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Six new species of aglajid opisthobranch mollusks from the tropical Indo-Pacific

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Abstract

Six new species of aglajid opisthobranchs are described from various localities in the tropical Indo-Pacific. *Philinopsis falciphallus* **n. sp.**, found from the Marshall Islands to the Red Sea, is distinguished by its reddish body color, a distinct black or maroon longitudinal line on the foot, a posterior projection on the posterior shield and a penis with a chitinous, sickle-shaped spine and numerous smaller spines. *Philinopsis coronata* **n. sp.**, known only from the Philippines, is similar to *P. falciphallus* but dominated by yellow body color and a ventral surface of the foot with yellow and maroon spots. It has a trumpet-shaped penis with a crown of rounded tubercles on the apex and anterior and posterior zones of penial spines. *Philinopsis ctenophoraphaga* **n. sp.** is found from the Philippines, Indonesia and the Red Sea. It feeds on platyctene ctenophores, including *Coeloplana meteroris*. It can be distinguished by its elongate posterior lobe of the headshield, reddish color with white spots, thinly muscularized buccal mass and simple, unarmed penis. *Chelidonura mandroroa* **n. sp.** is characterized by its black body with orange patches lined by yellow. It has a simple penis with a cuticularized apical papilla. This species has been found from Japan, Taiwan, the Philippines, Indonesia, Madagascar and Kenya. *Chelidonura alisonae* **n. sp.** is apparently restricted to the central and eastern Pacific of the Hawai'ian Islands, Johnston Island, the Marianas Islands and Easter Island. It is similar in coloration to *C. hirundinina*, but has orange lines on the dorsal and lateral shields and has a broad right posterior lobe rather than an acutely pointed one. The penis is simple and unarmed. *Odontoglaja mosaica* **n. sp.**, found from the Indian Ocean of Madagascar and South Africa, differs from *O. guamensis* by possessing a reticulate pattern on the notum rather than a pattern of brown spots. It also has a shorter penial papilla that is bifurcate rather than undivided one.

Key words: Aglajidae, Indo-Pacific, new species, biodiversity

Introduction

The members of the Aglajidae are widely distributed throughout the temperate and tropical regions of the world. The systematic relationships of the family have been reviewed by Rudman (1972a; 1972b; 1972c; 1974; 1978), Gosliner (1980), and Baba (1985).

The Indo-Pacific tropics support the greatest diversity of aglajid opisthobranchs with 23 described species documented from the region (Gosliner *et al.* 2008). Several relatively recently described species have been added to the Indo-Pacific region since the systematic reviews cited above. These include *Chelidonura flavolobata* Heller & Thompson, 1983; *Chelidonura castanea* Yonow 1994a; *Chelidonura livida* Yonow, 1994b and *Melanochlamys papillata* Gosliner, 1990. Recent field work around the Indo-Pacific from the Philippines and Madagascar has resulted in the discovery of specimens of several species of undescribed aglajid opisthobranchs, including three species of *Philinopsis*, two species of *Chelidonura* and a species of *Odontoglaja*. This paper describes these new taxa and compares them to previously described species.

Methods

Over the last two decades, new specimens of aglajids were collected from Batangas Province, Luzon Island, Philippines, the Hawaiian Islands and the Radama Islands of Madagascar and preserved for identification and analysis. Specimens collected prior to 2005 were generally preserved in Bouin's fixative and are therefore unlikely to be

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able to be effectively sequenced for molecular study. Specimens collected after 2005, were preserved in either 10% formalin for proper preservation of anatomical structures, or preserved entirely in 95% ethanol for later molecular study. Prior to preservation of any specimen in formalin, a tissue sample was taken from the animal and preserved in 95% ethanol for later molecular study.

Upon return to the California Academy of Sciences, dissections were completed, and drawings of anatomical structures were accomplished using a Nikon SMZ-U binocular microscope with drawing tube. Buccal mass structures of *Odontoglaja* specimens were dissected and cleaned by placing them in a 10% NaOH solution for 4–10 hours, and then prepared for scanning electron microscopy. The radula was separated and cleaned of any remaining tissue. It was then placed on glass cover slips, air-dried, and then mounted on a stainless steel stub. Specimens of copulatory organs were mounted on stubs and air-dried. Structures were then coated with gold/palladium using a Denton Desk II vacuum sputter coater. Scanning electron micrographs were produced by a LEO 1450 VP scanning electron microscope. Specimens and dissected structures were deposited at the California Academy of Sciences in the Invertebrate Zoology Department collection (CASIZ), and the American Museum of Natural History (AMNH).

Species descriptions

Family Aglajidae Pilsbry, 1895

Genus *Philinopsis* Pease, 1860

Type species: *Philinopsis speciosa* Pease, 1860, by monotypy

Philinopsis falciphallus n. sp.

(Figures 1A, B, 2A, 3, 4)

Philinopsis sp. 5 Gosliner *et al*., 2008: 42, upper photo.
Philinopsis sp. Rosenfeld, 1999; Abbott, 2007; Miller, 2008.
Aglajid sp. e518 Johnson, 2008.
Aglajid sp. 7 Rudman, 2005c.

Material examined. Holotype: CASIZ 181228, 12 m depth, Mainit Bubbles, Mabini, Batangas Province, Luzon, Philippines, 13.686025°S, 120.895167° E, 20 May 2009, T. M. Gosliner. Paratype: CASIZ, 177678, one specimen, dissected, 3 m depth, Matutunggil Point, Mabini, Batangas Province, Luzon, Philippines, 13.756132°S, 120.906889° E, 19 April 2008, T. M. Gosliner. CASIZ 174145, one specimen, dissected, 12 m depth, Mainit Bubbles, Mabini, Batangas Province, Luzon, Philippines, 13.686025°S, 120.895167° E, 24 May 2009, M. D. Miller. CASIZ 180406, one specimen, 3 m depth, old site of Seafari Resort, also known as Basura, Anilao, Mabini, Batangas Province, Luzon, Philippines, 13.756788°S, 120.921605° E, 17 May 2009, T. M. Gosliner. CASIZ 182236, one specimen, dissected, 8 m depth, on *Halimeda*, Bigej-Meck Reef, Kwajalein Atoll, Marshall Islands, Scott Johnson, 21 April 2008. CASIZ 182237, one specimen, 9 m depth, on *Halimeda*, Bigej-Meck Reef, Kwajalein Atoll, Marshall Islands, Jeanette Johnson, 16 November 2008.

Geographical distribution. Marshall Islands (Johnson 2008), Philippines (Rosenfeld 1999; Miller 2008; Lee 2008), Indonesia (Abbott 2007), Red Sea (Koretz 2005a).

Etymology. The name “falciphallus” is a combination of the Latin *falcis*, meaning sickle and the Greek *phallos*, meaning penis. This refers to the sickle-shaped structure associated with the penis of this species.

Natural history. This species is found on coral rubble in 5–15 m depth and has been observed depositing egg masses at the base of *Halimeda* plants (Johnson 2008). A specimen from the Red Sea was observed apparently feeding on polyclad flatworms (Koretz 2005a).

Description. *External morphology.* The living animals are 9 to 25 mm in length and 5–12 mm wide. The general body color of the living animal (Fig. 1A) is light pinkish to wine red with maroon with darker red pigment on the anterior portion of the head, along the parapodial margins and at the base of the posterior projection of the posterior shield. The entire dorsal and lateral surfaces of the body are ornamented with scattered irregular yellow spots and a few whitish patches. Specimens from the Marshall Islands (Johnson 2008) are much paler with dorsal and lateral whitish pigment and a few maroon spots on the head and parapodial margins. Small yellow to orange spots are also present over the body surface. The ventral surface of Philippine animals (Fig. 1B) is pale pink to wine red with a midventral longitudinal maroon line and two additional more lateral lines that may be interrupted as maroon spots. The foot has a few large yellow spots scattered over the ventral surface. A similar pattern is found on the foot of the Marshall Island specimens and also those from Red Sea (Koretz 2005a).

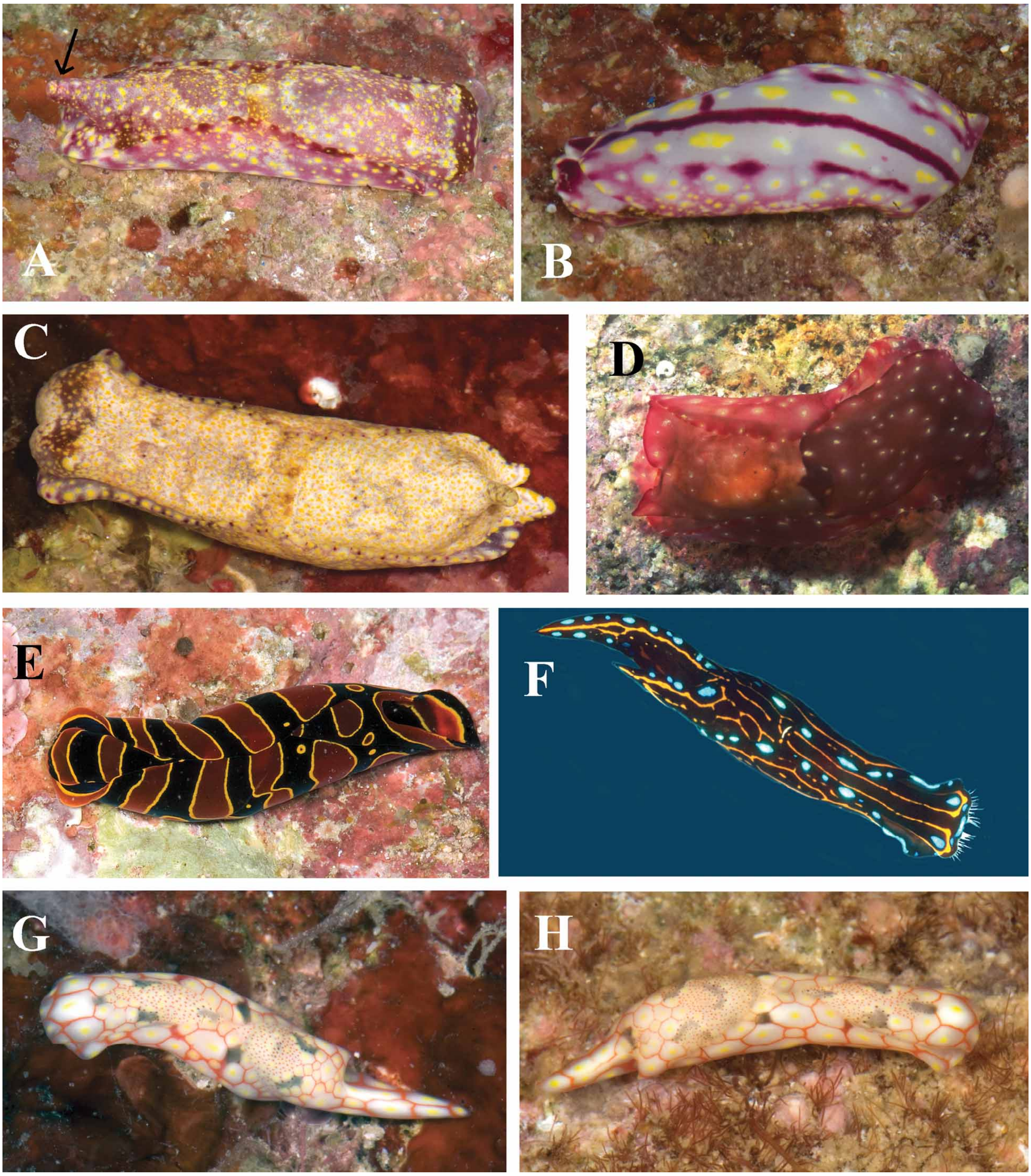

FIGURE 1. Living animals **A.** *Philinopsis falciphallus* **n. sp.**, paratype, CASIZ 177678, Mabini, Philippines, arrow indicates location of posterior lobe. **B.** *Philinopsis falciphallus* **n. sp.**, CASIZ 177678, Mabini, Philippines, ventral view showing markings on foot**. C.** *Philinopsis coronata* **n. sp.**, holotype, CASIZ 182887, Mabini, Philippines. D. *Philinopsis ctenophoraphaga* **n. sp.** CASIZ 096245, Mabini, Philippines, **E.** *Chelidonura mandroroa* **n. sp.**, holotype, CASIZ 173595, Radama Islands, Madagascar **F.** *Chelidonura alisonae* **n. sp.**, CASIZ 174177**. G.** *Odontoglaja mosaica*, paratype, CASIZ 173419, Radama Islands, Madagascar. **H.** *Odontoglaja mosaica*, paratype, CASIZ 173415, Radama Islands, Madagascar. Photos by T. M. Gosliner.

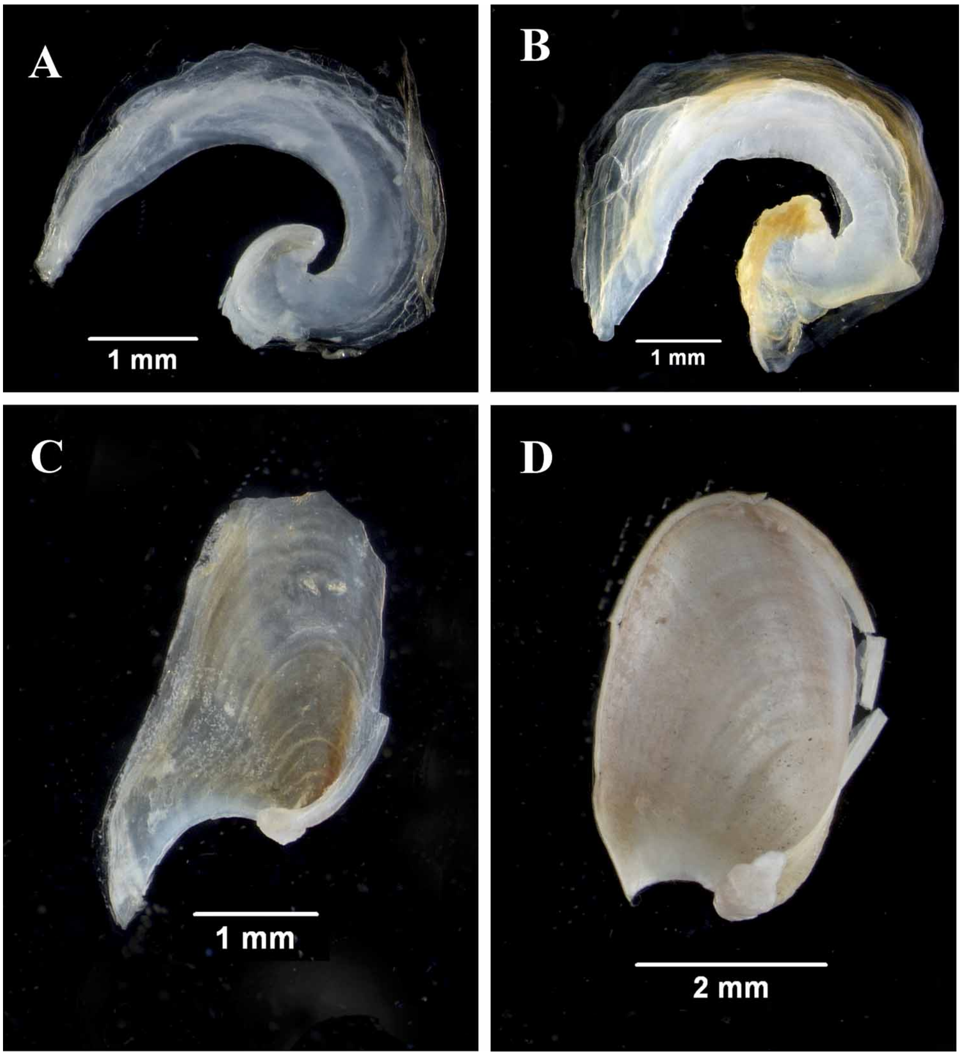

FIGURE 2. Shells. **A.** *Philinopsis falciphallus.* **n. sp.**, paratype, CASIZ 177678, Mabini, Philippines*.* **B.** *Philinopsis coronata* **n. sp.**, holotype, CASIZ 182887, Mabini, Philippines. **C.** *Chelidonura mandroroa* **n. sp.**, paratype, CASIZ 182002, Radama Islands, Madagascar **D.** *Chelidonura alisonae* **n. sp.**, paratype, CASIZ 174146, Easter Island.

Living animals are elongate, and wide. The anterior end of the cephalic shield is blunt and quadrangular. The cephalic shield is roughly rectangular and terminates posteriorly with a short, rounded papilla. The posterior shield is slightly rounded anteriorly and terminates in a medial, elongate conical posterior projection that is well-elevated from the base of the shield. The two lateral posterior lobes of the posterior shield are short and simply rounded. The parapodia are relatively short, leaving most of the cephalic and posterior shields visible. The gill is simply plicate consisting of 13 primary folds and is situated ventrally on the right posterior end of the animal.

Shell (Fig. 2A, 3A). The shell is relatively thickly calcified and consists of a narrow band that occupies the posterior extreme of the animal. There is a membranous periostracum that is slightly more extensive anteriorly than the calcified portion. The area at the base of the shell near the protoconch is more thickly calcified that the rest of the shell.

Digestive system (Fig. 3B). The buccal mass is large, highly muscularized and slightly elongating posteriorly and occupies the body cavity for the entire length of the cephalic shield. The buccal bulb entirely lacks any vestige of a radula. There is a large ventral oral gland and small dorsal oral glands were indistinct. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is large and saccate, wider than the buccal bulb. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

Central Nervous System (Fig. 3B): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both elongate with well-separated respective ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which has a distinct genital ganglion.

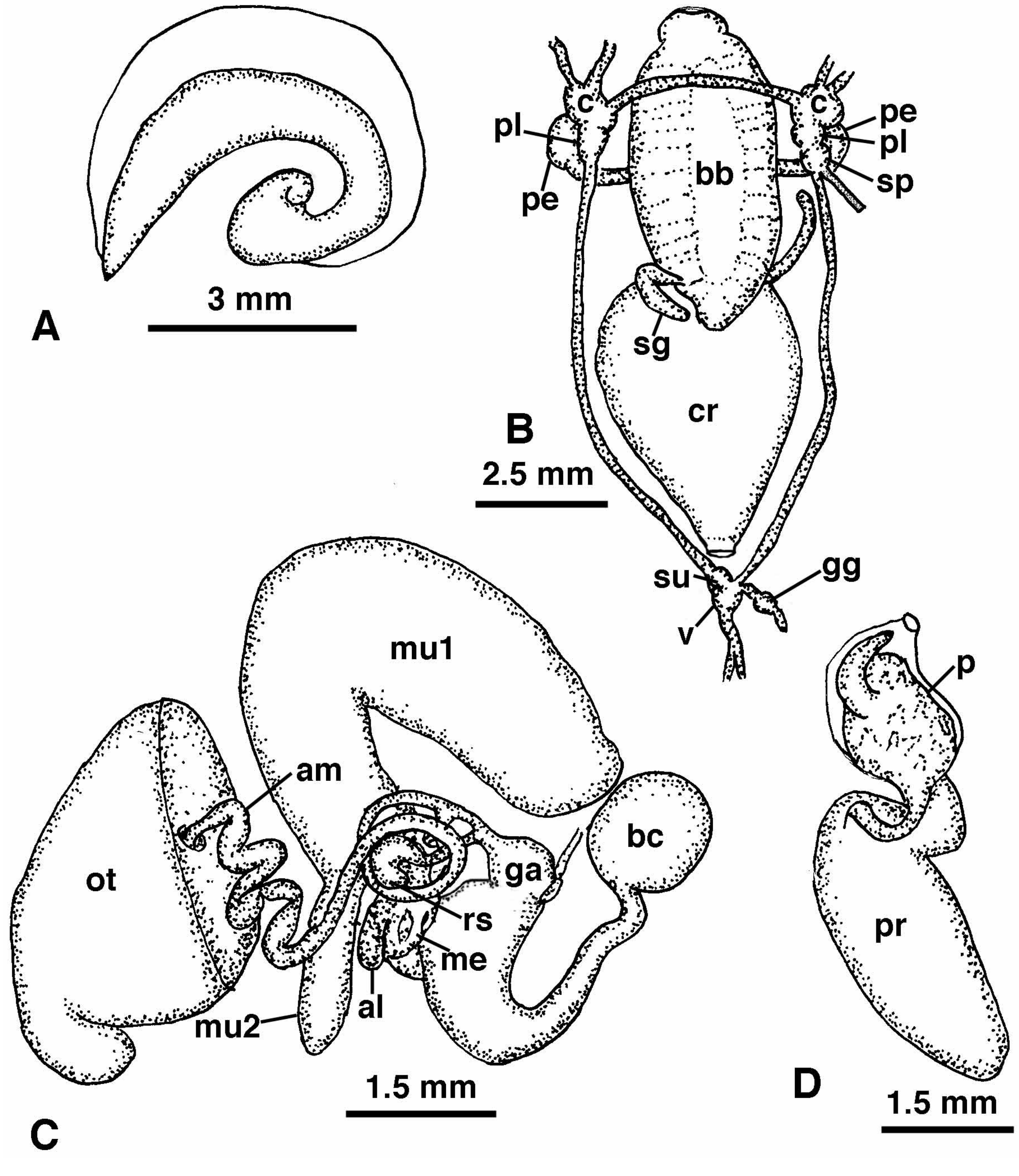

FIGURE 3. Internal anatomy, *Philinopsis falciphallus* **n. sp.** **A**. Shell, paratype, CASIZ 177678, scale = 3.5 mm. **B.** Digestive and central nervous system anatomy, paratype, CASIZ 174145, bb buccal bulb, c cerebral ganglion, cr crop, gg genital ganglion, pe pedal ganglion, pl pleural ganglion, sg salivary gland, sp supraintestinal ganglion, su subintestinal ganglion, v visceral ganglion. **C.** Posterior reproductive organs, paratype, CASIZ 174175, al albumen gland, am ampulla, bc bursa copulatrix, ga gential atrium, me membrane gland, mu1 mucous gland large, mu2 mucous gland small, ot ovotestis, rs receptaculum seminis. **D.** penis, paratype, Philippines, CASIZ 174145, p penial papilla, pr prostate.

Reproductive System (Fig. 3C–D). The arrangement of reproductive organs is essentially monaulic (as discussed by Gosliner 1994) but with a single branch of the hermaphroditic duct to the albumen and membrane glands

(Fig. 3C). From the large ovotestis, which is intermingled with the digestive gland, emerges the convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which curves around the receptaculum seminis and enters the short, coiled albumen and membrane glands by means of a single duct. The larger mucous gland is bilobed with a massive primary lobe and smaller secondary one. The hermaphroditic duct then joins the duct of the receptaculum seminis and continues to the genital atrium, where it joins the duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow where it joins the bursa and widens until its widest portion at the genital atrium. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 3D) consists of a penial sac and a lobate prostate gland that is joined to the penial sac by a narrow duct. Within the penial sac is a large penial papilla (Fig. 4) that is covered by a scattered series of large spines that are distributed over the surface of the penis and along its right base. Extending from the right surface of the penial papilla is a large curved, sickle-shaped chitinous spine.

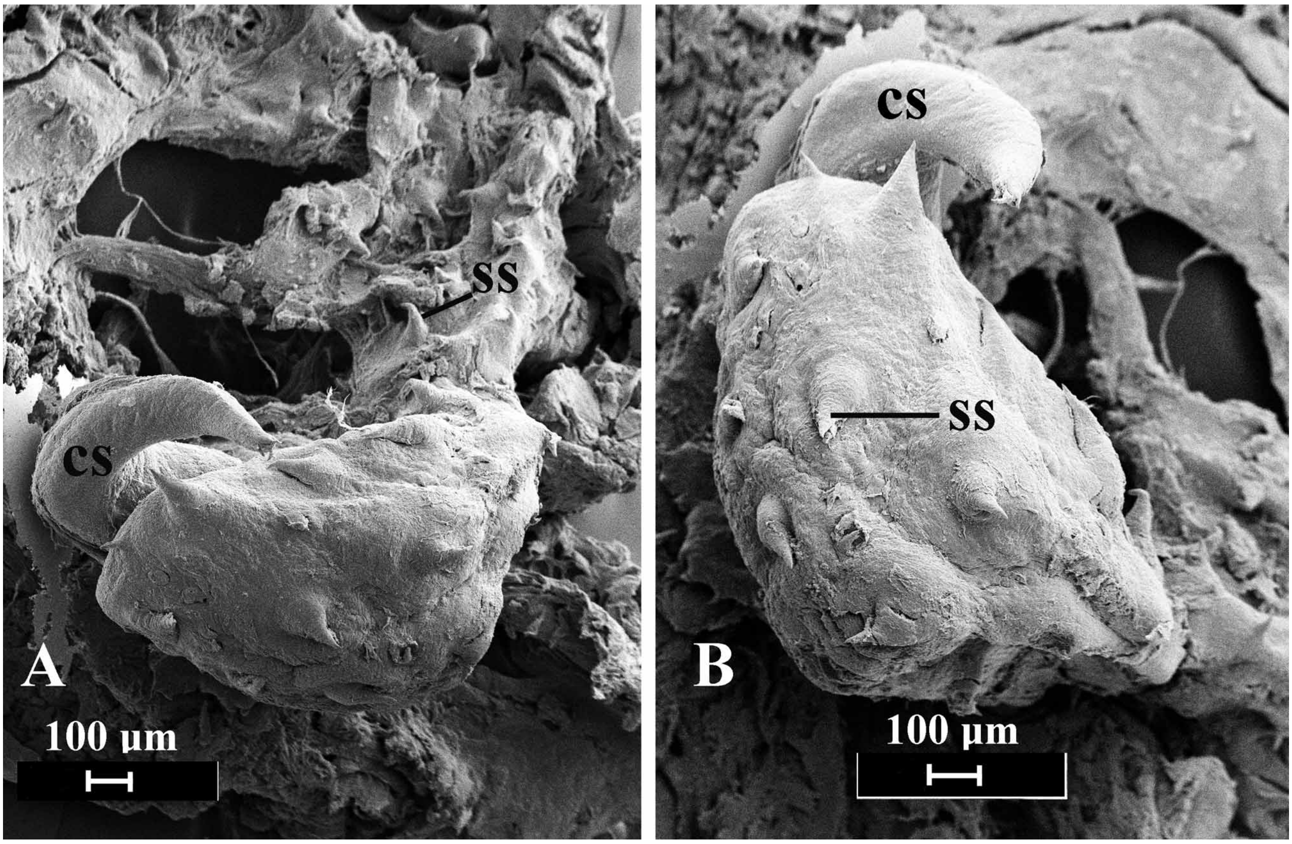

FIGURE 4. *Philinopsis falciphallus* **n. sp.**, Scanning eletron micrographs. **A., B.** Penis paratype, Philippines, CASIZ 174145, cs large penial spine, ss small penial spines.

Remarks. The presence of a quadrangular anterior end of the body, a posterior lobe of the cephalic shield, a large muscular bulb, the single branch of the hermaphroditic duct to the albumen and membrane glands, a bilobed mucous gland are all characteristics of species of *Philinopsis.*

In his review of *Philinopsis*, Rudman (1972a) indicated there were two distinct groups of species. Members of the first group are characterized by having a large quadrangular head, a bulbous buccal mass and a specialized penis with a basal elongate penial papilla and a short prostate (Marcus & Marcus 1967: fig. 12). Members of the second group have a rounded head with an elevated bulbous region (that resembles the front end of a Boeing 747) with prominent eyes visible at the base of the bulb, an elongate, tubular buccal bulb and a simple penis. Gosliner (1980) suggested that *Aglaja depicta* (Renier, 1807), placed by Rudman in *Aglaja*, had attributes more similar to the members of the quadrangular-headed species of *Philinopsis* and tranfered it to this genus. While the remainder of the anatomy of *P. depicta* is similar to the members of the quadrangular-headed group, it has a simple penis. *Philinopsis falciphallus* has a quadrangular head but differs from other members of this group in having a conical posterior lobe to the posterior shield. It also has a bulbous muscular buccal bulb. The penis of *P. falciphallus* is unique among described aglajids in several respects. It is the only species that has the prostate separated from the penial bulb by a narrow duct. It is also the only *Philinopsis* with an armed penis. Not only is the penis armed, but it has a series of spines on the papilla and a large curved chitinous spine. A few other aglajid species have an armed penis. *Melanochlamys diomedea* (Bergh) (Rudman 1972a) and *M. barryi* Gosliner (Gosliner 1990: fig. 14) have a single apical penial stylet. *Melanochlamys papillata* Gosliner (Gosliner 1990: fig. 8) and *Aglaja ocelligera* (Bergh) (Rudman 1974: fig. 13) have a penis with numerous papillae on the penial papilla. None of those structures resemble the elaborate armature present in *P. falciphallus*.

A preliminary molecular phylogenetic analysis (Gatdula *et al*. personal communication) using the 16S mitochondrial gene fragment has this species clustered with group of *Philinopsis* species that have a tubular buccal mass rather than those that have a bulbous buccal mass. This is despite the fact that *P. falciphallus* has a bulbous buccal bulb. More detailed analysis is required using multiple genes, but preliminary data clearly indicate that this species is nested within the clade of *Philinopsis* species.

***Philinopsis coronata* n. sp.**

(Figures 1C, 2B, 5, 6)

Material examined. Holotype: CASIZ 1822887, dissected, 12 m depth, Mainit Bubbles, Mabini, Batangas Province, Luzon, Philippines, 13.686025°S, 120.895167° E, 23 May 2010, P. Paleracio.

Geographical distribution. Known only from the Philippines (present study).

Etymology. The name “coronata” comes from the Latin *corona*, meaning crown. This refers to the ring of rounded tubercles at the apex of the penis, which resemble a crown.

Natural history. This species is found in the same habitat and at the same locality as the preceding species on coral rubble in 15 m depth. Little else is known about its biology.

Description. *External morphology.* The living specimen was 28 mm in length and 7 mm wide. The general body color of the living animal (Fig. 1C) is whitish with a “v”-shaped maroon patch present on the head. Maroon spots are present along the parapodial margins. The entire dorsal and lateral surfaces of the body are ornamented with scattered, irregular yellow spots and a few whitish patches. The ventral surface of the single animal is pale pink with a series of large yellowish and maroon spots on the foot. Living animals are elongate and wide. The anterior end of the cephalic shield is indented but blunt and quadrangular. The cephalic shield is roughly rectangular and terminates posteriorly with an elongate, rounded papilla. The posterior shield is slightly rounded anteriorly and terminates in an elongate conical posterior protrusion that is well-elevated from the base of the shield. The two lateral posterior lobes of the posterior shield are elongate and simply rounded. The left posterior lobe is longer than the right one. The parapodia are very short, leaving most of the cephalic and posterior shields visible. The gill is simply plicate consisting of 13 primary folds and is situated on the right posterior side of the animal.

Shell (Fig. 2B). The shell is relatively thickly calcified and consists of a narrow band that occupies the posterior extreme of the animal. There is a thin membranous periostracum that is slightly more extensive anteriorly than the calcified portion. The area at the base of the shell near the protoconch is more thickly calcified than the rest of the shell and a posterior lobe is present on the left side of the shell.

Digestive system (Fig. 5A). The buccal mass is large, highly muscularized and slightly elongate posteriorly. It occupies the entire length of the cephalic shield. The buccal bulb lacks any vestige of a radula. There is a large ventral oral gland and the small dorsal oral glands were indistinct. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is large and saccate, wider than the buccal bulb. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

Central nervous system (Fig. 5A): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both elongate with well-separated respective ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which has a distinct genital ganglion.

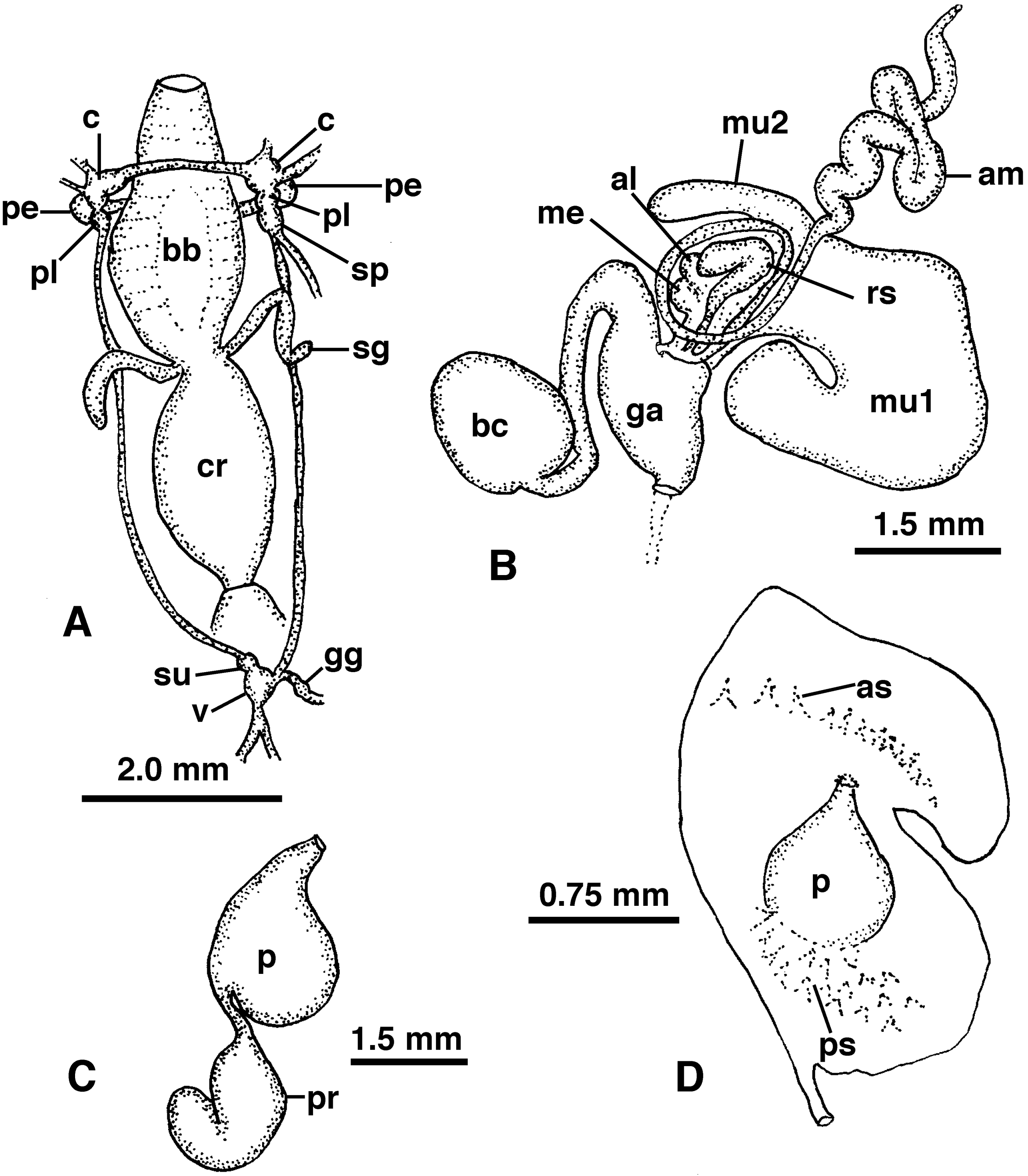

FIGURE 5. Internal anatomy, *Philinopsis coronata* **n. sp.**, holotype, CASIZ 182887 **A.** Digestive and central nervous system anatomy, bb buccal bulb, c cerebral ganglion, cr crop, gg genital ganglion, pe pedal ganglion, pl pleural ganglion, sg salivary gland, sp supraintestinal ganglion, su subintestinal ganglion, v visceral ganglion. **B.** Posterior reproductive organs, al albumen gland, am ampulla, bc bursa copulatrix, ga gential atrium, me membrane gland, mu1 mucous gland large, mu2 mucous gland small, ot ovotestis, rs receptaculum seminis. **C., D.** Penis, as anterior penial spine, p penial papilla, pr prostate, ps posterior penial spines.

Reproductive system (Fig. 5B, C, 6). The arrangement of reproductive organs is monaulic (Fig. 5A) with a single branch to the albumen and membrane glands. From the large ovotestis, which is intermingled with the digestive gland, emerges the convoluted ampulla. The ampulla narrows into the hermaphroditic duct, curves around the receptaculum seminis and has a single branch to the short, coiled albumen and membrane glands. The larger mucous gland is bilobed with a massive primary lobe and smaller secondary one. The ampulla then joins the duct of the receptaculum seminis and continues to the genital atrium where it joins the duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow where it joins the bursa and widens until its widest portion at the highly muscularized genital atrium. From the genital atrium, the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 5C, 6) consists of a penial sac and a lobate prostate gland that is joined to the penial sac by a narrow duct. Within the penial sac is a large, rigid conical penial papilla (Fig. 6A,B). Anterior to the penial papilla and posterior to it are two areas of spines on the folds of the penial sac (Fig. 5C, 6A). The apex of the papilla is covered with a ring of rounded tubercles.

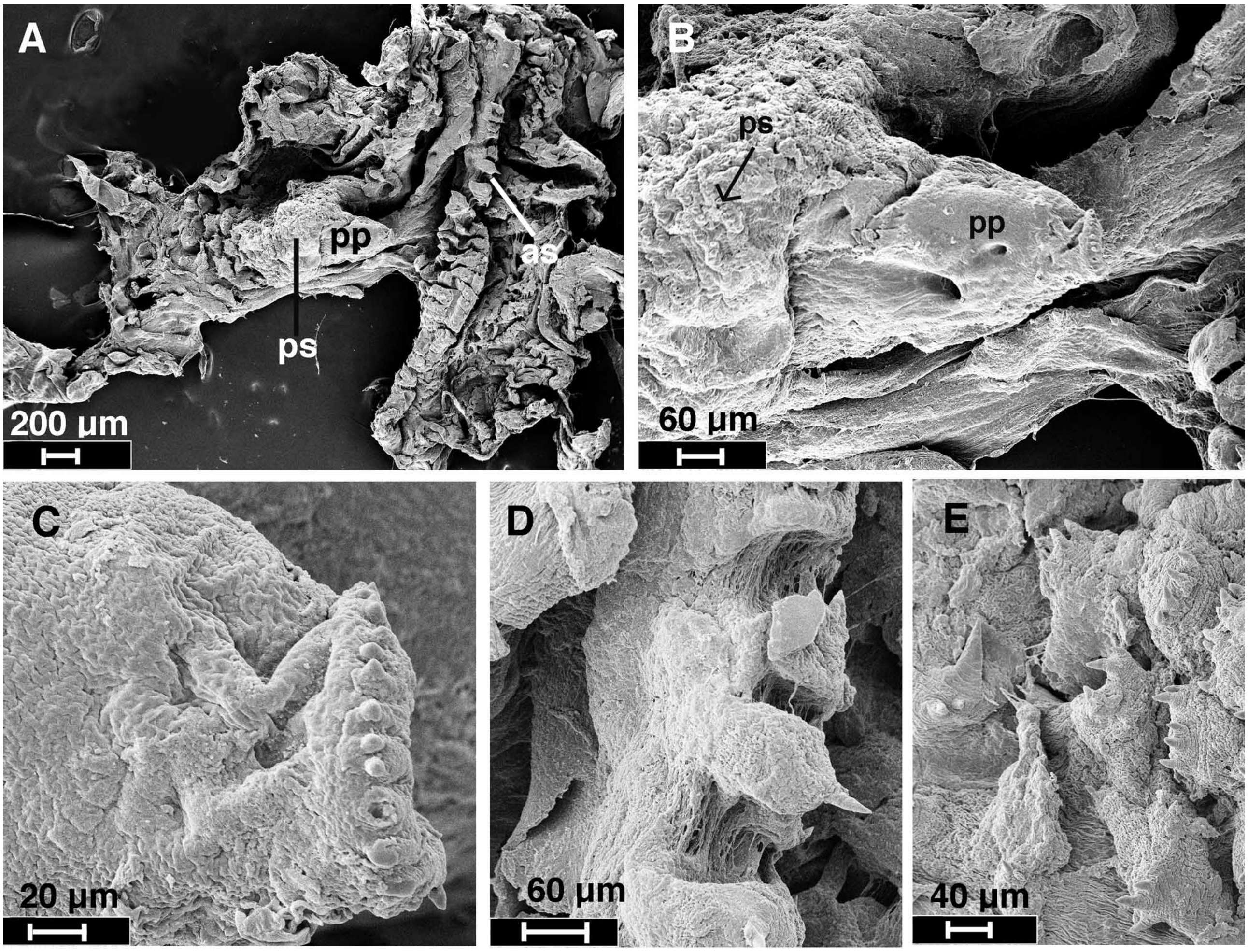

FIGURE 6. *Philinopsis coronata* **n. sp.**, holotype, CASIZ 182887, scanning electron micrographs of penis **A.** Penial sac showing location of as anterior spines, pp penial papilla, ps posterior spines **B.** Penial papilla and posterior spines **C.** Penial papilla showing ring of tubercles on apex. **D.** Detail of anterior spines. **E.** Detail of posterior spines.

Remarks. *Philinopsis coronata* is very similar in its external and internal appearance to *P. falciphallus*, described above. The external anatomy and color pattern are very similar. In *P. coronata*, there is more yellow pigment with less maroon and the posterior lobe of the posterior shield is more elongate than in *P. falciphallus*. Also, *P. coronata* has more elongate posterior extension of the foot than does *P. falciphallus*. Both species have yellow and maroon on the foot, but in *P. coronata* there is no maroon line, but rather a series of maroon spots. The shell of *P. coronata* has a more elongate posterior wing on the right side than is found in *P. falciphallus*. Internally, the digestive and central nervous systems of the two species exhibit no apparent differences. The arrangement of the posterior reproductive organs of the two is also quite similar, but the genital atrium of *P. coronata* appears to be more highly muscularized. The most significant difference between these two species is found in the structure of the penis. Both species have a simple penis and prostate connected by a narrow duct and both are the only species of *Philinopsis* with an armed penial papilla. Despite these similarities, the armature of the penis is markedly different in the two species. In *P. falciphallus*, there is a large chitinous spine and a series of smaller spines on the penial papilla. In *P. coronata* there are two regions of spines, one anterior to the penial papilla and the other one situated posteriorly to the papilla. The apex of the papilla of *P. coronata* has a ring of rounded tubercles that is not present in *P. falciphallus*. The specimens are similar in size and maturity so it is likely that the observed penial differences are due to differences in maturity or preservation. These significant differences in penial morphology confirm that these specimens represent distinct taxa.

Philinopsis ctenophoraphaga **n. sp.**

(Figures 1D, 7)

Philinopsis sp. Behrens, 2003.
Philinopsis sp. 1 Gosliner *et al*., 2008: 40, top photo.
Aglajid sp. 9 Rudman, 2005a; Koretz, 2005b; Francisco, 2008.
Aglajid sp. 11 Rudman, 2006a.

Material examined. Holotype: CASIZ 096249, 3 m depth, old site of Seafari Resort, also known as Basura, Anilao, Mabini, Batangas Province, Luzon, Philippines, 13.756788°S, 120.921605° E, 17 March 1994, Bob Jackson. Paratype: CASIZ 096245, one specimen, dissected, 3 m depth, old site of Seafari Resort, also known as Basura, Anilao, Mabini, Batangas Province, Luzon, Philippines, 13.756788°S, 120.921605° E, 16 March 1994, T. M. Gosliner.

Geographical distribution. Philippines (Behrens 2003), Indonesia (Francisco 2006) and the Red Sea (Koretz 2005b).

Etymology. The name comes from Ctenophora (Greek, meaning comb-bearer) and from the Greek phago, meaning to eat referring to the fact that this species has been observed feeding on benthic ctenophores.

Natural history. This species is nocturnally active. A specimen has been observed feeding on benthic ctenophores, identified here as *Coeloplana meteoris* Thiel (Francisco 2006).

Description. *External morphology.* The general body color of the living animal (Fig. 1D) is light pinkish to maroon red. The pigment is a darker red on the anterior portion of the head, along the parapodial margins and along the elongated appendage on the posterior end of the cephalic shield. The entire dorsal and lateral surfaces of the body are ornamented with scattered opaque white spots that are surrounded by a faint halo of lighter pigment. Living animals are elongate (18–40 mm long), and wide (6–15 mm). The anterior end of the cephalic shield is slightly trilobate. The cephalic shield is roughly rectangular and terminates posteriorly into an elongate triangular appendage (Fig. 7A) that is held upright when the animal is actively crawling (Gosliner *et al*. 2008, top figure). The posterior shield is slightly rounded anteriorly and terminates in a bilobed pair of extensions that are relatively short, forming a skirt around the edge of the mantle. The parapodia are relatively short, leaving most of the cephalic and posterior shields visible. The gill is simply plicate consisting of 10 primary folds and is situated on the right posterior side of the animal.

Shell. The shell was completely dissolved during fixation, but occupies only the posterior extreme of the animal. The membranous periostracum remains and is relatively thin and evenly arched.

Digestive system (Fig. 7B). The buccal mass is large and bulbous but is only weakly muscularized, without the thickened dense musculature observed in most other species of aglajids. The thin, translucent nature of the extruded buccal mass can be seen in the photo accompanying the comment on feeding of this species of ctenophores (Rudman, 2006b). The buccal bulb entirely lacks any vestige of a radula. Anterior to the buccal bulb are small ventral and dorsal oral glands. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is large and saccate, slightly narrower than the buccal bulb. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

Central nervous system (Fig. 7B): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both elongate with well-separated respective ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion there is no distinct genital ganglion.

Reproductive system (Fig. 7C, D). The arrangement of reproductive organs is monaulic (Fig. 7C). From the large ovotestis, which is intermingled with the digestive gland, emerges the convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which curves around the receptaculum seminis and enters short, coiled albumen and membrane glands with a single opening. At the point where the hermaphroditic duct coils around the receptaculum, it consists of several coils rather than being a straight duct. The larger mucous gland is bilobed with a massive primary lobe and smaller secondary one. The hermaphroditic duct then joins the duct of the receptaculum seminis and continues to the genital atrium where it joins the duct of the bursa copulatrix. The bursa is large and spherical. Its duct is short and of uniform diameter throughout its length, including where it joins the genital atrium. From the genital atrium, the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 7D) consists of a penial sac and a simple curved prostate gland that is joined to the penial sac by a wide duct. Within the penial sac is a large rounded simple penial papilla (Fig. 7D) that lacks any trace of armature.

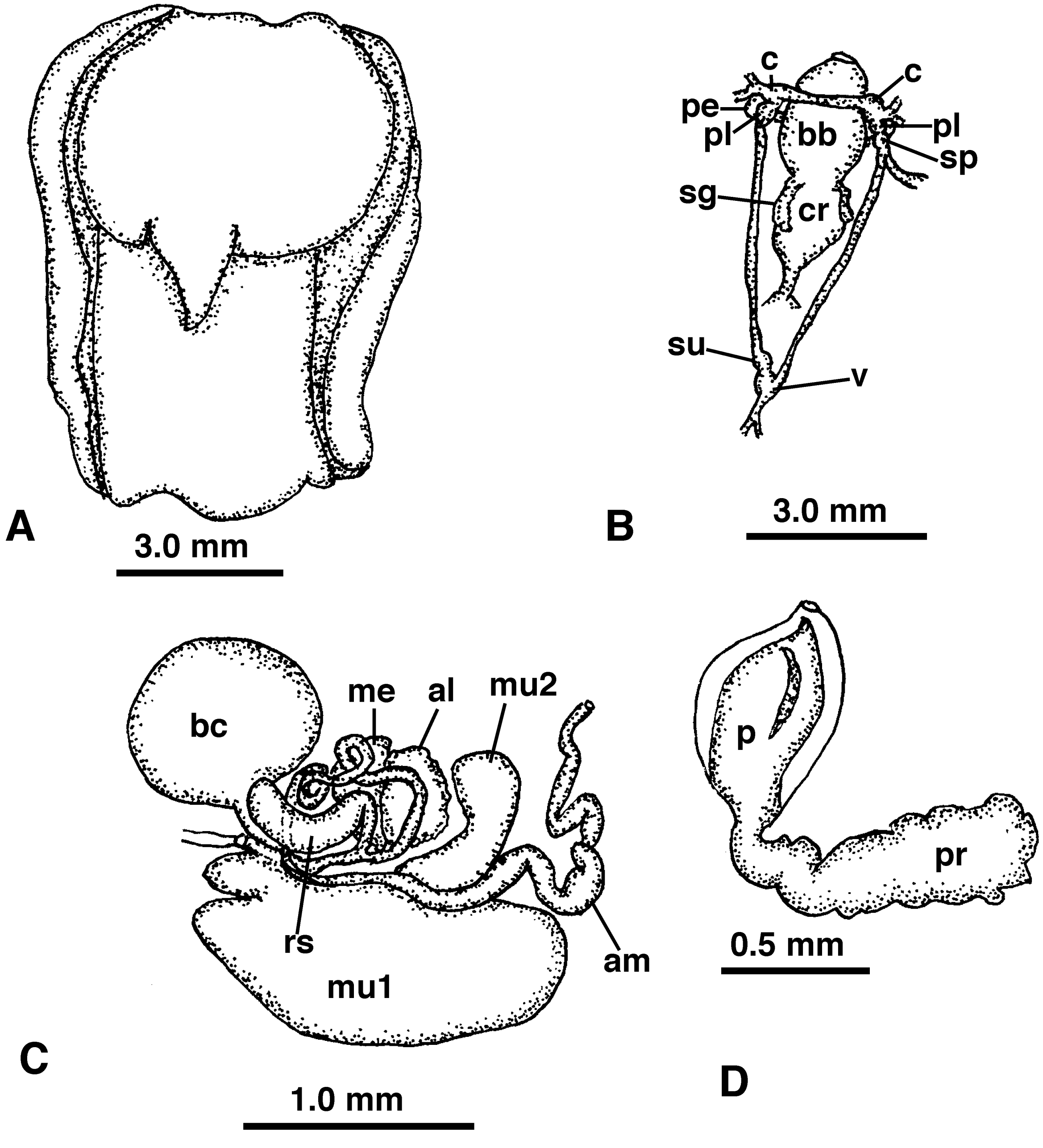

FIGURE 7. *Philinopsis ctenophoraphaga* **n. sp.**, paratype, CASIZ 096245. **A.** Dorsal view of preserved animal. **B.** Digestive and central nervous system anatomy, bb buccal bulb, c cerebral ganglion, cr crop, pe pedal ganglion, pl pleural ganglion, sg salivary gland, sp supraintestinal ganglion, su subintestinal ganglion, v visceral ganglion. **C.** Posterior reproductive organs, al albumen gland, am ampulla, bc bursa copulatrix, me membrane gland, mu1 mucous gland large, mu2 mucous gland small, rs receptaculum seminis. **D.** Penis, p penial papilla, pr prostate.

Remarks. *Philinopsis ctenophoraphaga* is the only species of *Philinopsis* with a pink to maroon coloration and opaque white spots. It is also unique in having a more elongate and acutely pointed triangular posterior end of the cephalic shield. In most other species of *Philinopsis*, the posterior end of the head shield is rounded and shorter. In most members of *Philinopsis,* as in the present species, the posterior end of the cephalic shield is held upright when the animal is actively crawling. *Philinopsis ctenophoraphaga* is clearly more similar to the group of *Philinopsis* species that have a highly muscularized bulbous buccal mass (such as *P. speciosa* Pease, 1860), but is unique having a weakly muscularized buccal bulb compared the thick mass with dense rings of muscles evident in other species. This may be an adaptation to feeding on benthic ctenophores rather than more solid and muscular molluscan prey. Most species of *Philinopsis* with a bulbous buccal bulb also have a specialized penial morphology and have a very specialized penial morphology that Marcus & Marcus (1966) called a type D penis. The only species in this group that lack this type of penis are *P. depicta* Renier (Gosliner 1980; present study) and *P. falciphallus* and *P. coronata* described here. These latter two species have elaborate penial armature. In *P. depicta* the simple penis and prostate are much longer the than the entire buccal bulb (Gosliner 1980; present study), while in *P. ctenophoraphaga* the penis and prostate are much shorter than the buccal mass. Several unique features of the external morphology, digestive system and reproductive anatomy clearly distinguish this species of aglajid from all other described taxa.

Genus *Chelidonura* A. Adams, 1850

Type species: *Bulla hirundinina* Quoy and Gaimard, 1832, by monotypy

Chelidonura mandroroa n. sp.

(Figures 1E, 2C, 8, 9)

Chelidonura sp. 1 Gosliner *et al.* 2008: 46, bottom figure.
Chelidonura sp. De Ponti, 2009; Chen, 2009.
Philinopsis sp. 1 Rudman, 2001.
Philinopsis sp. Behrens, 2005.

Material examined. Holotype: CASIZ 173595, not dissected, 11m depth, wall and reefs flat west of Nosy Valiha, Radama Islands, Madagascar, 14.15829° S 47.648473° E, 15 October 2005, T.M. Gosliner. Paratype: CASIZ 182002, dissected, molecular sample taken from foot, 13 m depth, wall and reefs flat west of Nosy Valiha, Radama Islands, Madagascar, 14.15829° S 47.648473° E, 15 October 2005, T.M. Gosliner. Paratype: CASIZ 112290, not dissected, Manado, Sulawesi, Indonesia, April 1988, Pauline Fiene and Mike Severns.

Geographic range. This species is known only from Japan (Nakano 2001), Taiwan (Chen 2009) Indonesia, Philippines (Gosliner *et al*. 2008) Tanzania (de Ponti 2009) and Madagascar (this study).

Etymology. The name *mandroroa* is the Malagasy word meaning to hallucinate. This refers to the striking, psychedelic color pattern that characterizes this species.

Natural history. This species is found on shallow reef flats, often under coral rubble or crawling in the open at 8–13 m depth.

Description. *External morphology.* The general body color of the living animal (Fig. 1A) is dark brown to black with burnt orange patches and circles each bordered by bright yellow. This pigment pattern is found on the cephalic and posterior shields, the parapodia and the foot. The living animals are elongate, and narrow. The anterior end of the cephalic shield is trilobate. The cephalic shield is triangular, broadest anteriorly and terminates posteriorly with a short rounded lobe. The posterior shield is well rounded anteriorly and terminates in two short, broad posterior lobes that are acutely pointed at their ends. They are approximately equal in length. The parapodia are relatively wide, largely covering most of the cephalic and posterior shields. The gill is plicate with 11 primary folds.

Shell (Fig. 2C, 8A). The shell is relatively thickly calcified and is a shiny white with a brownish tinge. It occupies the left third of the posterior shield. There is a broad anteriorly-directed wing and an elongate extension that is deeply imbedded in the posterior shield right to the end of the right posterior lobe.

Digestive system (Fig. 8B). The buccal mass is small, highly muscularized, occupying the anterior two-thirds of the cephalic shield. The buccal bulb entirely lacks any vestige of a radula. There is a small dorsal oral gland and a large ventral one. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is small and saccate, about the same width as the buccal bulb. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

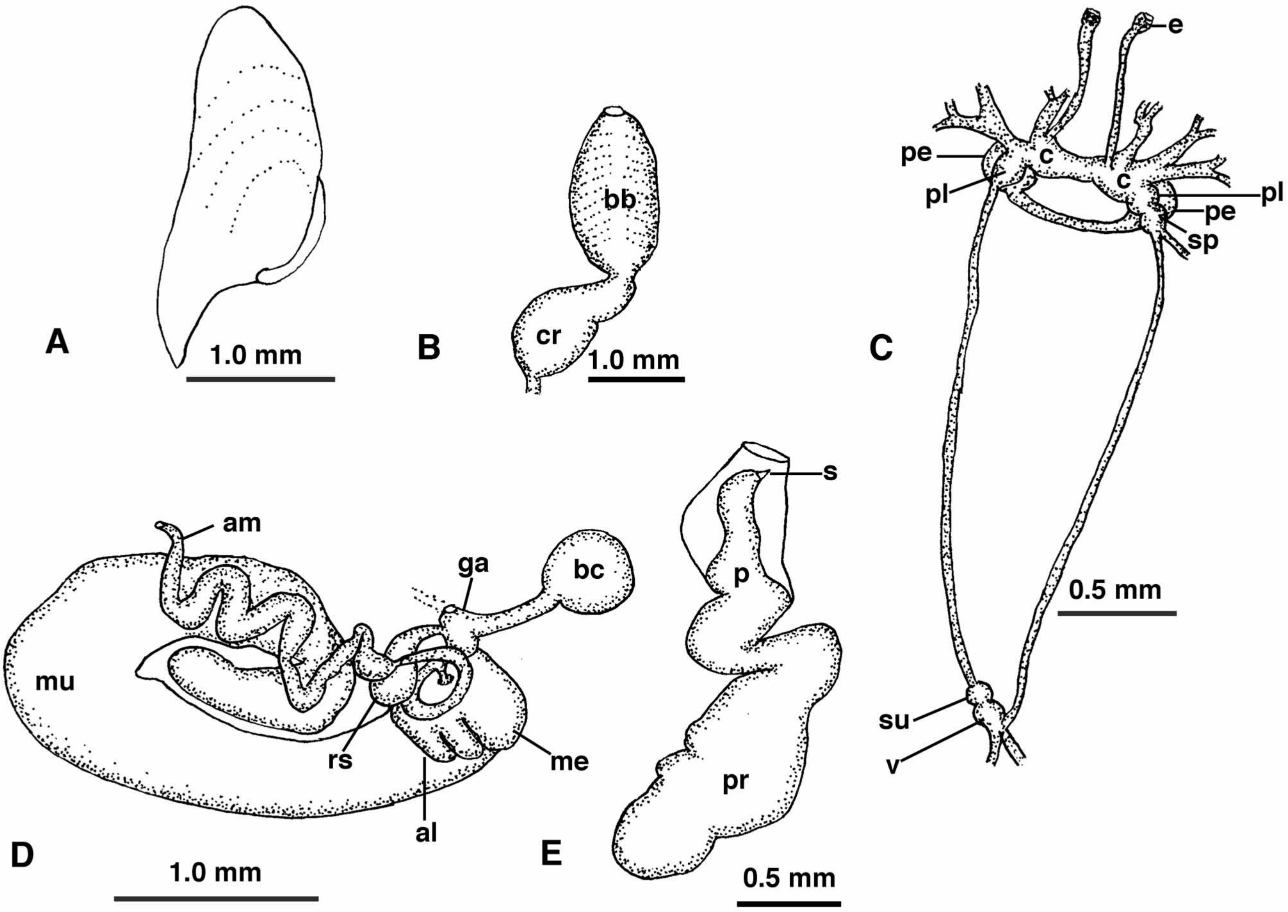

FIGURE 8. *Chelidonura mandroroa* **n. sp. A.** Shell. **B.** Buccal bulb and crop. bb buccal bulb, cr crop. **C.** Central nervous system, c cerebral ganglion, e eye, pe pedal ganglion, pl pleural ganglion, sp supraintestinal ganglion, su subintestinal ganglion, v visceral ganglion. **D.** Posterior genital system, al albumen gland, am ampulla, bc bursa copulatrix, ga genital atrium, me membrane gland, mu mucous gland, rs receptaculum seminis. **E.** Penis, p penial papilla, pr prostate, s stylet.

Central nervous system (Fig. 8C): The circumesophageal nerve ring consists of paired cerebral, pedal, pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both short with poorly separated ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters the visceral ganglion posterior to its junction with the subintesinal ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which lacks a distinct genital ganglion.

Reproductive system (Fig. 8D, E, 9). The arrangement of reproductive organs is a modified monaulic arrangement(Fig. 8D). From the large ovotestis, which is intermingled with the digestive gland, emerges the convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which curves around the receptaculum seminis and enters short, coiled albumen and membrane glands. It appears to have only a single entrance to these glands. Immediately prior to curving around the receptaculum, the hermaphroditic duct has a swollen, bulbous portion. The larger mucous gland is curved with a massive primary lobe. The hermaphroditic duct then joins the duct of the short receptaculum seminis and continues to the genital atrium where it joins the duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow and short and widens slightly at the genital atrium. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis (Fig. 8E, 9) consists of a penial sac and a lobate prostate gland that is joined to the penial sac by a wide duct. Within the penial sac is a large penial papilla that is smooth and conical. Extending from the apical end of the penial papilla is a small curved, apical stylet (Fig. 9C).

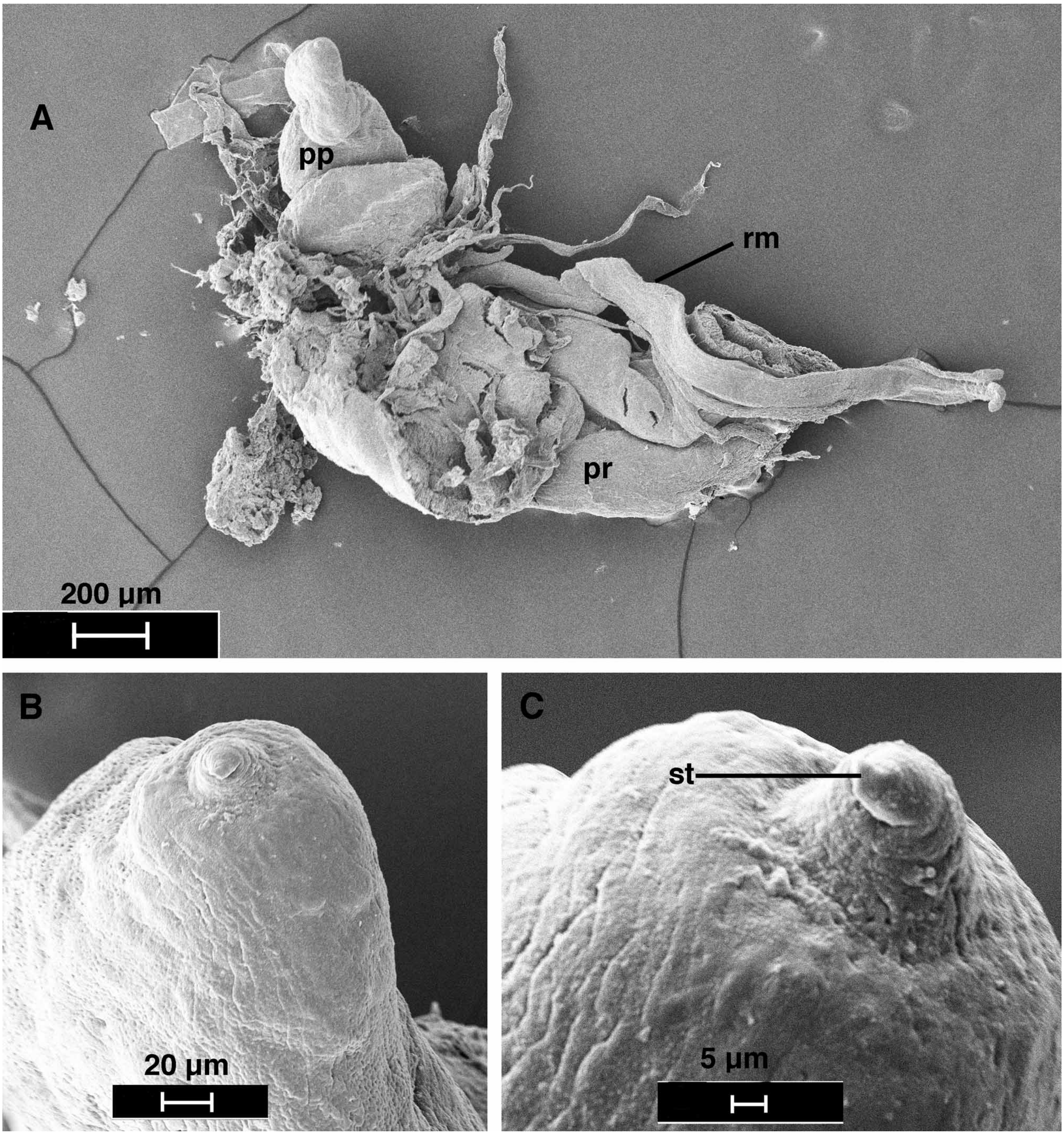

FIGURE 9. *Chelidonura mandroroa* **n. sp.** Scanning eletron micrographs of penis. A. Entire penis pp penial papilla, pr prostate, rm retractor muscle. **B.** Apex of penial papilla**. C.** Apex of penial papilla showing cuticular stylet, st stylet.

Remarks. Rudman (2001) suggested that this species was likely a species of *Philinopsis* based on the shape of its head, but later suggested it may be a species of *Chelidonura* (Rudman 2002). He also suggested that it likely had a tubular buccal bulb. Species of *Philinopsis* have either a rounded or quadrangular anterior end of the cephalic shield rather than the distinctly lobate one found in the present species. The head of *C. mandroroa* is similar in shape to that of *C. inornata* Baba, 1949; *C. electra* Rudman, 1970, *C. castanea* Yonow, 1994a; *C. punctata* Eliot, 1903 and *C. amoena* Bergh, 1905, (see Gosliner *et al.* 2008). Several other anatomical features support the placement of this species in *Chelidonura*. The shell is completely calcified with a broad anteriorly directed wing. The buccal mass is muscular but relatively small. The central nervous system has short cerebral and pedal commissures. The reproductive system has a distal receptaculum seminis and a single lobe of the mucous gland. In contrast, species of *Philinopsis* have a shell without a calcified expanded anteriorly-directed wing (Fig. 2C, 8A), a central nervous system with elongate commissures, a bilobed mucous gland and receptaculum seminis with an elongate duct.

A preliminary molecular phylogenetic analysis (Gatdula *et al.* personal communication) using the H3 nuclear gene fragment has this species clustered as sister taxon to *Chelidornura inornata*. More detailed analysis is required using multiple genes, but preliminary data strongly indicate that this species is nested within the clade of *Chelidonura* species.

Chelidonura mandroroa can be clearly distinguished from all other alglajids by its unique color pattern of a black body with orange patches surrounded by yellow lines. The shape of the anterior portion of the body is most similar to *C. inornata*, *C. electra*, *C. castanea*, *C. punctata* and *C. amoena*, but all of these species have elongate posterior extensions of the posterior shield, while *C. mandroroa* has short ones. *Chelidonura mandroroa* is the only species of *Chelidonura* that has been described with an apical cuticular stylet on the penis. The distinctive color pattern, lobed head with short posterior extensions of the posterior shield and the cuticular apex of the penis are all unique and distinctive attributes of this species.

***Chelidonura alisonae* n. sp.**

(Figures 1F, 2D, 10)

Chelidonura sp. 1 Gosliner *et al*., 2008; Pittman and Fiene, 2009.

Chelidonura sp. Hoover, 2006: 148, inset photo; Adams, 2009.

Chelidonura hirundinina (Quoy and Gaimard) Kay, 1979: 429, figure 138F; Bertsch and Johnson, 1981: 19, upper figure; Rudman, 2007, misidentifications.

Material examined. Holotype: CASIZ, 174176, intertidal reef platform, Diamond Head Beach Park, Honolulu, O’ahu, Hawai’i, 21.255795° N 157.810771° W, 8 February 1986, T.M. Gosliner. Paratypes: CASIZ, 073410, one specimen, intertidal reef platform, Diamond Head Beach Park, Honolulu, O’ahu, Hawai’i, 21.255795° N 157.810771° W, 8 February 1986, T.M. Gosliner. CASIZ 073408, one specimen, dissected, intertidal reef platform, Diamond Head Beach Park, Honolulu, O’ahu Hawai’i, 21.255795° N 157.810771° W, 8 February 1986, T. M. Gosliner and Michael T. Ghiselin. CASIZ 174177, one specimen, dissected, sea water tanks, Kewalo Marine Laboratory, Honolulu, O’ahu, Hawai’i, 25 October 1986, T.M. Gosliner and M. T. Ghiselin. CASIZ, 088428, four specimens, fish spot, outer reef, S. side Sand Island, Midway Atoll, Hawai’ian Islands, 2 June 1993, T.M. Gosliner and P. Fiene. CASIZ 088365, six specimens, fish spot, outer reef, S. side Sand Island, Midway Atoll, Hawai’ian Islands, 1 June 1993, T.M. Gosliner and P. Fiene. CASIZ 088575, one specimen, dissected, White Cross, N. E. side Sand Island, Midway Atoll, Hawai’ian Islands, 5 June 1993, T.M. Gosliner and P. Fiene. CASIZ 165872, one specimen, molecular sample removed, 1 m depth, Hekili Point, Maui, Hawai’ian Islands, 5 June 2003, C. Pittman. CASIZ 156080, seven specimens, one dissected, 3–8 m depth, Johnston Atoll, lagoon reefs near, Johnston Island, 23 April 2001, Phil Lobel. CASIZ 170052, 1–2 m depth, 1 specimen, natural tidal pool, Hotel Iorana, Easter Island, 27.15904°S, 109.442286° W, 15 December 2002, T. M. Gosliner. CASIZ 174146, two specimens, M36 84, Easter Island, Louis de Salvo. American Museum of Natural History 319376, one specimen, Anakena Beach, Easter Island, Christopher Boyko, 1999.

Geographic range. This species is known only from the Hawai’ian Islands (this study), Johnston Island (this study), Phoenix Island (Adams 2009), Moorea (C. Pittman personal communication), the northern Marianas Islands (Urasawa 2007) and Easter Island (Gosliner *et al.* 2008; this study).

Etymology. This species is named in honor of the late Dr. E. Alison Kay, Professor Emeritus of the University of Hawai’i. Dr. Kay was a superb mentor to many students including the author of this paper. She also pioneered the modern study of the molluscan fauna of the Hawai’ian Islands and the biogeography of the Central Pacific.

Natural history. This species is found on exposed intertidal reef platforms and shallow reefs in 1–10 m depth. It has been observed feeding on acoel flatworms of the genus *Convoluta* (Pittman & Fiene 2009; present study).

Description. *External morphology.* The general body color of the living animal (Fig. 1A, 10A) is black to brown. The head shield has a pair of bright blue spots, each of which is surrounded by a pair of orange lines that connect anteriorly and form a loop around the blue spots. The two outer bands terminate at the outer edges of the cephalic shield after a short distance, while the two inner bands continue to the posterior end of the cephalic shield where they converge. At the posterior end of the cephalic shield a white or blue band is usually present but may be absent in some specimens. There is also a large blue pigment spot on the anterior end of the head. The margins of the parapodia are decorated with five to seven pairs of bright blue spots. A submarginal orange line extends the length of the parapodia. Additional blue pigment spots are present on the dorsal portion of the posterior shield and on the surfaces of the two posterior extensions. Additional orange lines are present on the posterior shield including the posterior extensions. The lines may coalesce forming a reticulated network. Orange lines are also present on the ventral surface of the foot where they also form a network of interconnected lines. A specimen from Easter Island (CASIZ 170052) has less orange pigment on the cephalic shield. In this instance the inner orange lines do not extend to the end of the cephalic shield. This specimen also has opaque white spots scattered on the dorsal and ventral surfaces. A network of orange lines is still present on the foot.

The anterior end of the cephalic shield is trilobate. The cephalic shield is triangular, broadest anteriorly and terminates posteriorly with a short rounded lobe. Elongate sensory bristles are visible on the anterior end of the head (Fig. 10A). The posterior shield is well rounded anteriorly and terminates in two moderately elongate, broad posterior lobes that are acutely pointed at their ends. The left lobe is always longer than the right one. The parapodia are relatively wide largely covering most of the cephalic and posterior shields. The gill is plicate with 7–8 primary folds.

Shell (Fig. 2D). The shell is relatively thickly calcified and is a shiny white or brown. It occupies the almost the entire area of the posterior shield. There is a broad anteriorly-directed wing and a short extension that is deeply imbedded in the posterior shield right to the end of the right posterior lobe.

Digestive system (Fig. 10B). The buccal mass is small, highly muscularized, occupying the anterior two-thirds of the cephalic shield. The buccal bulb entirely lacks any vestige of a radula. There is a small dorsal oral gland and a large ventral one. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands. The crop is small and saccate, smaller than the buccal bulb. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

Central nervous system (Fig. 10C): The circumesophageal nerve ring consists of a paired cerebral, pedal and pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both short with short connectives to the adjacent ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters near the middle of the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which lacks a distinct genital ganglion.

Reproductive system (Fig. 10D, E–H). The arrangement of reproductive organs is a modified monaulic system (Fig. 10D). From the large ovotestis, which is intermingled with the digestive gland, emerges the slightly convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which curves around the receptaculum seminis and enters short, coiled albumen and membrane glands with a single duct. The hermaphroditic duct may have a portion that widens that may function as a proximal receptaculum seminis. The larger mucous gland is straight or curved with a massive primary lobe. The hermaphroditic duct then joins the duct of the elongate receptaculum seminis and continues to the genital atrium where it joins the duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow and elongate and does not widen at the genital atrium. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis is somewhat variable in shape (Fig. 10E–H), but consists of a penial sac and a lobate prostate gland that is joined to the penial sac by a wide duct. Within the penial sac is a large penial papilla that is smooth and conical. The penial papilla is devoid of any armature.

Remarks. *Chelidonura alisonae* is externally similar to the sympatric *Chelidonura hirundinina* (Quoy and Gaimard, 1832) and has often been misidentified with this species (Kay 1979; Bertsch and Johnson 1981; Rudman, 2007). Despite this similarity, there are consistent differences in external anatomy, which clearly distinguish these species. Both species have a black to brown body. *Chelidonura hirundinina* is quite variable in color but has a broad horizontal anterior yellowish or orange band. Behind this band is another blue or whitish transverse band that has a perpendicular connection to a mid-dorsal band of the same color that may extend to the posterior end of the

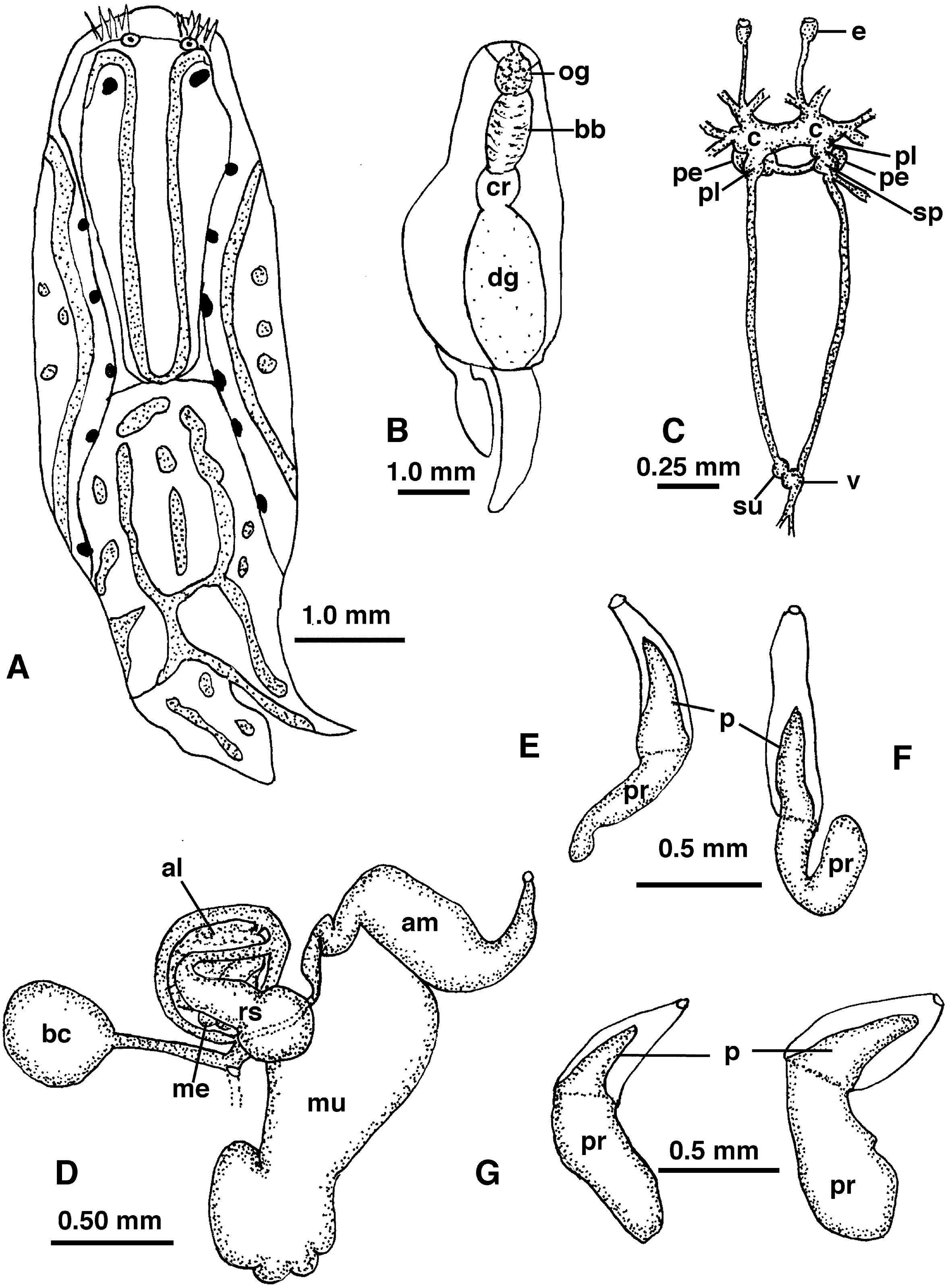

FIGURE 10. *Chelidonura alisonae* **n. sp. A.** Dorsal view of preserved specimen (CASIZ 073408). **B.** Ventral view, showing digestive system (CASIZ174177). Buccal bulb and crop. bb buccal bulb, cr crop, dg digestive gland, og ventral oral gland sg salivary gland, sp supraintestinal ganglion, **C.** Central nervous system, (CASIZ174177), c cerebral ganglion, e eye, pe pedal ganglion, pl pleural ganglion, sp supraintestinal ganglion, su subintestinal ganglion, v visceral ganglion. **D.** Posterior genital system, al albumen gland, am ampulla, bc bursa copulatrix, me membrane gland, mu mucous gland, rs receptaculum seminis. **E.** Penis (CASIZ 174177), p penial papilla, pr prostate. **F.** Penis (CASIZ 088575), p penial papilla, pr prostate. **G.** Penis (AMNH 319376), p penial papilla, pr prostate. **H.** Penis (CASIZ 156080), p penial papilla, pr prostate.

cephalic shield or may run just to its midsection. Most often there is a transverse opaque white crescent-shaped patch across the posterior shield, but this is occasionally absent. Generally, the parapodial margins are ornamented with a bright blue line, but occasionally this line is more greenish in color. There is a variable arrangement of orange lines on the cephalic shield, parapodia and posterior shield, but these lines never form a reticulating network as in *C. alisonae*. In contrast, *C. alisonae* always has a pair of blue spots on the head that is each surrounded by orange lines. No T-shaped opaque white or blue lines are present on the cephalic shield. An anterior blue patch rather than a yellow or orange one is present at the anterior end of the head. *Chelidonura alisonae* always has orange lines that form a reticulated network on the foot, but occasionally also on the posterior shield. The parapodial margins are ornamented with isolated blue spots rather than a continuous blue line. The posterior extensions of the posterior shield of *C. hirundinina* are always more elongate and finely tapered than those of *C. alisonae*.

There are also internal features that consistently separate the two species. In *C. hirundinina,* the right posterior end of the shell is slightly more elaborated than that of *C. alisonae* and it appears that the protoconch of the former is larger than that of the later. The central nervous system of *C. hirundinina* has a distinct genital ganglion (Gosliner 1988; present study) that is absent in *C. alisonae*. The mucous gland of *C. hirundinina* is tightly coiled, while that of *C. alisonae* is straight or curves only at the apex.

Pittman and Fiene (2009) have never observed copulation between specimens of *C. hirundinina* and *C. alisonae*.

We have conducted preliminary molecular studies (Camacho-Garcia, Gatdula & Gosliner personal communication.), using H3 nuclear and COI mitochondrial genes. In these studies, Caribbean and Indo-Pacific specimens of *C. hirundinina* cluster together, while a specimen of *C. alisonae* (CASIZ 165872) clusters with *Navanax* sp. (Gosliner *et al*. 2008: 48, bottom photo) and members of the *Chelidonura inornata* complex. *Chelidonura alisonae* differs from Caribbean and Australian specimens of *C. hirundinina* in its COI gene by 23% of its base-pairs.

Independent lines of evidence from external and internal morphology, species mate recognition systems and molecular markers clearly support the distinctness of *C. alisonae* from *C. hirundinina* and all other described species of *Chelidonura*.

Genus *Odontoglaja* Rudman

Type species *Odontoglaja guamensis* Rudman, 1978, by monotypy

Odonotoglaja mosaica n. sp.

(Figures 1G, H, 11–12)

Odontoglaja guamensis Koretz, 2005c; Ogden, 2005; Rudman, 2005b, misidentifications.
Odontoglaja sp. 1 Gosliner *et al.*, 2008: 38, bottom photo.

Material examined. Holotype: CASIZ 173402, 15m depth, NE Point of Nosy Kalakajoro, Radama Islands, Madagascar, 13.916819°S 47.760336° E, 20 October 2005, T.M. Gosliner. Paratypes: CASIZ 073539, one specimen, 3m depth, La Crique, Ile Saint Marine, Madagascar, 16.867978°S 49.901964° E, 8 April 1990, T.M. Gosliner. CASIZ 173419, two specimens, one dissected, W of Nosy Valiha, Radama Islands, Madagascar, 14.158167°S 47.648833° E, 21 October 2005, T.M. Gosliner. CASIZ 173415, one specimen, dissected, NW of Nosy Kalakajoro, Radama Islands, Madagascar, 13.894154°S 47.687500° E, 22 October 2005, T.M. Gosliner. CASIZ 173417, two specimens, one dissected, W of Nosy Valiha, Radama Islands, Madagascar, 14.174952°S 47.709251° E, 20 October 2005, T.M. Gosliner. CASIZ 175943, one specimen for shell and molecular study, 15m depth, NE Point of Nosy Kalakajoro, Radama Islands, Madagascar, 13.916819°S 47.760336° E, 20 October 2005, T.M. Gosliner.

Comparative material of *Odontoglaja guamensis*: CASIZ 069738, one specimen, dissected, 25 m depth, north reef north of "Pig Island" (Tab Island), Madang, Papua New Guinea, 24 August 1989. M. Gosliner. CASIZ 069738, one specimen, dissected, 10 m depth, Daphne's Reef, between Wongat Island and Sinub Island, Madang, Papua New Guinea, 26 July 1989, T. Gosliner. CASIZ 175764, sampled for molecular studies, 10 m depth, Ligpo Point, Balayan Bay, Batangas Province, Luzon Island, Philippines, 9 May 2001, T. Gosliner. CASIZ 175944, one specimen, portion of foot removed for molecular study, 22 m depth, Pineapple Point and Nudi wall, Pulau Tenggol, Malaysia, 30 September, 2007, D. W. Behrens.

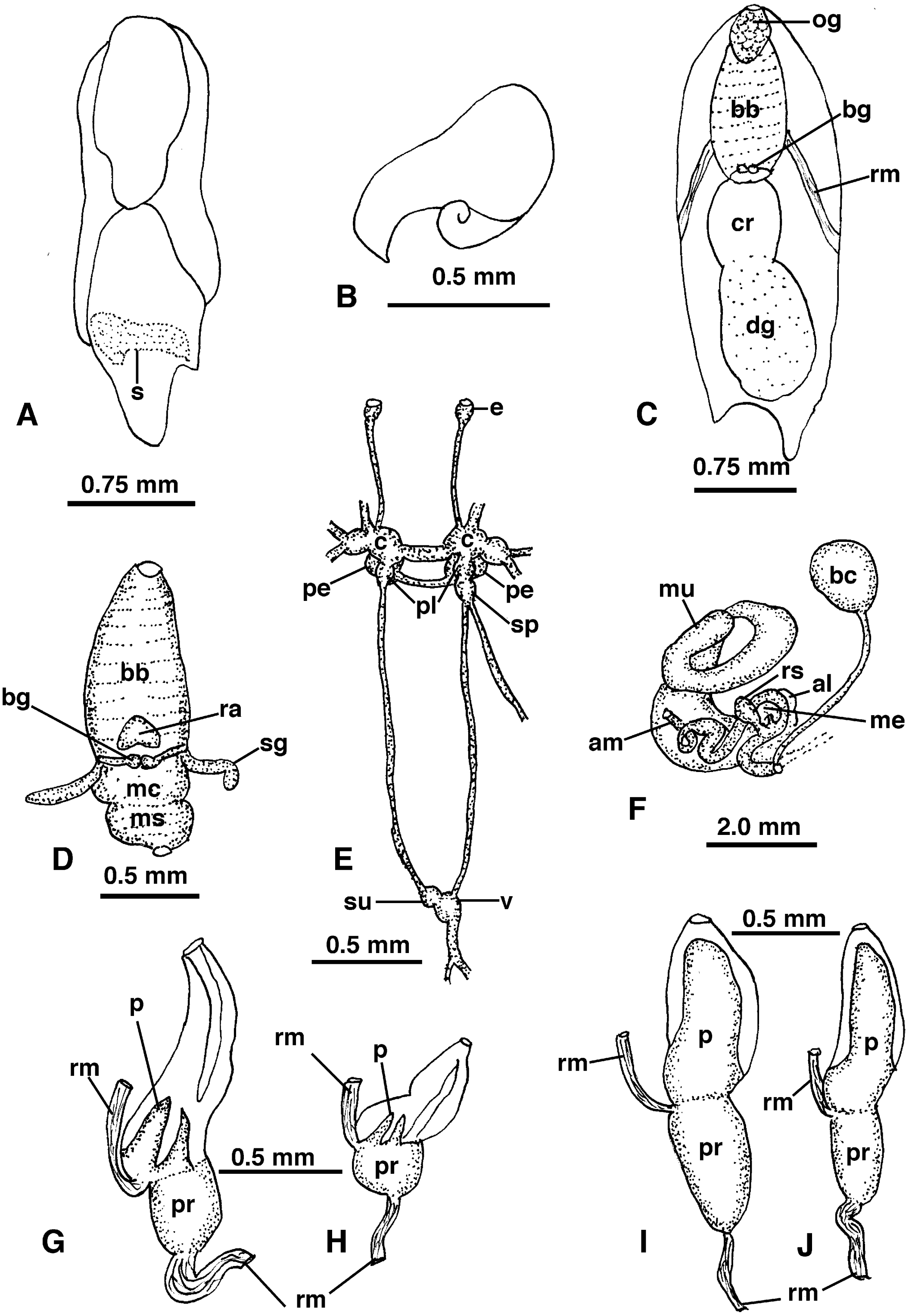

FIGURE 11. *Odontoglaja mosaica* **n. sp. A.** Dorsal view of preserved specimen (CASIZ 173415) showing location of shell, s shell. **B**. Shell, (CASIZ 175943). **C.** Ventral view, showing digestive system (CASIZ 173415). bb buccal bulb, bg buccal ganglion, cr crop, og ventral oral gland, rm retractor muscle, sp supraintestinal ganglion, **D.** Ventral detail of buccal bulb and crop, bb buccal bulb, mc membranous portion of crop, ms muscular portion of crop, ra radular sac, sg salivary gland. **E**. Central nervous system, (CASIZ 173415), c cerebral ganglion, pe pedal ganglion, pl pleural ganglia, sp supraintestinal ganglion, su subintestinal ganglion, v visceral ganglion. **F.** Posterior genital system, al albumen gland, am ampulla, bc bursa copulatrix, me membrane gland, mu mucous gland, rs receptaculum seminis. **G.** Penis (CASIZ 173415), p penial papilla, pr prostate, rm retractor muscle. **H.** Penis (CASIZ 173417), p penial papilla, pr prostate, rm retractor muscle. **I.** *Odontoglaja guamensis* Rudman, 1978, penis (CASIZ 069738), Papua New Guinea, p penial papilla, pr prostate, rm retractor muscle. **J.** *Odontoglaja guamensis* Rudman, 1978, penis (CASIZ 068671), Papua New Guinea, p penial papilla, pr prostate, rm retractor muscle.

Geographic range. This species is known from Madagascar (Gosliner *et al.* 2008) and South Africa (Ogden 2005). Specimens from the Red Sea (Koretz 2005c, Schrödl personal communication) likely represent this species as well.

Etymology. The name "mosaica" comes from Latin *mosaic,* referring to the reticulated pattern on the body appearing like a pattern of tiles.

Natural history. This species is found on shallow to moderately deep reefs where it is generally found under coral rubble in 3–22 m depth. No observations of feeding have been observed in the field, but one specimen dissected in this study had the entire crop filled with benthic copepods, on which it presumably feeds.

Description. *External morphology.* The general body color of the living animal (Fig. 1G, H) is white to cream. The anterior portion of the cephalic shield, the entire length of the parapodia and the posterior end of the posterior shield, including its posterior extensions, have a reticulated network of orange lines that form a mosaic-like pattern. In the center of each of these reticulations is a yellow spot. On the posterior portion of the cephalic shield and on the anterior portion of the posterior shield, where reticulations are absent, there are small, scattered orange spots. On the cephalic shield four brown spots are present that form a diamond-shaped pattern. A single brown patch is also present on each parapodium.

The living animals are elongate and narrow, 10–15 mm in length and 3–5 mm wide. The anterior end of the cephalic shield is blunt, angular and relatively narrow. It widens more posteriorly and again narrows to a rounded posterior termination. The posterior shield is also rounded anteriorly and terminates in a curved shelf. The left lateral posterior lobe of the posterior shield is elongate and wide, terminating in an acute apex. The right posterior lobe is short, triangular and acutely pointed. The parapodia are wide covering all of the cephalic and posterior shields near the middle of the animal. The gill is plicate with 3–5 primary folds.

Shell (Fig. 11A, B). The shell is relatively thickly calcified and is a shiny white. It occupies the posterior third of the posterior shield. There is a broad anteriorly-directed wing and an elongate extension that is deeply embedded in the posterior shield right to the end of the right posterior lobe.

Digestive system (Fig. 11C, D). The buccal mass is large, highly muscularized, occupying the anterior two-thirds of the cephalic shield (Fig. 11C). The buccal bulb contains a well-developed radula. The radular formula in two specimens examined was 36 x 1.0.1. (CASIZ 173415) and 29 x 1.0.1. (CASIZ 173417). The inner lateral teeth are broad with a sloping base. On the inner side of the tooth, near the middle of its length, is a short triangular denticle. The apex of the tooth bears a bifid apex with two distinct cusps. The inner cusp is longer than the outer one. Anterior to the buccal mass are a large ventral oral gland and a smaller dorsal one. At the posterior end of the buccal mass, near the junction with the crop, is a pair of elongate salivary glands (Fig. 11D). The crop is bilobed with a thin-walled anterior section that contained benthic copepods in one specimen (CASIZ 173415). The posterior portion is highly muscularized and contains thickened transverse areas that appear to be chitinous. The crop narrows posteriorly and enters the digestive gland. The intestine emerges from the right side of the digestive gland and terminates near the posterior end of the body near the base of the gill.

Central nervous system (Fig. 11E): The circumesophageal nerve ring consists of paired cerebral, pedal and pleural ganglia and a single supraintestinal ganglion on the right side. The cerebral and pedal commissures are both moderately long with some degree of separation between the cerebral ganglia and the pedal ganglia. Immediately adjacent and posterior to the right pleural ganglion is the supraintestinal ganglion. From its posterior end is the right branch of the visceral loop and the osphradial nerve. The two lateral branches of the visceral loop join posteriorly at the posterior ganglia. The left visceral loop enters the subintestinal ganglion, while the right lateral nerve enters near the middle of the visceral ganglion. The visceral ganglion is larger than the subintestinal ganglion. From the visceral ganglion is the genital nerve, which lacks a distinct genital ganglion.

Reproductive system (Fig. 11D, E–H). The arrangement of reproductive organs is monaulic (Fig. 11D). From the large ovotestis, which is intermingled with the digestive gland, emerges the highly convoluted ampulla. The ampulla narrows into the hermaphroditic duct, which around the receptaculum seminis and enters short, coiled albumen and membrane glands with a single branch to these glands. The larger mucous gland is tightly coiled with a massive primary lobe. The ampulla then joins the duct of the short receptaculum seminis and continues to the genital atrium where it joins the duct of the bursa copulatrix. The bursa is large and spherical. Its duct is narrow and elongate and does not widen at the genital atrium. From the genital atrium the open, ciliated sperm groove leads to the cephalic penis. The penis is in similar in shape in both specimens examined (Fig. 11G–H), but consists of a penial sac and a short lobed prostate gland that is joined to the penial sac by a wide duct. An anterior retractor muscle is connected at the junction of the prostate and the penis and curves anteriorly. From the posterior end of the prostate a second retractor muscle extend posteriorly and connects to the body wall. Within the penial sac is a short penial papilla that is smooth and bifid, dividing into two lobes at the apex. The penial papilla is devoid of any armature.

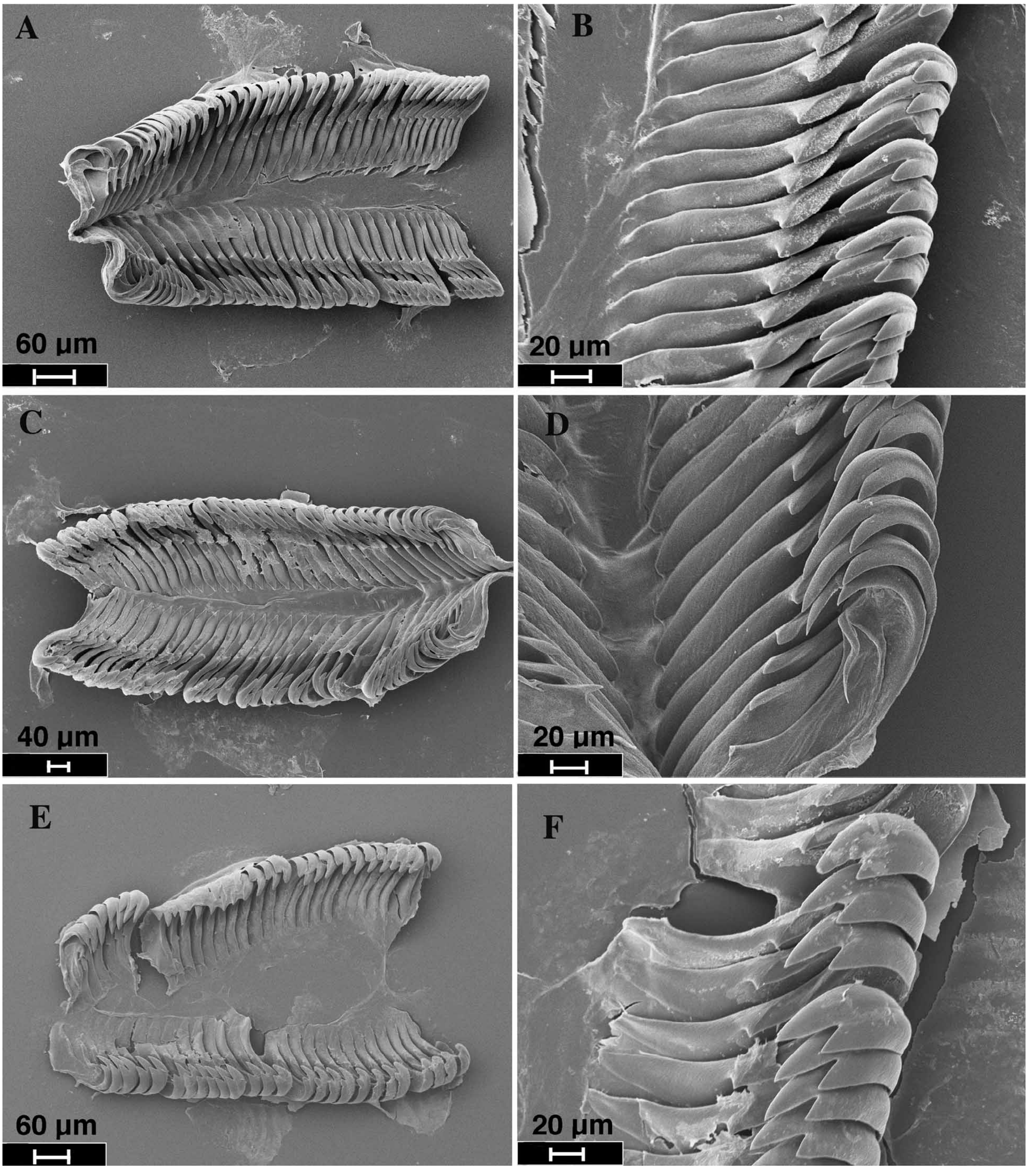

FIGURE 12. Scanning electron micrographs of radula. **A., B.** *Odontoglaja guamensis* Rudman, 1978 (CASIZ 068671), entire radula, inner lateral teeth. **C., D.** *Odontoglaja mosaica* **n. sp.** (CASIZ 173415), entire radula, inner lateral teeth. **E., F.** *Odontoglaja mosaica* **n. sp.** (CASIZ 173417), entire radula, inner lateral teeth.

Remarks. Following his original description of *Odontoglaja guamensis* (Rudman 1978), Rudman (2005b) considered specimens from southern Africa as being conspecific with *O. guamensis*. All the specimens from the western Indian Ocean that I describe here as *O. mosaica* (Rudman 2005b; Gosliner *et al*. 2008; present study) have a distinct pattern of orange reticulations that surround yellow spots that are distinct from the specimens of *O. guamensis* from the western Pacific. In *O. guamensis,* the body color is whitish with rounded white tubercles each with a pink or brownish center. Fine brown spots are scattered over the notum and additional brown patches may be present to varying degrees. *Odontoglaja guamensis* never has the orange reticulate markings found in *O. mosaica*, while *O. mosaica* never has the prominent tubercles found in *O. guamensis*. In *O. mosaica* the anterior end of the head is flat and angular, while in *O. guamensis* it is simply rounded. Both species are similar in size ranging in length from 10–11 mm. Specimens of the same size of the two species were dissected in this study.

The remainder of the external anatomy of the two species is quite similar. Both species have an elongate left posterior extension of the posterior shield and a short right one. Internally, the two species are also quite similar. The shell in both specimens is similar in shape (Rudman 1978: fig. 1b; present study, Fig. 11B). Both species have radular teeth with bifid cusps and a triangular basal denticle (Fig. 12) and a crop that has a membranous anterior section and a muscular posterior one. The central nervous system of *O. guamensis* was not described by Rudman, but the arrangement of ganglia is identical to that found in *O. mosaica* (present study). The most significant internal difference is the structure of the penis complex. The penis of *O. guamensis* was not described in detail nor illustrated, but was examined in two specimens in the present study (Figs. 11I, J). In O. *guamensis* the prostate is about the same size as the penial sac, while in *O. mosaica* (Figs. 11G, H) it is much shorter than the penial sac. Within the penial sac, the penial papilla of *O. guamensis* occupies most of the sac and is broad, muscular and paddle-shaped, being dorsoventrally flattened. In *O. mosaica*, the penial papilla is limited to the posterior quarter of the penial sac and consists of a bifid, less well-developed papilla.

Two specimens of *O. guamensis*, one from the Philippines (CASIZ 175764) and one from Malaysia (175944) were sequenced for the H3 nuclear gene together with one specimen of *O. mosaica* from Madagascar (CASIZ 175943). The two specimens of *O. guamensis* differed by 0.8 % in the H3 gene, while the specimen of *O. mosaica* differed from these two specimens of *O. guamensis* by 2.9% and 3.5% respectively. These molecular data further support the anatomical data that *O. mosaica* and *O. guamensis* represent distinct species.

Discussion

The species described here are indicative that diversity of Indo-Pacific aglajids remains incompletely known. Gosliner *et al*. (2008) illustrated 39 species of Aglajidae from the Indo-Pacific, including 16 possibly undescribed species, five of which are described here. The sixth species, *Philinopsis coronata*, did not appear in Gosliner *et al.* (2008). Other Indo-Pacific taxa were also not included in Gosliner *et al.* (2008). For example, *Melanochlamys papillata* Gosliner, 1990, has not been observed alive and was not included in Gosliner *et al.* (2008) as the living animal remains unknown. Two additional species of *Aglaja* have been documented by Anthes *et al*. (2008) from Australia. Other unidentified species of aglajids are present on the *Sea Slug Forum* and various other opisthobranch websites, and need to be more thoroughly investigated to determine whether they also represent undescribed species.

The six species described in the present work include three species of *Philinopsis*, two of *Chelidonura* and one of *Odontoglaja*. The three species of *Philinopsis* have several differences from other described species of this group (Rudman 1972b). All three species described here (*P. falciphallus*, *P. coronata* and *P. ctenophoraphaga*) have a bulbous buccal mass but have a simple penis. In Rudman's review of *Philinopsis*, only species with a tubular buccal mass had a simple penis rather than a type D penis (Marcus & Marcus 1966). Additionally, *P. falciphallus and P. coronata* are the only known members of *Philinopsis* with an armed penis.

The two species of *Chelidonura* described here, *C. mandroroa* and *C. alisonae*, have similarities to different described species of in the *Chelidonura inornata* complex of species. In both cases, there has been systematic confusion surrounding these species. In the case of *C. mandroroa*, this species has been tentatively placed in *Philinopsis* (Rudman 2001) based on external anatomy of the living animal. In this instance, both anatomical details and preliminary molecular data clearly support this species being placed in *Chelidonura*. In the case of *C. alisonae*, this species has been often confused with *C. hirundinina* (Kay 1979; Bertsch & Johnson 1981; Rudman 2007) based on their having a similar color pattern. Consistent morphological differences and preliminary molecular data clearly support the distinctness of these two taxa.

Odontoglaja has been considered as the only monotypic group within the Aglajidae. The discovery and description of at least one additional taxon will better permit the development of hypothesis of phylogenetic relationships within the Aglajidae. At present, the monophyly of most major groups that have been traditionally regarded as genera remains largely untested and needs to be the focus of future studies.

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