.163	0.150	0.161	0.189	0.189	0.181	0.180	0.184	0.161	0.159	0.208	0.195	0.02173913			
P. exigua	0.204	0.214	0.215	0.212	0.232	0.215	0.222	0.215	0.234	0.250	0.219	0.215	0.206	0.213	0.210	0.210	0.220	0.215	0.220	0.214	0.215	0.236	0.224	0.230	0.23410229		
P. indistincta	0.198	0.185	0.187	0.187	0.149	0.169	0.178	0.169	0.160	0.201	0.188	0.177	0.182	0.186	0.159	0.159	0.200	0.201	0.204	0.183	0.188	0.157	0.156	0.203	0.198	0.21910173	
P. scabra	0.181	0.192	0.189	0.192	0.153	0.175	0.182	0.175	0.164	0.211	0.193	0.182	0.185	0.191	0.163	0.163	0.202	0.206	0.210	0.191	0.194	0.160	0.166	0.210	0.199	0.223	0.07778984

Figure 4.1 *p*-distance matrix for Philinidae clade 1

Clade 2	P. ap.	14	12	15
P. aperta				
***P*. sp. 14**	0,131			
***P*. sp. 12**	0,121	0,047		
***P*. sp. 15**	0,124	0,019	0,047	
***P*. sp. 13**	0,109	0,038	0,047	0,019

Clade 3	11	10	9	8
***P*. sp. 11**				
***P*. sp. 10**	0,187			
***P*. sp. 9**	0,214	0,152		
***P*. sp. 8**	0,22	0,139	0,142	
P. sp. 3	0,271	0,225	0,255	0,257

Figure 4.2 *p*-distance matrix for Philinidae clade 2 and clade 3.

Clade 4	*P.quadri.*	*P. confusa*	*P. grandioculi*	*P. pruinosa*	*P. quadrata*
P. quadripartita					
P. confuse	0,260				
P. grandioculi	0,245	0,237			
P. pruinosa	0,272	0,227	0,238		
P. quadrata	0,262	0,213	0,237	0,219	
P. ventricosa	0,253	0,195	0,232	0,243	0,224

. **Figure 4.4 *p*-distance matrix for Philinidae clade 4.**

4.1.4 Systematic descriptions: the Philinidae *sensu lato*

Abbreviations: H = height, m = meters, spec. = specimens.

Philinidae Clade 1 (Philinidae *sensu stricto*)

Shell, oval to round, internal, transparent, smooth, spiral striae of indentations forming chain-like lines when present. Body white in preserved specimens, cephalic shield oval. Posterior shield extends to shell margin. Rachidian tooth absent, one inner lateral tooth with delicate denticulation along inner edge, outer lateral teeth absent. Salivary glands usually present and only attached in one end. Gizzard muscularised, calcified gizzard plates, gizzard plates usually not covered by muscular fibres on inactive surface, usually two paired plates and one smaller central unpaired gizzard plate, usually large pores or deep indentations on inactive surface of all plates. Usually long, convoluted prostate and species specific penial papillae.

Sub-clade B (*Praephiline)*

Synopsis: Shell, oval to round, internal, transparent, smooth, spiral striae of indentations forming undulating lines. Body white in preserved specimens, cephalic shield oval. Rachidian tooth absent, one inner lateral tooth with delicate denticulation along inner edge, outer lateral teeth absent. Long salivary glands usually present and only attached in proximal end. Gizzard muscularised, three equal spindle shaped gizzard plates, gizzard plates covered by muscular fibres on inactive surface. Long prostate with two distinct parts, posterior part nodulous, anterior part smooth.

PHILINE SP. 6

(FIGS 4.1 A-F, 4.2 A-F)

Diagnosis: Shell oval, internal, transparent, smooth; spiral striae of fused indentations forming undulating lines. Body white (preserves specs.), oval cephalic shield. Rachidian tooth absent, one inner lateral tooth with delicate denticulation along inner edge, outer lateral teeth absent. Long salivary glands, Gizzard surrounded by muscular fibres, three equal spindle shaped gizzard plates. Long prostate with two distinct parts, posterior part nodulous, anterior part smooth, penial atrium with long coiled caecum, bulbous penial atrium, ejaculatory duct coiling at the base of penis.

Barcode: IM-2009-4366: KF877709, IM-2009-4367: KF877692, IM-2009-4365: KF877696.

Material examined: 1 spec. (dissected and sequenced), Philippines, MNHN, Paris IM-2009-4366, H = 15 mm , 1 spec. (sequenced), Philippines, MNHN, Paris IM-2009-4367, H = 19 mm, 1 spec. (dissected and sequenced), Philippines, MNHN, Paris IM-2009-4365, H = 18 mm.

Shell (4.1B): Maximum H = 11 mm. Internal, thin; whitish transparent, oval, slightly obtuse apex, aperture wide. Shell sculpture not visible trough dermis, fused pits forming undulating spiral striae.

Animal (4.1A): Body white in preserved specimens. Cephalic shield oval, widens posteriorly, narrows anteriorly, median groove absent; small muscular parapodial lobes. Shallow posterior notch in posterior lobe. Long salivary glands.

Radula (4.2 A-B): Radular formula 17–18 x 1.0.1 Rachidian tooth absent. Inner lateral teeth with narrow base curved and rounded tips, inner edge delicately denticulate, with long thin dentricles.

Gizzard (4.1C-F): Gizzard elongate cylindrical, surrounded by thick muscular fibres, muscle fibre attachment of gizzard with consistent “zigzag” pattern latero-ventrally, contains three equal gizzard spindle shaped plates, active surface simple and concave, inactive surface with a cylindrical centre with a flattened surrounding rim.

Male reproductive system (4.2 C-E): Long prostate with two distinct parts, nodulous posteriorly, smooth anteriorly; bulbous penial atrium with long coiled blind caecum proximally on penial atrium; smooth prostate splits anteriorly into ejaculatory and incurrent sperm duct; ejaculatory duct longer than incurrent sperm duct; ejaculatory duct coiling within muscular tissue at the base of the penis.

Ecology: Occurs between 1184–1262 m likely on muddy-sand (as sand and mud was found in digestive system).

Distribution: Philippine Sea, east of Lamon Bay and Polillo Island, Philippines (4°59′N–123°15′E).

Remarks: These specimens likely belong to an undescribed species. The gizzard structure and gizzard plates are distinct in comparison to the other species described in this thesis as the elongate equal plates are more similar to those of *Philine finmarchica* Sars 1859 (Ohnheiser and Malaquias (2012), Page 15, Fig. 7 B-E), *P. kerguelensis* Thiele 1925, and *Philine polystrigma* Dall, 1908 (Gosliner (1994) page 305, Fig 38 B, C). The radula of *Philine* sp.6 is more similar to *P. finmarchica* as the teeth are narrower and more delicate than in subclade C and subclade D. *Philine* sp.6 also differ from all other species in Philinidae clade 1 as it has a large distinct penis with pronounced rib-like structures, and a long coiled blind caecum on the apical penial atrium. This species seem to be closely related, to *P. finmarchia*, *P. kerguelensis* and *P. polystrigma* based on internal morphology. However *Philine* sp.6 is the first species of this type recorded in the West Pacific (thus far only the Philippines) as *P. finmarchia* is found throughout the Atlantic (Ohnheiser and Malaquias, 2012), whereas *P. kerguelensis* only known from the Southern Ocean islands the Falklands and Kuergulen (Powell, 1951) and *P. polystrigma* is described form South Coronado Island, California , USA, (Behrens, 2004) .

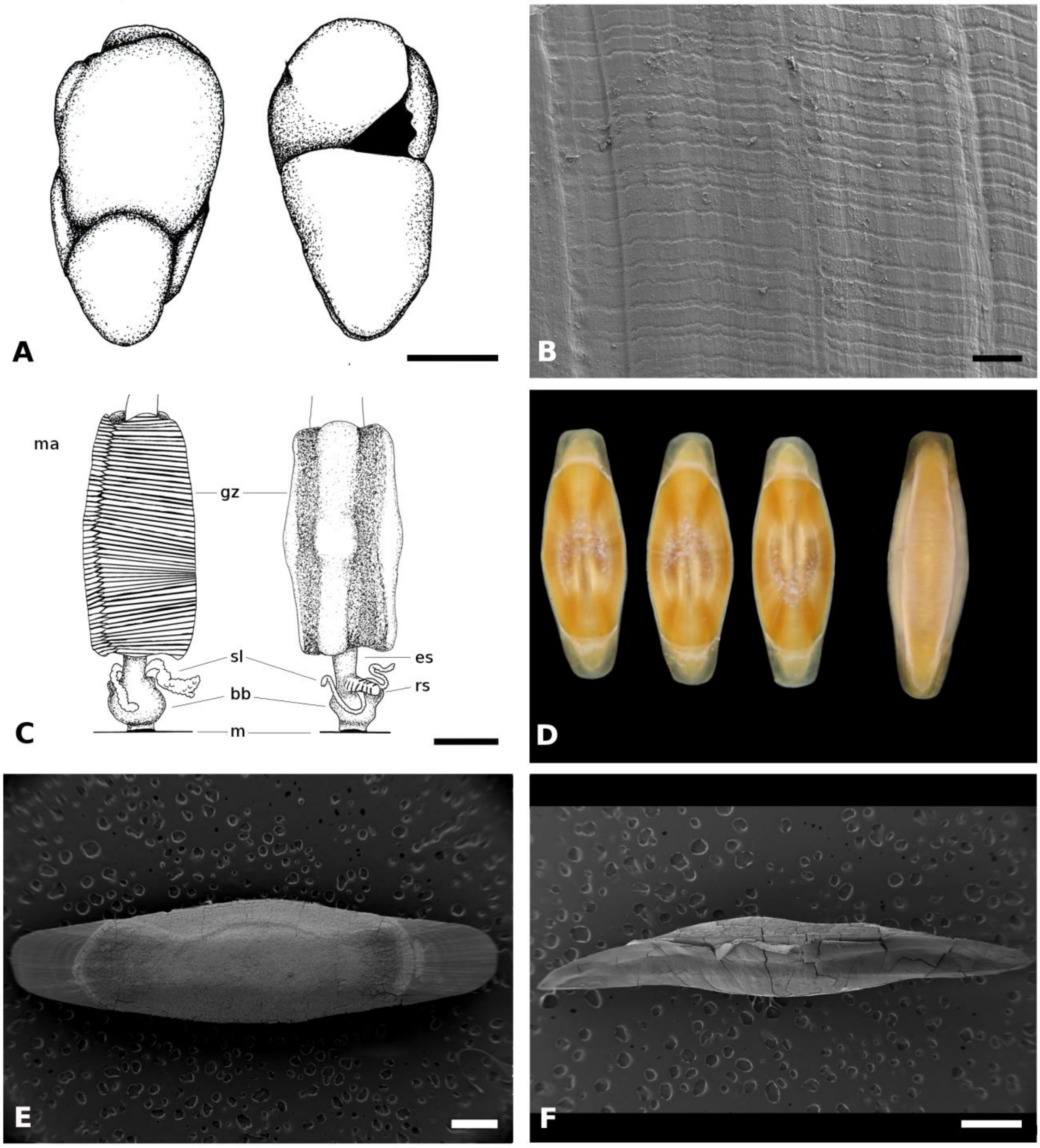


Figure 4.1 ***Philine* sp.6** A, Dorsal(left image) and ventral view(rigth image) illustration of complete animal (Philippines, IM-2009-4367, H= 19 mm) . B, SEM of shell sculpture (Philippines, IM-2009-4367, H= 19 mm). C, Dorsal(left image) and ventral view(rigth image) illustration of foregut (Philippines, IM-2009-4366, H= 15 mm). D, Active surface of 3 equal gizzard plates (left image) inactive surface of gizzaed plate (right image) (Philippines, IM-2009-4366, H= 15 mm). E, SEM of active surface of gizzard plate (Philippines, IM-2009-4366, H= 15 mm). F, SEM of lateral view of gizzard plate (Philippines, IM-2009-4367, H= 19 mm). Abbreviations: ma, muscle attachment. gz, gizzard. es, esophagus. bb, buccal bulb. sl, salivary glands. rs, radular sack. m, mouth. Scalebars: A=5mm, B=100µm, C=2,5mm, E-F=1mm.

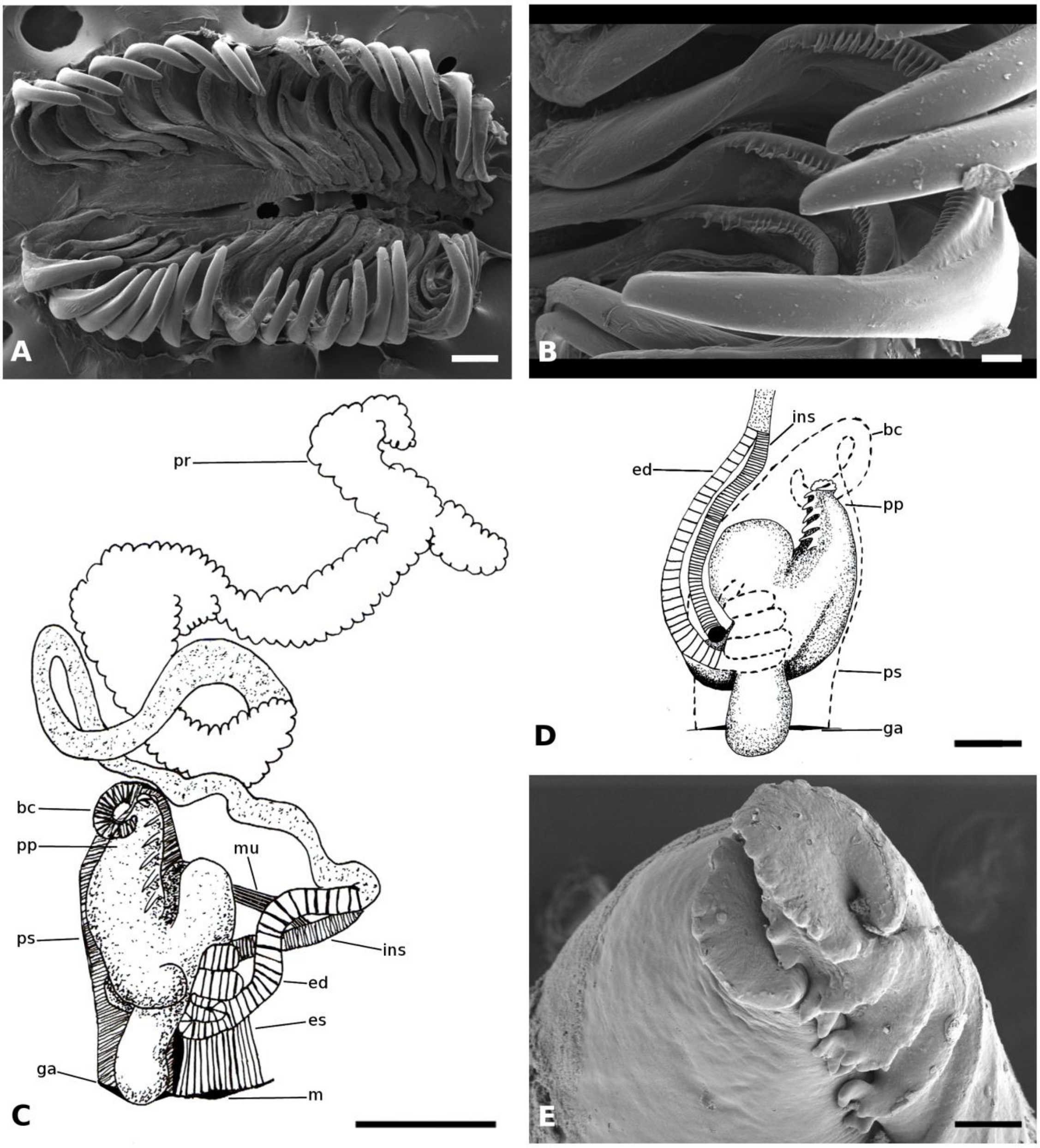


Figure 4.2 ***Philine*** **sp.6** A, SEM of radula (Philippines, IM-2009-4367, H= 19 mm). B, SEM detail of radula (Philippines,IM-2009-4367, H= 19 mm). C, Male reproductive system (Philippines, IM-2009-4367, H= 19 mm). D, detail of male reproductive system (Philippines, IM-2009-4367, H= 19 mm). E, detail of penial papilla (Philippines, IM-2009-4367, H= 19 mm). Abbreviations: pr, prostate. bc, blind caecum. pp, penial papilla. ps, penial sheath. ga, genital aperture. mu, muscle. ins, incurrent sperm duct (groove). ed, ejaculatory duct. es, esophagus. m, mouth. Scale bars: A=100µl; B=20µl; C=2mm; D=1mm; E=100µm.

Sub-clade C (*Philine)*

Shell, oval to round, internal, transparent, smooth, spiral striae of indentations forming chain-like lines when present. Body white in preserved specimens, cephalic shield oval. Posterior shield extends to margin of shell, may have posterior notch. Rachidian tooth absent, one inner lateral tooth with delicate denticulation along inner edge, outer lateral teeth absent. Salivary glands usually present and only attached in proximal end. Gizzard muscularised, calcified gizzard plates, gizzard plates usually not covered by muscular fibres on inactive surface, two paired plates and one smaller central unpaired gizzard plate, usually apparent round pores on inactive surface of all plates. Long, convoluted prostate and species specific penial papillae.

PHILINE SP.1

(FIGS 4.3 A–F, 4.4 A-D)

Diagnosis: Shell, oval, internal, transparent, smooth, no apparent spiral striae. Body white in preserved specimens, cephalic shield oval. Rachidian tooth absent, one inner lateral tooth with delicate denticulation along inner edge, outer lateral teeth absent. Salivary glands absent, Gizzard muscularised, gizzard plates not covered by muscles on inactive surface,, two paired plates and one smaller central unpaired gizzard plate, large pores on inactive surface of all plates.

Material examined: the Philippines, 1 spc. (dissected and sequenced), MNHN, Paris IM-2009-4380, H = 8 mm.

Shell: H = ca. 3 mm. Internal, fragile, thin; whitish transparent; oval, aperture wide; spiral striae not apparent. The shell of the studied specimen was broken.

Animal (4.3 A): Body white (preserved specimen); cephalic shield oval, median groove absent, shallow posterior notch present; thick short muscular parapodial lobes, salivary gland absent.

Radula (4.4 C-D): Radular formula 19 x 1.0.1 Rachidian tooth absent. Inner lateral teeth with narrow base curved and rounded pointed tips, inner edge delicately denticulate.

Gizzard (4.3 B-D, 4.4 A-B): Gizzard elongate cylindrical, muscular, contains three unequal gizzard spindle shaped plates not covered by muscles, two paired and one central unpaired, active surface simple and concave, inactive surface with deep large pores.

Ecology: Occurs at 280 m likely on muddy-sand (as sand and mud was found in digestive system).

Distribution: Between Mindanao and Aliguay Island (Bohol/Sulu Sea) (8°43'N–123°19'E), the Philippines.

Remarks: The shell of the single specimen available for study was fragmented. The buccal bulb was possibly damaged because a large radular sack was found loose within the body cavity; this may explain the fact that no salivary glands could be observed. No male reproductive system was found which may indicate this specimen to be a juvenile. Compared to other members of the subclade C which have great size differences between the large unpaired plates and the small central plate, this species have plates of more equal size; also it possesses plates that are more similar in shape. The paired plates are not as unsymmetrical as the other species in the clade. It is also noteworthy that the large plate pores are similar to the slits of subclade D . The overall morpho-anatomy of this specimen is an intermediate between species in the subclade C and subclade D but the fact that the specimen was damaged, and a juvenile hamper any proper comparison. The molecular analysis indicates this specimen to be a distinct species within the sublclade C, coming out basally in the subclade.

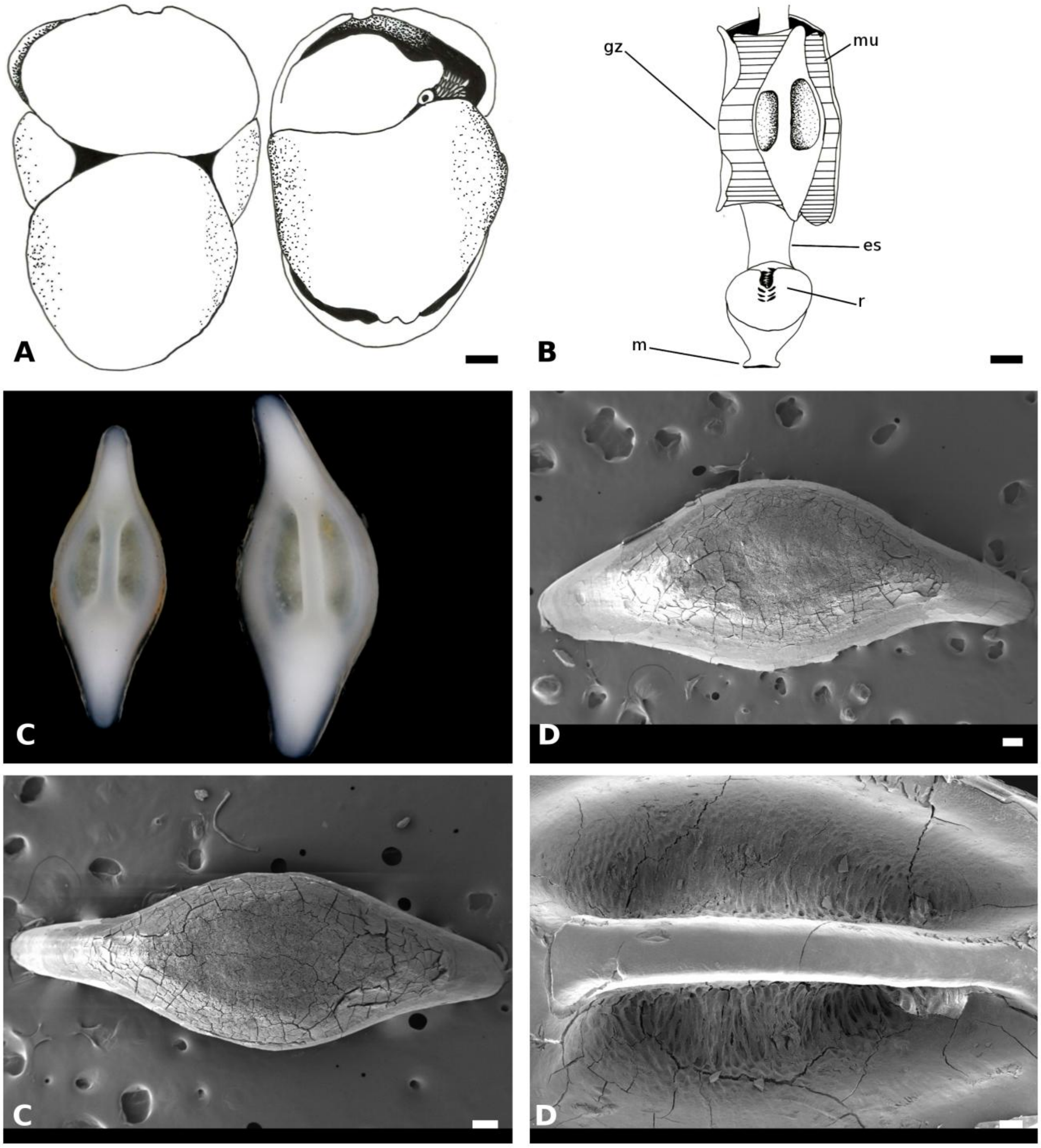


Figure 4.3 ***Philine*** **sp.1** (Philippines, IM-2009-4380, H = 8 mm) A, Dorsal (left image) and ventral view (rigth image) illustration of complete animal. B, illustration of foregut. C, inactive surface of central unpaired gizzard plate (left image) and paired gizzard plate (rigth image). D, SEM of active surface of paired gizzard plate. E, SEM, active surface of central gizzard plate. F, SEM, detail of microsculpture of plate pores. Abbreviations: mu, musculature. gz, gizzard. es, esophagus. bb, buccal bulb. r, radula. m, mouth. Scalebars: A = 0.66µm, B = 0.47µm, D =100µm, E =100µm, F =50µm.

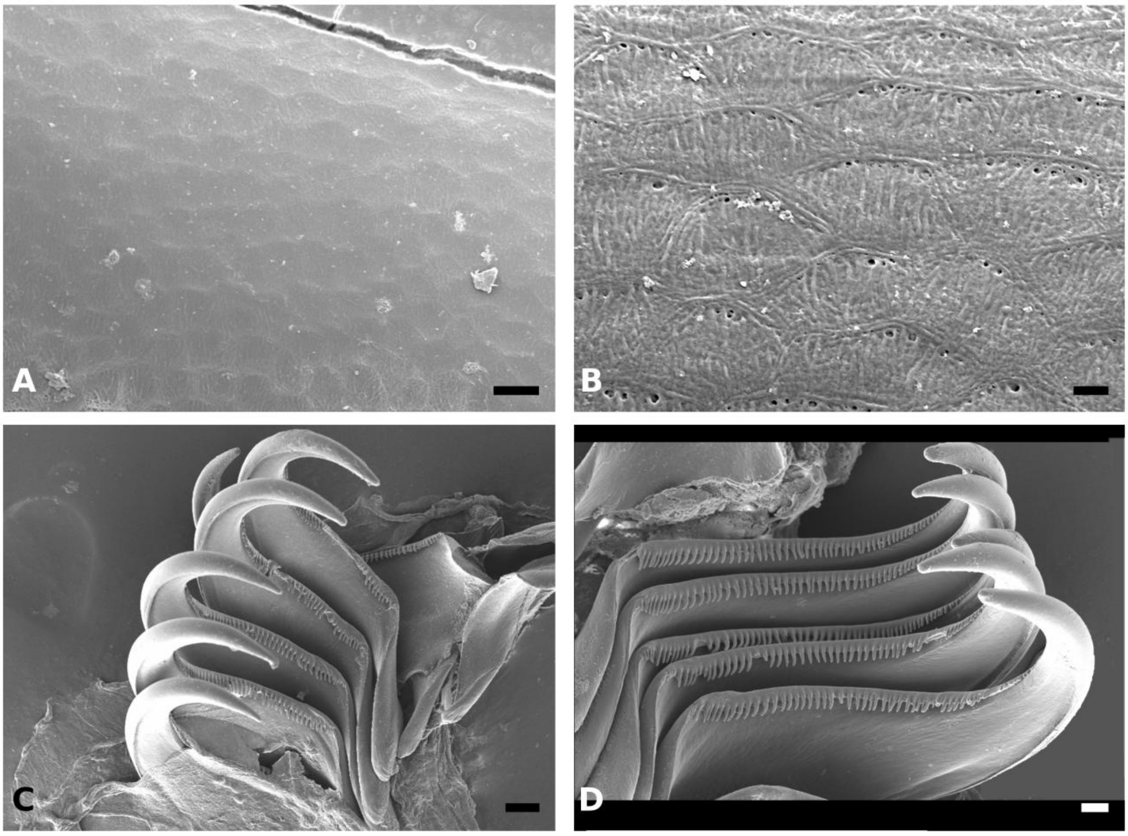


Figure 4.4 ***Philine*** **sp. 1** (Philippines, IM-2009-4380, H = 8 mm) A, SEM, microstructure of inactive surface of gizzard plate. B, SEM, detail of microstructure. C, SEM, Detail of radula. D, SEM, Detail of radula. Scalebars: A = 10µm, B = 2µm, C = 20µm, D = 10µm.

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PHILINE SP.2

(FIGS 4.5 A-F, 4.6 A-F)

Diagnosis: Shell oval-hemispherical, internal, transparent, smooth, spiral striae forming undulating lines. Body white in preserved specimens), rhomboid cephalic shield, shallow indentation posteriorly forming two lobes, posterior shield with shallow posterior notch. Rachidian tooth absent, one inner lateral tooth with denticulation along inner edge, denticulation oriented towards basis of tooth, outer lateral teeth absent, salivary glands present, gizzard muscularised, plates not covered by muscles on inactive surface,, two paired gizzard plates, one smaller central unpaired gizzard plate. Long and convoluted prostate, bulbous penial atrium, ejaculatory duct long, incurrent sperm duct short, penial papilla club shaped, basis of penial papilla forming penial envelope surrounding penial papilla.

Barcode: MNHN, Paris IM-2009-4360: KF877697

Material examined: New Caledonia, 1 spec. (dissected and sequenced), MNHN, Paris IM-2009-4359, H = 14.2 mm. New Caledonia, 1 spec. (dissected and sequenced), MNHN, Paris IM-2009-4360, H = 16.8 mm.

Shell (4.5 B): Maximum H = ca.8 mm. Shell oval-hemispherical; internal; transparent; spiral striae forming undulating lines. Both shells were broken.

Animal (4.5 A): Body white in preserved specimens. Cephalic shield rhomboid, posterior notch present forming two lobes, median groove absent; thick muscular parapodial lobes; shallow posterior notch on rear part of posterior shield, salivary glands present.

Radula (4.6 A-B): Radular formula 18-20 x 1.0.1. Rachidian tooth absent; inner lateral teeth with narrow base curved and rounded tips, inner edge delicately denticulate.

Gizzard (4.5 C-F): Gizzard cylindrical, muscular, gizzard plates not covered by muscular fibres on inactive surface, contains two large paired gizzard plate and one small central unpaired gizzard plate, inactive surface with two pores.

***Male reproductive system (4.6 C-E*)**:** Long ejaculatory duct and short incurrent sperm duct, all of equal diameter. Incurrent sperm duct splits posteriorly to ejaculatory duct and prostate. Long convoluted prostate. Penial atrium bulbous; penial papilla simple and club shaped, the basis of penial papilla forms a penial envelope that surrounds the papilla,

Ecology: Occurs at 415 m likely on muddy-sand (as sand and mud was found in digestive system).

Distribution: New Caledonia between Surprise and Pott Island (18°58'S–163°19'E)

Remarks: These specimens likely belong to an undescribed species. Among sublclade C only this species and *Philine* sp.4 have penial envelops surrounding the penial papilla. However, these two species differs in the connections of the ducts and shape of penial papilla, as *Philine* sp.2 has a elongate tear-shaped penial papilla, whereas *Philine* sp.4 has a club-shaped penial papilla. The gizzard plate microstructure of this species have a honeycombed pattern that is similar to the remaining species in subclade C (and the *P. aperta* clade; (*P. orientalis:* Price et al. (2011), page 34-36, Fig. 27, C, D 28 D, Fig. 29 D; *P. quadripartita:* Ohnheiser and Malaquias (2013), page 36, fig. 24F), but differ in not having deep pores in the gizzard plate microstructure, which is solid. The morphological differences separating *Philine* sp. 2 and *Philine* sp. 4 was also supported by the bayesian analysis of all genes combined as both species were monophyletic with high support, and branched separately. P-distance analysis also support the separation of the species, minimum p-distance and maxiumum p-distance between the species is 11.4% and 13% respectively, these results might be higher than reality as the single COI sequence for *Philine* sp. 2 was quite short (317 bp) compared to the remaining species (644 bp).

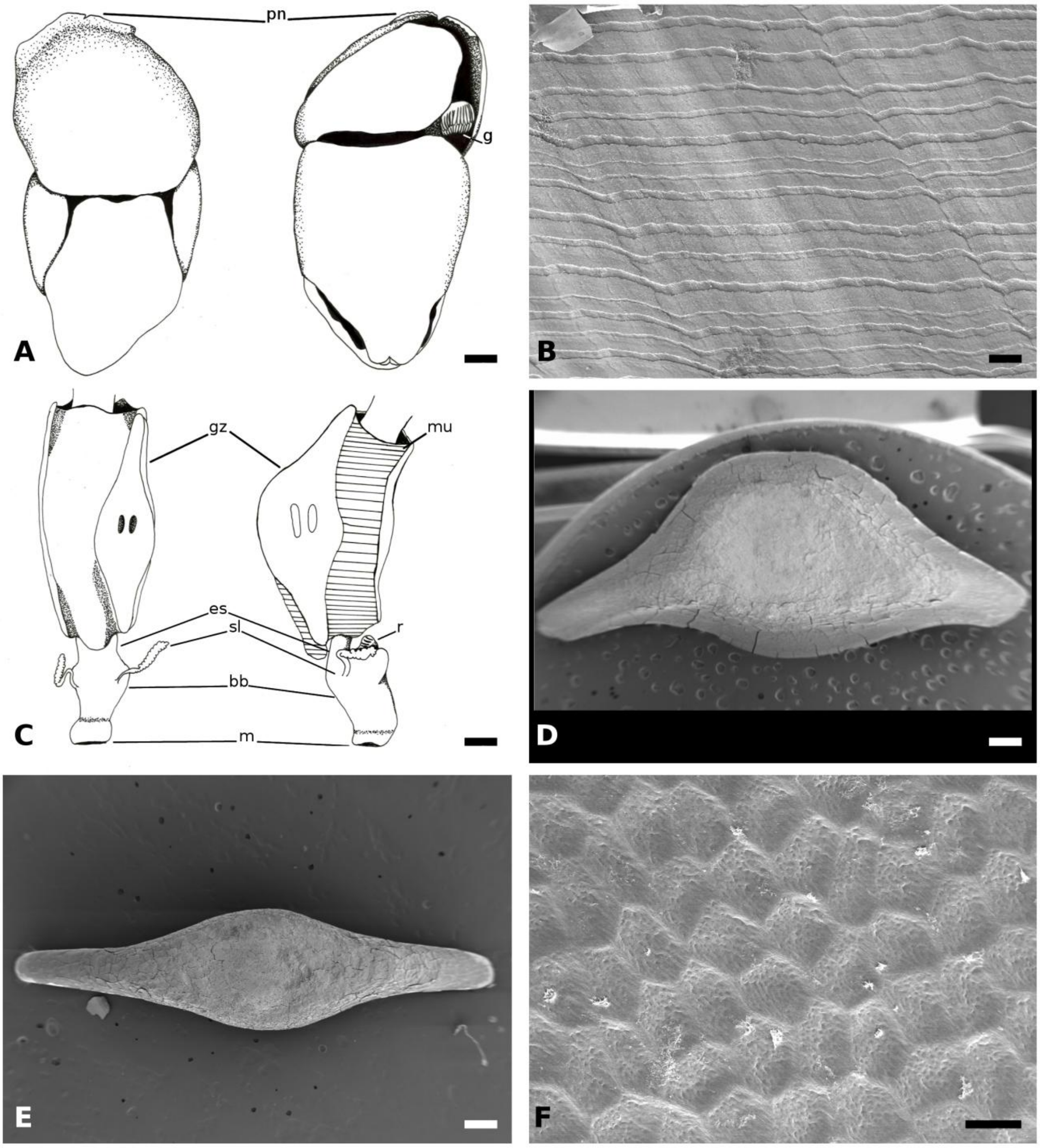

Figure 4.5 ***Philine sp.2*** A, Dorsal(left image) and ventral view(rigth image) illustration of complete animal (New Caledonia IM-2009-4360, H = 16.8 mm). B, SEM, Surface of shell (New Caledonia IM-2009-4360, H = 16.8 mm). C, Dorsal view (left image) and lateral view (rigth image) illustration of forgut (New Caledonia IM-2009-4360, H = 16.8 mm). D, SEM, active surface of paired gizzard plate (New Caledonia IM-2009-4359, H = 14.2 mm). E, SEM, active surface of unpaired gizzard plate (New Calaledonia IM-2009-4360, H = 16.8 mm. F, SEM, microstructure of gizzard plate (New Caledonia IM-2009-4360, H = 16.8 mm). Abbreviations: mu, musculature. gz, gizzard. g, gill. sl, salivary glands. bb, buccal bulb. r, radula. m, mouth. pn, posterior notch. Scalebars: A = 1.6mm, B = 50µm, C = 1.25mm, D,E = 0.5mm, F = 10µm.

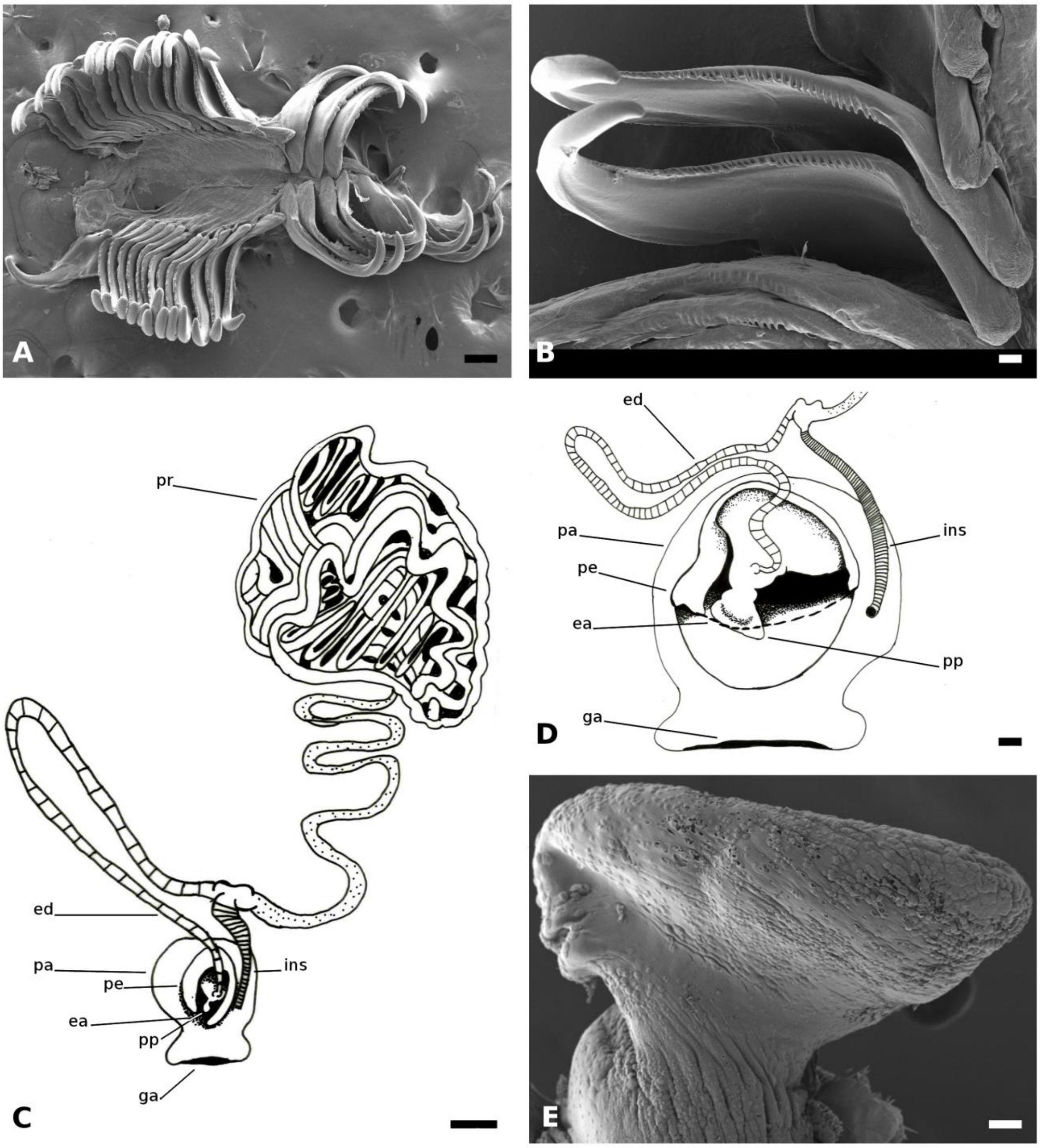

Figure 4.6 *Philine sp.2* A, Sem, radula (New Caledonia IM-2009-4359 H = 14.2 mm). B, SEM, detail radula (New Caledonia IM-2009-4360, H = 16.8 mm.) C, SEM, lateral view illustration of male reproductive system (New Caledonia IM-2009-4360, H = 16.8 mm). D, dorsal view illustration male reproductive system (New Caledonia IM-2009-4360, H = 16.8 mm). E, SEM, penial papilla (New Caledonia IM-2009-4359 H = 14.2 mm). Abbreviations: pr, prostate. ins, incurrent spermduct (groove). ed, ejaculatory duct. pa, penila atrium. pe, penial envelope. pp, penial papilla. ga, genial aperture. ea, envelope aperture. Scalebars: A = 100µm, B = 20µm, C = 1mm, D = 2mm, E = 50µm.

PHILINE SP. 3

(FIGS 4.7 A-F, 4.8 A-F, 4.9 A-D)

Diagnosis: Shell round-hemispherical, internal, transparent, smooth, smooth. Body white (preserves specs.), rhomboid cephalic shield, shallow posterior notch on posterior shield. Rachidian tooth absent, one inner lateral tooth with denticulation along inner edge, outer lateral teeth absent. Short salivary glands. Gizzard muscularised, plates not covered by muscles on inactive surface,, two paired gizzard plates, one smaller central unpaired gizzard plate. Long and convoluted prostate, penial atrium bulbous with short blind caecum; ejaculatory duct long, incurrent sperm duct thick and solid.

Barcode: IM-2009-4333: KF877708, IM-2009-4334: KF877690, IM-2009-4335: KF877707, IM-2009-4354: KF877701, IM-2009-4355: KF877700, IM-2009-4357: KF877699, Paris IM-2009-4358: KF877698, Paris IM-2009-4368: KF877691.

Material examined:

1 spec. (dissected and sequenced) Solomon Islands, MNHN, Paris IM-2009-4333, H = 32 mm, 1 spec. (sequenced) MNHN, Solomon Islands, Paris IM-2009-4334, H = 29 mm,, 1 spec. (sequenced) MNHN, Solomon Islands, Paris IM-2009-4335 H = 32 mm, 1 spec. (sequenced) MNHN, New Caledonia, Paris IM-2009-4354, H = 26 mm, 1 spec. (sequenced) New Caledonia, MNHN, Paris IM-2009-4355, H = 24 mm, 1 spec. (sequenced) New Caledonia, MNHN, Paris IM-2009-4356, H = 25 mm, 1 spec. (sequenced) New Caledonia, MNHN, Paris IM-2009-4357, H = 22 mm, 1 spec. (dissected and sequenced) MNHN, Paris IM-2009-4358 H = 28 (18°59′S–163°08′E), 1 spec. (dissected and sequenced) the Philippines, MNHN, Paris IM-2009-4368, H = 37 mm.

Shell (4.7 B): Maximum H = 18 mm. Shell fragmented; round-hemispherical; internal; transparent, smooth; spiral striae not apparent. Shells were partially broken.

Animal (4.7 A): Body white in preserved specimens. Cephalic shield rhomboid, median groove absent; small muscular parapodial lobes. Shallow notch on rear part of posterior shield. Short salivary glands.

Radula (4.8 A-C): Radular formula 19–21 x 1.0.1 Rachidian tooth absent. Inner lateral teeth with narrow base curved and rounded tips, inner edge with regular denticles or grouped in bundles.

Gizzard (4.7 C-F): Gizzard cylindrical, muscular, gizzard plates not covered by muscles on inactive surface, contains two large paired gizzard plate and one small central unpaired gizzard plate, inactive surface with two pores.

Male reproductive system (4.8 D-F, 4.9 A-C): Bulbous penial atrium; short bulbous blind caecum proximally on penial atrium; thick incurrent sperm duct seem to have two openings into penial atrium, the smaller posterior duct carries a muscle and might be a hollow tissue attachment; incurrent sperm duct splits posteriorly into ejaculatory duct and duct leading to a long convoluted prostate; ejaculatory duct longer than incurrent sperm duct.

Ecology: Occurs between 456–875m likely on muddy-sand (as sand and mud was found in digestive system).

Distribution: Know from south of Vangunu Island, off Kavachi, Solomon Islands, between Surprise and Pott island, New Caldeonia, and Baler Bay, the Philippines.

Remarks: These specimens likely belong to an undescribed species. The male reproductive system resembles that of *Philine orientalis* from Nagasaki, Japan (Price, et al. 2011, page 32, Fig 25 B, C) but differs in some respects as the penial papilla is hammer-shaped with two lobes and a elongate basis, while *P. orientalis* has two lobes and a cussion like basis, *Philine* sp.3 also has unique “brain-like” folds on the surface of the penial papilla. The ejaculatory duct seems to be a bit shorter than in *P. orientalis* the incurrent sperm duct splits posteriorly to the prostate and ejaculatory duct, while in *P. orientalis* (Price, et al. 2011, page 32, Fig 25 B, C) it seems to split into two ducts, which both lead to the prostate. According to Price et al. (2011) the prostate of *P. orientalis* is granular while in *Philine* sp.3 it is largely smooth. A species that occurs in the same geographical area is *P. habei* Valdés 2008 (Valdés (2008), Page 719, Fig 65 E) which also has a hammer-shaped papilla, and similar duct system but this has more lobes and the lobes are not as elongate as in *Philine* sp.3. They also differ in that the ducts of the prostate of *P. habei* (Valdés (2008), Page 719 ,Fig 65 D,) narrows distally while *Philine* sp.3 has a smaller prostate with ducts of equal size throughout the prostate. The penial atrium also have a bulbous blind caecum apically which has previously only been recorded in *P. quardripartita* from European waters (Ohnheiser and Malaquias, 2013). The pores of the gizzard plates of *Philine* sp.3 are also deeper and more prominent than in *P. orientalis*. *Philine* sp.3 was found monophyletic with maximum support (PP = 1; Tree 7.5.8) in the bayesian analysis of all genes combined, *Philline orientalis* was found as sister to the remaining subclade C with good support (PP = 0.99; Tree 7.5.1) however only 16S sequences were available for this species. In the 16S analysis (Tree 7.1.2) subclade C was poorly resolved, but *Philine* sp.3 and *Philine orientalis* did not cluster together.

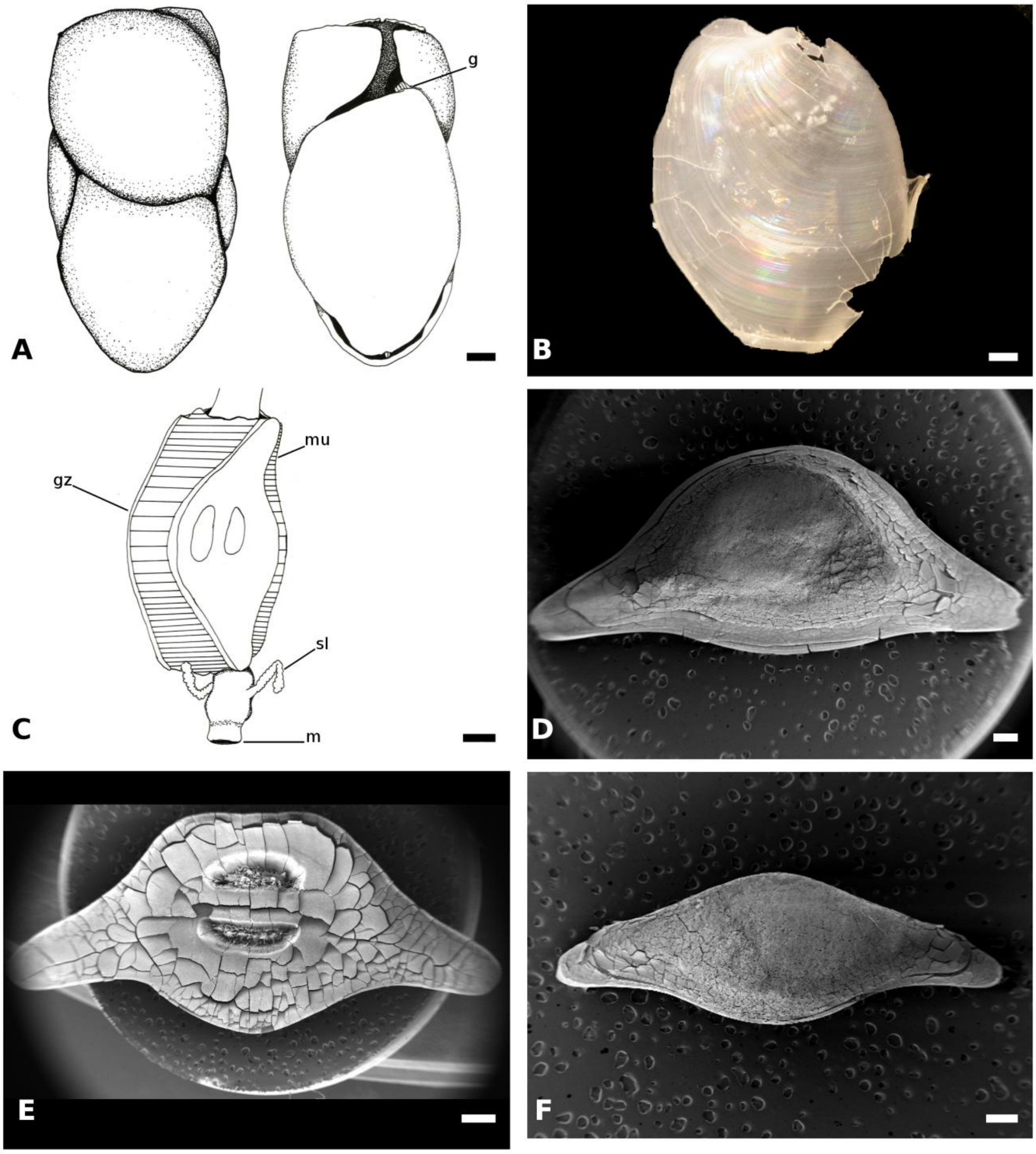

Figure 4.7 ***Philine* sp.3** A, Dorsal(left image) and ventral view (rigth image) illustration of complete animal (Solomon Is. IM-2009-4358, H = 25 mm). B, Dorsal view of fractured shell (Solomon Is. IM-2009-4358, H = 25 mm). C, Dorsal view illustration of forgut (Solomon Is. IM-2009-4358, H = 25 mm). D, SEM, active surface of paired gizzard plate (New Caledonia IM-2009-4333, H = 32 mm). E, SEM, inactive surface of paired gizzard plate (Philipines IM-2009-4368, H = 37 mm). F, SEM, active surface of central unpaired gizzard plate (New Caledonia IM-2009-4333, H = 32 mm). Abbreviations: mu, musculature. gz, gizzard. g, gill. f, foot. sl, salivary glands. Scalebars: A = 0.9 mm, B = 1 mm, C = 1.6 mm, D = 0.5 mm, E = 1 mm, F = 0.5 mm.

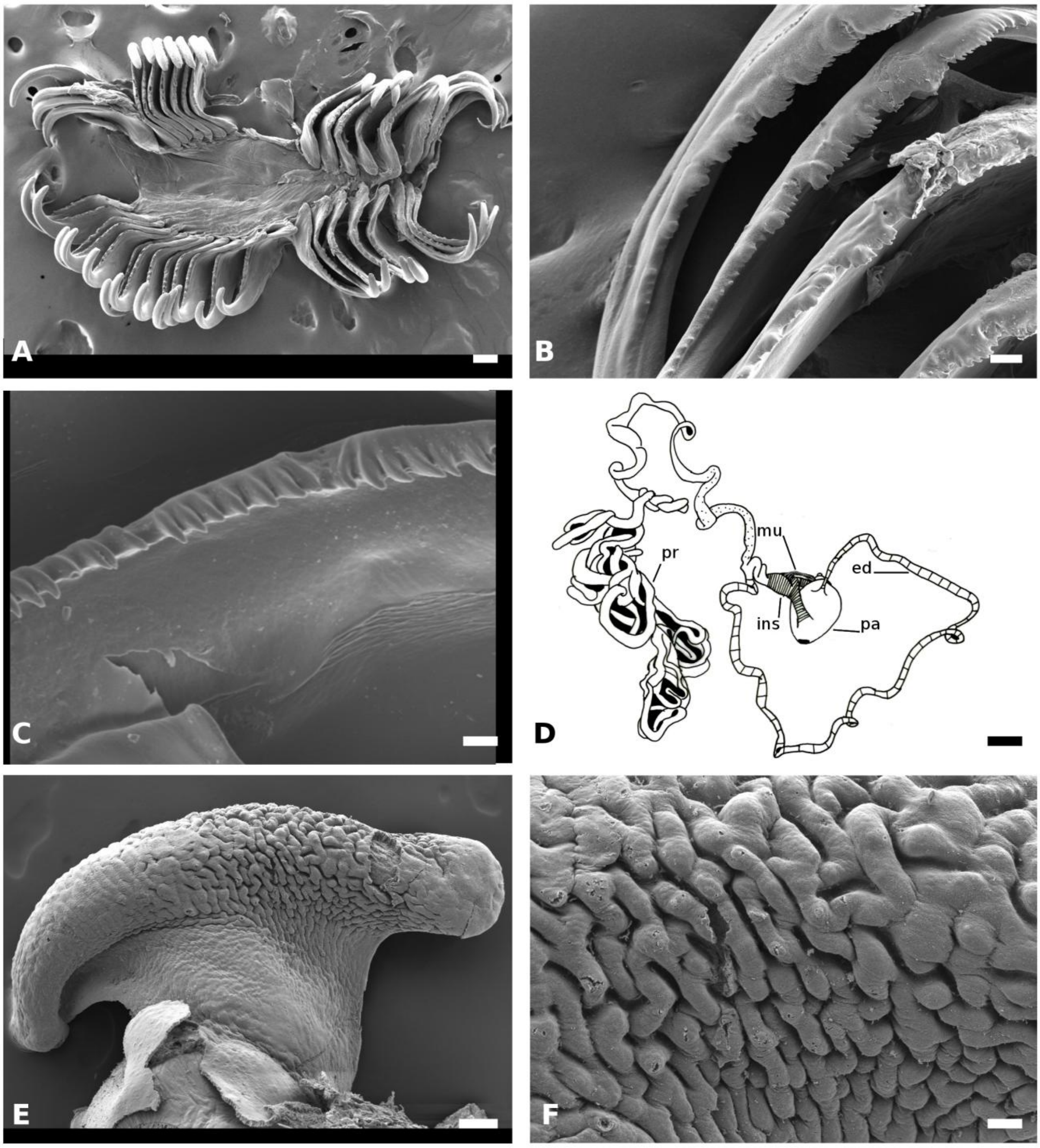

Figure 4.8, *Philine* sp.3 A, SEM, radula (Philippines IM-2009-4368, H = 37 mm). B, SEM, detail of bunched denticulation of inner lateral teeth (Philippines IM-2009-4368, H = 37 mm). C, SEM, detail of ordered denticulation of inner lateral tooth(Solomon Is. IM-2009-4358, H = 25 mm). E, Dorsal view illustration of male reproductive system. (Solomon Is. IM-2009-4358, H = 25 mm) E, SEM, dorsal view penial papilla. F, SEM, microstructure of short lobe penial papilla (New Caledonia IM-2009-4333, H = 32 mm). F, SEM, Microstructure of short lobe of penial papilla (New Caledonia IM-2009-4333, H = 32 mm). Abbreviations: mu, muscle. pr, prostate. ins, incurrent sperm duct (groove). ed, ejaculatory duct. pa, penial atrium. pp, penial papilla. ga, genial aperture. bc, blind caecum. Scale bars: A = 100µm, B = 20µm, C = 10µm, D = 1.5 mm, E = 100µm, F = 20 µm.

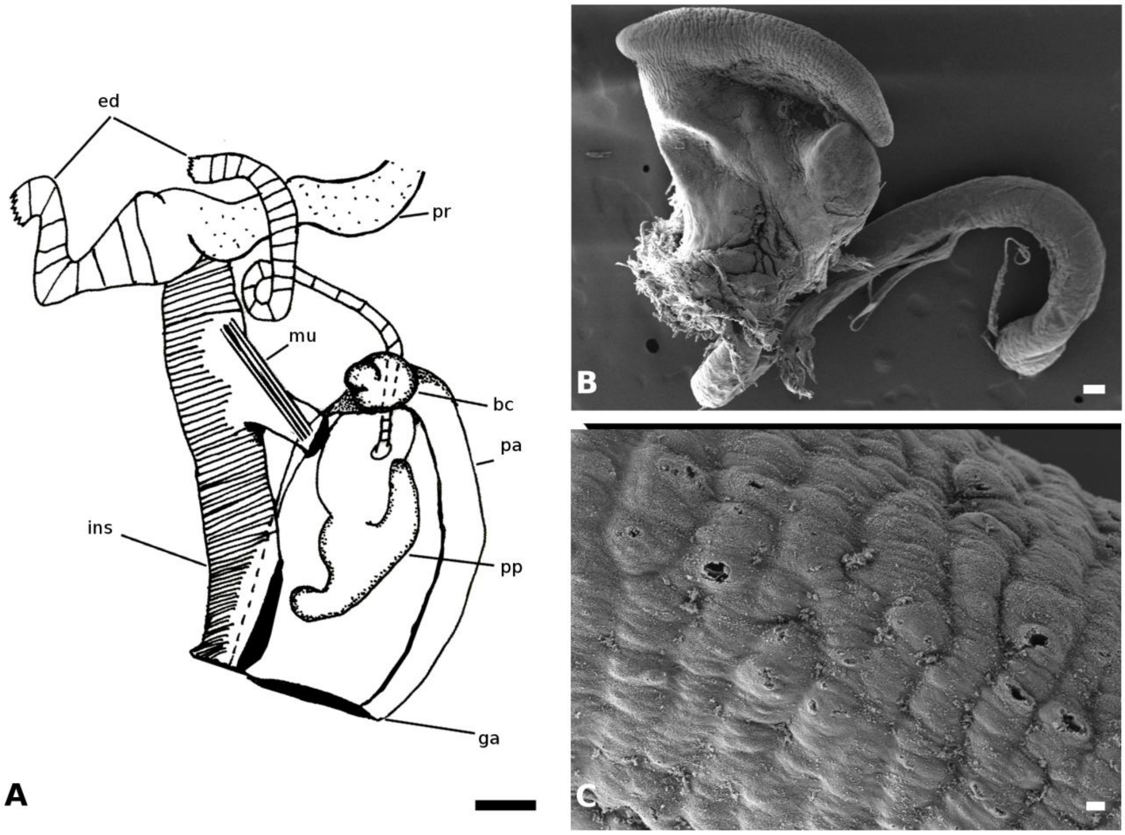

Figure 4.9 ***Philine*** **sp.3** A, Dorsal view illustration of male reproductive system (New Caledonia IM-2009-4333, H = 32 mm). B, SEM, ventral view penial papilla (Philippines IM-2009-4368, H = 37 mm). C, SEM, microstructure of longer lobe of penial papilla (Philippines IM-2009-4368, H = 37 mm). Abbreviations: pp, penial papilla. ins, incurrent sperm duct. pr, prostate. ed, ejaculatory duct. pa, penial atrium. ga, genial aperture. bc, blind caecum. Scale bars: A = 0.2 mm, B = 100µm, C = 6,7µm.

PHILINE SP.4

(FIGS 4.10 A-F, 4.11 A-F)

Diagnosis: Shell fragmented, round-hemispherical, internal, transparent, smooth, spiral striae forms undulating lines. Body white (preserves specs.), cephalic shield oval, narrows posteriorly, shallow indentation forming two lobes. Rachidian tooth absent, one inner lateral tooth with delicate denticulation along inner edge, outer lateral teeth absent. Short salivary glands. Gizzard muscularised, plates not covered by muscles, two paired gizzard plates, one smaller central unpaired gizzard plate, long and convoluted prostate, cylindrical penial atrium, ejaculatory duct long, incurrent sperm duct thick, penial papilla tear shaped, basis of papilla forms penial envelope that surrounds papilla.

Barcode: IM-2009-4336: KF877706, IM-2009-4337: KF877705, IM-2009-4338: KF877704, IM-2009-4328: KF877689

] ***Material examined:*** 1 spec. (Sequenced and dissected), Indonesia, MNHN, Paris IM-2009-4336, H = 11 mm, 1 spec. (Dissected), Indonesia, MNHN, Paris IM-2009-4337, H = 10 mm, 1 spec. (Dissected), Indonesia, MNHN, Paris IM-2009-4338, H = 8 mm, 1 spec., (dissected and sequenced), Taiwan, MNHN, Paris IM-2009-4328, H=14 mm..

Shell (4.10 B): Maximum H = 7 mm. Shell round-hemispherical, internal, transparent, with spiral striae forming undulating lines. All shells were partially broken.

Animal (4.10 A): Body white in preserved specimens. Cephalic shield oval, narrowing posteriorly, shallow indentation forming two lobes, median groove absent; thick muscular parapodial lobes. Short salivary glands.

Radula (4.11 A-B): Radular formula 20 x 1.0.1 Rachidian tooth absent. Inner lateral teeth with narrow base, curved and pointed tips, inner edge delicately denticulate.

Gizzard (4.10 C-F): Gizzard cylindrical, muscular, gizzard plates not covered by muscles, contains two large paired gizzard plate and one small central unpaired gizzard plate, inactive surface with two pores, microstructure of inactive surface honeycombed, largely solid with few pores.

Male reproductive system (4.11 C-E): Long convoluted prostate, cylindrical penial atrium, thick incurrent sperm duct, ejaculatory duct longer than incurrent sperm duct, tear shaped penial papilla, basis of penis forms a penial envelope that surrounds penial papilla.

Ecology: Occurs between 216–331m m likely on muddy-sand (as sand and mud was found in digestive system).

Distribution: Known from the Bohol Sea off Panglao island (9°30'N–123°52'E), and from off Taiwan (24°48'N–122°08'E).

Remarks: These specimens likely belong to an undescribed species. This species is similar to *Philine* sp.2 which also has a penial envelope surrounding the penial papilla. However the penial papilla of Philine sp.2 is club-shaped not elongate tear shaped. There are also differences in the duct system of the species, Philine sp. 4 have a incurrent sperm duct that connects to the ejaculatory duct and the prostate duct of this species is not connected to the ejaculatory or incurrent sperm duct, but instead connects to the penial atrium, this was observed in both specimens, while most other members of the *Philine aperta* clade (subclade C) have a incurrent sperm duct that splits to form the ejaculatory and prostate duct. Superficially the two species are similar, however *Philine* sp.4 does not have a posterior notch in the posterior shield like *Philine* sp.2 *Philine* sp.4 also have shorter thicker gizzard plates with straighter and more symmetrical outline, than *Philine* sp.2, which have more defined elongated tips and a more circular central part of the plates. The morphological differences separating *Philine* sp. 2 and *Philine* sp. 4 was also supported by the Bayesian analysis of all genes combined as both species were monophyletic with high support, and branched separately. P-distance analysis also support the separation of the species, minimum p-distance and maximum p-distance between the species is 11.4% and 13% respectively. As previously mentioned these results might be higher than reality as the single COI sequence for *Philine* sp. 2 was quite short.

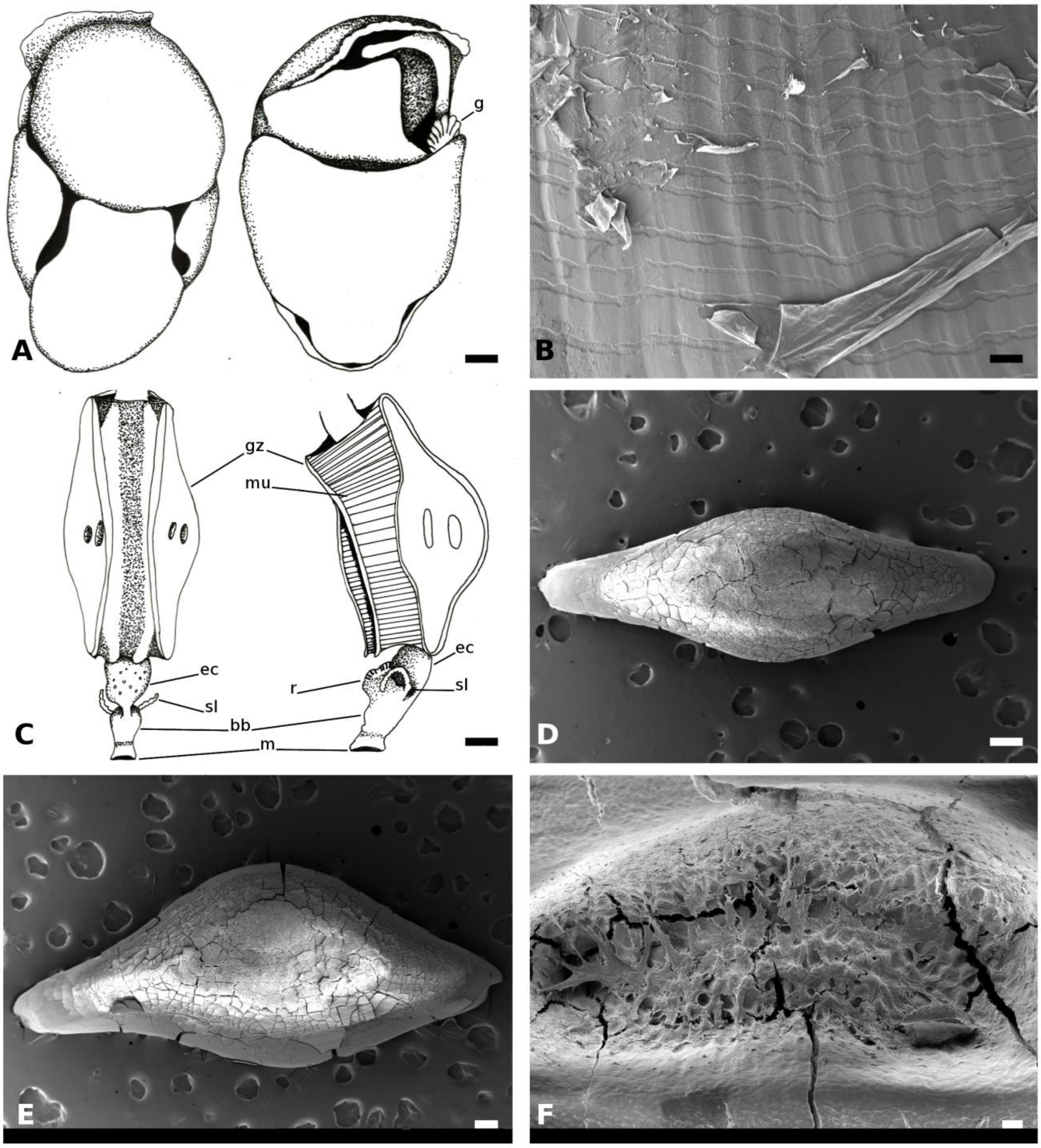

Figure 4.10 ***Philine* sp.4** A, Dorsal (left image) and ventral view (rigth image) illustration of complete animal (Hong Kong, IM-2009-4328, H = 14 mm). B, SEM, Surface view of fractured shell (Hong Kong, IM-2009-4328, H = 14 mm). C, Dorsal view (left image) and lateral view (rigth image) illustration of forgut (Hong Kong, IM-2009-4328, H = 14 mm). D, SEM, active surface of unpaired gizzard plate (Philippines, IM-2009-4336, H = 11 mm). E, SEM, active surface of paired gizzard plate (Philippines, IM-2009-4336, H = 11 mm).. F, SEM, microstructure of gizzard pore (Philippines, IM-2009-4336, H = 11 mm).. Abbreviations: mu, musculature. m, mouth. gz, gizzard. bb, buccal bulb. r, radula. ec, esophageal crop. sl, salivary glands. g, gill. Scalebars: A=1.25mm, B=100µm, C=1mm, D,E=200µm, F=20µm.

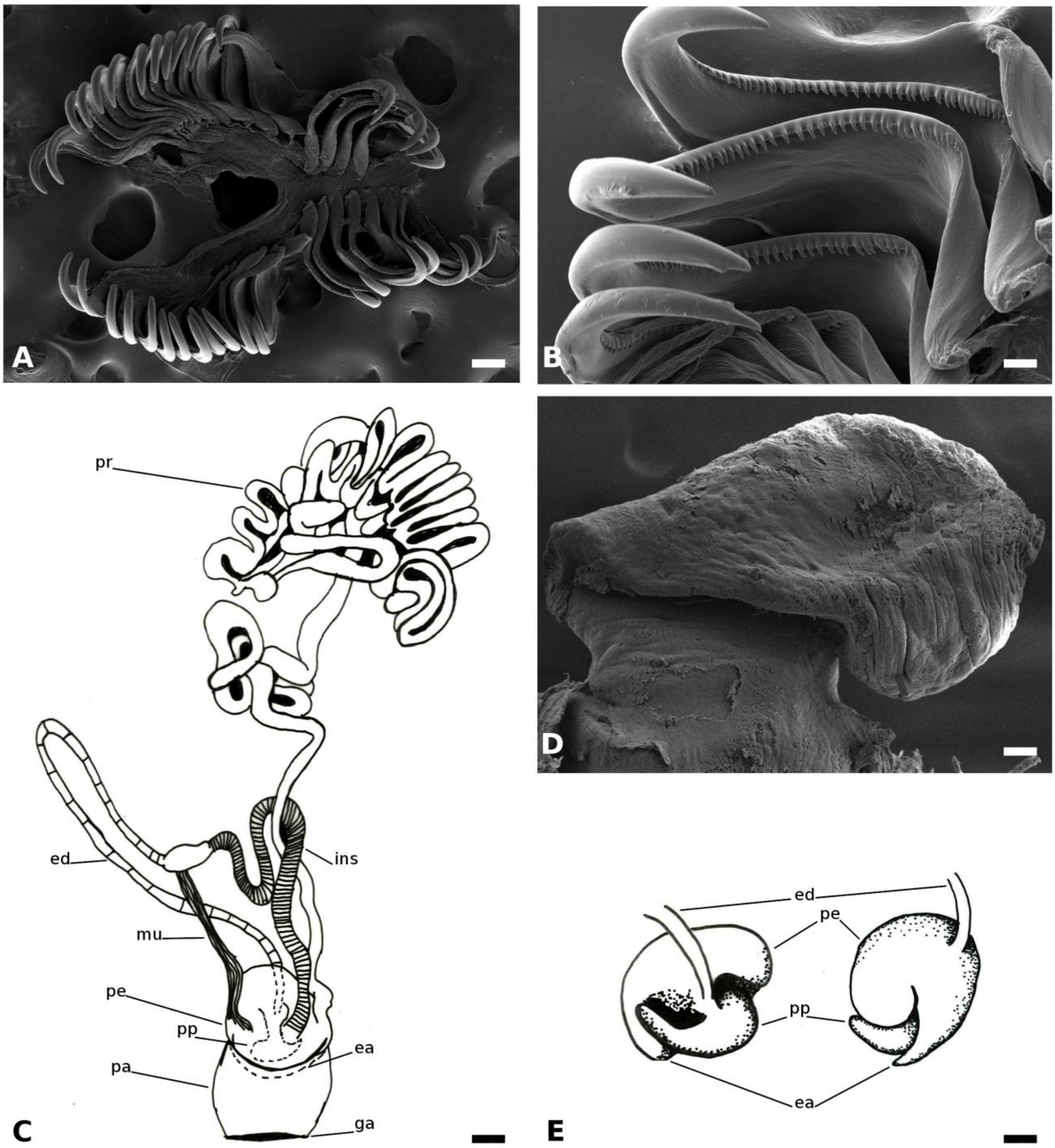

Figure 4.11 ***Philine* sp.4** A, SEM, Radula (Hong Kong, IM-2009-4328, H = 14 mm). B, SEM, detail of inner lateral tooth (Philippines,, IM-2009-4336,H = 11 mm). C, Dorsal view illustration of male reproductive system (Hong Kong, IM-2009-4328, H = 14 mm). D, SEM, penial papilla (Hong Kong, IM-2009-4328, H = 14 mm). E, Ventral (left image) and lateral view (rigth image) of penial papilla andpenial envelope (Hong Kong, IM-2009-4328, H = 14 mm). Abbreviations: mu, muscle. pr, prostate. ins, incurrent sperm duct (groove). ed, ejaculatory duct. pa, penial atrium. pp, penial papilla. ga, genial aperture. pe, penial evelope. ea, envelope aperture. Scalebars: A = 100µm, B = 25µm, C = 0.66mm, D = 50µm, E = 0.25mm.

PHILINE SP.5

(FIGS 4.12 A-F, 4.13 A-F)

Diagnosis: Shell oval-hemispherical, slightly obtuse apex, internal, transparent, smooth, spiral striae with indentations forming chain-like lines . Body white (preserves specs.), rhomboid cephalic shield, shallow indentation posteriorly forming two lobes, posterior shield with deep posterior notch. Rachidian tooth absent, one inner lateral tooth with denticulation along inner edge, denticules regularly spaced or clustered in hand-like bundles, outer lateral teeth absent. Salivary glands present. Gizzard muscularised, plates not covered by muscles, two paired gizzard plates, one smaller central unpaired gizzard plate. Long and convoluted prostate, penial atrium bulbous, ejaculatory duct long, incurrent sperm duct thick, incurrent and ejaculatory duct fuses to form thick prostate duct, penial papilla oblong, cylindrical and mushroom shaped.

Barcode: IM-2009-4373: KF877694, IM-2009-4374: KF877695, IM-2009-4375: KF877693

Material examined: 1 spec. (dissected and sequenced), New Caledonia, MNHN, Paris IM-2009-4373, H = 9.2 mm, 1 spec. (dissected and sequenced), New Caledonia, MNHN, Paris IM-2009-4374, H = 11 mm. 1 spec. (sequenced), New Caledonia, MNHN, Paris IM-2009-4375, H = 15 mm.

Shell (4.12 B): Maximum H = 5 mm. Shell oval-hemispherical; slightly obtuse apex; internal; transparent; spiral striae of fused pits forming chain like lines. All shells were partially broken.

Animal (4.12 A): Body white in preserved specimens. Cephalic shield rhomboid, splits posteriorly to form two lobes, median groove absent; thick and long parapodial lobes; deep notch on posterior lobe. Salivary glands present.

Radula (4.13 A-C): Radular formula 20 x 1.0.1 Rachidian tooth absent. Inner lateral teeth with narrow base curved and rounded tips, inner edge delicately denticulate.

Gizzard (4.12 C-F): Gizzard cylindrical, muscular, gizzard plates not covered by muscles, with two large paired gizzard plates and one small central unpaired gizzard plate, inactive surface with two pores.

Male reproductive system (4.13 D-E): Oblong penial papilla with a mushroom like shape, incurrent and ejaculatory duct meets posteriorly to form a much thicker prostate duct that may function as a seminal vesicle.

Ecology: Occurs at 305 m likely on muddy-sand (as sand and mud was found in digestive system).

Distribution: Surprise Island, New Caledonia (18°30'S–163°04'E).

Remarks: These specimens likely belong to an undescribed species. The two most similar species to *Philine* sp.5 are *P. puka* and *P. paucipapillata*. Externally *Philine* sp.5 resembles *P. puka* as illustrated in Price et al. (2011). The penial papilla and duct system are similar to those of *Philine puka* (Price et al. (2011), Page 40, Fig 32, B , C,) and *P. paucipapillata* (Price et al. (2011), Page 38, Fig 30, B , C), but the penial papilla is simpler with an elongate mushroom like-shape, whereas *P. puka* has a hammer shaped papilla with two lobes, one is distinct, long and slightly convoluted (Price et al. (2011), Page 40, Fig 32, B). The penial papilla of *P. paucipapillata* is club shaped with two short lobes, giving it the tip a rounded appearance (Price et al. (2011), Page 38, Fig 30, B). Of the species described here *Philine* sp.5 is most similar to *Philine* sp. 2 and *Philine* sp. 4 but lacks a penial envelope. The microstructure of the gizzard plates is coarsely indented with depressions, which is different from both *P. puka* and *P. paucipapillata* which have a honeycombed microstructure with small pores (Price et al. (2011), *P. paucipapillata* Page 39, Fig 31, D; *P. puka*, Page 42, Fig 33, B),but as plates are brittle this character is difficult to interpret. The denticulation of the radula differs between the three species (Price et al. (2011), *P. paucipapillata* Page 39, Fig 31, E; *P. puka*, Page 42, Fig 33, E). In *Philine* sp.5 denticulation is more conspicuous than in *P. paucipapillata* but more delicate and narrow than in *P. puka*. Like in *Philine* sp. 3 intraspesiffic variations was found in this character as denticules can be regularly spaced or clustering in bundles resembling human hands with fingers. This denticulation in this species is however longer and deeper than in *Philine* sp.3. Nevertheless, the denticulation of the radula might not be a good trait for recognizing species of *Philine*; as highlighted by the variation found in the species *Philine* sp. 3 and *Philine* sp.5. Lemche (1948) has suggested that "The presence or lack of serrulation of the teeth has again and again proved valueless as a systematic character in *Philine*" (from Marcus (1974)). *Philine* sp.5 was retrieved as monophyletic with maximum support in the bayesian analysis of all genes (PP = 1; Tree 7.5.9). Of the described species it was most similar to *Philine* sp. 2, minimum and maximum p-distance between these two species is 10.9% and 11.5 respectively, and with *Philine* sp. 4 minimum and maximum p-distance between these two species are 11.6% and 13.5% respectively,

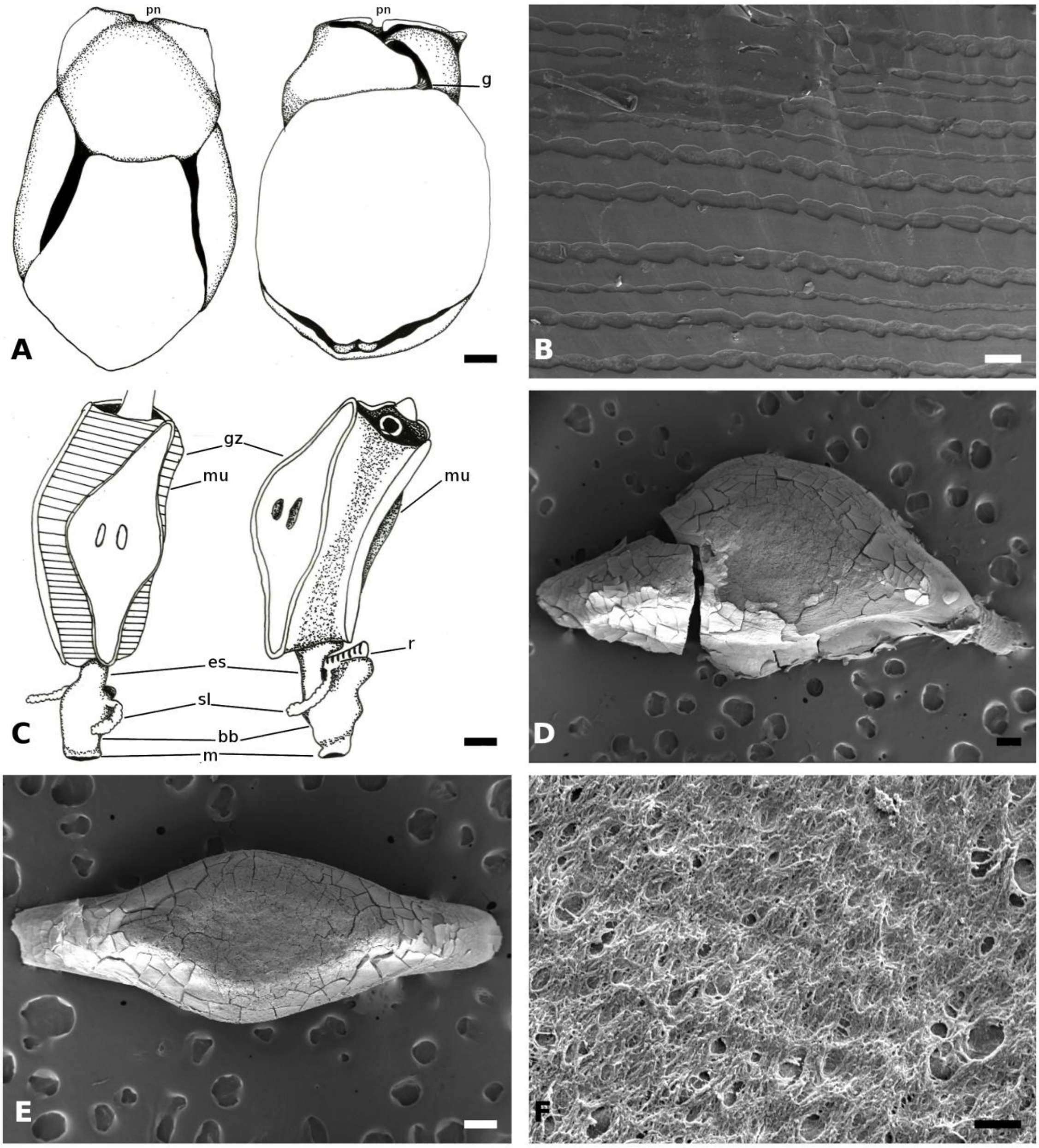

Figure 4.12 ***Philine* sp.5** A, Dorsal (left image) and ventral view (rigth image) illustration of complete animal (New Caledonia IM-2009-4374, H = 11 mm). B, SEM, Surface of shell (New Caledonia IM-2009-4374, H = 11 mm). C, Dorsal view (left image) and lateral view (rigth image) illustration of forgut (New Caledonia IM-2009-4374, H = 11 mm). D, SEM, active surface of paired gizzard plate (New Caledonia IM-2009-4373, H = 9.2 mm), . E, SEM, active surface of unpaired gizzard plate (New Caledonia IM-2009-4373, H = 9.2 mm). F, SEM, microstructure of gizzard plate (New Cal. IM-2009-4373, H = 9.2 mm). Abbreviations: mu, musculature. gz, gizzard. g, gill. sl, salivary glands. bb, buccal bulb. r, radula. m, mouth.mu, musculature. pn, posterior notch. Scalebars: A=1mm, B=100µm, C=0.8mm, D=200µm, E=200µm, F=10µm.

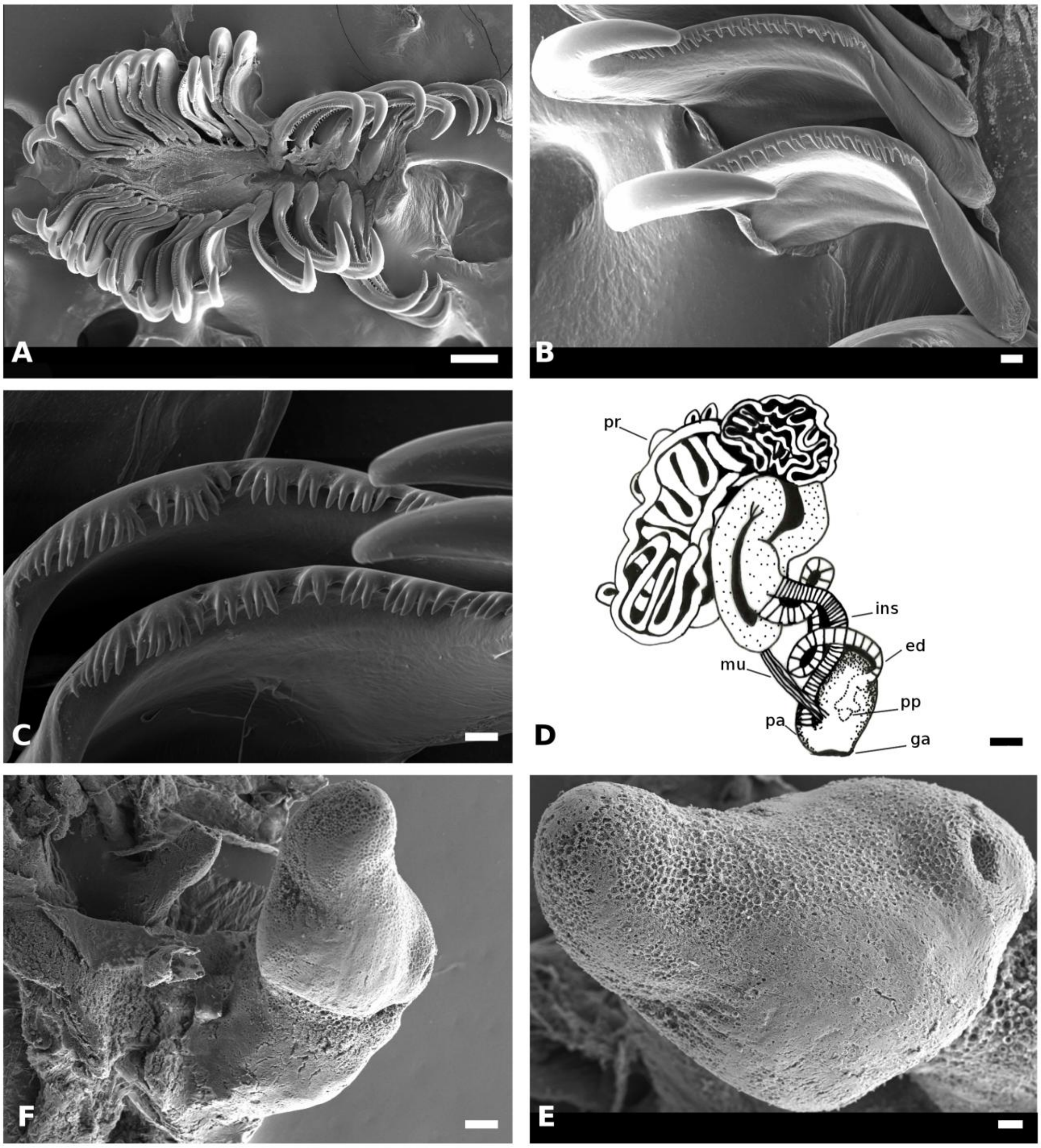

Figure 4.13, *Philine* sp. 5 A, SEM, radula (New Caledonia IM-2009-4374, H = 11 mm). B, SEM, detail of ordered denticulation (New Caledonia IM-2009-4373, H = 9.2 mm). C, Detail of ordered denticulation (New Caledonia IM-2009-4374, H = 11 mm). D, Illustration of male reproductive syatem. E, SEM, anterio-dorsal view penial papilla (New Caledonia IM-2009-4373, H = 9.2 mm). F, SEM, tip of penial papilla (New Cal. IM-2009-4373, H = 9.2 mm). Abbreviations: pp, penial papilla. ins, incurrent sperm duct (groove). pr, prostate. ed, ejaculatory duct. pa, penial atrium. ga, genial aperture. Scale bars: A=100μm, B=10μm, C=10μm, D=0.2mm, E=20μm, F=10μm.

Sub-clade D (New genus)

Synopsis: Shell globose to cylindrical; internal, transparent, smooth, spiral striae forming undulating lines. Body white (in preserved specs), elongate cephalic shield. Rachidian tooth absent, inner lateral tooth with denticulation along inner edge, outer lateral teeth present. Gizzard surrounded by muscular fibres, gizzard plates not covered by muscles on inactive surface, usually large pores in the form of slits along the edges of inactive surface, one larger unpaired gizzard plate wit no slits on inactive surface, and two paired gizzard plates with raised edges on active surface and longitudinal slits along inner side of inactive surface. Salivary glands present. Long and convoluted prostate, long ejaculatory duct.

PHILINE BABAI Valdés, 2008

(FIGS 4.14 A-F, 4.15 A-F)

Diagnosis: Shell globose, internal, transparent, mostly smooth, with shallow spiral striae, forming undulating lines. Body white (preserved specs.), elongate-rounded cephalic shield. Rachidian tooth absent, inner lateral tooth with denticulation along inner edge, smaller outer lateral teeth present, long and narrow. Gizzard muscular, gizzard plates not covered by muscular fibres on the inactive surface, inactive surface covered by thin tissue, one larger unpaired gizzard plate, and two paired gizzard plates with raised edges and longitudinal slits along inner side of edges. Long salivary glands. Long and convoluted prostate, seminal, bulbous penial atrium, long incurrent sperm duct, long ejaculatory duct.

Barcode: IM-2009-4344: KF877703, IM-2009-4352: KF877702.

Type locality: Fiji, 478–500 m (BORDAU 1: stn CP 1468; 18°16’S–178°41’W).

Material examined:, 1 spec. (dissected and sequenced), the Philippines, MNHN, Paris IM-2009-4344, H = 8 mm. 1 spec. (dissected and sequenced), the Philippines, MNHN, Paris IM-2009-4352, H = 12.7 mm.

Shell (4.14 B): Maximum H = 5mm. Internal, thin; whitish transparent; oval in shape with flattened apex, protoconch slightly raised, aperture wide. Shell surface mostly smooth, shallow undulating spiral striae present.

Animal (4.14 A): Body white in preserved specimens, shallow posterior notch on posterior shield. Cephalic shield rounded anteriorly, square posteriorly, median groove absent. Thick muscular, broad parapodial lobes that widens posteriorly. Long salivary glands.

Radula (4.15 A-B, D): Radular formula 16–17 x 1.1.0.1.1. Rachidian tooth absent. Inner lateral teeth with narrow base, curved with rounded tips, inner edge delicately denticulate. Outer lateral teeth, smaller than inner laterals, long, straight and narrow with pointed tips.

Gizzard (4.14 C-F): Gizzard short and compact, muscularised, gizzard plates not covered by muscle fibres on inactive surface, thin film covers gizzard plates the inactive surface; unpaired gizzard plate larger than paired plates, paired plates curved on both sides; raised edges on active surface, deep slits present on inactive side of plates,.

Male reproductive system (FIG.15C-E): Prostate convoluted; proximal with broader duct; prostate connected to penial atrium via long incurrent seminal duct, a long prostate duct and long ejaculatory duct, all three ducts diverge anterior of the prostate.

Ecology: Occurs between 243–786 m likely on muddy-sand (as mud and sand were found in the digestive system) (Valdés, 2008; present study).

Distribution: Known from Indonesia, Fiji, New Caledonia, Tonga and Wallis Island; Bohol Sea, around Siquijor Island, the Philippines, (9°28' N–123°38' E and 8°53' N–123°34' E).

Remarks: *Philine babai* was resolved in a monophyletic clade with maximum support (PP = 1; Tree 7.5.1) together with *P. aurifomis* (Suter, 1909) and *Philine* sp.7 in the bayesian analysis of all genes, but the species was poorly supported. However *Philine babai* was monophyletic with high support in all remaining analysis. The plates of the previously described specimens of *P. babai* have undulating (ruffled) edges (see Valdès, (2008) page 718, Fig 64, E) (Price et al., 2011), which differed from the straight edges of these specimens, however this may be due to a fixation artefact (Valdés pres. Com.). As all specimens were fixated in formalin (Valdés pers. Com) it may have affected the shape of the gizzard plates..

As previously mentioned the gizzard plates are most similar to *Philine* sp. 7, however the central gizzard plate is blunted and have no extensions. The interspeciffic p-distance between these species is 5.5% indicating them to be closely related but separate species.

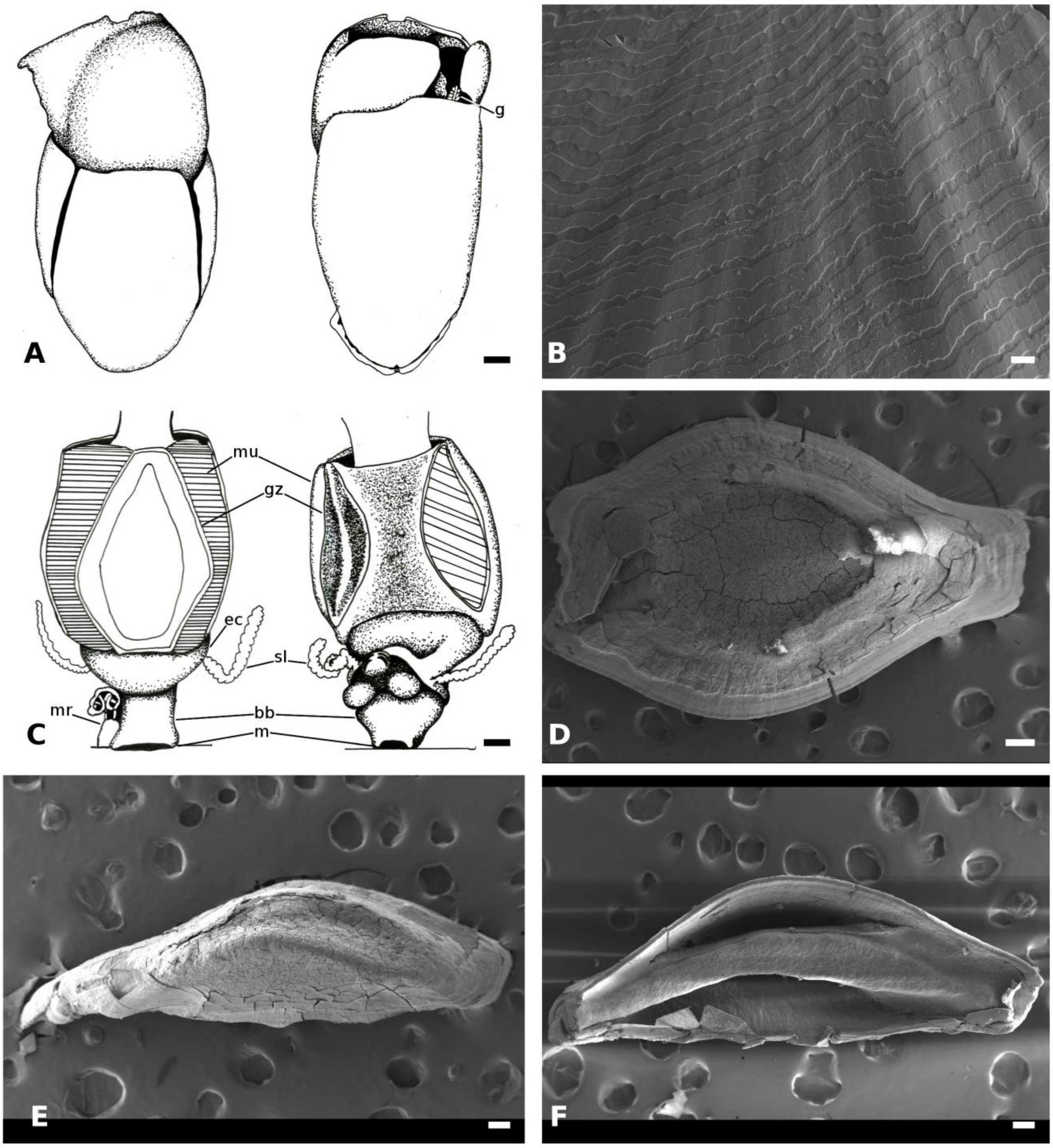

Figure 4.14, *Philine babai* (Philippines, IM-2009-4352, H = 12.7mm) A, Dorsal (left image) and ventral view (rigth image) illustration of complete animal. B, SEM of apical part of shell. C, Dorsal (left image) and lateral view (rigth image) illustration of foregut. D, Active surface of unpaired gizzard plate. E, Active surface of paired lateral gizzard plate. F, Inactive surface of paired lateral plate. Abbreviations: g, gill. gz, gizzard plate. ec, esophagial crop. bb, buccal bulb. sl, salivary glands. rs, radular sack. m, mouth. mu, musculature. Scale bars: A = 1mm, B = 50µm, C = 0.25mm. D = 200µm, E = 100µm, F = 100µm.

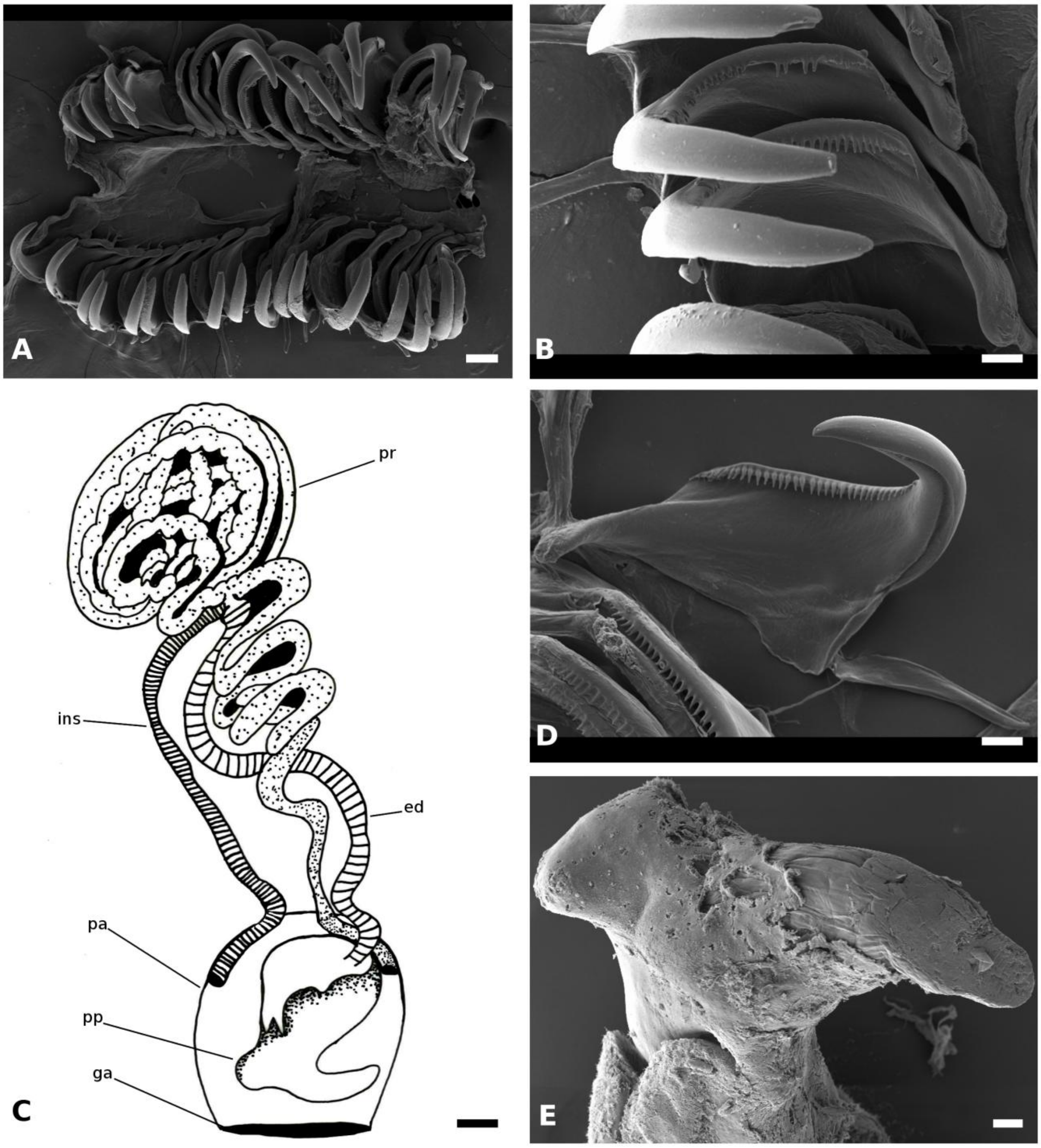

Figure 4.15 ***Philine babai*** A, SEM of radula (Philippines, IM-2009-4352, H = 12.7 mm). B, SEM detail of radula (Philippines,IM-2009-4352, H = 12.7 mm). C, Illustration of male reproductive system (Philippines, IM-2009-4352, H = 12.7 mm). D, SEM, detail of inner and outer lateral teeth of radula (Philippines, IM-2009-4344, H = 8mm). E, SEM, penial papilla (Philippines, IM-2009-4352, H = 12.7 mm). Abbreviations: pp, penial papilla. pa, penial atrium. ins, incurrent sperm duct (groove). ed, ejaculatory duct. pr, prostate. Scale bars: A=50μm, B = 20 μm, C = 0.12 mm, D = 20 μm, E = 33μm.

PHILINE **SP.7**

(FIGS 4.16 A-F, 4.17 A-F)

Diagnosis: Shell oval, oblong and cylindrical; internal, transparent, smooth, with few spiral striae posteriorly. Body white (preserved spec.), elongate-squarish cephalic shield. Rachidian tooth absent, inner lateral tooth with denticulation along inner edge, outer lateral teeth present. Gizzard surrounded by muscular fibres, gizzard plates not covered by muscles, one larger unpaired gizzard plate wit no slits on inactive surface, and two paired gizzard plates with raised edges on active surface and longitudinal slits along inner side of inactive surface. Short salivary glands. Long and convoluted prostate; seminal vesicle with bulbous caecum, bulbous penial atrium,, short incurrent sperm duct, ejaculatory duct long encircling prostate.

Barcode: KF877696

Material examined: 1 spec. (dissected and sequenced), the Philippines, MNHN, Paris IM-2009-4341, H = 23 mm .

Shell (4.16 B-C): Maximum H = 10 mm. Internal, thin; whitish transparent; oval, oblong and cylindrical in shape with flattened apex, protoconch slightly raised, aperture wide. Shell surface smooth anteriorly, spiral striae present posteriorly.

Animal (4.16 A): Body white in preserved specimen. Cephalic shield elongate, square posteriorly, median groove absent. Thick, muscular and elongated parapodial lobes. Shallow posterior notch on posterior lobe. Short salivary glands.

Radula (4.17 A-B): Radular formula 22 x 1.1.0.1.1. Rachidian tooth absent. Inner lateral teeth with narrow base, curved with rounded tips, inner edge delicately denticulate. Smaller outer lateral teeth long, straight and narrow with rounded tip.

Gizzard (4.16 D-F): Gizzard elongate, muscularised; gizzard plates not covered by muscle fibres on inactive surface of all plates,, thin film covers inactive surface of all gizzard plates, unpaired gizzard plate larger than paired plates with no slits on inactive surface; paired plates straight on one side with outer expansion at mid-point on opposite side; raised edges on active surface, slits present on inactive surface.

Male reproductive system (4.17 C-E): Prostate convoluted with two distinct parts; prostate separated from penial atrium by short incurrent seminal duct; bulbous caecum present on seminal vesicle; ejaculatory duct long, encircling prostate.

Ecology: Occurs at 786 m likely on muddy-sand (as mud and sand were found in the digestive system).

Distribution: Known from the southern opening of Cebu Strait, Philippines (Cebu Strait/Bohol Sea) (9°27′N–123°34′E).

Remarks: This specimen likely corresponds to an undescribed species. The gizzard plates are similar to those of *Philine fenestra* Price, Gosliner and Valdés 2011, *P. infundibulum* Dall 1889, and *P. sarcophaga* Price, Gosliner and Valdés 2011, *P.auriformis* Suter 1909 and *P. babai* Valdés 2008. However the unpaired gizzard plate has a pointed posterior end, whereas *P. infundibulum*, *P. sarcophaga* and *P. babai* have a rhomboid unpaired plate (*P. infundibulum* Marcus and Marcus, (1967) page 607, Fig 21; *P. sacrophaga* :Price et al., (2011) page 47, Fig 37), while *P. fenestra* (Price et al., (2011) page 25, Fig 18) have three identical spindle shaped plates. The ejaculatory duct in *Philine* sp. 7 is longer than in the other similar species encircling the large prostate and foregut. Although all the aforementioned species all have an unusually long ejaculatory duct compared for example to the Philinidae subclade C. *Philine* sp.7 is also the only to have a bulbous caecum on the seminal vesicle. The similarities on the anatomy of the male reproductive system of these six species suggest that they are closely related. This is support in the Bayesian analysis of all genes where *Philine* sp. 7, *P. babai* and *P. auriformis* cluster together in a clade with maximum support (PP = 1; Tree 7.5.1) however the clade was poorly resolved internally. P-distance analysis support that *Philine* sp.7 and *P. babai* as separate species as the uncorrected p- distance between them wa 5.5%. Among these species, three are only know from the West Pacific, namely *Philine* sp.7 in the Philippines (present study), *P. aurifomis* in New Zealand (introduced to San Fransisco Bay, USA; Krug et al. 2012), and *P. babai* know in New Caledonia, Tonga and Walis island (Valdés, 2008; Price et al., 2011). The species *P. infundibulum* occur along the western

Atlantic from Brazil to Cape Cod, US, whereas *P. fenestra* and *P. sacrophaga* seem to be restricted to the Indian Ocean coast of South Africa Price et al. 2011).

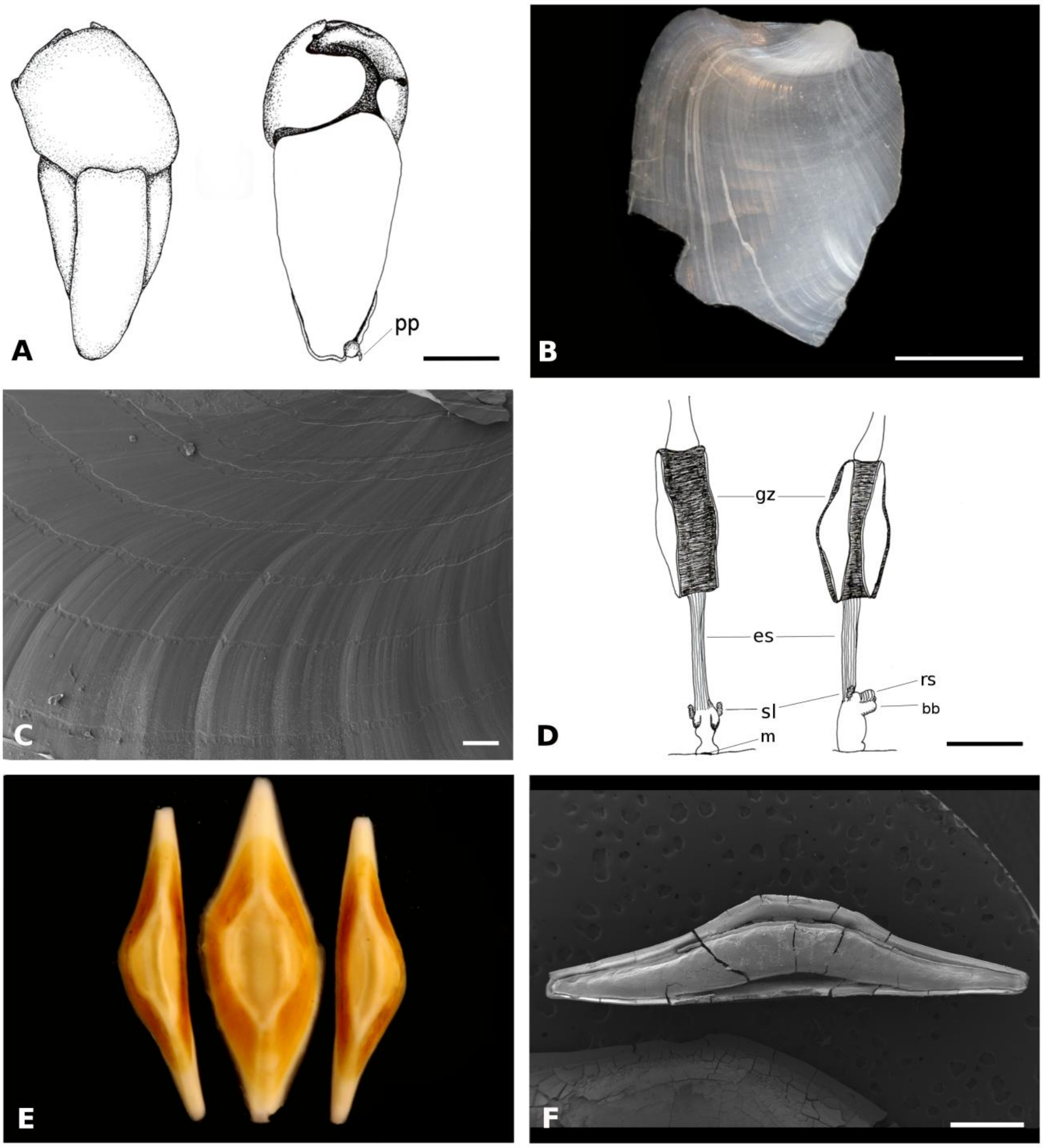

Figure 4.16, *Philine* sp.7 (Philippines, IM-2009-4341, H = 23mm) A, Dorsal (left image) and ventral view(rigth image) illustration of complete animal. B, Apical part of shell. C, SEM of apical part of shell. D, Dorsal (left image) and lateral view (rigth image) illustration of foregut. E, Active surface of gizzard plates. F, Inactive surface of paired lateral plate. Abbreviations: pp, everted penial papilla. gz, gizzard, es, esophagus. bb, buccal bulb. sl, salivary glands. rs, Radular sack m, mouth.. Scale bars:. A,BD = 5 mm, C = 100 µm, F = 1 mm.

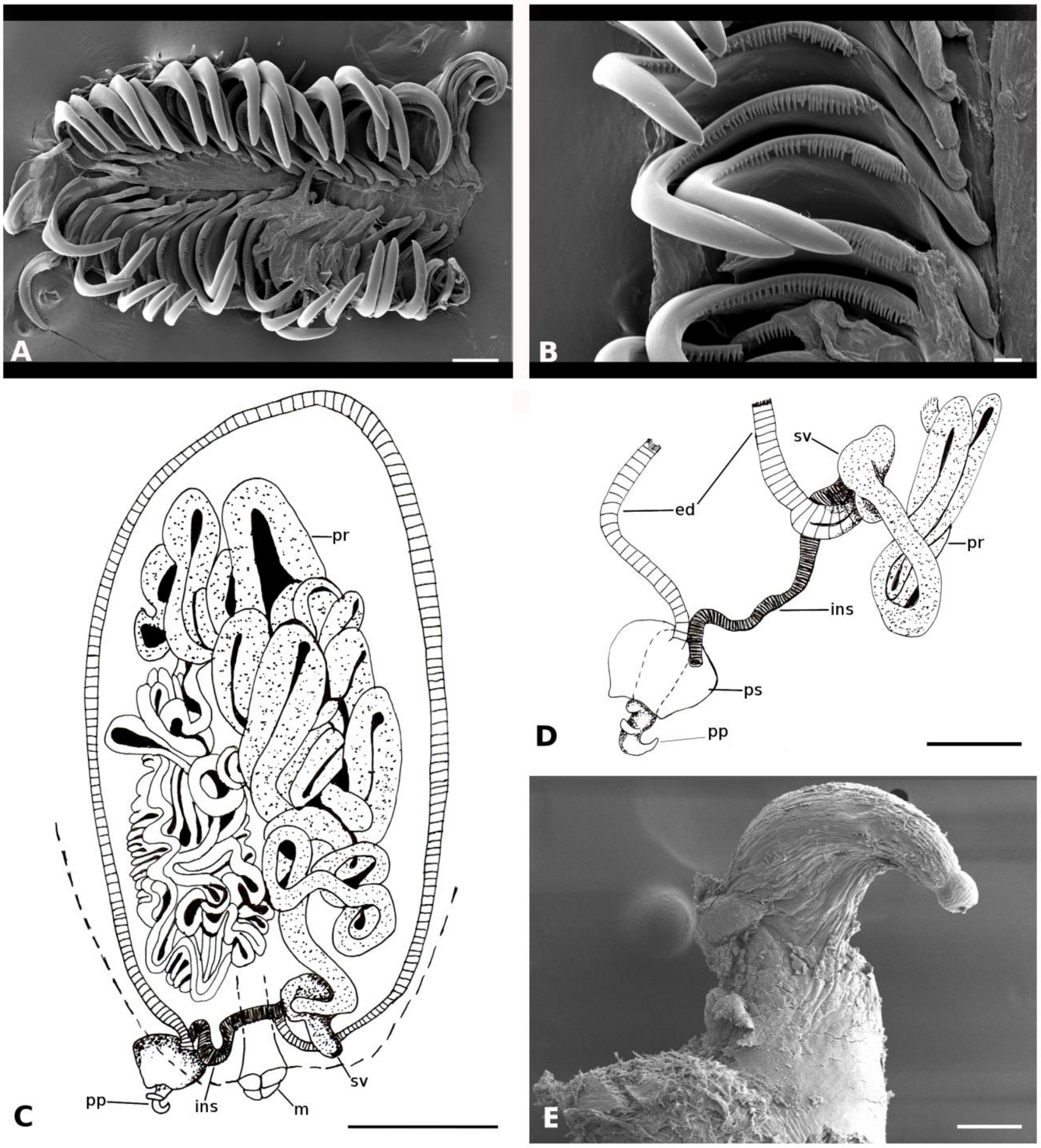

Figure 4.17 ***Philine*** **sp.7** (Philippines, IM-2009-4341, H = 23mm) A, SEM of radula. B,SEM detail of radula. C, male reproductive system. D, detail of male reproductive system. E, Penial papilla. Abbreviations: m, mouth. pp, penial papilla. ps, penial sheat. ins, incurrent sperm duct(groove). ed, ejaculatory duct. sv, seminal vesticle (seminal sac). pr, prostate. Scale bars: A = 100 μm B = 20 μm C = 2,5 cm D = 1 mm, E = 100 μm

Philinidae Clade 2 (*Philinorbis)*

Synopsis: Shell concave-flat, plate-like, internal, transparent, smooth, spiral striae in the form of slightly raised fields when present. Round to rhomboid cephalic shield, usually lobed posteriorly. Posterior lobe usually extends beyond shell apex, often long. Rachidian tooth absent, inner lateral tooth with smooth inner edge, outer lateral teeth present. Salivary glands usually present dorsally on buccal bulb. Muscular buccal bulb, gizzard reduced, relatively small gizzard plates, plates equal and chitinous. Simple tubular prostate, usually conical penial atrium, Peneal atrium imbedded in tissue.

PHILINE SP.12

(FIGS 4.18 A-F, 4.19 A-F)

Diagnosis: Shell concave-flat, plate-like, internal, transparent, smooth, with micro-structural spiral striae consisting of slightly raised fields. Round cephalic shield, lobed posteriorly. Posterior lobe extending just beyond shell margin. Rachidian tooth absent, inner lateral tooth with smooth inner edge, outer lateral teeth present. Short salivary glands present dorsally on buccal bulb. Muscular buccal bulb, gizzard not surrounded by muscular fibres, relatively small, equal, gizzard plates. Simple tubular prostate and quadriobed penial papilla, inside a round penial envelope,; conical penial atrium, ejaculatory duct short.

Material examined: 1 spec. (dissected and sequenced), New Caledonia MNHN, Paris IM-2009-4316, H = 47 mm.

Shell (4.18 C-D): H = ca. 25.4 mm. Internal, thin; whitish-transparent; plate-like, aperture wide. Shell surface smooth with micro-structural spiral striae consisting of raised granulose fields.

Animal (4.18 A-B): Body yellowish-white in preserved specimens. Posterior lobe extending just beyond shell margin. Cephalic shield round, lobed posteriorly, median groove absent. Narrow parapodial lobes, visible dorsally. Muscular buccal bulb. Salivary glands short with free distal end. Short salivary glands present dorsally on buccal bulb.

Radula (4.19 A-C): Radular formula 13–14 x 2.1.0.1.2. Rachidian tooth absent. Inner lateral teeth with narrow base, broad, curved with rounded tips, inner edge smooth. Outer lateral teeth smaller, curved with rounded tip.

Gizzard (4.18 E-F, 4.19 E-F):, Gizzard small, reduced and not muscular, with crop present anteriorly; brown gizzard plates of equal size and shape.

Male reproductive system (4.19 D): Prostate long and tubular, Penial atrium conical, penial atrium imbedded in tissue. Penial papilla quadrilobed, with tree short and one long thin lobe, inside bulbous penial envelope.

Ecology: Know from 628 mm likely on muddy-sand (as mud and sand were found in the digestive system).

Distribution: North of New Caledonia, between Surprise Island and Pott island (18°50′S–163°14′E).

Remarks: This single specimen likely belongs to an undescribed species. The internal anatomy of this species hints a close phylogenetical relationship to *Philine alba* Mattox 1958 (Mattox, 1958 page 99-101, Plate 33, 34; Price et al (2011) page 10-11, Fig 5, 6), *P. albioides* Price, Gosliner and Valdès. 2011 (Price et al (2011) page12-13, Fig 7,), *Philine* sp. 13, and *Philine* sp 14. Philine sp. 12 differ from *P. alba* and *P.albioides* , *Philine* sp. 13, and *Philine* sp 14 externally by having a more rounded rather than elongate shape, additionally the cephalic shield of Philine sp.12 is posteriorly lobed whereas in *alba*, *P.albioides* and *Philine* sp.14 it is not lobed. The penial papilla is quadrilobed but with smaller lobes than in *P. alba* but more complex than in *P. albioides* and *Philine* sp.14. The bulbous penial envelope of *Philine* sp.12, is not found in the other species. The male reproductive system of *Philine* sp.12 differ from *Philine* sp.13 in that it is not completely imbedded in the tissue and does not have penial glands or a long narrow penial papilla. The inner lateral teeth of the radula of *P. alba* has reduced denticulation whereas *Philine* sp.12 have smooth inner lateral teeth. The raula teeth of *Philine* sp. 12 is narrower and sharper than in *P. albioides* and Philine sp. 14. Regarding the distinction from *Philine* sp. 13, and *Philine* sp 14, this is supported by the molecular phylogenetic results (PP = 1; Tree 4.5). Philinidae clade 2 had low success in amplification of COI, however the interspeciffic p-distance of 16S rRNA between this species and *Philine* sp. 13 (4.7%) and *Philine* sp 14 (4.7%) and support their distinction.

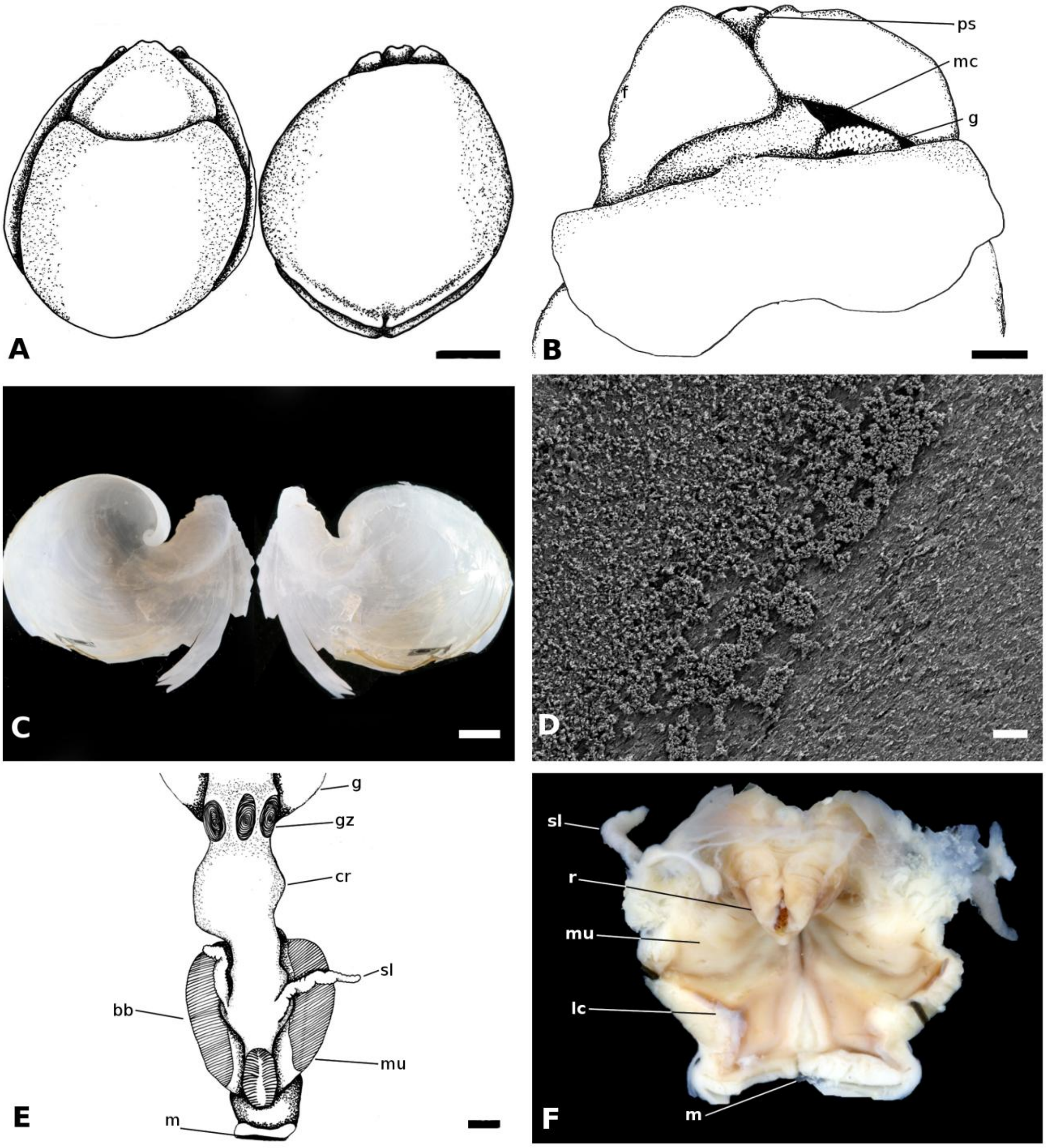

Figure 4.18 ***Philine* sp.12** (New.Caledonia IM-2009-4316, H = 47mm) A, Dorsal (left image) and ventral view (rigth image) illustration of complete animal. B, mantle cavity. C,Ventral (left image) and dorsal view (rigth image) image of complete shell. D, Micro structure, SEM of shell surface. E, illustration of foregut. F, Dorsal view of opened buccal bulb. Abbreviations: mu, Dense musculature. gz, gizzard. g, gill, mc, mantle cavity. f, foot. bb, buccal bulb. sl, salivary glands. r, radula. ps, posterior shield cr, crop m, mouth. lc, labial cuticle. Scalebars: A = 1cm, B = 3.3mm, C = 4mm, D = 10µm, E = 2.5mm.

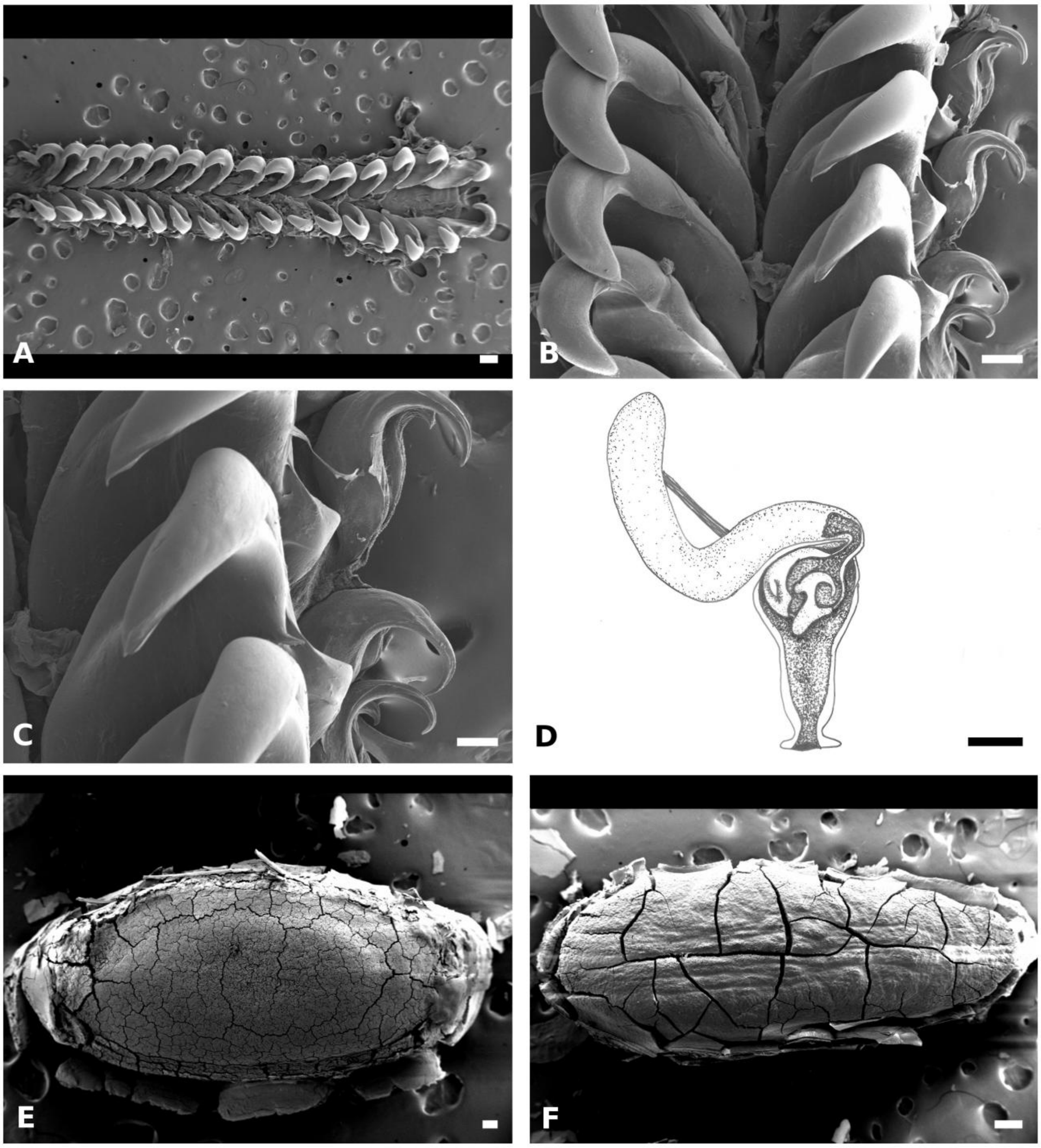

Figure 4.19 ***Philine*** **sp. 12** (New.Caledonia IM-2009-4316, H = 47mm) A, SEM, radula. B,C, SEM, detail of radula. D, Male reproductive system. E, Active surface of gizzard plate. F, Inactive surface of gizzard plate. Abbreviations: pr, prostate. mu, muscle. pa, penial artrim. pp, penial papilla. ga, genital aperture. Scalebars: A = 200µm, B = 100µm, C = 50µm, D = 2mm, E = 100µm, F = 200µm.

***PHILINE* SP.13**

(FIGS 4.20 A-F, 4.21 A-D)

Diagnosis: Shell flat, plate-like, internal, transparent, smooth, with no spiral striae. Rhomboid-squarish cephalic shield, forming lobes posteriorly. Posterior lobe long, extending beyond shell apex. Rachidian tooth absent, inner lateral tooth with smooth inner edge, outer lateral teeth present. Long salivary glands connected to buccal bulb and crop. Muscular buccal bulb. Gizzard reduced, gizzard plates absent. Simple tubular prostate ending in a globular seminal vesicle; conical penial papilla with penial glands around basis; conical penial atrium connected to a prostatic atrium; penial atrium, entire male reproductive system deeply imbedded in tissue anterior of body cavity.

Barcode: KF877715

Material examined: 1 spec. (dissected and sequenced), the Philippines, MNHN, Paris IM-2009-4369, H = 76 mm .

Shell (4.20 B): H = 27.5 mm, Internal, thin; whitish-transparent; plate-like, aperture wide. Shell surface smooth with no spiral striae; growth lines present.

Animal (4.20 A): Body yellowish in preserved specimens. Cephalic shield rhomboid to squarish, lobed posteriorly, median groove absent. Posterior lobe long, extending beyond shell apex. Narrow muscular parapodial lobes, visible dorsally. Thick muscular buccal bulb. Salivary glands long, attached at both ends in buccal bulb and crop.

Radula (4.21 A-D): Radular formula 14 x 2.1.0.1.2. Rachidian tooth absent. Inner lateral teeth with narrow base, broad, curved with rounded tips, inner edge smooth. Outer lateral teeth smaller, curved and sickle shaped with pointed tip.

Gizzard: Absent,

Male reproductive system (4.20 E): Simple tubular prostate ending in globular seminal vesicle; conical penial papilla with penial glands around basis; conical penial atrium connected to a prostatic atrium; entire male reproductive system deeply imbedded in tissue anterior of body cavity. Neither penial or prostatic atrium extends into the body cavity.

Ecology: Known from 509 m likely on muddy-sand, (as mud and sand were found in the digestive system). An unidentified Aplacophora was found in the crop.

Distribution: North East of Lamon Bay, the Philippines (Philipine Sea), (14°48′N–123°08′E).

Remarks: This single specimen likely belongs to an undescribed species. It is conspicuously large and its internal anatomy suggests a close phylogenetic relationship with *Philine alba* (Mattox, 1958), *P.albioides* Price, Gosliner and Valdés 2011), *Philine* sp.12, and *Philine* sp.14. As remarked in discussion of previous species all these species have similar radulae, however the sickle shaped outer lateral teeth of this species is less curved than previously mentioned species, extending from its basis at a straight angle. The internal anatomy and buccal bulb is also similar to the enigmatic genus *Pseudophiline* Habe 1976, but differ from *P. hayashii* Habe 1976 (Kitao and Habe, 1982; page 63, Fig 3, 4, 5) in having longer salivary glands, gizzard plates, and much larger outer lateral teeth. The male reproductive system is more complex than in previously mentioned species. The entire system is contained within the tissue anterior of the body cavity, whereas in the previously discussed species this usually only concern the penial atrium and the prostate is found in the body cavity. It also differs in that the long narrow prostate is contained within a prostatic atrium and connects proximally to a seminal vesicle. The penial papilla is long and conical and connects posteriorly to the seminal vesicle. The penial papilla carries numerous nodulous penial glands not shared by similar species.

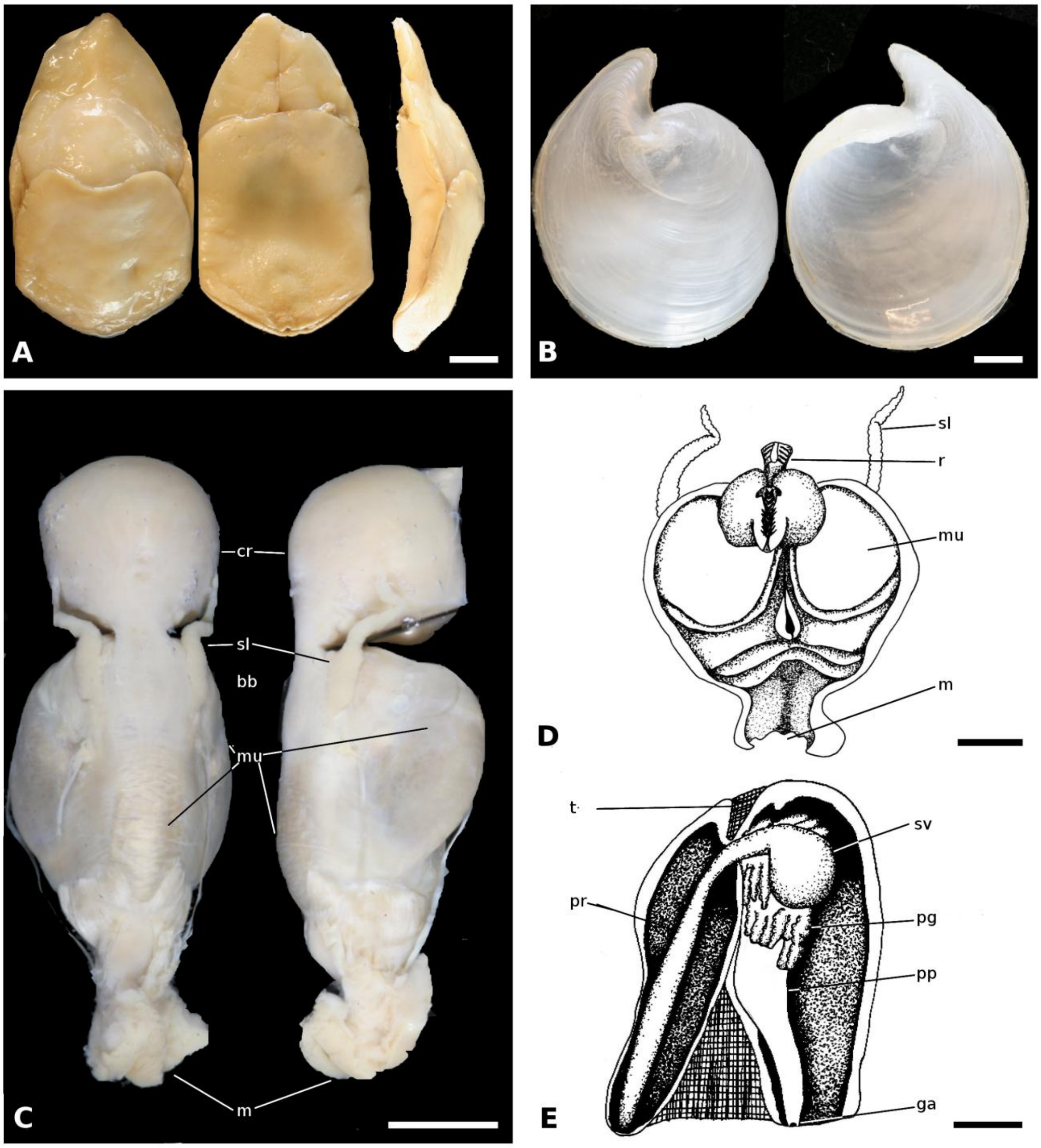

Figure 4.20 ***Philine*** **sp.13** (Phillippines IM-2009-4369, H = 76mm) A, Left dorsal (left image) and ventral (middle image) and lateral view (right image) of whole animal. B, Dorsal (left image) and ventral view (rigth image) of complete shell. C, Dorsal (left image) and lateral view (right image) of foregut. D, Dorsal view illustration of opened buccal bulb. E, Illustration of male reproductive system. Abbrevations: m, mouth. mu, dense muscle. cr, crop. r, radula. bb, buccal bulb. sl, salivary glands. pa, penial atrium. pr, prostate. sv, seminal vesticle. pg, penial gland. pp, penial papilla. ga, genial aperture. t, dense tissue. Scale bars: A = 1.5cm, B = 5mm, C = 5.4mm, E = 1.25mm.

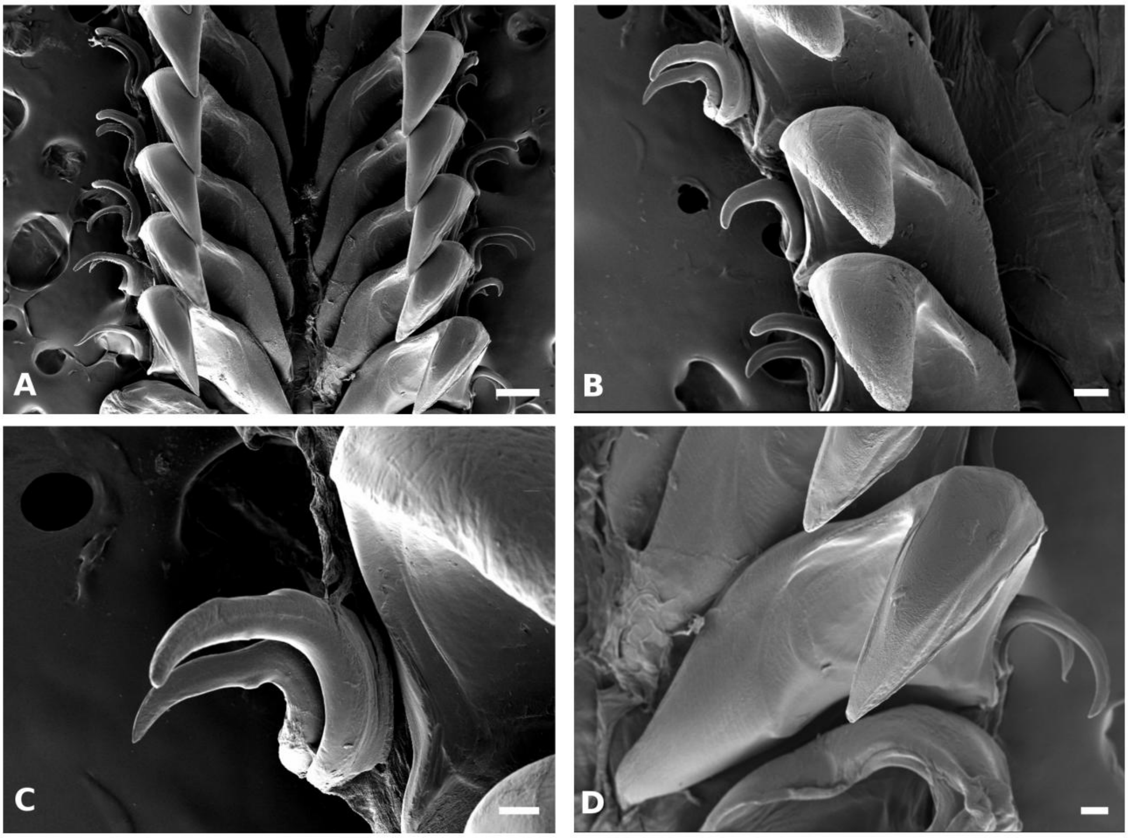

Figure 4.21 ***Philine*** **sp.13** (Philippines IM-2009-4369, H = 76mm) A, SEM of radula. B, SEM, detali of radula. C, SEM, detail of outer lateral teeth . D, SEM, detail of inner lateral tooth. Scale bars: A = 200µm, B = 100µm, C = 50µm, D = 50µm.

PHILINE SP.14

(FIGS 4.22 A-F, 4.23 A-F)

Diagnosis: Shell flat, concave ,plate-like, internal, transparent, smooth, with few spiral striae. Rhomboid-squarish cephalic shield. Posterior lobe long, extending beyond shell apex. Rachidian tooth absent, inner lateral tooth with smooth inner edge, outer lateral teeth present. Muscular buccal bulb. Salivary glands not present. Gizzard not surrounded by muscular fibres, relatively small gizzard plates, one slightly oblong unpaired gizzard plate, and two paired oval gizzard plates with raised conical central part of active surface. Simple bulbous prostate and trilobed penial papilla; conical penial atrium.

Barcode: KF877716

Material examined: 1 spec. (dissected and sequenced), the Philippines MNHN, Paris IM-2009-4353, H = 11mm.

Shell (4.22 E): H = 4,6 mm. Internal, thin; whitish-transparent; concave, plate-like, aperture wide. Shell surface smooth with spiral striae formed by broad straight indentations separated by narrow raised fields. The shell was partially broken.

Animal (4.22 A): Body white in preserved specimens. Cephalic shield rhomboid-squarish, tapering posteriorly, median groove absent. Posterior lobe long, extending beyond shell apex. Narrow muscular parapodial lobes, visible dorsally. Salivary glands absent.

Radula (4.23 F): Radular formula 14 x 2.1.0.1.2. Rachidian tooth absent. Inner lateral teeth with narrow base, broad, curved with rounded tips, inner edge smooth. Outer lateral teeth smaller, curved with rounded tip.

Gizzard (4.22 B-C, F, 4.23 F):, Gizzard small, not muscular, crop present anteriorly; unpaired gizzard plate narrower than paired plates, paired plates oval, central part of active surface conical slightly curved backwards.

Male reproductive system (4.22 D): Prostate short and bulbous; penial atrium conical, penial papilla tri-lobed, with two short and one long thin lobe.

Ecology: Known from 543 m likely lives on muddy-sand (as mud and sand were found in the digestive system).

Distribution: Bohol Sea, between Siquijor and Mindanao Island, the Philippines (8°53′N–123°34′E),.

Remarks:

This single specimen likely belongs to an undescribed species. The internal anatomy of this species shows that it is closely related with previously discussed *Philine alba* (Mattox, 1958 page 99-101, Plate 33, 34; Price et al (2011) page 10-11, Fig 5, 6), *Philine* sp.12, *Philine* sp.13 and *Philine* sp.14. It differs from these species in not having domed smooth gizzard plates, but raised central fields which are more similar to *P. albioides* (Price et al. (2011) page13-14, Fig 7, 8) however the raised central part of the active surface is more pointed and curves slightly backwards. The male reproductive system is also more similar to *P. albioides* as the penial papilla has the same general shape of one long and one short lobe, but does however have a shorter and straighter prostate. The unique spiral striae that forms narrow raised lines in-between deeper broader fields, differentiates this species from the previously mentioned species who all have smooth shells, this feature, similar to the Pacific genus *Philinorbis* Habe 1950 of the Aglajidae and Philine sp. 15. As previously mentioned the molecular analyses show that this species is distinct from the other discussed members of Philinidae clade 2 (PP = 1; Tree 4.5).

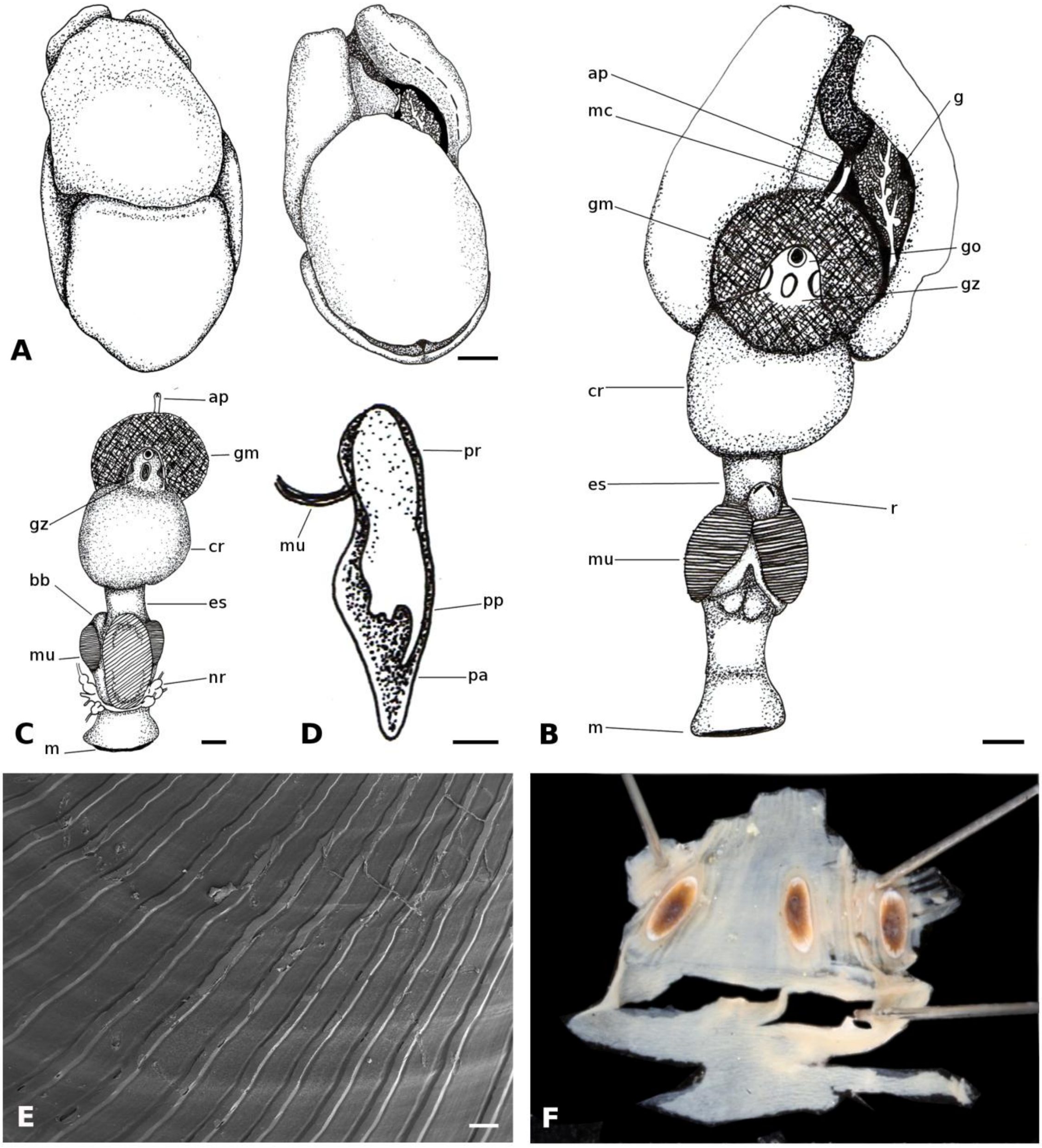

Figure 4.22 ***Philine*** **sp.14** (Philippines IM-2009-4353, H = 11mm) A, dorsal (left image) and ventral view (rigth image) illustration of complete animal. B, ventral view of digestive system and mantle cavity. C, dorsal view of digestive system. D, Male reproductive system. E, SEM of shell surface. F, interior of thin walled gizzard. Abbreviations: ap, anal papilla. gm, gutmass. gu, gut opening. gz, gizzard. cr, crop. es, esophagus. bb, buccal bulb. mu, muscle. nr, nerve ring. m, mouth. pr, prostate. pp, penial papilla. pa, pemial atrium. g, gill. mc, mantle cavity. r, radula. Scale bars: A = 1.25 mm, B,C = 500 µm, D = 170 µm, E = 100 µm.

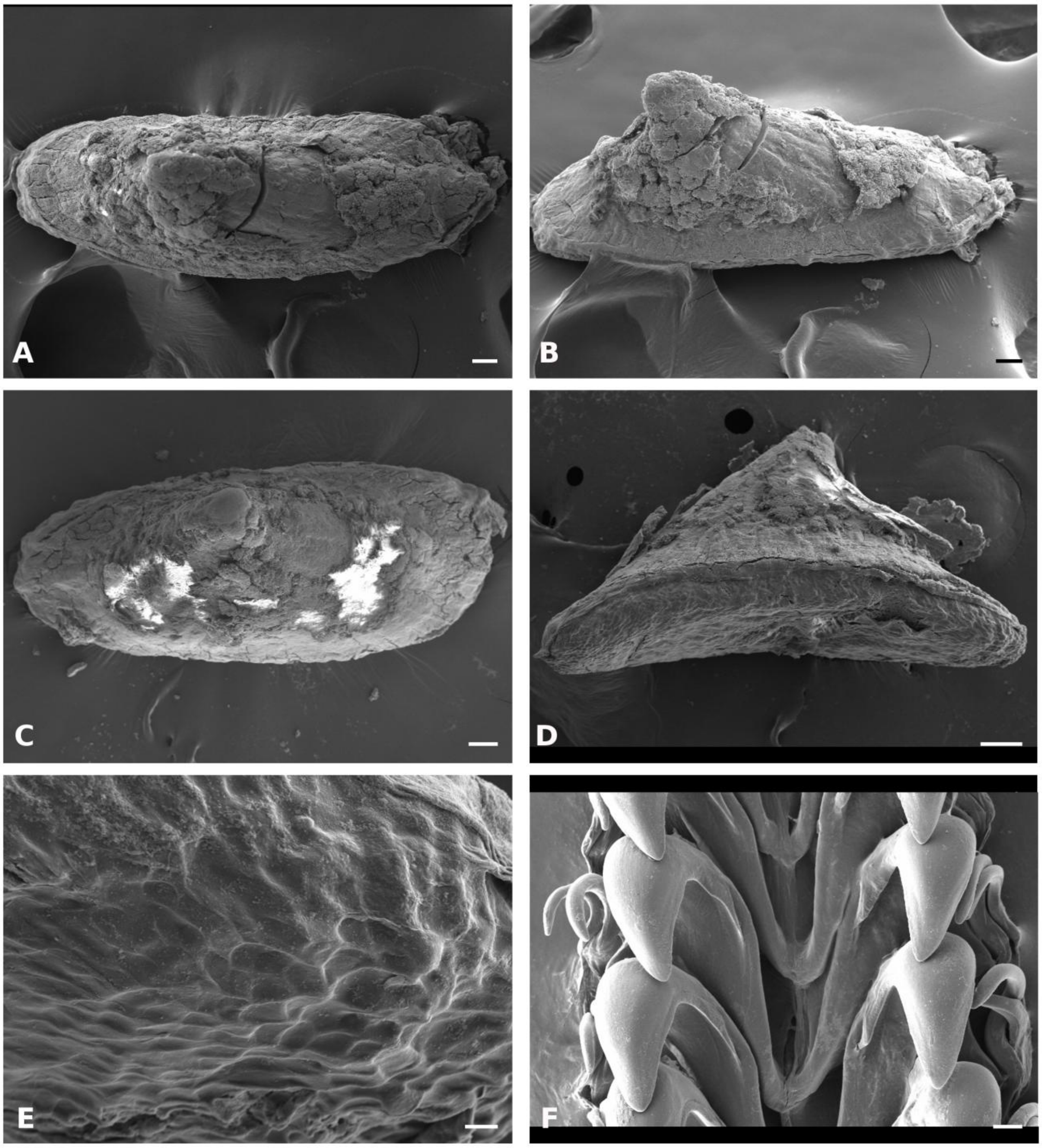

Figure 4.23 ***Philine*** **sp.14** (Philippines IM-2009-4353, H = 11mm) A, SEM of active sufrace unpaired gizzard plate. B, SEM of lateral view of unpaired gizzard plate. C, SEM of active surface of paired gizzard plate. D,SEM of lateral view of paired gizzard plate. E, SEM of microstructure of inactive surface of gizzard late. F, SEM of detail of radula. Scale bars: A, B, C = 33 µm. D = 50 µm. E = 5 µm. F = 20 µm.

PHILINE SP.15

(FIGS 4.24 A-F)

Diagnosis: Shell flat, concave, plate-like, internal, transparent, smooth, with spiral striae of deep straight indentations. Rhomboid-squarish cephalic shield. Posterior lobe long, extending beyond shell apex. Radula absent; muscular buccal bulb. Salivary glands absent. Gizzard not apparent, gizzard plates absent. Simple, tubular prostate, conical penial papilla; penial atrium conical. salivary glands absent.

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Material examined:,1 spec. (dissected and sequenced), Indonesia, MNHN, Paris IM-2009-4340, H = 23 mm.

Shell (4.24 E-F): H = 10 mm., Internal, thin, concave, plate-like; whitish-transparent; aperture wide. Shell surface with spiral striae formed by broad straight indentations separated by narrow raised fields. The shell was partially broken.

Animal (4.24 A): Body brown in preserved specimens. Cephalic shield rhomboid-squarish, tapering posteriorly, median groove absent. Posterior lobe long, extending beyond shell apex. Narrow muscular parapodial lobes, visible dorsally, cephalic shield. Salivary glands absent.

Radula: Absent.

Gizzard: Absent.

Male reproductive system (4.24 B): Simple bulbous and tubular prostate; conical penial papilla; atrium conical.

Ecology: Occurs at 304 m.

Distribution: Between the islands of Flores and Timor, Indonesia (Savu Sea). (8°58′S–123°21′E).

Remarks: This single specimen may belong to an undescribed species. This species is similar to *Philine alba*, *P. albioides* (Price et al. (2011) page13-14, Fig 7, 8), and *Philine* sp.14, but differs from these in having a thicker prostate and a large conical uni-lobed penial papilla extending the length of the penial atrium. It also differs from other similar species in sharing the unique spiral striae of Philine sp.14. It must be emphasised that the studied specimen was damaged, which may explain the lack of gizzard and radula. Molecular phylogenetic data (PP = 1; Tree 4.5) clustered this specimen in Clade 4 together with *Philine* sp.12, *Philine* sp.13, and Philine sp.14, minimum and maximum genetic distance from these species was 1.9%–4.7% (16S *p*-distance) supporting its distinction.

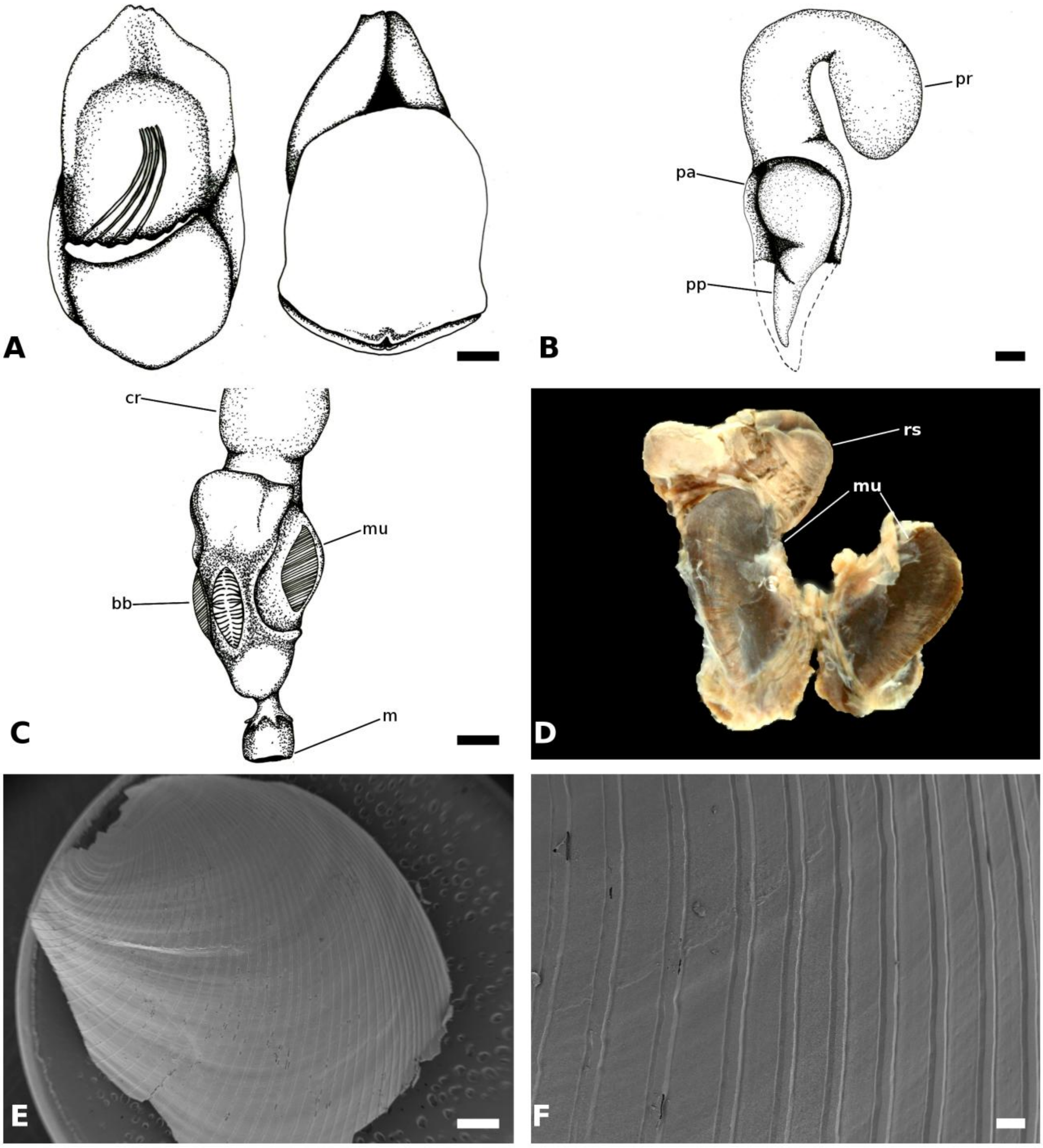

Figure 4.24 ***Philine* sp.15** (Indonesia, IM-2009-4340, H = 23mm) A, Dorsa l(left image) and ventral view(rigth image) illustration of complete animal. B, Illustration of male reproductive system. C, Illustration of foregut. D, Dense muscules of buccal bulb. E, SEM of dorsla view of shell. F, SEM detail of shell sufrace. Abbreviations: mu, Dense musculature. gz, gizzard. g, gill. bb, buccal bulb. rs, radular sack. cr, crop m, mouth. pr, prostate. pa, penial atrium. pp, penial papilla Scalebars: A = 0.5cm, B = 0.25mm, C = 0.66mm, E = 1mm, F = 100µm.

Philinidae Clade 3 (New genus, new family)

Synopsis: Shell globose, to elongate, thick, whitish transparent, smooth, spiral striae with deep fused indentations. Body yellow to white (in preserved spec.), oval cephalic shield, slightly folded. Posterior shield or lobe usually extends far beyond shell apex. Radula may be absent, when present: rachidian tooth present, inner lateral tooth with robust denticulation along inner edge, outer lateral teeth present. Long salivary glands usually present. Muscular buccal bulb, which may be reduced. Gizzard reduced, simple, equal chitinous gizzard plates, usually a large crop; simple chitinous gizzard plates, Simple male reproductive system.

PHILINE SP.8

(FIGS 4.25 A-F, 4.26 A-F)

Diagnosis: Shell globose, thick, internal, transparent, smooth, spiral striae with deep fused indentations. Body yellow white (preserved spec.), oval cephalic shield, slightly folded. Posterior lobe squarish extending beyond shell apex. Radula absent, muscular buccal bulb. Long salivary glands attached in both ends to gizzard and crop. Gizzard reduced , chitinous, simple gizzard spines in anterior gizzard and posterior crop; simple chitinous gizzard plates , moderately calcified on active surface, one oblong unpaired gizzard plate with raised posterior active surface, and two oval paired gizzard plates with raised central active surfaces. nodulous prostate narrow penial atrium, bulbous sperm vesicle.

Barcode: KF877714

Material examined: 1 spec. (dissected and sequenced), the Philippines, MNHN, Paris IM-2009-4361, H = 9mm.

Shell (4.25 B-D): H = 6.7 mm. Internal thick; whitish transparent; globose. Aperture narrow, tapering posteriorly; aperture lip raised over apex on left side forming a short wing. Spiral striae made up of fused indentations; broad raised fields separate spiral striae; between anterior end and mid-length the raised fields contain intermediate spiral striae made up of fused indentations of smaller size.

Animal (4.25 A): Body yellow white in preserved specimens. Cephalic shield oval, slightly folded due to shell margin, median groove absent. Posterior lobe, squarish extending beyond shell apex. Parapodial lobes narrow. Posterior lobe extends beyond shell. Long salivary glands attached in both ends to gizzard and crop.

Gizzard (4.25 E, 4.26 A-F): Gizzard reduced, small gizzard spines of variable size and shape present, large crop present anteriorly to gizzard; large gizzard plates slightly calcified on active surface, raised central fields of active surface, translucent reddish-brown in colour; unpaired central gizzard plate slightly longer than paired plates, raised surface on posterior active side; paired plates oval with raised middle active surface.

Male reproductive system (4.25 F): Nodulous prostate separated from penial atrium and sperm sac.

Ecology: Found at 442 m likely on sand (sand was found in the digestive system).

Distribution: North of Lamon Bay, between Luzon island and Polillo island, the Philippines (15°04′N–121°41′E).

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Remarks: This single specimen corresponds likely to an undescribed species. It was not obvious whether the shell was internal or partially external as it is here interpreted. In fact the mantle could have been ripped apart during sampling. Only the study of additional specimens can clarify this feature. The gizzard plates are similar to other *Philine* designated as “less derived” in older studies (Cylichnidae-like; Rudman, 1972; 1978), however they show some deviation from the usual smooth oval plates as the central part of the active surface is raised and seem to be lightly calcified on the active surface. *Philine* sp.8 retains gizzard spines, which are simple and of slightly different sizes and shapes. The spines are loose and fall out easily, but this may be an effect of fixation. These spines are much simpler than those found in other cephalaspids genera (e.g. Bullidae; Malaquias and Reid, 2008). Thereduced buccal bulb and gizzard with a large anterior crop is similar to *Philine* sp.10 and *P. falklandica* Powell 1951 (Rudman (1972) page 173, Fig 1, A). The shell is similar to that of *P. kawamurai* Habe 1958, (Okutani. 2000, page 750, Plate 375, 4), however compared to *Philine* sp.8 the previous species has a shell where the upper lip does not extend beyond the apex and the anterior part is more elongate (Okutani, 2000). The shell is also similar to the phylogenetically closely related species *Philine* sp.9, where the shell seems to be equally partially external but with a wing that does not extend beyond the apex. Moreover, *Philine* sp.9 lacks the raised central fields of the of the gizzard plates of *Philine* sp.8 and lacks gizzard spines. *Philine* sp.8 forms a monophyletic clade with Philine sp. 9 with maximum support (PP = 1; Tree 4.5) in the bayesian analysis of all genes, the interspeciffic p-distance between these species is 14.2% confirming they are separate species.

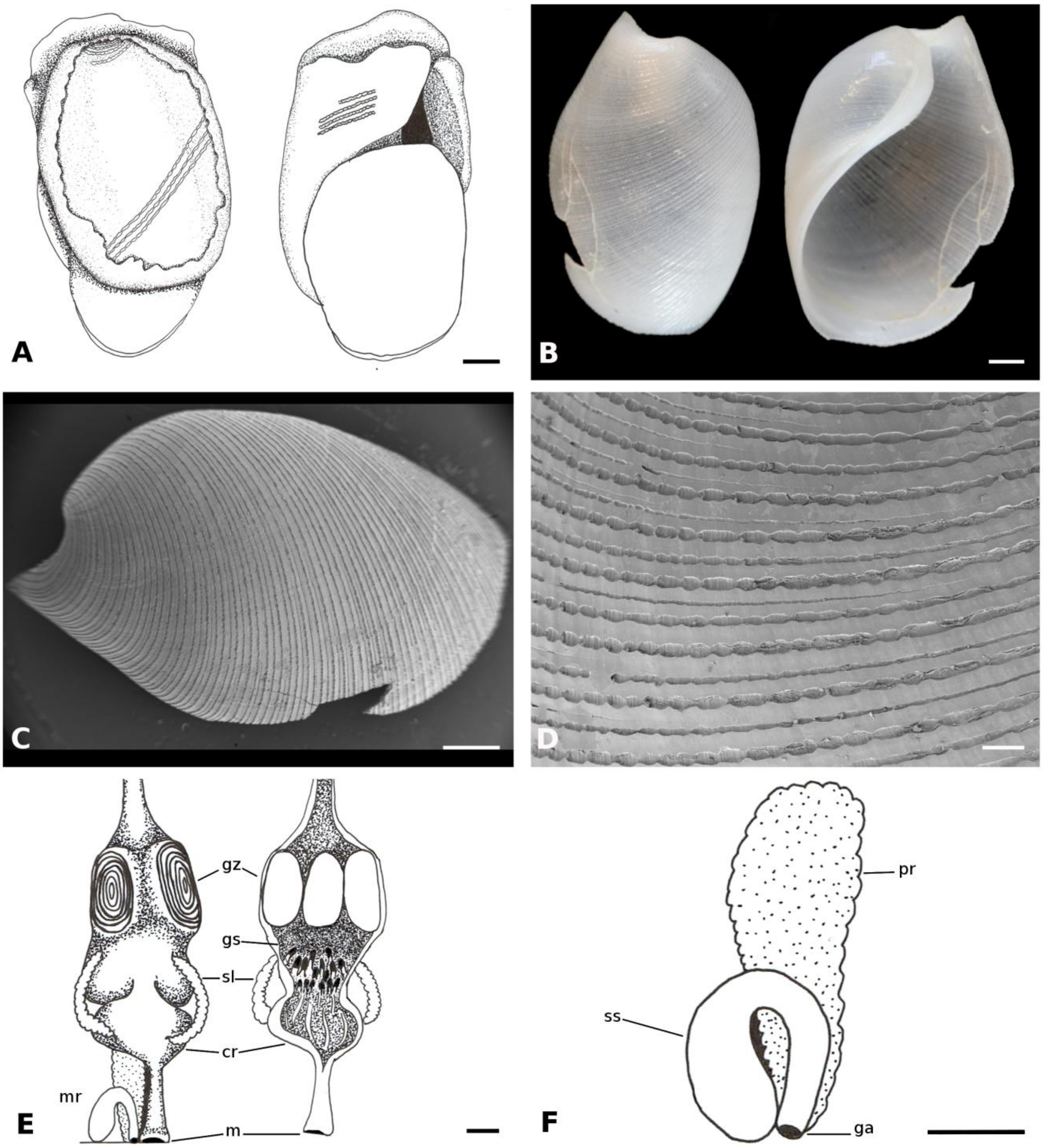

Figure 4.25, *Philine* sp.8 (Philippines IM-2009-4361, H = 9mm) A, Dorsal(left image) and ventral view (rigth image) illustration of complete animal. B, Dorsal (left image) and ventral view(rigth image) of complete shell. C, SEM of whole shell. D, SEM of shell sculpture. E, Dorsal exterior view (left image) and dorsal interior view (rigth image) illustration of foregut. F, male reproductive system. Abbreviations: gz, gizzard plates, gs, gizzard spines, sl, salivary glands. cr, crop. m, mouth. mr, male reproductive system.. ss, sperm sack pr, prostate. ga, genial aperture. Scale bars: A,B, C = 1mm, D = 200µm, E,F = 0.5mm.

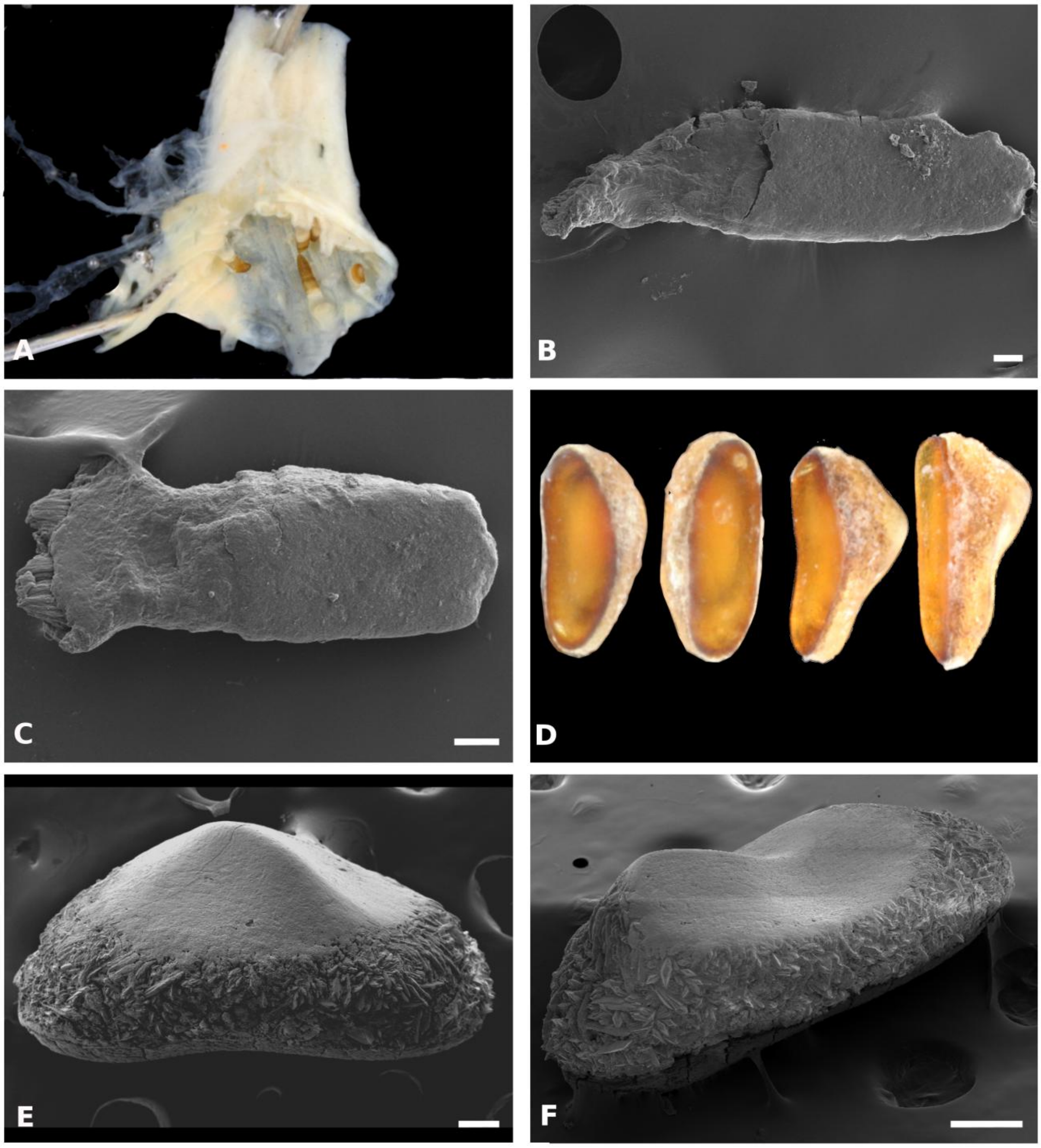

Figure 4.26 *Philine* sp.8 (Philippines IM-2009-4361. H = 9mm) A, ventral view of lower gizzard with spines. B, C, gizzard spines. D, inactive surface of gizzard plats(left image) lateral view of gizzard plates (rigth image). D, SEM of lateral view of paired gizzard plate. E, Posterio lateral wiev of unpaired central plate. Scale bars: B, C = 20µm. E = 100µm, F = 200µm.

PHILINE SP.9

(FIGS 4.27 A-F, 4.28 A-F)

Diagnosis: Shell globose, thick, internal, whitish transparent, smooth, spiral striae of fused indentations. Body yellow white (preserved spec.). Oval cephalic shield, slightly folded. Posterior lobe does not extend beyond apex of shell. Radula absent, buccal bulb reduced. Long salivary glands attached in both ends to anterior and posterior end of buccal bulb. Gizzard reduced, chitinous gizzard plates, one oblong unpaired gizzard plate, and two oval paired gizzard plates. Simple prostate fused with penial atrium.

Barcode: KF877713

Material examined: 1 spec. (dissected and sequenced), the Philippines MNHN, Paris IM-2009-4362, H = 5.8 mm.

Shell (4.27 B, D-F): H = 5.5 mm. Internal,, thick; whitish-transparent; globose, Aperture narrow, tapering posteriorly; aperture lip raised over apex on left side forming a blunt wing. Spiral striae made up of fused indentations; broad raised fields separate spiral striae; between anterior end and mid-length the raised fields contain intermediate spiral striae made up of fused indentations of smaller size.

Animal (4.27 A): Body yellow white in preserved specimens. Cephalic shield oval, slightly folded due to shell margin, squarish posteriorly, median groove absent. Posterior lobe does not extend beyond apex of shell. Buccal bulb reduced, Long salivary glands attached in both ends to anterior and posterior end of buccal bulb.

Gizzard (4.27 C, 4.28 B-F): Gizzard not muscularised with large crop anteriorly located; , gizzard plates translucent reddish-brown, unpaired central gizzard plate slightly longer than paired plates, paired plates oval.

Male reproductive system (4.28 A): Simple prostate fused with penial atrium, large genital aperture.

Ecology: Known from 380 m likely on sandy-mud (sand was found in the digestive system).

Distribution: Philippine Sea, North East of Lamon Bay, Philippines (14°48′N–123°43′E).

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Remarks: This unique specimen likely belongs to an undescribed species. Externally this species resembles *Philine* sp.8 as in the latter species it was not obvious whether the shell was internal or partially external because the mantle could have been ripped apart during sampling. Anatomically this species differs from *Philine* sp.8. As highlighted before the shell is similar to the phylogenetically closely related *Philine* sp.8 but the wing does not extend beyond the apex. *Philine* sp.9 lacks the pronounced points present in the gizzard plates of *Philine* sp.8 and has no trace of gizzard spines. The male reproductive system also differ in that the prostate and penial atrium is fused, thick and much smaller than the system found in *Philine* sp.8, it also lacks a nodulous prostate and apparent sperm sack. The lack of a nodulous prostate gland may be due to fixation artefacts, but this cannot be verified until more specimens are found ad investigated. As referred in the Remarks' section of *Philine* sp.8 the COI *p*-distance between these two species is 14.2%.

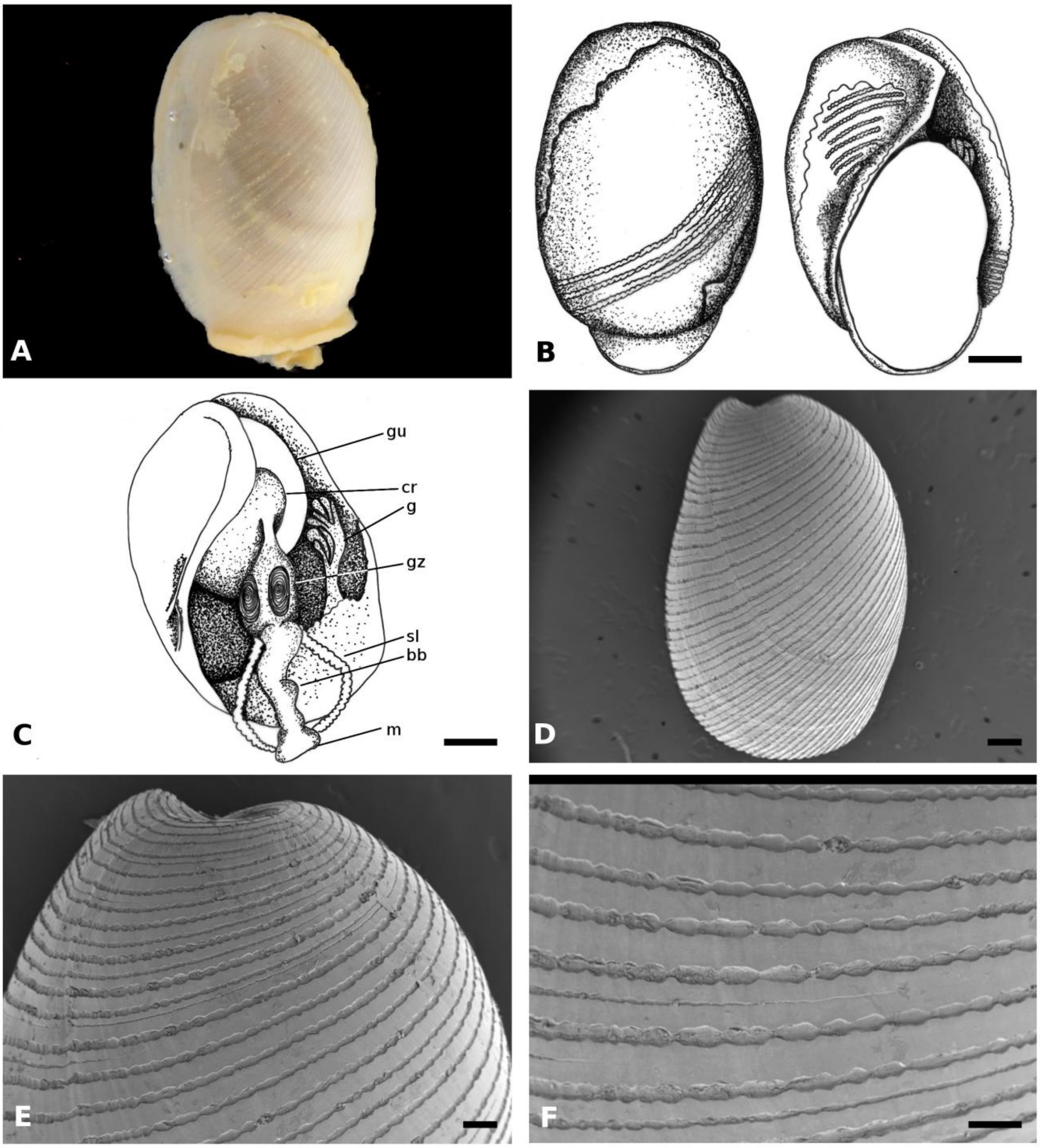

Figure 4.27 ***Philine*** **sp.9** (Philiååines IM-2009-4362, H = 5.8mm) A, Dorsal view of complete animal. B, Dorsal (left image) and ventral view (rigth image) illustration of complete animal. C, Illustration of internal anatomy with digestive system and gill. D, SEM of shell surface. E, SEM apex of shell. F, SEM, detail of shell surface. Abbreviations: gz, gizzard. g, gill. bb, buccal bulb. sl, salivary glands. cr, crop m, mouth. gu, gut. Scalebars: B = 0.83mm, C = 0.85mm, D = 0.5mm, E = 100µm, F = 200µm.

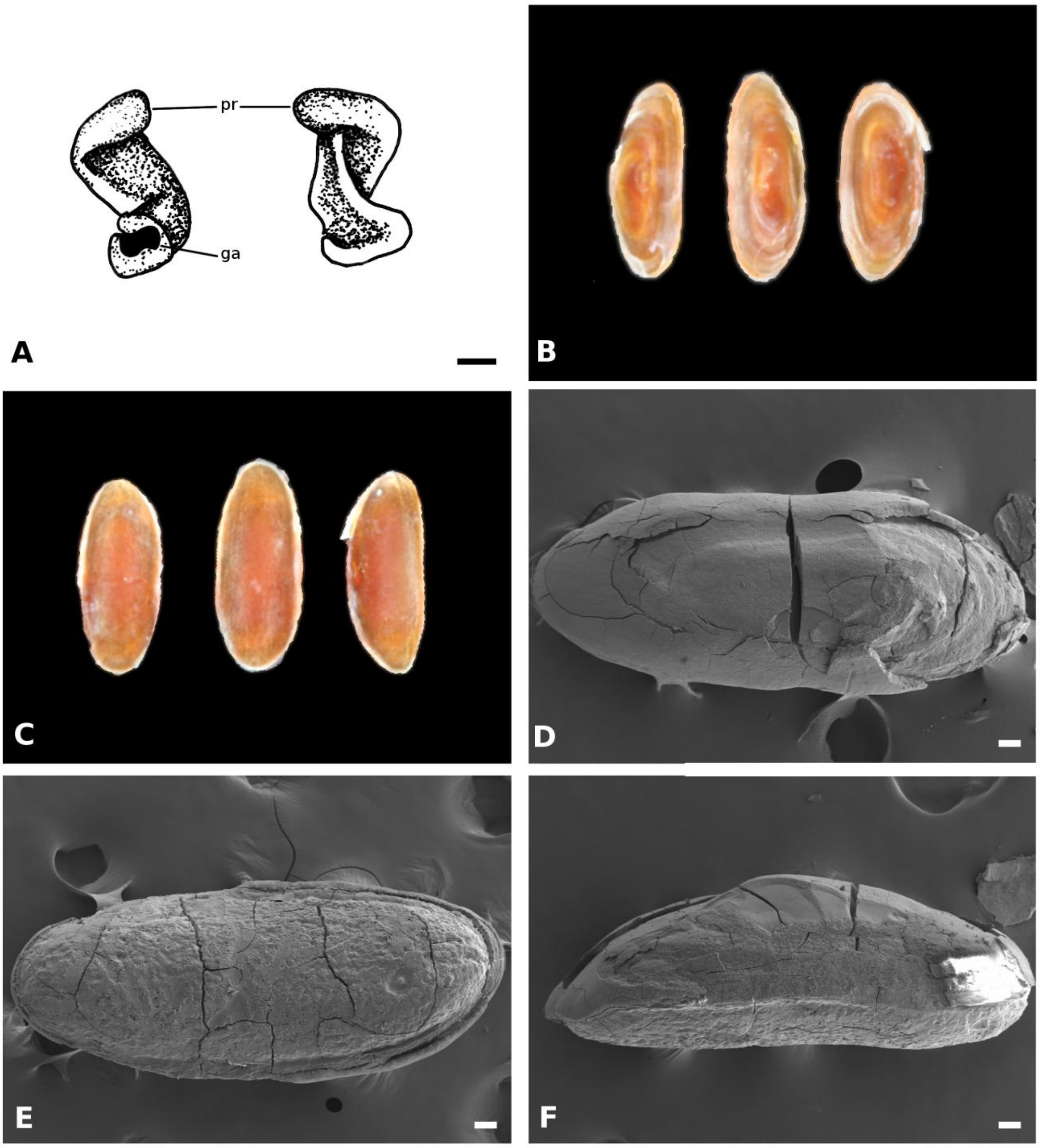

Figure 4.28 ***Philine* sp.9** (Philippines IM-2009-4362. H = 5.8mm) A, Dorsal (left image) and ventral view (rigth image) illustration of male reproductive system. B, Dorsal view of gizzard plates. C, ventral view of gizzard plates. D, SEM of active surface of gizzard plate. E, SEM of inactive surface of gizzard plate. F, SEM, lateral view of gizzard plate. Abbreviations: pr, prostate. ga, genital aperture. Scalebars: A = 160µm, D,E,F = 50µm.

PHILINE SP.10

(FIGS 4.29 A-F, 4.30 A-F)

Diagnosis: Shell internal, white, large, solid, wide anteriorly, narrow posteriorly, cylindrical, widest in middle part, spiral striae of fused pits. Body yellowish-white (preserved spec.), oval cephalic shield. Posterior lobe does not extend beyond apex of shell. Rachidian tooth present, inner lateral tooth with robust denticulation along inner edge, outer lateral teeth present. Long salivary glands attached in both ends to buccal bulb and crop. Muscularised buccal bulb. Gizzard not heavily muscularised, oval smooth gizzard plates, with flattened active surface, unpaired gizzard plate oblong, two paired plates. Male reproductive system small; bulbous penial papilla and penial atrium; comparatively large prostate. Salivary glands long, attached at both ends.

Barcode: KF877712

Material examined: 1 spec. (dissected and sequenced), New Caledonia, MNHN, Paris IM-2009-4372, H = 9.2 mm.

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Shell (4.29 B-C): H = 8 mm. Internal, large, solid, white, cylindrical; raised lateral lip of equal height to apex; aperture widest anteriorly, narrowing posteriorly; Spiral striae present formed by chains of rounded pits fused together, in parts main spiral striae intercalated by thinner striae.

Animal (4.29 A): Body white in preserved specimens. Cephalic shield oval. Posterior lobe does not extend beyond apex of shell. Parapodial lobes short, not visible dorsally. Long salivary glands attached to buccal bulb and crop. Buccal bulb well developed and muscularised. Long salivary glands attached in both ends to buccal bulb and crop.

Radula (4.30 C-F): Radular formula 15 x 1.1.1.1.1. Rachidian tooth present, trapezoidal in shape, two simple lateral denticules, one miniscule central denticle; inner lateral teeth, triangular, with narrow base, curved with sharp tips, inner edge robustly denticulate with 4–6 denticules, two innermost fused and leaf-like. Outer lateral teeth long, thick, sharp and curved.

Gizzard (4.29 D-F,4.30 A): Gizzard reduced, gizzard plates small, oval, with flattened central portion of active surface, unpaired gizzard plate longer and narrower than paired plates. Large crop present anteriorly to gizzard.

Male reproductive system (4.30 B): Small, prostate simple and bulbous, same size as penial atrium, penial papilla bulbous.

Ecology: Occurs at 407 m likely on muddy-sand (as clay-like particles and sand grains were found in the animal).

Distribution: Between Surprise and Pott Island, New Caledonia (19°00′S–163°14′E).

Remarks: This single specimen likely belongs to an undescribed species. The shell of *Philine* sp. 10 most closely resembles *Philine cumingii* Adams 1862 as described by Valdés (2008). However, the aperture of *P. cumingi* is wider anteriorly while *Philine* sp.10 has comparatively straighter sides and is more cylindrical. In *P. cumingii* the lip of the shell forms a wing that extends beyond the apex (Valdés, 2008), while in *Philine* sp.10 this wing is of equal height as the apex. Notable differences between these two species are: The active surface of the gizzard plates in *P. cumingii* is domed (Valdés, 2008: Page, 715, Fig. 63, E), whereas the gizzard plates of *Philine* sp.10 has a flattened central field. In the denticulation of the inner lateral teeth, *P. cumingii* lacks the prominent cusp and coarser denticulation of *Philine* sp.10 (Valdés, 2008: Page, 715, Fig. 63, F). In the penial papilla of *P. cumingii* the prostate and penial papilla are small and simple and contained within a common duct (Valdés, 2008: Page, 714, Fig. 62, C), whereas *Philine* sp.10 have clearly separate prostate and penial atrium and a large conical penial papilla.. The radula of *Philine* sp.10 resembles that described by Valdés' (2008) under the name "*Philine* sp.2" (Valdés, 2008: Page, 725, Fig. 69E) but the rachidian tooth is squarish (instead of rounded) and has less denticules. Also, the outer laterals of "*Philine* sp.2" are straight whereas those of *Philine* sp.10 are curved, nothing is known about the internal soft anatomy of "*Philine* sp.2" as all specimens investigated by Valdés (2008) were dried or lacking soft parts. In the bayesian analysis of all genes *Philine* sp.10 clusters with *Philine* sp.8 and *Philine* sp.9 with maximum support (PP = 1; Tree 4.5) noticeable morphological differences is the cylindrical shell of *Philine* sp. 10 versus the globular shell of the aforementioned species, the presence of a developed buccal bulb, a radula and the more complex male reproductive system with a clearly separate prostate and penial atrium and a large conical penial papilla. The interspeciffic p-distance between *Philine* sp.10 to *Philine* sp.8 is 13.9%, an to *Philine* sp.9 is 15.2%,

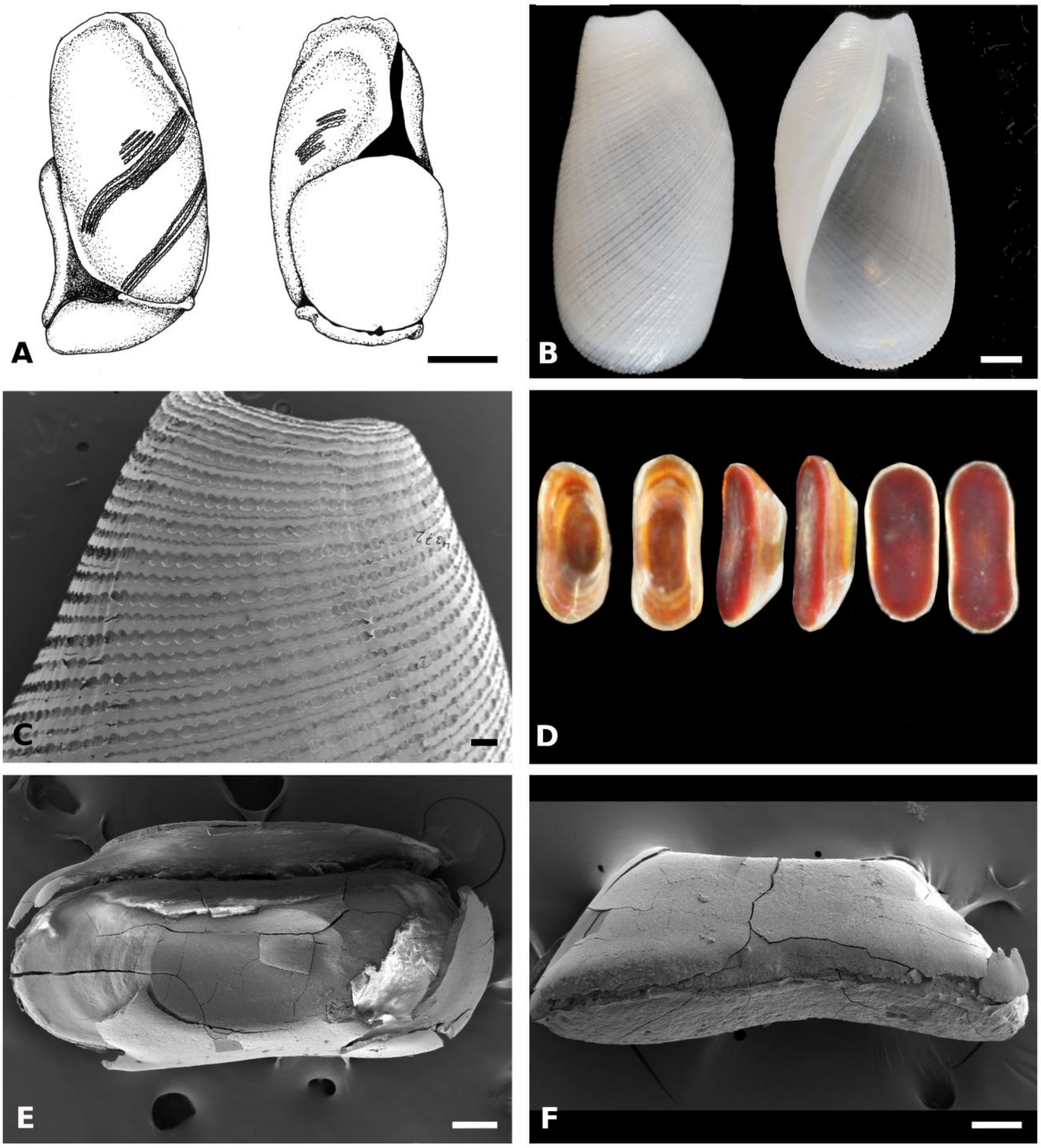

Figure 4.29 ***Philine*** **sp.10** (New Caledonia IM-2009-4372, H = 9.2mm) A, Left dorso latral(left image) and ventral view (rigth image) illustration of whole animal. B, Dorsal (rigth image) snd ventral view (rigth image) of complete shell. C, SEM of apicla palrt of shell. D, Active surface(left image) lateral view(middle image) and inactive surface (rigth image) of 1 paired and the central gizzard plate. E, SEM of central unpaired gizzard plate. F, SEM of lateral view of paired gizzard plate. Scale bars: A = 2mm, B = 1mm, C = 200µm, E,F = 100µm.

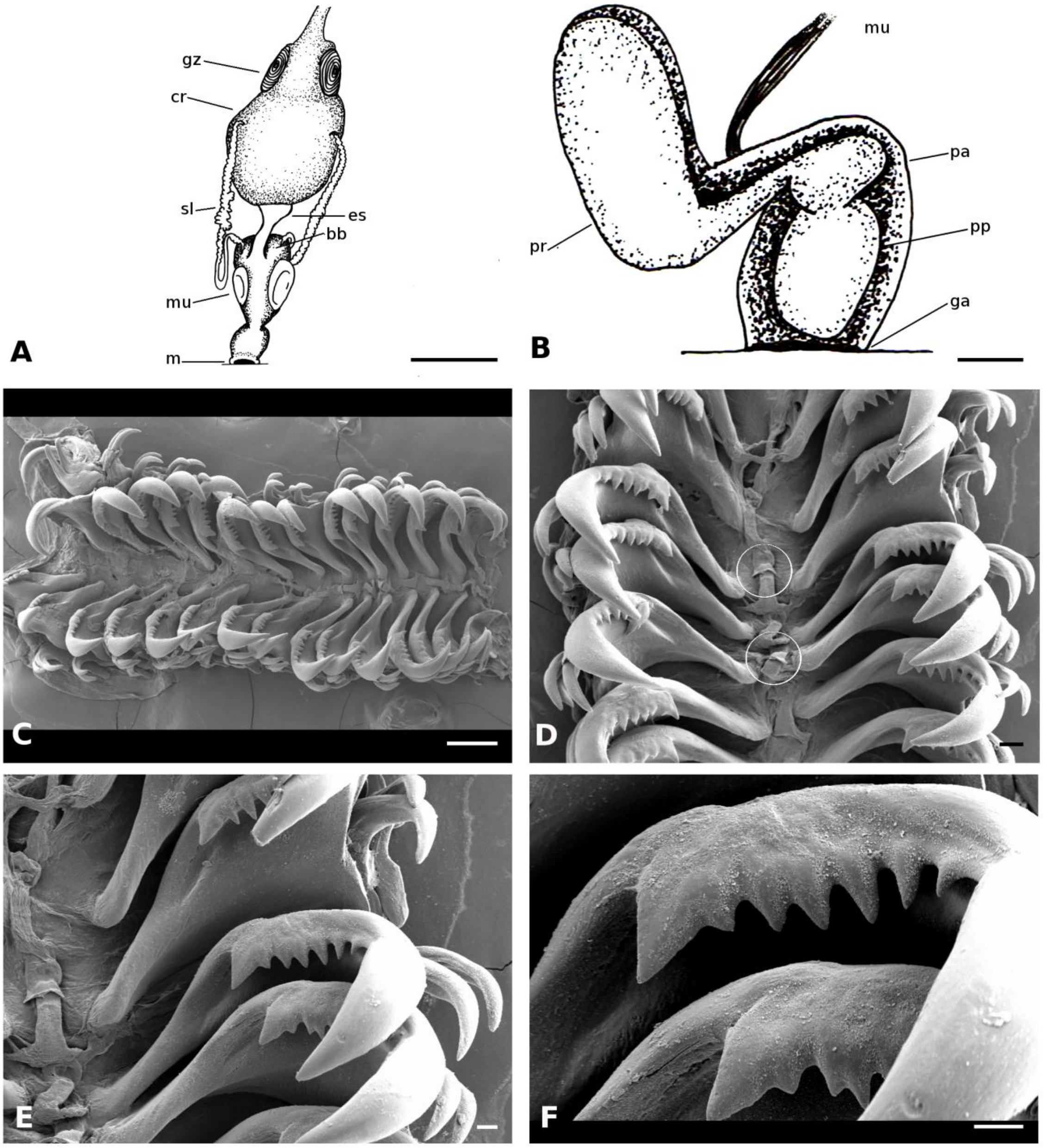

Figure 4.30 ***Philine* sp.10** (New Caledonia IM-2009-4372, H =9 .2mm) A, dorsal view of forgut. B, male reproductive system. C, radula. D, middle radula, rachidian tooth encircled. E, detail of rigth latral teeth. F, detail of denticulation on teeth. Abbreviations: gz, gizzard plates. cr, sediment filled crop. sl, salivary glands. es, esophagus. bb, buccla bulb containing radula. mu, dense muscle. m, mouth. pr, prostate, pa, penial atrium. pp, penial papilla. Scale bars: A = 1.7mm, B = 250μm, C = 100μm, C = 20μm, D, E, F = 10μm.

PHILINE SP. 11

(FIGS 4.31 A-F)

Diagnosis: Shell oval trapezoidal, external, whitish-transparent, spiral striae of fused indentations, undulating thin lines between thicker spiral striae. Body brownish-yellow (preserves specs.). Radula unknown. Gizzard unknown. Reproductive system unknown.

Barcode: KF877711

Material examined: 1 spc. (dissected and sequenced), the Philippines, MNHN, Paris IM-2009-4363, H = 5.1 mm

Shell (4.31 E): H = 5.1 mm. External, thick; whitish transparent; oval trapezoidal, slightly obtuse apex, aperture wide. Shell sculpture deep, fused pits forming undulating spiral striae, thinner striae in between.

Animal (4.31 A-D): Body yellowish brown (preserved specimens).

Ecology: Known from 380 m likely on sandy mud (as sand and mud was found in digestive system).

Distribution: Philippines Sea, North East of Lamon bay, the Philippines (14°48′N, 123°43′E),.

Remarks: This single specimen likely belongs to an undescribed species; however there is too little data to ascribe it either to a new species or any known species. The only known characters are the shell, some internal organs, and the DNA because the cephalic region of the single specimen available was damaged; the foregut and male reproductive system were not possible to study. Whether this is a new species or not will not be possible to ascertain until more complete specimens are found. The shell is similar to that of *P. infantilis* Habe 1950 (Okutani. 2000, page 750, Plate 375, 8, as *Hermania infantilis*), however, in the latter species the wing is more rounded, while in *Philine* sp.11 is sharper and pointed. It is also similar to the shell of *Philine* sp.8 and *Philine* sp.9, but differ from these in that the shell is external, the aperture wider and more oblong (trapezoidal) rather than globular. In the bayesian analysis of all genes this species is resolved basally within Philinidae clade 3 with maximum support (PP = 1; Tree 4.5) Interspeciffic p-distance to *Philine* sp.8 (22%), *Philine* sp.9 (21.4%) and *Philine* sp.10 (18.7%), show that this species is genetically more similar to *Philine* sp.10 rather than the morphologically more similar *Philine* sp.8 and *Philine* sp.9.

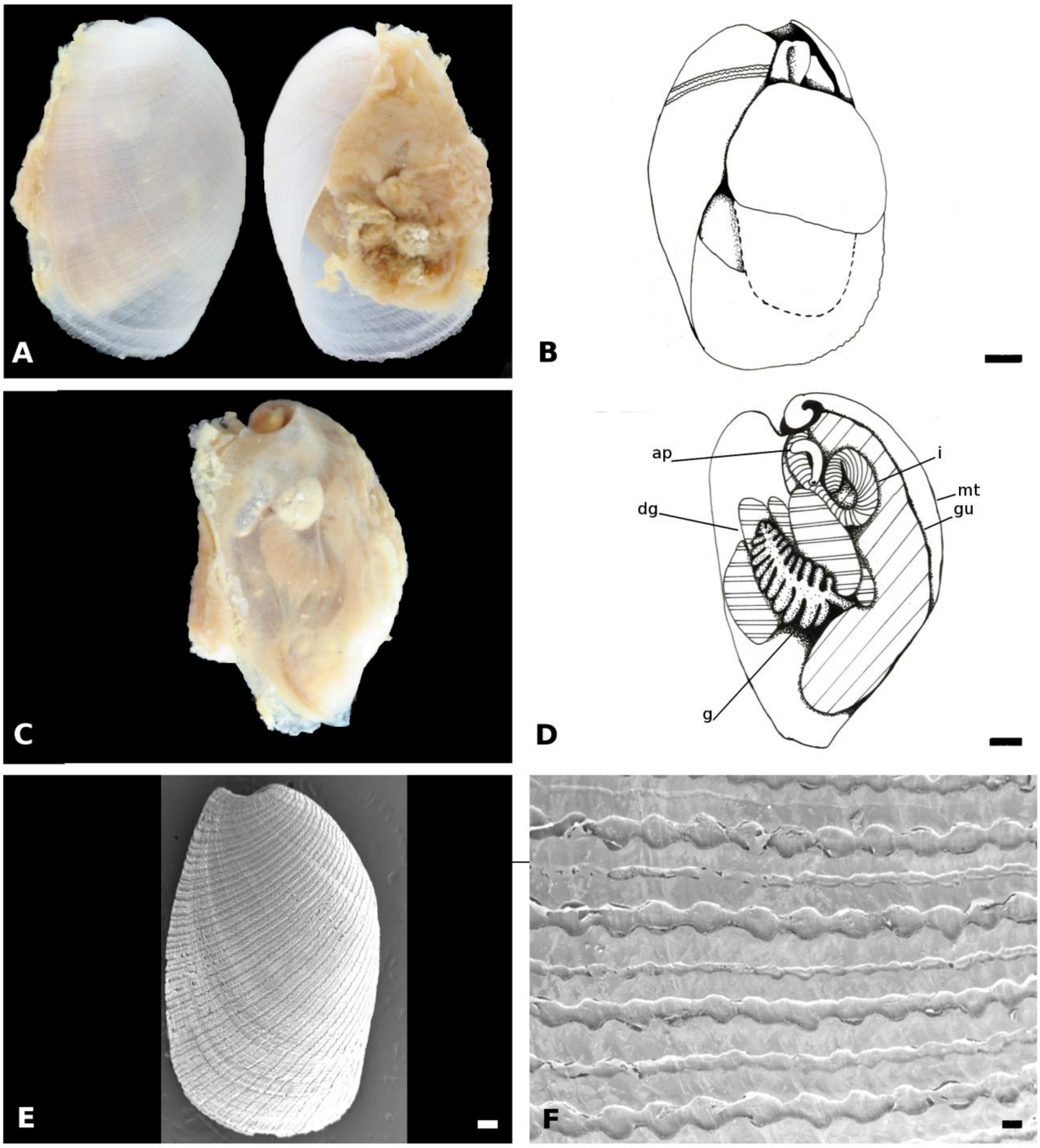

Figure 4.31 ***Philine* sp.11** (Phillippines IM-2009-4363, H = 5.1mm) A, Dorsal (left image) and ventral view (rigth image) of complete animal. B, Ventral view, illustration of complete animal. C, Dorsolateral view of mantle. D, Dorsolateral view fo internal anatomy. E, SEM of complete shell. F, SEM, detali of shell surface. Abbreviations: g, gill. dg, digestive glands. i, intestine. ap, anal papilla. g, gut. mt, mantle Scalebars: B = 0.55mm, D = 0.5mm, E = 200µm, F = 50µm.

5. Discussion

5.1 Cephalaspidea phylogeny and family relationships

In line with several previous studies this research confirmed the monophyly of Cephalaspidea without the Runcinacea, an hypothesis suggested earlier by Malaquias et al. (2009a), Dinapoli & Klussmann-Kolb (2010), Jörger et al. (2010), (Schrödl et al., 2011a) and Wägele et al. (2013) (see Tree 4.1). Philinoidea and Bulloidea (*sensu* Bouchet and Rocroi, 2005) were retrieved polyphyletic which is congruent with the results of Malaquias et al. (2009a). However as many traditionally Philinoidean families form a well supported clade (PP = 1; Tree 4.1), the superfamily Philinoidea can be redefined and reinstated with Philinidae Clade 1, Aglajidae, "*Colpodaspis* + *Colobocephalus*", Gastropteridae, Philinoglossidae, Scaphandridae, *Roxania*, Philinidae Clade 2 (*Philinorbis*; see Discussion 5.2), Philinidae Clade 3, and Philinidae Clade 4 (*Laona*; see Discussion 5.2). While Retusidae and Cylichnidae, two non-monophyletic families (see Tree 4.2 and Tree 4.3), in need of redefinition are excluded from Philinoidea.

Mikkelsen (1996) on her cladistic analysis of the Cephalaspidea *s. l.* noted that *Acteocina* (a traditional genus of the Cylichnidae) previously had often been regarded as separate from other cylichnids, in its own family Acteocinidae, something that was seemingly supported in her analysis as *Cylichna* and *Acteocina* clustered separately. The results in this thesis are not conclusive about the phylogenetic placement of *Acteocina* but they suggest exclusion of the genus from the Cylichnidae. Therefore, it is here suggested the reinstatement the family Acteocinidae Dall 1913 (considered a junior synonym of Cylichnidae). *Acteocina* has a radula similar to *Cylichna*, but with a much lower number of outer laterals and unlike *Cylichna* the gizzard plates are calcified with one trilobed central plate and oblong paired plates, somewhat similar to gizzard plates of *Scaphander* (Marcus, 1977; Rudman, 1978; Eilertsen and Malaquias, 2013).

Roxania species did not cluster within Scaphandridae. Their phylogenetic position as sister to Philinidae Clade 4 (*Philinorbis*) (PP = 1) suggests a new family assignment (see Tree 4.1). Previously they have been included in Cylichnidae (Thiele, 1931; Just et al., 1985; Thompson,

1988) and Haminoeidae (Bouchet, 1975; Høisæter, 1986; Gosliner, 1987). Little is known about their internal anatomy; the penis has both a prostate and a “seminal bulb” (Burn and Thompson, 1998). The radula has a broad rachidian tooth bearing large and small denticles (Pilsbry, 1893; Burn and Thompson, 1998; Valdés, 2008), and triangular lateral teeth (Pilsbry, 1893; Valdés, 2008) or quadrate lateral teeth that may bear denticles (Burn and Thompson, 1998). According to Gantes and Cornet (1981) the rachidian tooth has a large middle cusp with five denticles on either side; the lateral teeth seem to bear a cusp separate from the main tooth and overlaying the tooth of previous row. This type of radula differs drastically from the phylogenetically closely related *Philinorbis* (Price et al., 2011, as *Philine*; this study Clade 4), which have thick curved inner laterals with light or no denticulation (see Results). Most studies report no gizzard plates in *Roxania* (Burn and Thompson, 1998), but Gantes & Cornet (1981) found small reduced chitinous amber coloured gizzard plates, which are somewhat similar to those of *Philinorbis* and Philinidae Clade 3.

The status of Retusidae and Rhizoridae are uncertain, since the relationships between species of these two families were not fully resolved. The latter two families clustered in the same clade together with *Acteocina* and Bullidae but with no support (PP = 0.58; see Tree 4.3). As there are few morphological similarities between these families, further molecular and morphological analyses including additional samples is warranted. Mikkelsen (1996) referred that *Cylichna*-*Acteocina*-*Retusa* taxa are superficially similar but previously Mikkelsen (1993; 1994) had suggested *Retusa* to be more closely related to Bullidae/Bulloidea. Ghiselin (1966) have also pointed a possible close relationship between Retusidae and Bulloidea based on the presence of a “spermatic bulb”.

Malaquias et al. (2009a) excluded the genus *Ventomnestia* Iredale 1936 from Haminoeidae, however the authors have only included this taxon on their 28S rRNA analyses. This study confirmed the exclusion of *Ventomnestia* from Haminoeidae, but the phylogenetic affinity of the genus was not resolved (see Tree 4.1 and Tree 4.3). Early studies usually assigned *Ventomnestia* to *Cylichna* due to similarities in the shell (e.g. (Gould, 1859; Pease, 1860), but also to Retusidae (Mikkelsen, 1996), while the ridged gizzard plates suggest their affinity to Haminoeidae (Carlson and Hoff, 2000). In Haminoeidae two diagnostic characters are the reabsorbtion of the protoconch and presence of transverse ridges on the gizzard plates (Mikkelsen, 1996). This is also the case for *V. villica*, but while the radular formula of *V.*

villica is 2.1.2 (Carlson and Hoff, 2000) typically Haminoeidae taxa have a higher number of lateral teeth (Burn and Thompson, 1998).

The Diaphanidae was found to be polyphyletic, which is congruent with the results of Malaquias et al. (2009a). *Diaphana globosa* was basal and sister to the remaining Cephalaspidea. *Toledonia globosa* clustered together with *Cylichna* taxa (PP = 1) and *Colpodaspis* + *Colobocephalus* formed a clade (PP = 1) sister to Gastropteridae (PP = 0.94), while specimens of an undescribed species of "*Diaphana*" from the Philippines branched off alone (see Tree 4.1 and Tree 4.2). The monophyly of Diaphanidae has been disputed, because the family was loosely defined, lacks synapomorphies and is largely united by plesiomorphies (Jensen, 1996). Taxa in this family show great differences in shell morphology and internal anatomy (Marcus, 1976; Brown, 1979; Warén, 1989; Jensen, 1996; Burn and Thompson, 1998; Schiøtte, 1998; Ohnheiser and Malaquias unpublished data).

Species of *Diaphana* usually have an external, globose and thin shell while the radula might have thin pointed outer lateral teeth when present, long, strong inner laterals with a broad basis and delicate denticulation along the inner edge and a bilobed, rectangular and denticulate rachidian tooth (Warén, 1989; Schiøtte, 1998; Ohnheiser and Malaquias unpublished data). *Newnesia* Smith 1902 (not tested in this study) has a shell and inner laterals similar to *Diaphana*, however the unilobed, denticulated rachidian tooth resembles *Toledonia* (Smith, 1902; Marcus, 1976; Schiøtte, 1998). Jensen (1996) and Schiøtte (1998) suggested that *Newnesia*, *Toledonia*, and *Bogasonia* are closely related genera, and possibly constitute their own family. *Toledonia* and *Bogasonia* have shells with a raised apex, while as previously mentioned the rachidian tooth is unilobed and usually denticulate, they may have plate-like lateral teeth (Marcus, 1976; Warén, 1989; Ohnheiser and Malaquias unpublished data). *Colobocephalus* and *Colpodaspis* have internal, globose shells with raised apexes, the radulae differ from the aforementioned Diaphanidae by not having rachidian tooth; inner and outer laterals are curved with a broad based and no denticulation (Brown, 1979; Ohnheiser and Malaquias unpublished data). As pointed above *Colpodaspis* and *Colobocephalus* formed a distinct clade and a new family name is necessary to reflect this novel phylogenetic hypothesis.

The genus *Diaphana* seems to be polyphyletic with a separation between Atlantic and Indo-Pacific species, but additional taxa are necessary to investigate and conclude about the systematics of this taxon. The "*Diaphana*" specimens from the Philippines used in this study belong to a species that is likely the same as *Diaphana* sp.1 illustrated on the *Sea Slugs of Hawaii* webpage (Pittman and Fiene, 2013b). Interestingly, the shells of this species resembles those of the elusive *Notodiaphana* spp. studied by Thiele (1912, 1917) who erected the new genus and family *Notodiaphana* and Notodiaphanidae (Thiele, 1917). The original species of *Notodiaphana* were described as *Bulla fragilis* and *Bulla divae* by Velain (1877), but later both were considered synonyms and included in *Diaphana* as *D. fragilis* (Tyron and Pilsbry, 1879). Thiele (1912, 1917) studied specimens that he ascribed to *Notodiaphana*, and showed that the radula lack rachidian tooth and had plate-like inner and outer laterals where the inner carried three cusps, while the outer laterals were more square with one cusp (Thiele, 1912, 1917; Boss, 1982). Burn and Thompson (1998) raised the possibility that the single inner lateral could be a broken rachidian tooth, which then will make this radula very similar to *Roxania.*

Toledonia globosa Hedley 1916 was resolved within Cylichnidae *sensu stricto* with *Cylichna gelida* Smith 1907 and *Cylichna cylindracea* Pennant 1777. This clade was retrieved basally in the tree sister to the remaining Cephalaspidea (PP = 0.97) with *Diaphana globosa* as mentioned above occupying the most basal position in the Cephalaspidea tree. The radula of *Toledonia* has a unilobed, oblong denticulate rachidian tooth with plate-like outer lateral teeth and is quite different from the cylichnid radula (see (Marcus, 1976; Gosliner, 1994), which usually have a broad bilobed denticulate rachidian, inner curved pointed laterals with a broad basis and denticulation. The outer lateral teeth are usually simple, hook shaped with a broad basis. The radula of *Cylichna* is indeed more similar to *Diaphana*; the main differences are that the diaphanid radula has a prominent basis on the rachidian teeth, which extends to the depression separating the denticulate lobes, the inner lateral teeth are more angular and less curved, and the denticulation extends throughout the length of the tooth; when present the outer laterals are thin and needle like (see Schiøtte, 1998). One noticeable similarity between the rachidian teeth of *Cylichna* and *Toledonia* is that the denticles usually are orientated at a more or less 90° angle from the main surface of the tooth. *Cylichna* usually have jaws and chitinous gizzard plates (Lemche, 1956) which are absent in *Diaphana* and *Toledonia* (Ohnheiser and Malaquias, unpublished data).

The shells are variable; many species as *C. cylindracea* and *C. gelida* have cylindrical shells while others may have oval to round shell, with the aperture running the length of the shell and the spire in sunken. The more rounded shells of *C. occulta* and *C. densistriata*, *C. magna* (see Lemche, 1956) and *C. lemchei* are similar to *Diaphana cretica*, *D. hiemalis*, *D. minuta* and *D. globosa* (see Hardy, 2013), while shells of *Toledonia* have a prominent developed spire. Based on the results of this study it is suggested the inclusion of the genus *Toledonia* in the family Cylichnidae.

One of the novel phylogenetic results retrieved in this study was the sister relationship between the monophyletic *Colobocephalus* + *Colpodaspis* clade and the Gastropteridae (PP = 0.94). *Colobocephalus* and *Colpodaspis* show some morpho-anatomical resemblance with the Gastropteridae genus *Siphopteron*, which has a globular visceral hump (Gosliner 1989) which is superficially similar to the internal globular shells of *Colpodaspis* (see Brown (1979), page 203, Plate I, a, b). However a few similarities seem, to be unique for these two clades within the Cephalaspidea. According to Gosliner (1989) an apomorphy of the Gastropteridae is the anteriorly cleft foot in *Sagaminopteron*, but this is also present in *Colobocephalus* and *Colpodaspis* and may constitute a synapomorphy of the clade *Colobocephalus* + *Colpodaspis* + Gastropteridae, that has been lost in several lineages of the Gastropteridae. It remains to confirm whether the anteriorly cleft foot in *Sagaminopteron*, *Colobocephalus* and *Colpodaspis* is homologous of those found in some species of *Diaphana*.
Another trait that seems to be shared between Gastropteridae and *Colobocephalus* + *Colpodaspis* is an elaborated cephalic shield with enhanced chemoreceptors. *Colpodaspis* have elongate rolled cephalic tentacles (referred to as rhinophores by Brown (1979)) while *Colobocephalus* and larval *Colpodaspis* have stunted anterior cephalic tentacles (Brown , 1979; Ohnheiser and Malaquias unpublished data). Whereas Gastropteridae have a posterior siphon that possibly acts as a chemosensor (Gosliner, 1989).

This study found Philinoglossidae monophyletic and sister to the clade containing *Colobocephalus* + *Colpodaspis* and Gastropteridae (PP = 1; see Trees 4.1. and 4.2). Scaphandridae clustered in a sister position to the latter lineages but with no support (PP = 0.73); a result consistent with Malaquias et al. (2009a), but Jörger et al. (2010) found support for a sister relation between *Scaphander* and *Philinoglossa*, yet this may result from limited taxon sampling. A close relationship between the Gastropteridae and Philinoglossidae has been suggested by Malaquias et al. (2009a) and Göebbler and Klussmann-Kolb (2011) where the two families were retrieved sister to each other. The previous works also suggested a sister relationship between the latter clade (Gastropteridae + Philinoglossidae) and a clade containing Aglajidae + Philinidae, but the relationships between these four lineages were not resolved in the present study (see Tree 4.1).

Philinoglossidae are highly specialized and have lost many traits present on other members of the Cephalaspidea. Most have a head shield fused to the rest of body; members of the genus *Abavopsis* however, have a short head shield similar to Gastropteridae (Salvini-Plawen, 1973; Gosliner, 1989; Brenzinger et al., 2013). Philinoglossidae retain a radula that has an arrangement largely similar to that of Philinidae and Gastropteridae (Gosliner 1994: fig. 22, A–D,) and the teeth morphology is similar to the Gastropteridae (Gosliner, (1989; Cadien, 1998; Behrens, 2004).

Brenzinger et al. (2013) pointed out that a trend in Aglajidae and Gastropteridae is that the male genital opening is placed under the anterior cephalic shield (e.g. as illustrated in Anthes, 2007) rather than on the right side of the head as in other philinoideans (Rudman, 1972a). This configuration is similar to Philinoglossidae, where however the male genital opening is situated inside the mouth (Marcus, 1953; Marcus and Marcus, 1958; Marcus, 1959; Salvini-Plawen, 1973; Brenzinger et al., 2013). This may result from an adaption to a meiofaunal lifestyle, as other interstitial groups of gastropods also have an anteriorly orientated male reproductive system (Swedmark, 1964; Challis, 1969; Jörger et al., 2008; Jörger et al., 2009; Brenzinger et al., 2012).

5.2 The systematics of Philinidae *sensu lato*

A novel result of this research was the polyphyly of the family Philinidae, which showed to be made up of four divergent clades (Clades 1–4; Trees 4.1 and 4.3). Clade 1 (PP = 1) sister to Aglajidae, contains the "true" Philinidae (Philinidae *sensu stricto*) with type species *Philine aperta*. This clade is defined by the synapomorphies: Internal shell, usually fragile, well developed, muscular gizzard, calcified gizzard plates, no rachidian tooth, usually convoluted prostate and species specific penial papilla. Within the Philinidae *sensu stricto* four sub-clades were recognized based on molecular phylogenetic evidence and morpho-anatomical characters (Sub-clades A–D; Tree 4.4).

Sub-clade A, (PP = 1), includes the species *Philine scabra*, *P. indistincta*, and *P. exigua*. Previously the first two species have been included in the genera *Hermania* by Monterosato (1884) based on the shape of the shell and the scalloped edge of the aperture, but Ohnheiser and Malaquias (2013) recently considered *Hermania* a synonym of *Philine*, but the larger dataset here analysed supports the validity of the genus and recognized the presence of unique features among this philinids, such as the presence on an elongate-cylindrical internal shell, scalloped outer lip, gizzard surrounded by muscles, only central part of the inactive surface of the gizzard plates covered by muscular fibres, inactive surface of gizzard plates with central slits in the form of semicircular indentations (Ohnheiser and Malaquias, 2013). The species *P. exigua* shows reduction of many of these features due to its interstidial lifestyle (Jörger et al. 2009; 2010; Schrödl and Neusser, 2010;) which may indicate a derived or pleisomorphic condition of this species, or alternatively an artificial clustering resulting from limited representation of the diversity of Philinidae.

Philine sp. 6 formed a separate sub-clade within the Philinidae (sub-clade B; genus *Praephiline*). Only one species is included in this sub-clade and therefore its phylogenetic/systematic status is difficult to ascertain, but due to shared unique similarities with species like *P. finmarichia* and *P. polystrigma* such as simple elongate-oval, spindle shaped and equally sized gizzard plates, inactive surface of plates with a raised field centrally surrounded by a transparent margin, well developed gizzard and gizzard plates completely surrounded by muscular fibres, and male reproductive system with a long prostate smooth on proximal half, nodulous on distal half, penial papilla with a verrucose crest or spine like structures on upper part (Marcus et al., 1969; Gosliner, 1994; Behrens, 2004; Chaban and Soldatenko, 2009b; Price et al., 2011; Ohnheiser & Malaquias, 2013; this study), it is here suggested the validity of this clade to which the genus name *Praephiline* Chaban and Soldatenko 2009 is available. *Praephiline* was purposed by Chaban and Soldatenko (2009a) for the north Atlantic species *P. finmarchica* based on the presences of three equal, flat and elongate gizzard plates, gizzard completely surrounded by annular musculature, subequal ducts of the male reproductive system and a muscular mass at the basis of the penis. This genus was recently synonymised with *Philine* by Ohnheiser & Malaquias (2013) and is here reinstated as valid. Following Chaban and Soldatenko (2009a) *P. chilla* (Marcus et al., 1969) and *P. thurmanni* (Marcus et al., 1969) should also be included in the genus. Ultimately the validity of this genus rests on testing the placement of its type species (*P. finmarchia*) using molecular phylogenetics.

Sub-clade C, corresponds to genus *Philine* and includes *P. aperta* (PP = 0.95). *Philine* (sub-clade C) includes species with apomorphic traits such as a long, large convoluted prostate, calcified spindle shaped gizzard plates with small round to bean shaped pores on the inactive suface, with a consistent pattern of a rounded central field and tapering extensions anteriorly and posteriorly, where one plate is small symmetrical and unpaired, and two large paired unsymmetrical and mirrored plates. The radula in *Philine* is made up only by inner lateral teeth with delicate denticulation along the inner edge (Price et al., 2011; Ohnheiser and Malaquias, 2013; present study). Based on this study and the recent work by Price et al. (2011) the true *Philine* include the species: *Philine aperta* Linneaus 1767, *P. quadripartita* Ascanius 1772, *P. paucipapillata* Price, Gosliner and Valdés 2011, *P. orientalis* A.Adams 1854, *P. angasi* Crosse,1865, *P. elegans* Bergh 1905, *P. habei* Valdès 2008, *P. puka* Price, Gosliner and Valdés 2011, *P. kinglipini* Tchang 1934, , *Philine* sp.1, *Philine* sp.2, *Philine* sp.3, *Philine* sp.4, and *Philine* sp.5. The molecular phylogenetic analysis in this study largely supports the results of Price et al. (2011), but showed that species with large slits on the inactive surface of the gizzard plates likely belong to a separate new genus (Sub-clade D).

A clade consisting of *Philine babai* (Valdès, 2008), *P. auriformis* (Suter, 1909) and P. sp. 7, formed the last clade within the Philinidae (PP = 1; sub-clade D). These and similar species like *P. infundibulum* (Dall and Agassiz, 1889) and the recently described *P. sarcophaga* (Price, Gosliner, Valdés, 2011) and *P. fenestra* (Price, Gosliner, Valdés, 2011) shared several apomorphies especially in the gizzard plates like The active surface of the plate carries raised fields and ridges in the central portion, whether other clades have smooth active surfaces. The inactive surface of the gizzard usually carry deep elongate slits along the lateral sides of the plate, these are larger and more extensive than the central pores ore indentations of other species of this clade. These slit may be reduced on the central plate in some species, and may be reduced on side of the lateral plate but is always present on the convex edge of the plate. The outer lateral teeth are long, narrow, flattened, un-curved and does not have a broad basis, whereas the other subclades usually have curved outer laterals with a broad basis. The ejaculatory duct is much longer compared to the other sub-clades. (Rudman and Miller, 1998; Price et al. 2011; Ohnheiser and Malaquias, 2012; this study). No genus name is available for this clade containing species which have always been ascribed to the genus Philine.

Clade 2 (PP = 1; see Trees 4.1 and 4.5) includes four species (*Philine* sp.12, *Philine* sp.13, *Philine* sp.14, and *Philine* sp.15). Their anatomy suggest that they are closely related with the well described species *Philine alba* Mattox 1958 from the Eastern Pacific and *P. albioides* Price, Gosliner and Valdes 2011 from the Caribean region, but also to species ascribed to the elusive West Pacific genera *Pseudophilne* (*Pseudophiline hayashii*) and *Philinorbis* (*Philinorbis teramachii)* so far two genera of doubtful validity and uncertain systematics status (Chaban, 2011b). Externally species in Clade 2 have a long, rhomboid cephalic shield, a long often tapering posterior lobe lacking a rear notch, and narrow parapodial lobes. This differs from the usual round-oval cephalic shield, posterior shield wrapping the shell and thick, broad or absent parapodial lobes (Price et al., 2011; present study). Anatomically, there are common traits as a flat, concave, circular plate-like shell, without spiral striae (as described in *Pseudophiline hayashii*, *P. alba*, and *P. albioides*; Mattox, 1958; Marcus, 1974; Habe, 1976; Price et al., 2011) or with narrow raised spiral striae as described in *Philinorbis teramachii* (Habe, 1950; Okutani, 2000; Chaban, 2011b) . All these previous species are characterized by the unique presence of a reduced gizzard with small brown chitinous gizzard plates, which may be absent, and by a developed broad highly muscular buccal bulb. The position and size of gizzard plates indicate that the gizzard maybe non functional, (Mattox, 1958; Kitao and Habe, 1982; Price et al., 2011; Chaban, 2011b; present study). The radula of all these species is 2.1.0.1.2, with outer lateral teeth smaller compared with the thick and well developed inner laterals, which bear great similarities in all species, all lack apparent denticulation, except *P. alba* but the denticulation of this species is much simpler than in the other clades (Mattox, 1958; Price et al., 2011). As in *P. alba* (Mattox, 1958: pl. 34, fig. 4) all species in Clade 2 have the penial atrium embedded in the tissue anterior of the body cavity**,** a unique feature of this clade. In all other Philinidae *s. l.* the penial atrium lies within the anterior body cavity, and is only connected to the tissue in the anterior end.

The morpho-anatomical similarities of species in Clade 2 with species of *Pseudophiline* and *Philinorbis* suggests they generic placement within one of these two genera. Although the only morphological feature separating these genera is the spiral striae of the shell and therefore, *Pseudophiline* Habe, 1976 is here purposed as a junior synonym of *Philinorbis* Habe, 1950, which has been previously suggested by Chaban (2011). Thus, the genus name *Philinorbis* is here purposed for species in this clade showing the automorphies discussed above and highlighted in the systematic part of the Results. A new family name is required for this clade of philinids.

Species in Clade 3 all have minute shells with spiral striae of fused pits and wide aperture. Their internal anatomy also reveals minute differences that easily could be overlooked without a molecular framework. The most noticeable feature of this clade is the comparatively large size in relation to the animal length of the gizzard plates, and the presence of a light calcification on the active surface of the plates. In Clade 2 the gizzard plates are comparatively much smaller and not calcified. All species in Clade 3 share a massive crop. *Philine* sp.8 and *Philine* sp.9 are sister species and have a reduced buccal bulb lacking a radula while *Philine* sp.10 have a small muscular buccal bulb and a radula with inner lateral teeth that have strong prominent coarse denticulation, and a small vestigial cusped rachidian tooth not present in other clades of the Philinidae *s. l.* (see Price et al., 2011; Ohnheiser and Malaquias, 2013), but in the putatively closely related *Philine* (=*Philinorbis*) *alba* (Price et al., 2011), which has a rounded plate-like reduced rachidian tooth. The high interspeciffic distance between species in Clade 3 may indicate that the diversity of this clade is underrepresented. Two species not studied here that show morpho-anatomical similarities with those in Clade 3 are *Philine gibba* and *Philine falklandica* (Rudman, 1972: 173, 174, figs 1a–b, 2a). No genus and family names area available for this clade.

Clade 4 (PP = 0.98) includes some species with a net-like structure similar to *Laona zonata* from the West Pacific described by A. Adams (1865) based on shells alone (Adams, 1865; Habe, 1976; Okutani, 2000: pl. 373, 11). Adams (1865) emphasised the netlike sculpture and suggested that the European *Philine (Laona) pruinosa* should be included in the genus due to similarities in the shell. Nothing is known about the anatomy of the type species *Laona zonata*, but *Philine pruinosa* was included in this analysis and therefore, it is here suggested to reinstate the genus *Laona* as valid to name species in Clade 4. *Laona* was recently considered a synonym of *Philine* by Ohnheiser and Malaquias (2013), but as highlighted earlier the authors only analysed a reduced dataset including Scandinavian species.

Species in Clade 4 show some variability in shell shape (rounded to quadrate; the latter only in *P. quadrata*), shell ornamentation (net-like, smooth, chain-like spiral lines; the latter only in *P. quadrata*). The sculpture of the shell is a poor character because it is not shared between all species. However, all species have a shell where the first part of the teloconch extends into the aperture covering part of the posterior columella. The radula largely similar, but *P. quadrata* has a longer and more rectangular radula and *P. pruinosa* has six outer lateral teeth). All species lack gizzard plates and all have a simple prostate and a tubular penial atrium

(Ohnheiser and Malaquias, 2013). The morpho-anatomical differences found in *P. quadrata* and the fact that this species branched basally as sister to the remaining *Laona*, may indicate a different phylogenetic "affiliation" of this species, but to confirm this an extended taxa set is necessary.

6. LITERATURE CITED

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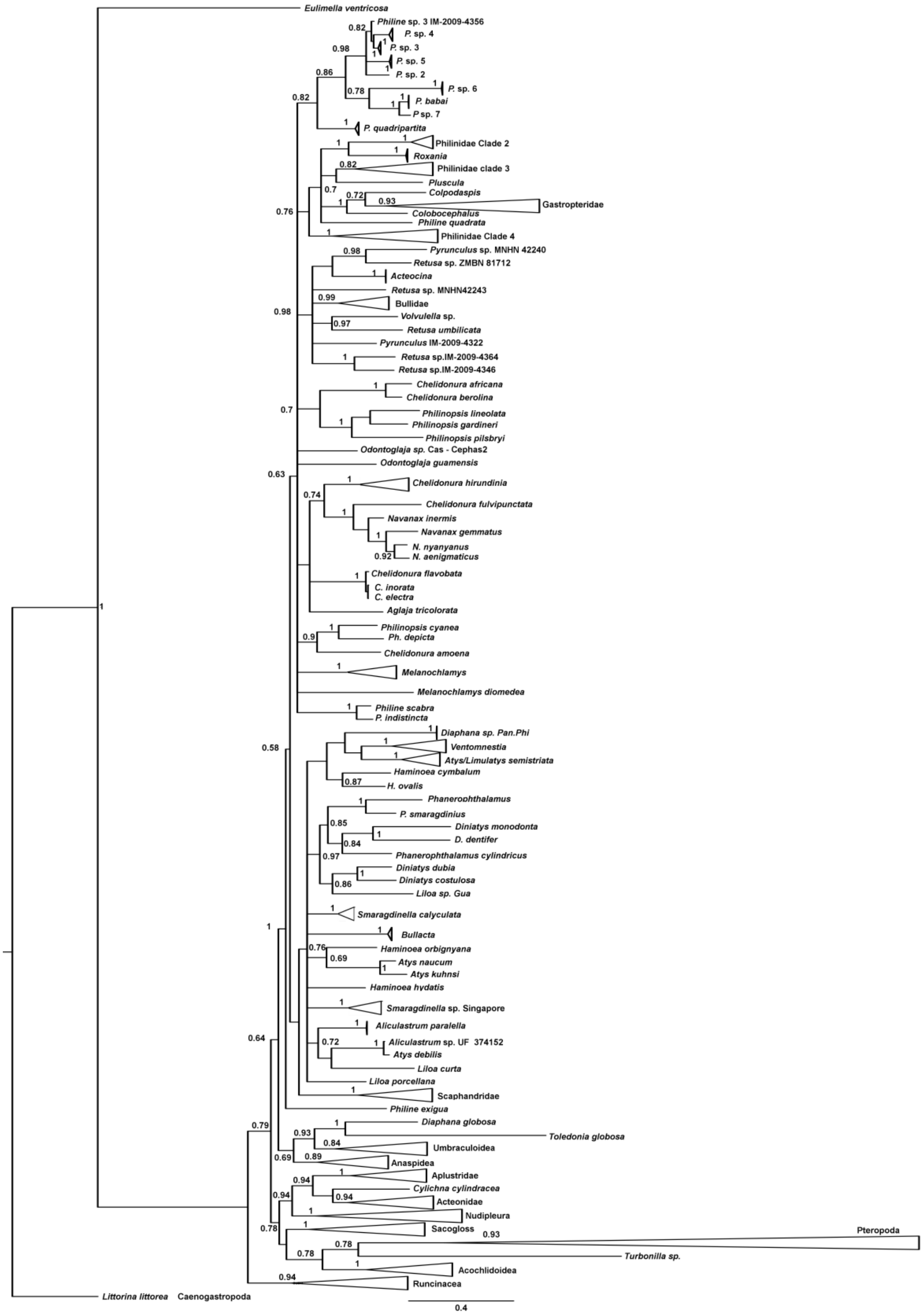
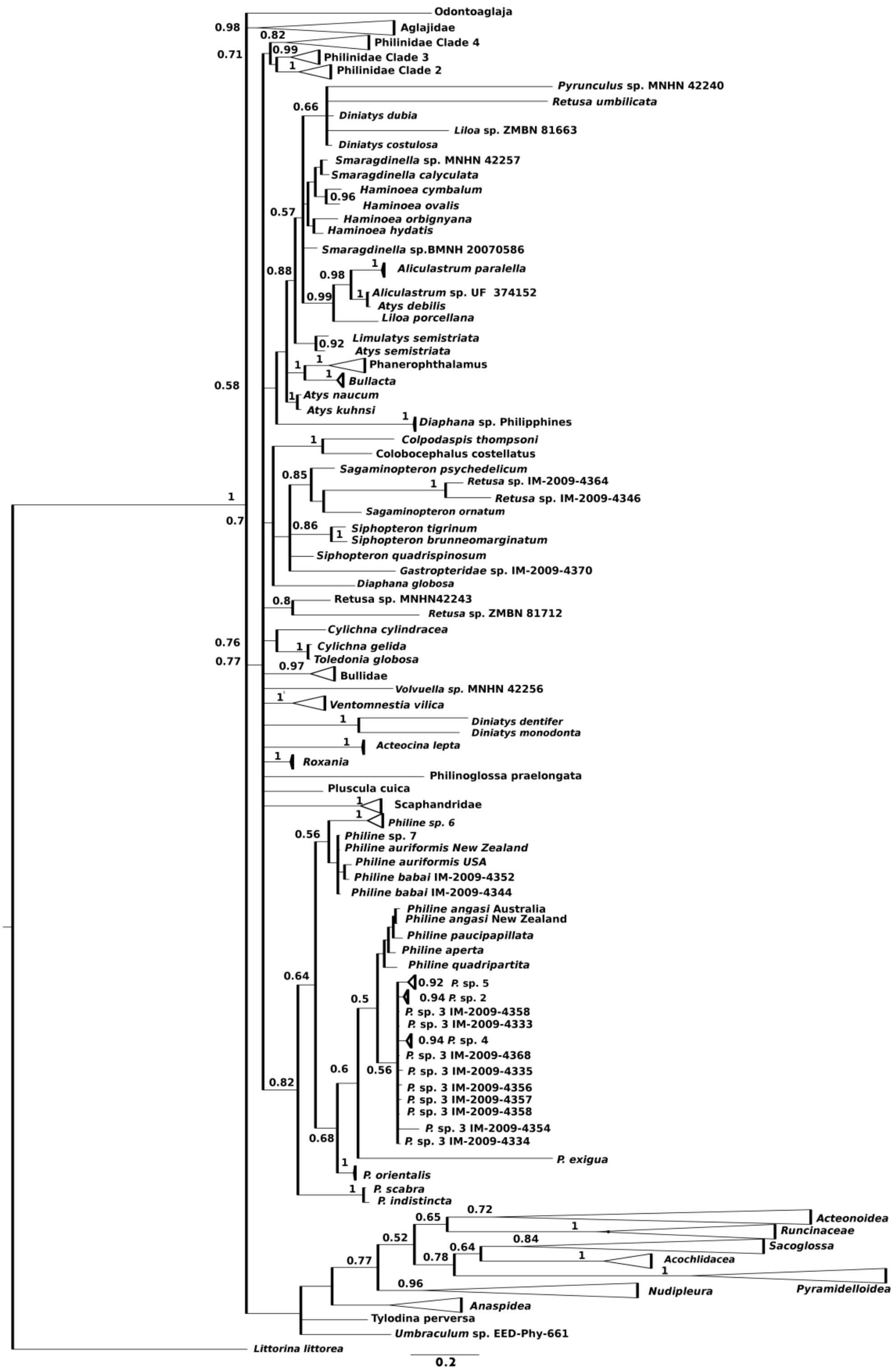
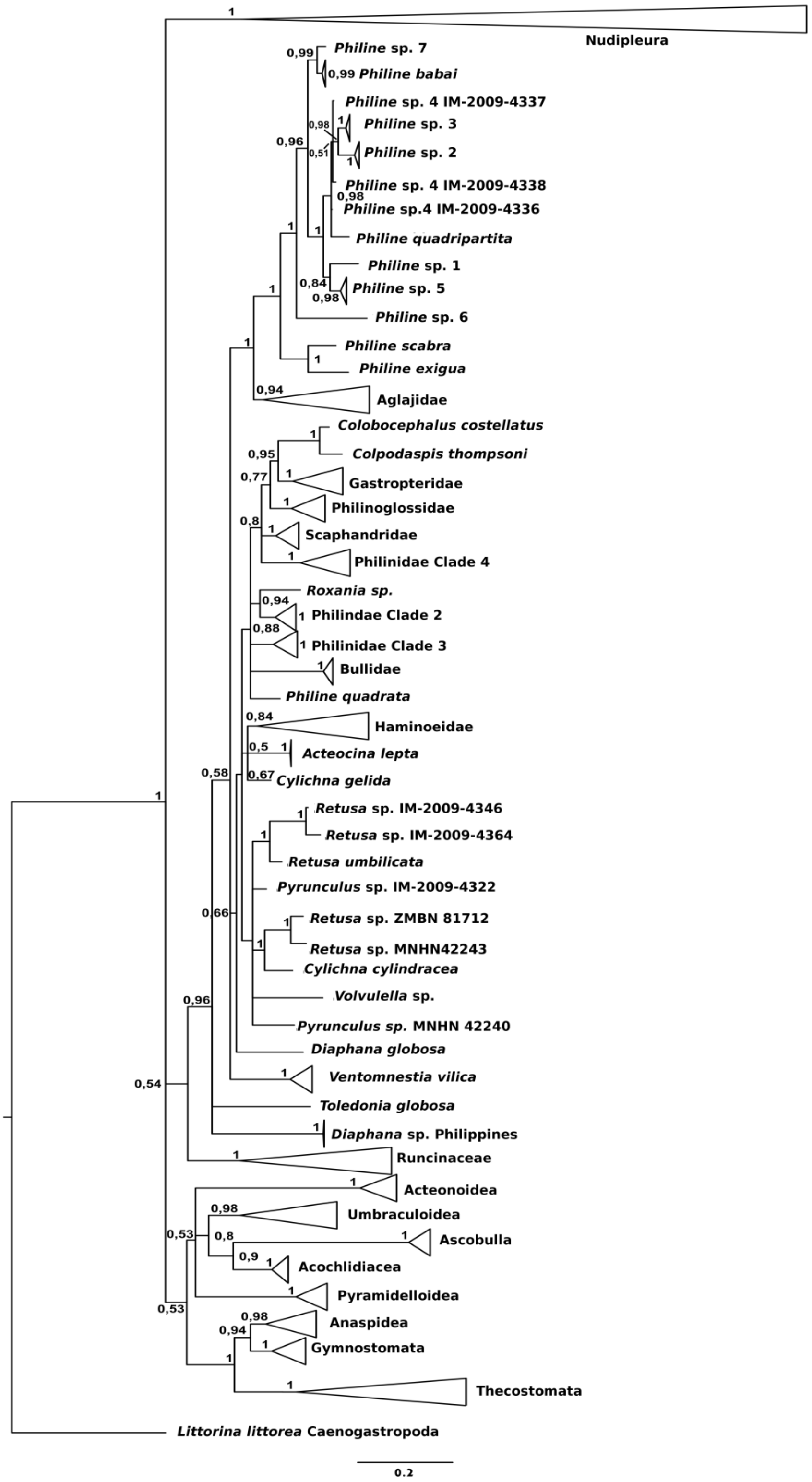
7. Appendix



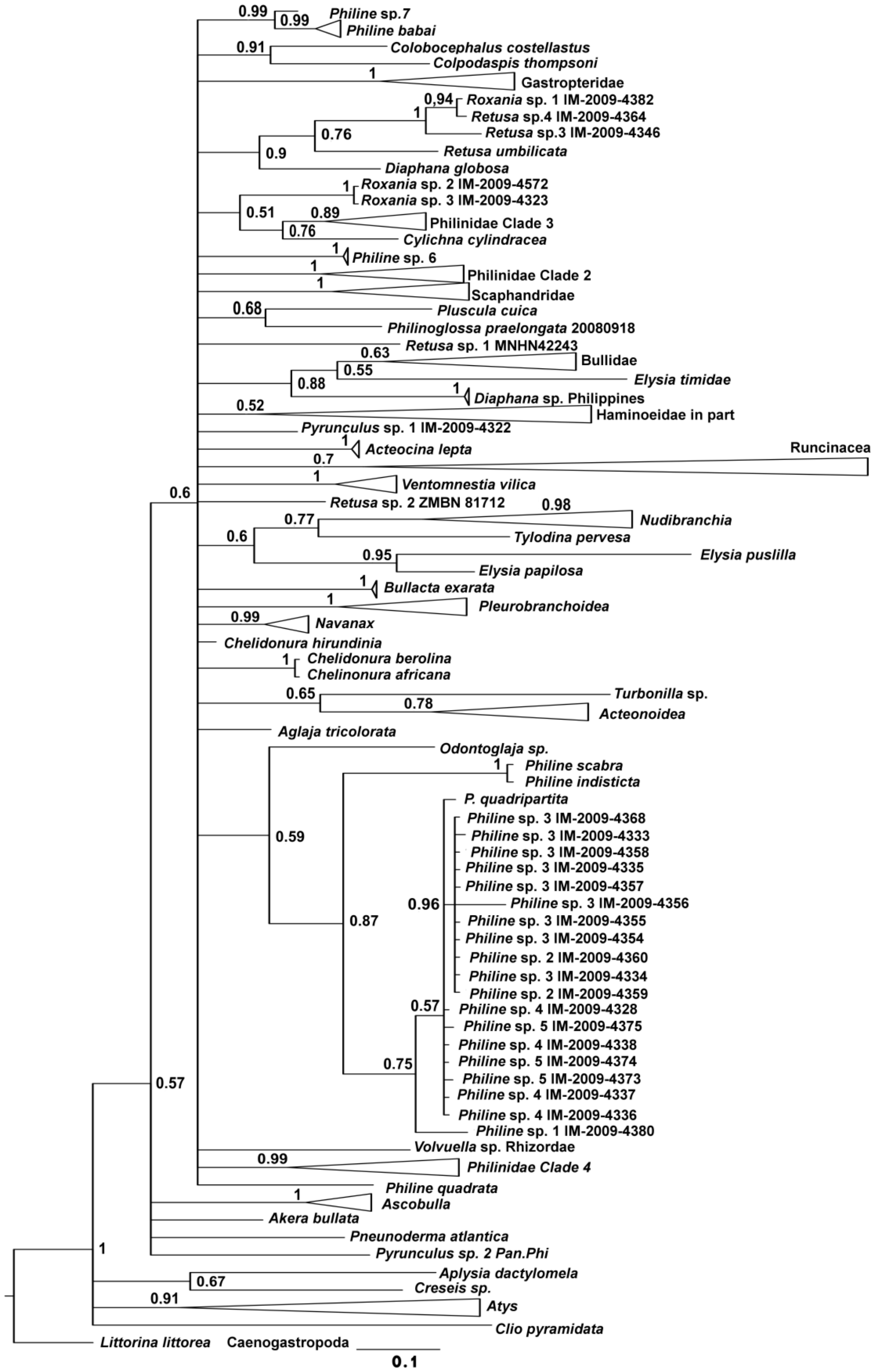
Tree 7.1.1 Bayesian phylogeny of the Cephalaspidea based on the analysis of the mitochondrial COI. Figures on nodes are posterior probabilities. The tree was rooted with the Caenogastropod species *Littorina littorea*.



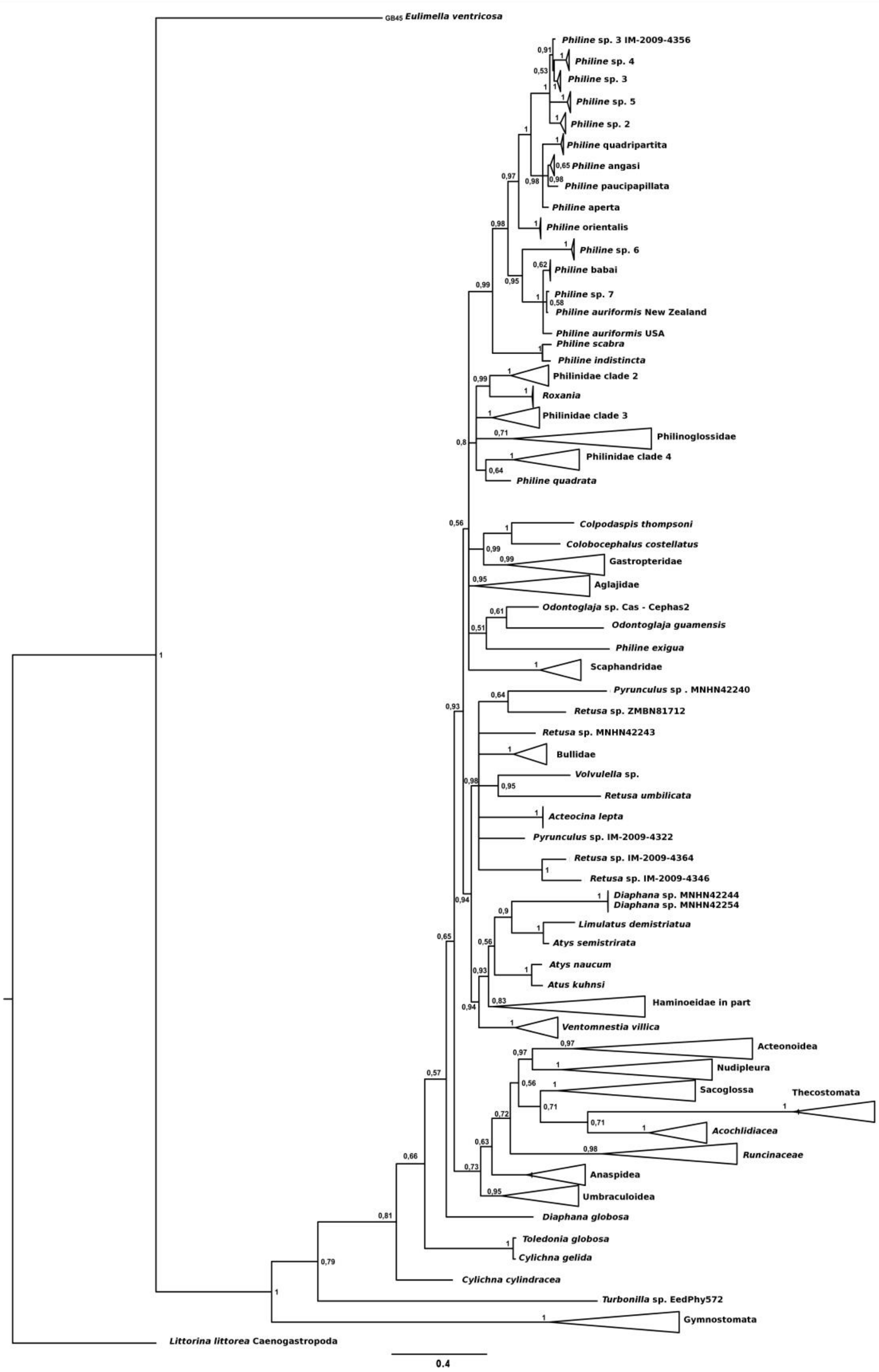
Tree 7.1.2 Bayesian phylogeny of the Cephalaspidea based on the analysis of the mitochondrial 16S rRNA. Figures on nodes are posterior probabilities. The tree was rooted with the Caenogastropod species *Littorina littorea*.



Tree 7.2.1 Bayesian phylogeny of the Cephalaspidea based on the analysis of the nuclear 28S rRNA. Figures on nodes are posterior probabilities. The tree was rooted with the Caenogastropod species *Littorina littorea*.

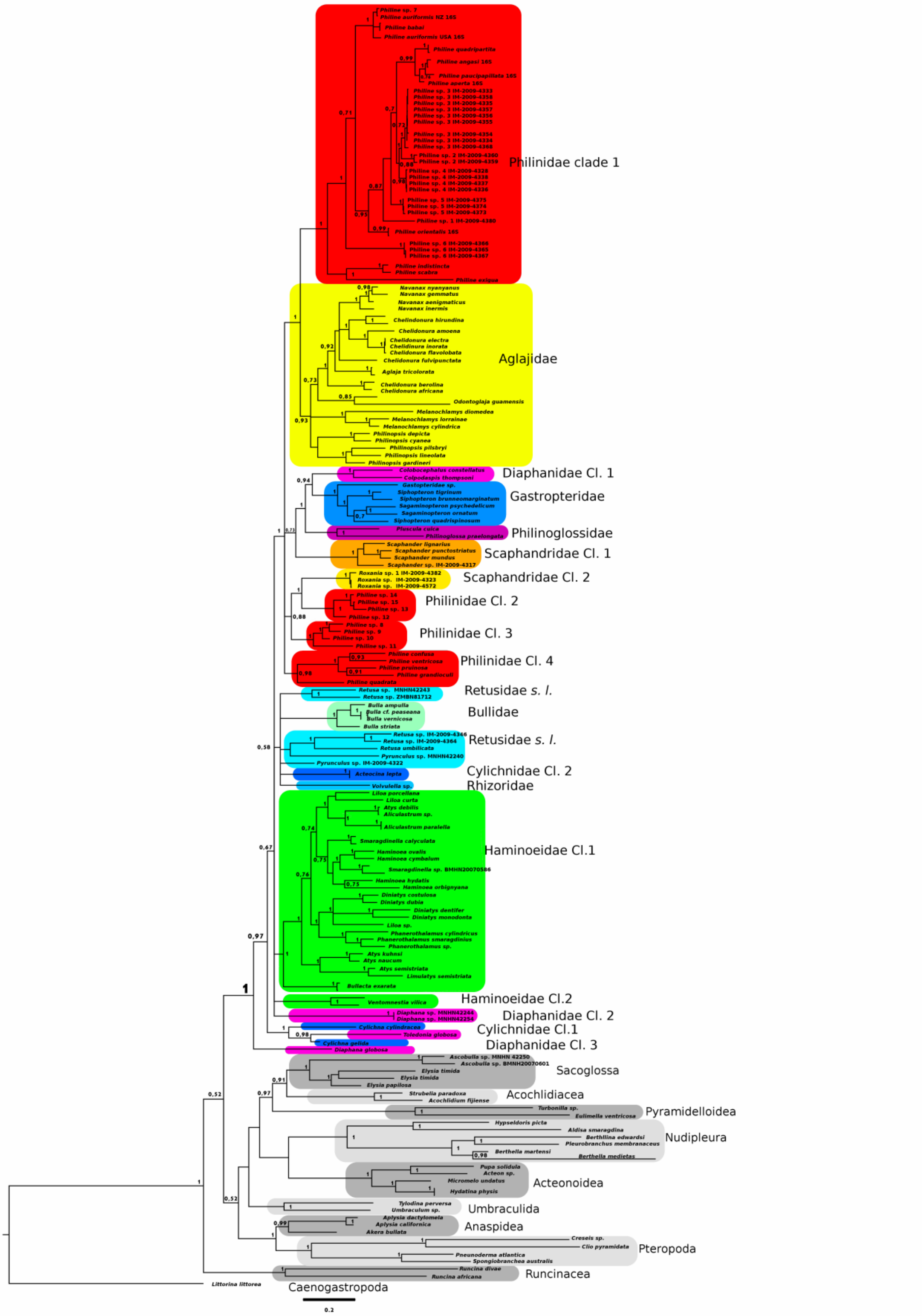


Tree 7.2.2 Bayesian phylogeny of the Cephalaspidea based on the analysis of the nuclear Histone 3. Figures on nodes are posterior probabilities. The tree was rooted with the Caenogastropod species *Littorina littorea*.

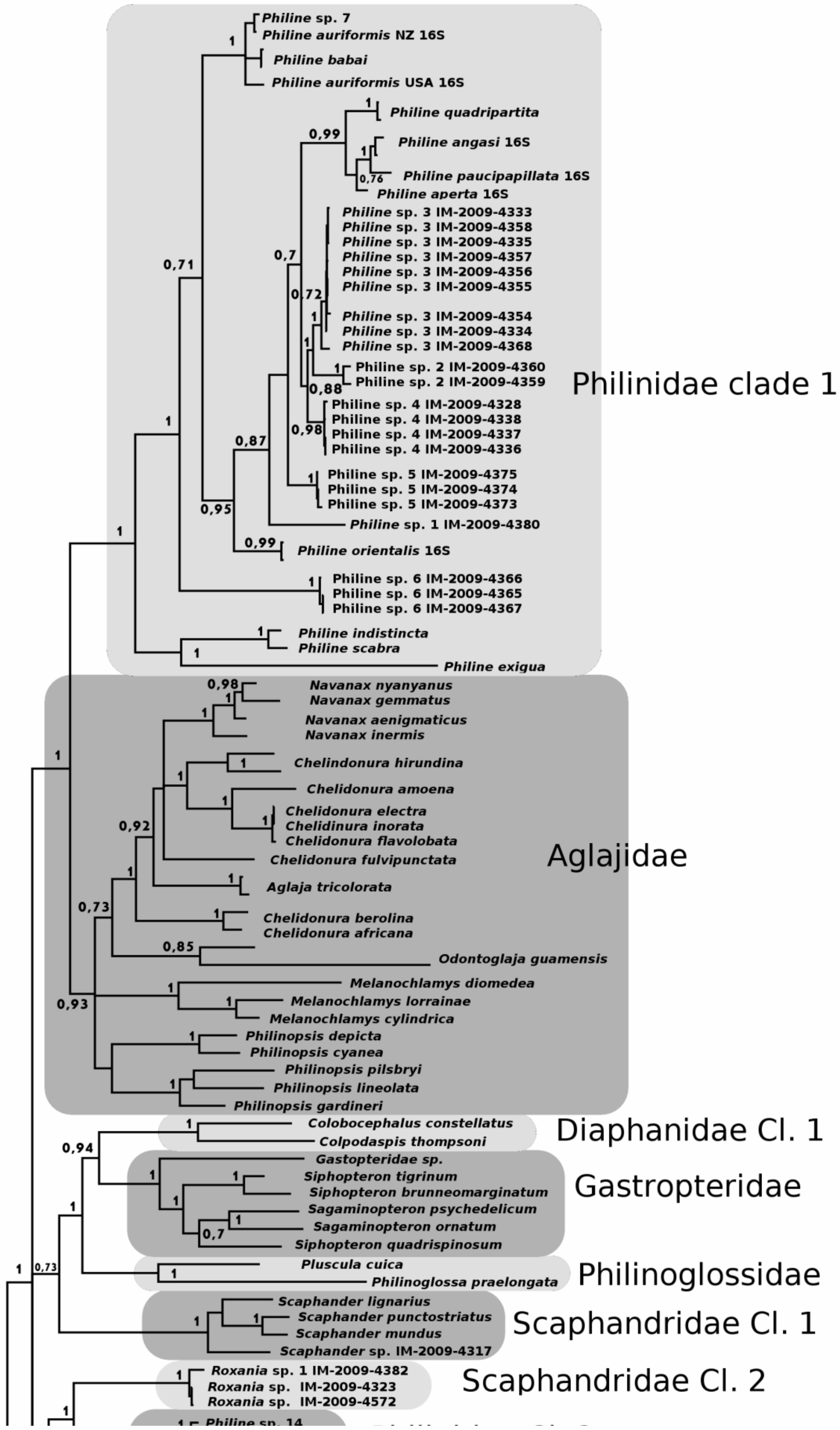


Tree 7.3 Bayesian phylogeny of the Cephalaspidea based on the combined analysis of the mitochondrial COI + 16S rRNA. Figures on nodes are posterior probabilities. The tree was rooted with the Caenogastropod species *Littorina littorea*.

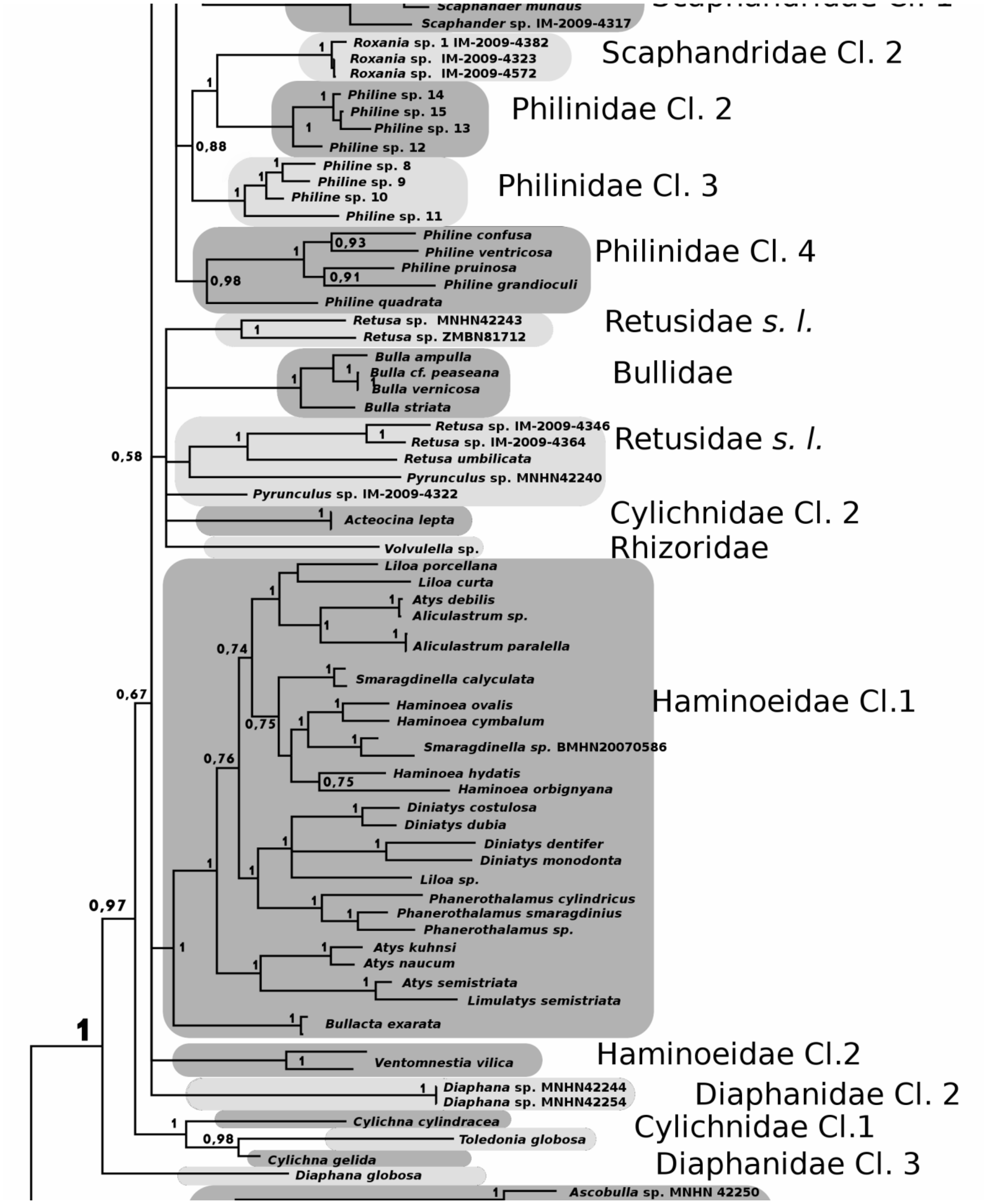
Tree 7.4 Bayesian phylogeny of the Cephalaspidea based on the combined analysis of the nuclear 28S + H3. Figures on nodes are posterior probabilities. The tree was rooted with the Caenogastropod species *Littorina littorea*.



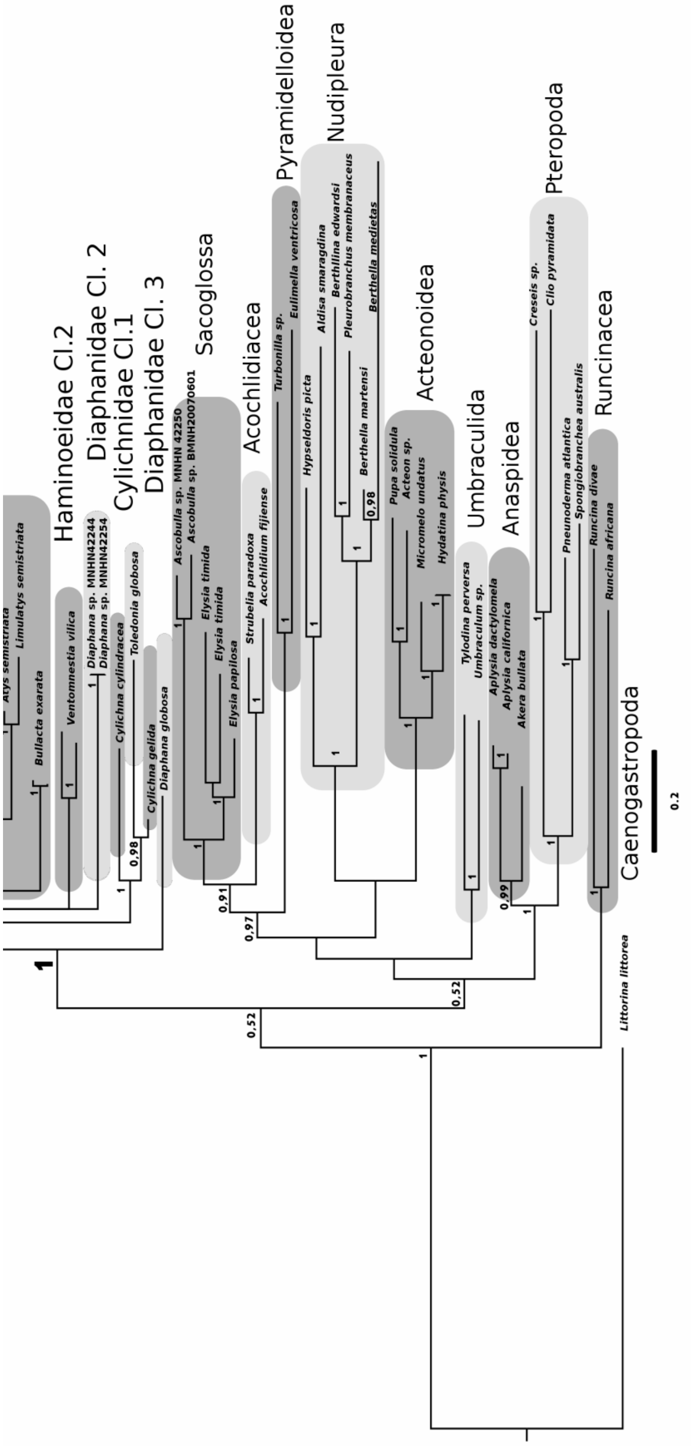
Tree 7.5 Bayesian phylogeny of the Cephalaspidea based on the combined analysis of COI, 16S rRNA, 28S rRNA and Histone 3. Figures on nodes are posterior probabilities. The tree was rooted with the Caenogastropod species *Littorina littorea*.



Tree 7.5.1 Part of tree depicted in figure Tree 7.5 : Philinidae *s. s.* Clade 1, Aglajidae, Diaphana Clade 1, Gastropteridae, Philinoglossidae, Scaphandridae Clade 1 and Clade 2.



Tree 7.5.2 Part of tree depicted in figure Tree 7.5 : Scaphandridae Clade 2, Philinidae Clade 2, Clade 3 and Clade 4, Retusidae *sensu lato*, Bullidae, Cylichnidae Clade 2, Rhizoridae, Haminoeidae Clade 1, Haminoeidae Clade 2, Diaphanidae Clade 2, Cylichnidae Clade 1 and Diaphanidae clade 3.



Tree 7.5.3 Part of tree depicted in figure Tree 7.5 : Haminoeidae Clade 2, Diaphanidae Clade 2, Cylichnidae Clade 1 and Diaphanidae clade 3, Sacoglossa, Acochlidacea, Pyramidelloidea, Nudipleura, Acteonoidea, Umbraculida, Anaspidea, Pteropoda, Runcinacea and Caenogastropoda.

Table 7. 1 List of accepted valid families, genera and type species of Cephalaspidea. Type genera and species highlighted in bold font.

Family	**Genus**	**Type Species**
Aglajidae Pilsbry, 1895	***Aglaja* Renier, 1807**	***Aglaja tricolorata* Renier, 1807**
	Chelidonura A. Adams, 1850	*Chelidonura hirundinina* (Quoy & Gaimard, 1833)
	Melanochlamys Cheeseman, 1881	*Melanochlamys cylindrica* Cheeseman, 1881
	Navanax Pilsbry, 1895	*Navanax inermis* (J.G. Cooper, 1863)
	Nakamigawaia Kuroda & Habe, 1961	*Nakamigawaia spiralis* Kuroda & Habe, 1961
	Noalda Iredale, 1936	*Noalda exigua* (Hedley, 1912)
	Spinoaglaja Ortea, Moro & Espinosa, 2007	*Spinoaglaja petra* (Ev. Marcus, 1976)
	Odontoglaja Rudman, 1978	*Odontoglaja guamensis* Rudman, 1978
	Philinopsis Pease, 1860	*Philinopsis speciosa* Pease, 1860
Bullidae Gray, 1827	***Bulla* Linnaeus, 1758**	***Bulla ampulla* Linnaeus, 1758**
Cylichnidae H. Adams & A. Adams, 1854	*Adamnestia* Iredale, 1936	*Adamnestia arachis* (Quoy & Gaimard, 1833)
	Acteocina J. E. Gray, 1847	*[?]*
	***Cylichna* Lovén, 1846**	***Cylichna nitidula* Lovén, 1846**
	[?] Bullinella Newton, 1891	*[?]*
	Cylichnella Gabb, 1873	*Cylichnella bidentata* (d'Orbigny, 1841)
	Mamillocylichna Nordsieck, 1972	*Mamillocylichna richardi* (Dautzenberg, 1889)
	Paracteocina Minichev, 1966	*Paracteocina vitjazi* Minichev, 1966
	Truncacteocina Kuroda & Habe, 1955	*Truncacteocina oyamai* (Kuroda & Habe, 1954)
	Tornatina A. Adams, 1850	*Tornatina decorata* (Pilsbry, 1904)
	Sphaerocylichna Thiele, 1925	*Sphaerocylichna atyoides* (Thiele, 1925)
Diaphanidae Odhner, 1914	*Colpodaspis* M. Sars, 1870	*Colpodaspis pusilla* M. Sars, 1870
	Colobocephalus M. Sars, 1870	*Colobocephalus costellatus* M. Sars, 1870
	Woodbridgea S.S. Berry, 1953	*Woodbridgea williamsi* S. S. Berry, 1953
	***Diaphana* T. Brown, 1827**	***Diaphana minuta* T. Brown, 1827**
	Bogasonia Warén, 1989	*Bogasonia volutoides* Warén, 1989
	Newnesia E.A. Smith, 1902	*Newnesia antarctica* E.A. Smith, 1902
	Toledonia Dall, 1902	*Toledonia perplexa* Dall, 1902
Gastropteridae Swainson, 1840	***Gastropteron* Kosse, 1813**	***Gastropteron meckeli* Blainville, 1825**
	Sagaminopteron Tokioka & Baba, 1964	*Sagaminopteron ornatum* Tokioka & Baba, 1964
	Siphopteron Gosliner, 1989	*Siphopteron tigrinum* Gosliner, 1989
	Enotepteron Minichev, 1967	*Enotepteron flavum* Minichev, 1967
Haminoeidae Pilsbry, 1895	*Cylichnatys* Kuroda & Habe, 1952	*Cylichnatys angusta* (Gould, 1859)
	Aliculastrum Pilsbry, 1896	*Aliculastrum cylindricum* (Helbling, 1779)
	Diniatys Iredale, 1936	*Diniatys dentifer* (A. Adams, 1859)

	Cylichnium Dall, 1908	*[?] Utriculus domitus* Dall, 1889
	***Haminoea* Turton & Kingston, 1830**	***Haminoea hydatis* (Linnaeus, 1758)**
	Nipponatys Habe, 1952	*Nipponactys volvulina* (A. Adams, 1862)
	Weinkauffia Monterosato, 1884	*[?] Weinkauffia diaphana* (Aradas, A. & Maggiore, 1840)
	Liloa Pilsbry, 1921	*[?] Liloa tomaculum* Pilsbry, 1918
	Limulatys Iredale, 1936	*Limulatys reliquus* Iredale, 1936
	Bullacta Bergh, 1901	*Bullacta exarata* (Philippi, 1849)
	Phanerophthalmus A. Adams, 1850	*Phanerophthalmus luteus* (Quoy & Gaimard, 1833)
	Smaragdinella A. Adams, 1848	*Smaragdinella calyculata* (Broderip & G. B. Sowerby I, 1829)
	Hamineobulla Habe, 1950	*Hamineobulla kawamurai* Habe, 1950
	***Atys* Montfort, 1810**	***Atys naucum* (Linnaeus, 1758)**
	Austrocylichna Burn, 1974	*[?] Austrocylichna exigua* (A. Adams, 1850)
	Micratys Habe, 1952	*Micratys ovum* Habe, 1952
	Mnestia H. Adams & A. Adams, 1854	*Mnestia marmorata* (A. Adams, 1850)
	Ventomnestia Iredale, 1936	*Ventomnestia colorata* Iredale, 1936
Notodiaphanidae Thiele, 1931	***Notodiaphana* Thiele, 1917**	***Notodiaphana fragilis* (Vélain, 1877)**
Philinidae Gray, 1850	***Philine* Ascanius, 1772**	***Philine aperta* (Linnaeus, 1758)**
	Philinorbis Habe, 1950	*Philinorbis teramachii* Habe, 1950
	Pseudophiline Habe, 1976	*Pseudophiline hayashii* Habe, 1976
	Spiniphiline Gosliner, 1988	*Spiniphiline kensleyi* Gosliner, 1988
	[?] Choshiphiline	
	Yokoyamaia Habe, 1950	*[?] Yokoyamaia ornatissima* (Yokoyama, 1927)
	Globophiline Habe, 1958	*[?]*
Philinoglossidae Hertling, 1932	***Philinoglossa* Hertling, 1932**	***Philinoglossa helgolandica* Hertling, 1932**
	Abavopsis Salvini-Plawen, 1973	*Abavopsis latosoleata* (Salvini-Plawen, 1973)
	Sapha Marcus, 1959	*Sapha amicorum* Marcus, 1959
	Pluscula Er. Marcus, 1953	*Pluscula cuica* Er. Marcus, 1953
Retusidae Thiele, 1925	*Pyrunculus* Pilsbry, 1895	*[?]*
	Cylichnina Monterosato, 1884	*Cylichna laevisculpta* Granata-Grillo, 1877
	***Retusa* T. Brown, 1827**	***Retusa obtusa* (Montagu, 1803)**
	Relichna Rudman, 1971	*[?]*
	Sulcoretusa J.Q. Burch, 1945	*Sulcoretusa* sulcata (d'Orbigny, 1841)
	Volvulopsis Schepman, 1913	*[?]*
Rhizoridae Dell, 1952	***Rhizorus* Montfort, 1810**	***Rhizorus adelaidis* Montfort, 1810**
	Volvulella Newton, 1891	*Volvulella acuminata* (Bruguière, 1792)
Scaphandridae G.O. Sars, 1878	*Roxania* Leach in Gray, 1847	*Roxania utriculus* (Brocchi, 1814)
	***Scaphander* Montfort, 1810**	***Scaphander lignarius* (Linnaeus, 1758)**

	Kaitoa Marwick, 1931	*[?]*
	Meloscaphander Schepman, 1913	*Meloscaphander sibogae* Schepman, 1913
	Micraenigma Berry, 1953	*Micraenigma oxystoma* Berry, 1953