

NEW DATA ON *CHELIDONURA AMOENA* BERGH, 1905 (OPISTHOBRANCHIA: CEPHALASPIDEA: AGLAJIDAE).

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ABSTRACT

Chelidonura amoena Bergh, 1905 is redescribed, principally on material from Australia. The single extant type specimen is designated as lectotype. Considerable intraspecific colour variation is evident, with that relating to the caudal lobes being greatest. The variation in coloration and shape observed in one specimen from Belau lies outside those described for *C. amoena* and we believe it could be explained as the product of hybridisation with *C. electra* Rudman, 1970. Aggregation for the purpose of breeding is shown to be normal for *C. amoena*. The collection data and observations indicate *C. amoena* is widely distributed in the tropical western Pacific and eastern Indian Oceans with disparate limits on the eastern and western coasts of the Australian continent.

KEYWORDS: Mollusca, Opisthobranchia, Cephalaspidea, Aglajidae, *Chelidonura*, taxonomy, intraspecific variation, hybridisation.

INTRODUCTION

Chelidonura amoena Bergh, 1905 is a little-known member of the Aglajidae, a family of advanced, carnivorous, cephalaspidean opisthobranchs. The species was described from two specimens collected in 1899 at "Saleyer" (= Selayar) Island, southern Sulawesi, Indonesia, during the "Siboga" Expedition and it was not reported again until Coleman (1975) illustrated it in his popular book *What Shell is That?*. That report was based on a specimen from Coral Bay, central Western Australia, found in 1972. Ho (1989) wrote an illustrated account about a specimen from Pulau Kapas, Malaysia. More recently, photographs of specimens from Western Australia have appeared in books by Wells *et al.* (1990) and Wells and Bryce (1993), and the name has been used in taxonomic (Rudman 1970, 1974; Gosliner 1980) and faunal (Wells and Slack-Smith 1986) checklists. However, at no time have authors actually compared their material with the original specimens, or has the species been redescribed on live or freshly collected material.

Spurred by finding one specimen on the Great Barrier Reef, Queensland, Australia, we have accumulated data on external morphology, internal anatomy (shell, buccal bulb, penial complex), reproductive behaviour and geographic range pertaining to this distinctive and interesting opisthobranch. The extent of intraspecific variation in coloration in this species has turned out to be considerable - seemingly greater than that recorded in any other species of *Chelidonura*. One animal from Belau (= Palau) possibly represents a hybrid with *C. electra* Rudman, 1970. Finally, the geographic range of *C. amoena* has turned out to be much more extensive than previously appreciated, and the species has proven to be relatively common in parts of this range.

Abbreviations used in the text are as follows: AMS, Australian Museum, Sydney; NMV, Museum of Victoria, Melbourne; NTM, Museum and Art Gallery of the Northern Territory, Darwin; WAM, Western Australian Museum, Perth; ZMA, Zoologisch Museum, Universiteit van Amsterdam, the Netherlands.

SYSTEMATICS

Family Aglajidae Pilsbry, 1895
Genus *Chelidonura* A. Adams, 1850
Chelidonura amoena Bergh, 1905
(Plate 1, Figs 1-4)

Chelidonura amoena Bergh, 1905: 45, 46, pl. 3, fig. 7. - Rudman 1970: 10; - Rudman 1974: 207; - Coleman 1975: 107, no. 312; - Gosliner 1980: 333; - Wells and Slack-Smith 1986: 52; - Ho 1989: 58, 59; - Wells et al. 1990: 66, pl. 43, no. 303; Wells and Bryce 1993: 36, 37, species number 28.

Through the courtesy of Mr R. Moolenbeek, ZMA, we have been able to examine the type material of *Chelidonura amoena* Bergh. (All the existing type material of species described by Bergh from the *Siboga* Expedition is deposited in ZMA.) The type material consists of an intact, 18 mm specimen, plus a 6 mm long piece of black, sickle-shaped tissue. The intact animal is unquestionably the smaller of Bergh's syntypes, and we herein designate it as lectotype. Apparently Bergh completely disposed of the larger syntype after dissecting it because the piece of black tissue cannot be matched with any external structure or internal organ mentioned in the original description; it is probably only a contaminant.

Type material. LECTOTYPE. Here designated. Intact preserved specimen (18 mm long by 5 mm maximum width), with tail bent to the left side, collected on (presumably low-tidal) reef, "Saleyer" (= Selayar) Island, southern Sulawesi, Indonesia - 06°00'S, 120°30'E, 26 October 1899 (*Siboga* Expedition, Station 213). Deposited in ZMA.

Additional material. QUEENSLAND - One specimen (Fig. 1), 30 mm extended crawling length, 10 metres depth, Davies Reef, N. E. of Townsville, central section, Great Barrier Reef, Queensland, Australia - 18°50'S, 147°39'E, R. Cattaneo-Vietti, 13 November 1986 (Italian Great Barrier Reef Expedition, Station 30.) Specimen observed and photographed live by R. Cattaneo-Vietti, dissected by R. C. Willan. Dissected body in AMS C166226. **WESTERN AUSTRALIA** - Two specimens, crawling lengths not recorded, depths not recorded, western side of North Lagoon, Scott Reef, northern Western Australia - 14°00'S, 121°45'E, C. W. Bryce, September 1984, WAM 2417-84; two specimens, 21, 16 mm crawling length, 1.2 metres

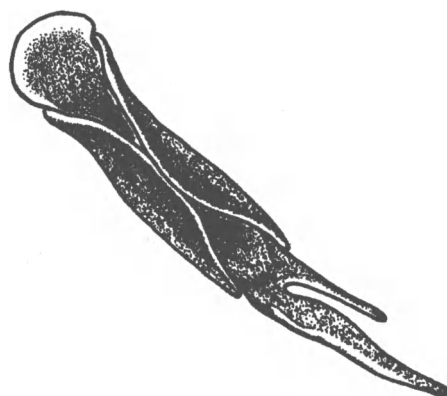


Fig. 1. *Chelidonura amoena*. Specimen from Davies Reef, Queensland, Australia, crawling actively, 13 November 1986, length 30 mm. Drawn from slide.

depth, Bernier Island, Dampier Archipelago, northern Western Australia - 24°52'S, 113°08'E, C. W. Bryce, March 1980, WAM 2417-84; three specimens, crawling lengths of the larger two recorded as 26 and 21 mm, photographed *in situ*, subtidally, Steep Point, Shark Bay, central Western Australia - 26°08'S, 113°10'E, C. W. Bryce, March 1986, WAM 345-85; one specimen, 35 mm crawling length, on crustose algae, 2 metres depth, Coral Bay, south of Learmonth, central Western Australia - 23°00'S, 113°49'E, N. Coleman, 14 July 1972, NMV. (Mr Bryce kindly made available a list of 105 specimens of this species in WAM. These specimens were collected from Ashmore Reef, Timor Sea, south to Rottnest Island, Western Australia, between 1980 and 1986.)

Photographic material. WESTERN AUSTRALIA - Many individuals (some shown here in Plate 1), crawling lengths not recorded, 6 metres depth, western side of Marney Bay, Malus Islands, Dampier Archipelago, northern Western Australia - 20°31'S, 116°41'E, W. R. Rowlands and G. McGarvie, 4 November 1990, four colour transparencies examined; one specimen, 16 mm crawling length, photographed *in situ*, subtidally, Rottnest Island, southern Western Australia - 32°00'S, 115°30'E, C. W. Bryce, November 1980, colour transparency examined. One specimen, 24 mm crawling length, photographed *in situ*, subtidally, Rottnest Island, southern Western Australia - 32°00'S, 115°30'E, C. W. Bryce, December 1981, colour transparency examined. **BELAU (= PALAU)** - Two specimens (Fig. 4), crawling lengths not recorded,

selected from a breeding population in a sandy area on the edge of Rengrak Channel, Re'au - 7°30'N, 124°30'E, C. Carlson, 28 June 1969, colour transparency examined. RYIKYU ISLANDS - Two specimens, both approximately 30 mm extended crawling length, collected intertidally on Okuma Island, Okinawa - 26°21'N, 127°36'E. J. Hamanai, 4 November 1991, colour print of one specimen examined.

Description. (Based on Queensland specimen.) Living animals illustrated in Plate 1.

Extended length to 40 mm (Ho 1989), though 30-35 mm is more usual for adults.

When alive, body shape corresponded to Rudman's (1974: 201-202) generic diagnosis. When crawling actively, parapodia occupied 60% of entire body length (measured from anterior margin of head shield to posterior tip of left caudal lobe).

Anterior margin of head shield broad, immovably, slightly trilobed with no movements or sensory bristles visible. Head shield tapering gradually toward pointed posterior end beneath parapodia. Anterior margin of foot slightly enlarged, its margins folding outwards, but never forming funnels. Parapodia relatively low, touching one another only in dorsal midline and not overlapping. Both caudal lobes elongate, flattened left lobe almost three times length of dorsally keeled right lobe.

Head shield pale grey on account of numerous, microscopic, evenly spaced black specks, darkest mid dorsally. Interspersed with these black specks are numerous, fine, white flecks. Anterior margin of head shield, including frontolateral corners, marked with broad, pale cream band. Foot sole uniformly grey. Parapodia appearing uniformly grey-black to naked eye, but magnification reveals fine, black reticulum, darkest closest to midline. Black pigmentation shading to pale cream-gold margin that is narrower than cream band on front of head shield. This pale margin separated from black area by a very irregular line. Posterior shield dark grey dorsally, equivalent in intensity to head shield, speckled with tiny pallid areas but not reticulate. Dark grey pigmentation of mantle shield continuing without interruption onto dorsal surfaces of both caudal lobes. Margins of caudal lobes cream-gold, sharply delimited from central dark area of mantle shield. Apices of caudal lobes with no yellow pigmentation.

When examined after preservation in methanol, body pale grey, darkening on antero-lateral cor-

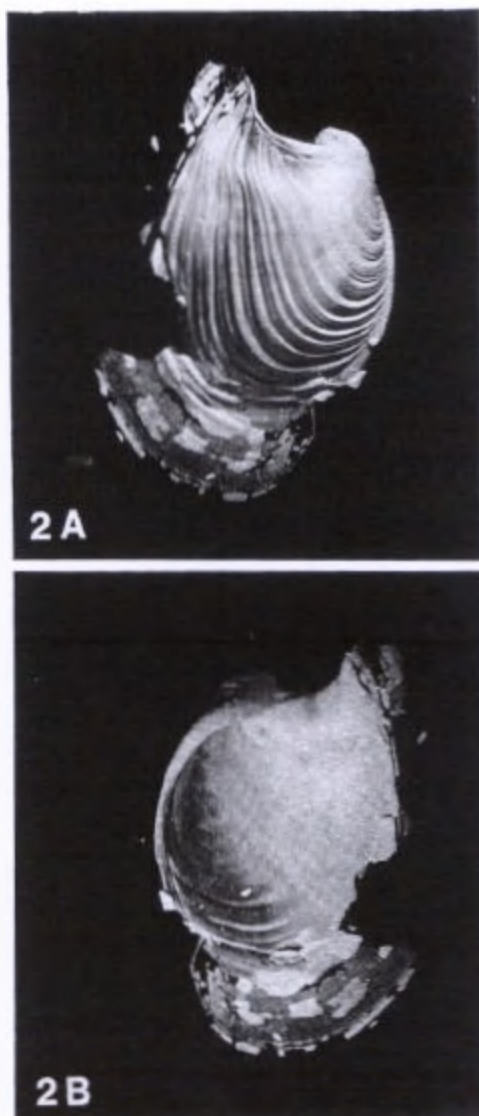


Fig. 2. *Cleobalanus amoena* shell from specimen shown in Figure 1, length 4.9 mm. A, exterior; B, interior.

ners and posterior margin of head shield, parapodial margins, and dorsal ridges of caudal lobes. Interiors of parapodia white.

Shell (Fig. 2) with dimensions 4.9 x 2.9 mm, located internally underneath posterior shield, calcareous but thin, white, consisting of calcified apex and greatly expanded, flattened body whorl. Protoconch and spire whorls heavily calcified, with superficial microsculpture of irregular, small pustules and ridges. Body whorl

relatively large, subrectangular, calcified, exterior glossy from membranous, overlying periostracum, interior shallow and dull white. Anterior margin broadly rounded and lightly calcified. Posterior margin short, deeply concave, defined by calcified ridge internally, produced into long, erect, narrow spine, elevated above level of protoconch. Shell's right (i.e. columellar) margin evenly convex. Shell surface ornamented externally with approximately 20, strong, broad, flattened concentric ridges. Ridges all of variable width, all becoming narrower toward posterior margin.

Buccal bulb 3 mm in length (i.e. approximately $\frac{1}{4}$ preserved body length excluding caudal lobes), forming most conspicuous organ within anterior visceral cavity, barrel-shaped, elongate, parallel-sided, consisting of three, large, longitudinal blocks of muscle - two lateral, and one, a little shorter, mid-ventral. Inner walls of all 3 muscle blocks completely smooth. Salivary glands short, located at extreme hind end of buccal bulb, ducts opening either side of ventral muscle block. No vertical sheet of tissue (diaphragm) separating crop and organs of visceral mass.

Penial complex (Fig. 3). Penis eversible, located inside head cavity to right of mouth and below right fronto-lateral corner of head shield. Penial complex unpigmented, narrower than and only $\frac{2}{3}$ length of buccal bulb beside which it lies. When retracted, penial complex elongate and circular, consisting of two sections of about equivalent length. Proximal section, the penial sheath (= vestibule) containing penial papilla, fusiform and thin-walled. Upon entering this sheath, ventral fold of external seminal groove enlarges threefold, forming inner wall of deep

interior seminal groove located on floor to right of papilla; this internal groove running directly to base of papilla. Penial papilla $\frac{1}{2}$ length of sheath, muscular and conical, flattened, margins enfolded to form deep ventral groove for entire length. Distal part of penial complex (i.e. prostatic section) fusiform and circular, narrower and slightly longer than sheath, tapering very gradually to bluntly rounded apex where two retractor muscles insert dorsally. Walls of prostatic section thick and glandular, but not distinctly granular. Tall ridge passing through interior of prostatic section. Depression on right of ridge continuous with both internal seminal groove and groove on outside of penial papilla. Penial retractor muscles short and broad, originating from floor of visceral cavity.

DISCUSSION

Colour variation. The specimens and photographs of *Chelidonura amoena* now available indicate that the species possesses considerable colour variation. The head shield and posterior shield are relatively constant in colour, whereas the parapodia and caudal lobes are variable from individual to individual.

With the exception of one of the animals from Palau (see below), the head shield is greyish black with white speckles, becoming paler anteriorly, and merging gradually into the relatively broad cream-gold to yellow-gold band that borders the front of the head. This differs from Bergh's (1905) original illustration of a pale, longitudinal, medial bar extending rearward from this band into the dark area. No

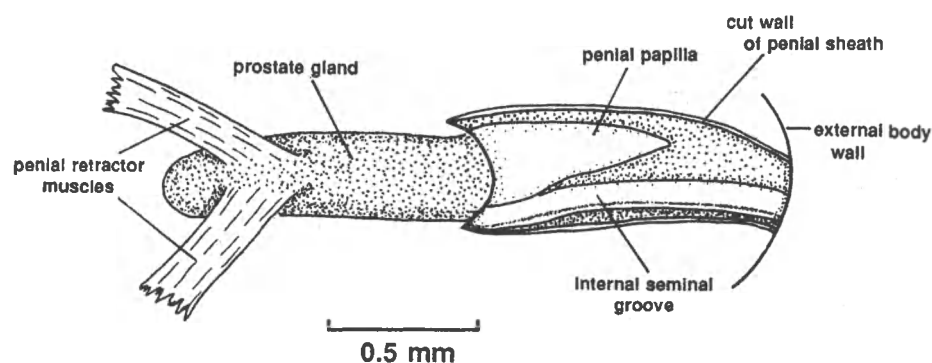


Fig. 3. *Chelidonura amoena* penial complex of specimen shown in Figure 1. Sheath cut away dorsally to reveal internal seminal groove and papilla.

animal resembling Bergh's illustration has ever been seen again and the illustration is probably inaccurate. Further, the golden margin along the front of the head would probably have been more vivid than the depiction would indicate.

The parapodia are dark dorsally with quite vivid yellow-gold anterior corners. The parapodia are generally black and peppered with white to the extreme margin (Plate 1). In the Queensland specimen, a narrow, white line clearly demarcates the parapodial margins (Fig. 1). We have never seen a specimen matching that depicted by Bergh with a relatively broad white margin to the parapodia. The extent of black pigment on the parapodia is quite variable. Generally, they become lighter gradually, through a reticulate intervening section, to the pale grey foot, but in the specimen depicted by Bergh and in WAM 2417-84, only the upper half of the parapodia is black. Actually, in WAM 2417-84, the upper half of the right parapodium is black and there are only two large blotches on the left parapodium (see Wells and Bryce 1993: 36).

The posterior shield is usually uniformly dark (pale grey to sooty black) with microscopic white speckles. In approximately half the animals, there is an unpigmented area on either side resulting in an hour-glass pattern lying across the top of the shield. This marking is well shown in Bergh's animal. The specimen illustrated by Coleman (1975) is unique in having an opaque white shield with a single, large, black blotch mid-dorsally.

The pigmentation of the caudal lobes is the most variable element of this species' coloration.

In the Queensland specimen, the caudal lobes are dark throughout their length (both inside and outside), with a narrow, dull cream margin. In the specimens illustrated by Bergh (1905), Ho (1989) and Wells *et al.* (1990), and in the smaller animal photographed in Palau (Fig. 4A), these lobes are black anteriorly, pale cream marginally and vivid gold apically. The caudal lobes of Coleman's specimen are opaque white with cream-gold tips. Those of the Okinawan specimen are cream with a narrow, black stripe on the dorsal face of the left lobe.

The larger animal from Belau (Fig. 4B) seems to lie outside the range of colour variation just described for *Chelidonura amoena* in several ways. Its entire head shield was translucent white. Its parapodia were translucent white with yellow margins and, symmetrically, irregular black blotches on the anterior third. Its posterior shield was opaque white. Both its caudal lobes were opaque white with pale yellow margins. This specimen was part of a breeding aggregation of *C. amoena* (see below), and it was photographed deliberately because its pale coloration rendered it conspicuous amongst the mass of otherwise dark individuals (C. Carlson pers. comm. 1990). Unfortunately the specimen was not retained by the collector.

Several explanations could account for this anomalous individual. It could have been an extreme colour form of *Chelidonura amoena*, but in view of the hundreds of specimens of that species now known that seems unlikely, as the individual lies too far outside the variation of that species. Secondly, it could have been a specimen of the closely related *C. electra* Rudman

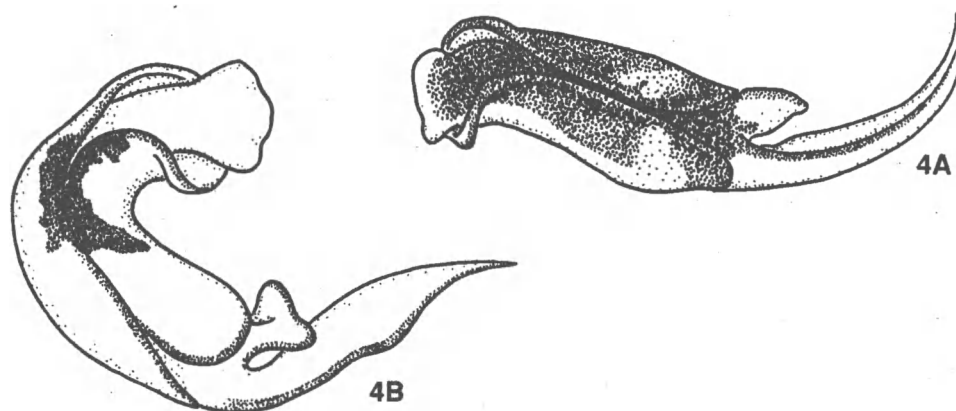


Fig. 4. *Chelidonura amoena*. Specimens from breeding aggregation at Rengrak Channel, Belau, 28 June 1969, lengths not recorded. Drawn to same scale from slide by C. Carlson. Specimen 4B is possible *C. amoena* x *C. electra* hybrid. Black pigmentation represented by heavy stipple; gold or yellow marginal lines represented by lighter stipple.

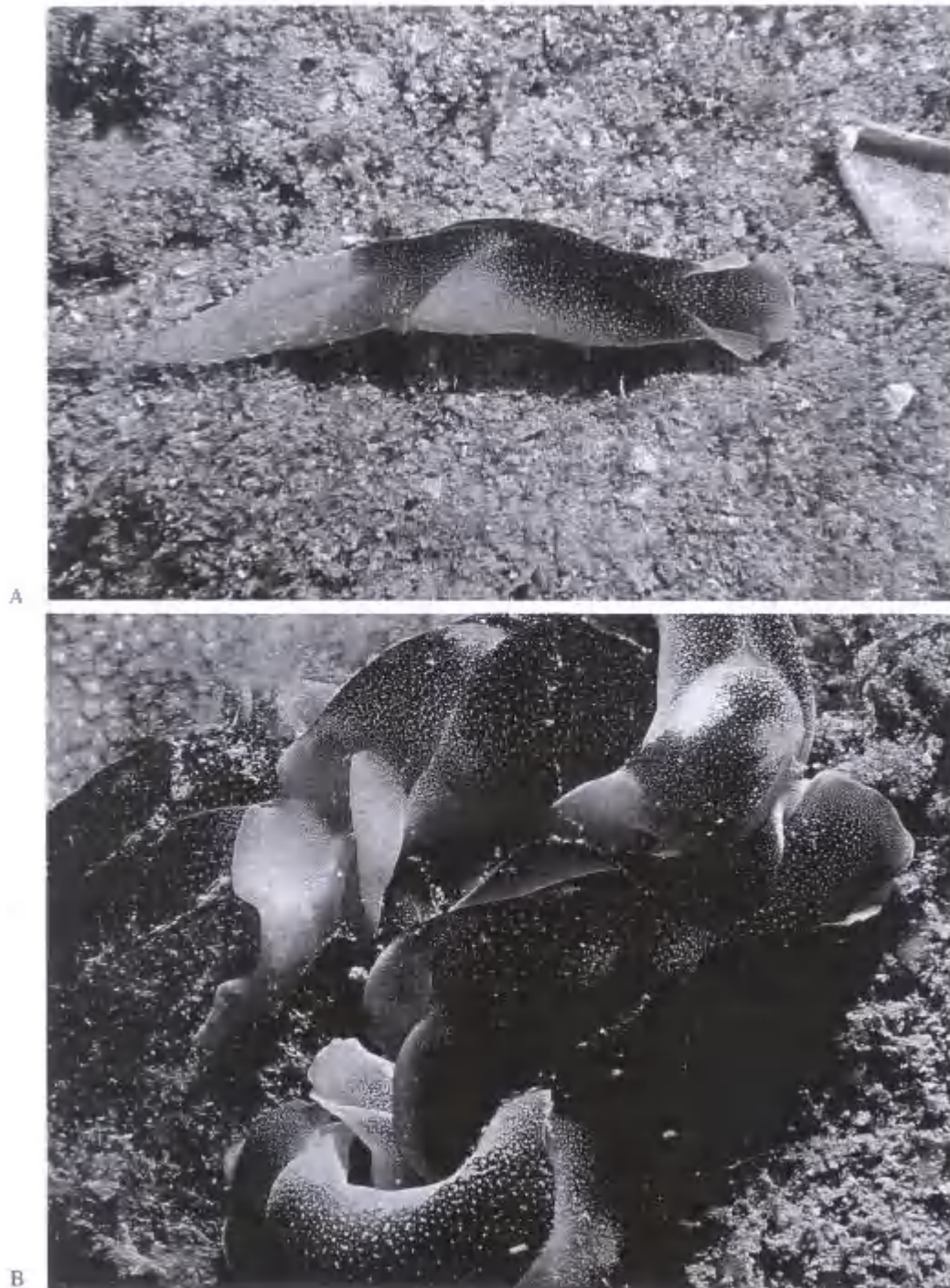


Plate 1. A. *Chelidonura amoena*. Actively crawling specimen separated from the breeding aggregation at Dampier Archipelago for photography, 4 November 1990, length not recorded. Reproduced from slide by G. McGarvie.
B. specimens from the breeding aggregation at Dampier Archipelago, 4 November 1990. Note the small individual to the left of centre. Reproduced from slide by G. McGarvie.

1970, that had been attracted by pheromones released from all the *C. amoena* in the aggregation. The characters of *C. electra* exhibited by this specimen (in contrast to *C. amoena*) are its longer body, longer and narrower head shield, translucent areas, pale yellow (not gold) borders, opaque white posterior shield and caudal lobes, and longer, taller, and more attenuated caudal lobes. *Chelidonura electra* has not yet been recorded from Belau, but little intensive collecting has been done there to this date (C. Carlson pers. comm. 1992). Thirdly, and in our opinion the most likely scenario, is that this individual was hybrid between *C. amoena* and *C. electra* because it possesses pigmentation and shape characteristic of both species.

Hybridisation has already been strongly suspected in prosobranch gastropods (e.g. Springsteen and Leobrera 1986: 69; Marshall 1995: 85, 87), but it is not presently recognised as occurring in any opisthobranch.

We conclude that colour variation is considerable in *Chelidonura amoena* and this variation can neither be correlated with geographical occurrence nor interpreted as clinal. For example, two of the Australian specimens (the one illustrated by Coleman (1975) and the specimen from Queensland) differ more from each other than either does from the Indonesian one depicted by Bergh (1905). The largest population for which data on colour variation is available is that from the Dampier Archipelago where an aggregation of dozens of individuals was encountered in November 1990. Members of this population displayed most of the colour variation described above for the species as a whole (W. R. Rowlands pers. comm. 1994). Data on large populations such as this are unavailable at present to quantify the components of chromatic variation.

Comparison with similar species. The genus *Chelidonura* is circumtropical and consists of approximately 20 species (Rudman 1973, Perrone 1990, Martinez *et al.* 1993, Yonow 1994). R.C.W. has had the opportunity to study living specimens of seven other Indo-Pacific species besides *C. amoena*: *C. electra*; *C. fulvipunctata* Baba, 1938 (= *C. conformata* Burn, 1966; for synonymy, see Gosliner 1980: 334, 335); *C. hirundinina* (Quoy and Gaimard, 1832) (= *C. philinopsis* Eliot, 1903; for synonymy, see Gosliner 1987: 42 and Gosliner 1988: 91); *C. inornata* Baba, 1949; *C. pallida* (Risbec, 1951); *C. tsurugensis* Baba and Abe, 1959; and *C. varians* Eliot, 1903.

In comparison to *Chelidonura amoena*, *C. electra* is larger when adult (to 52 mm extended crawling length), more elongate, more translucent, and there is a pale yellow (not gold) edging to the head shield, parapodia and caudal lobes. Dark forms of *C. amoena*, like the Queensland specimen and the one illustrated by Wells *et al.* (1990), resemble *C. inornata* and *C. tsurugensis*. However, *C. inornata* has a uniform soot-black head shield with a broad, opaque white frontal band and orange antero-lateral corners, soot-black parapodia with white spots and a narrow white band, and uniform soot-black posterior shield and caudal lobes. *Chelidonura tsurugensis*, although exceedingly variable in coloration itself, is most often uniformly black. *Chelidonura tsurugensis* can always be distinguished from all the other *Chelidonura* species by its reduced right caudal lobe.

R.C.W. had previously considered partitioning the species of *Chelidonura* into two species groups. One character contemplated for this separation was pigmentation. It seemed possible to recognise a group with translucent, colourless bodies (e.g. *C. pallida* and *C. electra*) and a second group with heavily pigmented, black or dark brown bodies (e.g. *C. inornata*, *C. fulvipunctata* and *C. tsurugensis*). However, in possessing great variability in pigmentation on the parapodia and caudal lobes, *C. amoena* could be placed in either group depending on the intensity of its pigmentation. Such an observation forces us to reject the hypothesis.

The wording by Risbec (1928:42), translated from the French: "Entire body and parapodia displaying a conspicuous greenish-maroon network over a yellow background" initially led us to consider the possibility that *Doridium perparvum* Risbec, one of the most enigmatic of aglajid names (Rudman 1974: 209; Gosliner 1980: 284), might have been a junior synonym of *Chelidonura amoena* based on a dark colour form. However, other characters contained in Risbec's (1928) original description and subsequent revised account (Risbec 1951: 134, pl. 8, fig. 8; as *Chelidonura perparava* [sic]) force us to discount this possibility. The shell of *D. perparvum* is neither calcified nor does it have a spine on its posterior margin. The buccal bulb of *D. perparvum* is "enormous" and spherical, and its lining possesses numerous, glistening, soft hooks (Risbec (1928) used the term "papillae" to describe them in the legend to his Figure 18). None of these characters is concordant

with *C. amoena* and there is no justification for synonymising *D. perparvum* with this species. Indeed, *D. perparvum* may not even be a species of *Chelidonura*, because according to Gosliner (1980: 334), the shell of all species in that genus should be "thinly but completely calcified". The identity of *D. perparvum* remains unresolved.

Breeding aggregations. We are aware of three instances of breeding aggregations in *Chelidonura amoena*, only one of which has been mentioned previously in the literature. On each occasion, observers discovered aggregations of many individuals, all forming clusters. Within these clusters, individuals were crawling over each other and/or laying spawn. In June 1969, Mr C. Carlson observed such an aggregation intertidally at Rengrak Channel, Belau. He came across 50 to 70 animals in a sandy area on the edge of the channel. The presence of spawn was interpreted as indicating a breeding aggregation. Wells and Bryce (1993: 37) reported that mating and spawning individuals were found at South Passage, Shark Bay, in March 1986. In November 1990, Messrs W. Rowlands and G. McGarvie observed an aggregation subtidally at Malus Islands, Dampier Archipelago. All the specimens in this aggregation were crawling actively in tight clusters of up to a dozen individuals (Plate 1b). The only growth on the silty rocks on which the specimens were amassed was a low stubble of filamentous algae. Some animals were actually laying masses of spawn when the aggregation was observed, so this behaviour was interpreted as a mass spawning event. The spawn consisted of a white tangle inside a clear, flaccid sac. Interestingly, there were a few very small animals less than half the size of the majority amongst the clusters (Plate 1). Either these animals were diminutive adults that were engaged in the spawning, or else they were non-reproducing juveniles attracted by the pheromones emitted by all the other mature animals.

Since discrete mating pairs have not been observed in *Chelidonura amoena*, we assume that aggregation for breeding always takes place in this species. Aggregation as a normal part of the reproductive process has already been recorded for *Philineopsis cyanea* (Martens), and one other member of the Aglajidae (Allan 1950: 217). This phenomenon of aggregation for breeding has also been well documented in sea hares

(Allan 1950: 211, Kandel 1979, Carefoot 1987).

Spawning events could take place more than once in a year in *Chelidonura amoena* because the two sets of observations on the coast of northern Western Australia were five months apart.

Geographical distribution. Far from being restricted to Indonesia, as the original record of *Chelidonura amoena* might indicate, it is now apparent that this species occurs widely throughout the western Pacific (i.e. Ryukyu Islands, Belau, eastern Australia) and eastern Indian Oceans (i.e. Western Australia, Christmas Island, Indonesia, Malaysia). The northern boundary apparently lies south of Japan and Guam because no specimens have been found at either locality despite many years of intensive opisthobranch study (K. Baba pers. comm. 1990, C. Carlson pers. comm. 1991). Neither are there any records of *C. amoena* from the "Top End" of Australia, that is the northern coastline between Cape York and the Kimberley coast.

The majority of records of *Chelidonura amoena* now available come from Western Australia, but instead of indicating the species is relatively more common on this coast than in other parts of its range, the records may simply reflect the greater number of opisthobranch observers there than elsewhere in the range. Within the continent of Australia, however, two biogeographical patterns are certainly evident. *Chelidonura amoena* extends further south on the west coast than on the east coast. On the west coast, it extends to Rottnest Island (32°S), whereas on the east coast it is only known from Davies Reef (18°S) which is part of the northern Great Barrier Reef. The greater influence of the Leeuwin Current on the west coast than the East Australian Current on the east coast probably explains this anomaly. Secondly, *C. amoena* is relatively much more abundant on the west coast of Australia than on the east coast. Hundreds of specimens have been observed along the north-west coast over the last decade (W. R. Rowlands, G. McGarvie, C. W. Bryce pers. comm.), whereas only a single individual has been discovered on the east coast. At present we have no idea what might be responsible for this imbalance. We note, however, that the converse can also be true for some species of *Chelidonura*. There is only a single record of *C. fulvipunctata* from Western Australia (Wells and Bryce 1993), yet the species is "common" along the east coast as far south as Cape Byron (pers. obs.).

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