AN OUTLINE OF THE SYSTEMA TICS AND CLASSIFICA TION OF NUDIBRANCHIA (GASTROPODA, OPISTHOBRANCHIA)

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ABSTRACT

The Nudibranchia (Mollusca: Gastropoda: Opisthobranchia) is the largest order within the Opisthobranchia. The total number of species is presently estimated to be about 2000 in the Indo-Pacific, of which more than 30% may be undescribed. Nudibranchs are carnivores and most species are dietary specialists. Porifera, Cnidaria and Bryozoa are the most common prey organisms. Nudibranchs are usually brightly coloured and attractive for SCUBA divers. Current classification subdivides the Nudibranchia into four suborders, Doridacea, Arminacea, Dendronotacea, and Aeolidacea. Recent studies involving molecular methods and cladistic analysis indicate that these are not all monophyletic and that classification will have to be changed. In the present study the four suborders and the families included are characterised, and some representatives for each suborder are illustrated.

INTRODUCTION

The Nudibranchia is the most speciose order of Opisthobranchia; Boss (1982) estimated 1000 species worldwide. More recently the estimate has risen to 2000 species just in the Indo-Pacific region (Gosliner *et al.* 1996), and new species are continuously added (Rudman & Willan 1998). The Nudibranchia are shell-less in the post-larval stage. They are carnivores, and most species are dietary specialists. Porifera, Cnidaria and Bryozoa are the most common prey organisms for nudibranchs, but some species have more peculiar diets, e.g. fish eggs, barnacles, polychaete worms, or other opisthobranchs (Thompson 1976). Many nudibranchs sequester or synthesise secondary metabolites for defense (Avila 1995); these chemicals have elicited an enormous interest from natural product chemists, who are looking for new pharmaceutical compounds. As these compounds are generally species-specific, correct identification becomes important. Also, many species are brightly coloured and attract much attention from SCUBA divers and amateur collectors (Coleman 1989; Debelius 1996). Very little is known about the ecology, life histories, and evolutionary relationships of the Nudibranchia, and it has been estimated that 30% or more of the Indo-Pacific species are undescribed (Gosliner & Draheim 1996). Unfortunately taxonomy at the present time is rather unstable, but in recent years modern phylogenetic approaches have been applied to several nudibranch genera and smaller families (Gosliner & Willan 1991; Brunckhorst 1993; Kolb & Wägele 1998; Tholleson 1999b; Gosliner & Johnson 1999). Many species and genera have been scantily described, and it is highly probable that classification will be rearranged in the coming years. Current classification (Odhner in Franc 1968; Boss 1982; Rudman & Willan 1998) is based exclusively on morphological

characters. Recent molecular studies have indicated that major changes will be necessary (Thollesson 1999a). In the present study an outline of current classification and definitions of suprageneric taxa occurring in the tropical and subtropical Indo-West Pacific Region, will be presented. This will be illustrated by selected species from the South China Sea and Thailand.

CLASSIFICATION

Traditionally the Opisthobranchia has been classified as one of three subclasses of Gastropoda. Recent changes in classification of Gastropoda based on phylogenetic analysis reduce the Opisthobranchia to ordinal level (Ponder & Lindberg 1997; Ponder 1998), which implies that the Nudibranchia are reduced to a suborder at the most. However, this change in taxonomic levels has not yet been universally accepted (Rudman & Willan 1998), and until further stabilisation in the classification of the higher gastropods (Heterobranchia) has been achieved, it is considered prudent to retain ordinal level for the Nudibranchia. Classification always reflects the conflict between the need for stability of names and the need for adopting the most recent changes based on phylogenetic studies and/or rules of nomenclature.

It is usually assumed that the Notaspidea (side-gilled seaslugs) are more closely related to the Nudibranchia than to other opisthobranch orders, i.e. they are sister-groups (Schmekel 1985; Willan 1987). However, in some studies the Notaspidea is considered paraphyletic, or one nudibranch suborder, the Doridacea, is excluded from the Nudibranchia *sensu stricto* (Schmekel 1985; Salvini-Plawen 1990). In these cases the other three suborders of Nudibranchia appear to form a monophyletic group.

Parallel evolution has been rampant in the Opisthobranchia (Gosliner & Ghiselin 1984), and members of the order Sacoglossa may have an external appearance very similar to members of the Nudibranchia. The most striking homoplasy is the development of dorso-lateral cerata containing a branch of the digestive gland in the sacoglossan superfamily Limapontioidea and in the nudibranch suborders Dendronotacea, Arminacea and Aeolidacea. However, the Sacoglossa are almost exclusively herbivores.

Order Nudibranchia

The Nudibranchia are characterised by a number of synapomorphies (Table 1), and they have usually been considered a monophyletic group (Schmekel 1985; Rudman & Willan 1998). Current classification subdivides the order into 4 suborders (Boss 1982; Rudman & Willan 1998). However, it is usually acknowledged that one suborder, the Doridacea, also called the Ctenidiacea (Schmekel 1985) or Anthobranchia (Salvini-Plawen 1980), is more distantly related to the remaining three suborders, which form a monophyletic group variably called Actenidiacea (Schmekel 1985), Cladobranchia (Willan 1987) or Nudibranchia *sensu stricto* (Salvini-Plawen 1990). Molecular studies indicate that the Doridacea may not be included in a monophyletic group with the other three suborders (Thollesson 1999b). Two suborders, the Arminacea and Dendronotacea, are probably not monophyletic (Rudman 1998b; Willan 1998), and in molecular studies species from all three actenidiacean suborders cluster together (Thollesson 1999a), so the division into 3 suborders may be unwarranted. At family level classification is even less stable in most of the suborders.

Table 1. Synapomorphies of the order Nudibranchia.

1. Shell lost in postlarval stage
2. External bilateral symmetry
3. Visceral ganglion on right side
4. Reproductive system generally triaulic
5. Specialized vacuole cells present

Anatomically the Nudibranchia are highly diverse. Jaws and radular teeth are important characters for identifying species. In an older classification, the Nudibranchia were divided into two subgroups based on branching of the digestive gland; the Holohepatica with a solid digestive gland and Cladohepatica with a branched digestive gland (Bergh 1892); this classification roughly corresponds to the division into Ctenidiacea and Actenidiacea. The position of anus, nephridial pore and genital opening are "also important for identification. There is only one genital opening, usually on a distinct papilla. In some species only the penis and oviduct open into the genital papilla; this is called diaulic (meaning 'two pipes'). In the majority of species there is also a vaginal duct opening into the genital papilla; this is called triaulic. The nervous system is highly concentrated, with a short, untwisted visceral cord. In many species intestinal as well as abdominal ganglia are fused with the cerebro-pleural ganglia, but some species have one ganglion on the visceral cord, which may be the abdominal ganglion, which may or may not have fused with one or both intestinal ganglia. It is located on the right side of the visceral cord. The nervous system has also been used previously for classification (Schmekel 1985), but parallel evolution has probably been common (Gosliner & Ghiselin 1984; Gosliner 1991), so this cannot be used to establish phylogenetic relationships.

Suborder: Doridacea
Synonyms: Ctenidiacea, Anthobranchia, Doridina

This is the largest suborder of nudibranchs; the number of species is higher than for the remaining 3 suborders combined. The group is considered monophyletic (Schmekel 1985; Salvini-Plawen & Steiner 1996; Thollesson 1999a,b). However, there is some discussion about the inclusion of a few aberrant taxa (Wägele 1989, 1998; Salvini-Plawen 1990). Also, phylogenetic relationships within the suborder are highly debated. The Doridacea is usually considered the sister-group of the remaining nudibranchs (Schmekel 1985; Wägele 1989).

The dorids have a dorsal mantle, sometimes called the notum, overhanging the visceral mass and foot, and sometimes also the head. Most species have a dorsal circlet of branched gills surrounding the anus. The rhinophores are usually lamellate and in most species can be retracted into small pockets. Synapomorphies for the suborder are listed in Table 2. The dorids are traditionally divided into two subgroups: (1) Cryptobranchia, in which the gills can be retracted into a pocket so that only a small opening is visible in most preserved specimens, and (2) Phanerobranchia, in which there is no gill pocket. The Phanerobranchia may be further divided into Suctoria and Non-suctoria based on pharyngeal morphology, the Suctoria having a muscular, dorsal pouch on the pharynx. These groups probably do not reflect phylogenetic relationships.

Table 2. Synapomorphies of the suborder Doridacea

1. No cuticular lining in oesophagus
2. Triaulic genital system
3. Blood gland close to cephalic ganglia
4. Gill glands
5. ? Pericardial "glands"

Three families do not fit into these two groups, the Corambidae, the Dendrodoridae and the Phyllidiidae. The Corambidae is usually included in the Phanerobranchia because of its suctorial pharynx. The Phyllidiidae and the Dendrodoridae lack jaws and radula and are sometimes united in the Porostomata (Brodie *et al.* 1997), sometimes included in the Cryptobranchia (Brunckhorst 1993; Rudman 1998a). Recent anatomical studies have indicated that at least the Dendrodoridae should be included in the Cryptobranchia (Wägele *et al.*

1999), but also that the Cryptobranchia and Phanerobranchia may not be monophyletic groups.

An exact taxonomic level has not been given to the above taxa, though most workers call them superfamilies. However, superfamily-names have to be based on a valid genus-level taxon, and neither Cryptobranchia nor its synonym Eudoridina (=Eudoridoidea) are based on existing genera; the same is true for the Phanerobranchia (=Anadoridina; Anadoridoidea) and Porostomata (=Porodoridoidea). As phylogenetic relationships remain uncertain, no new taxon-names will be introduced here. The family division, with one exception, follows that of Rudman (1998a).

The Cryptobranchia, including the Porostomata, are usually sponge-feeders, whereas the Phanerobranchia feed on bryozoans, ascidians, barnacles and other prey. One family, the Gymnodorididae, is voracious predators of other opisthobranchs.

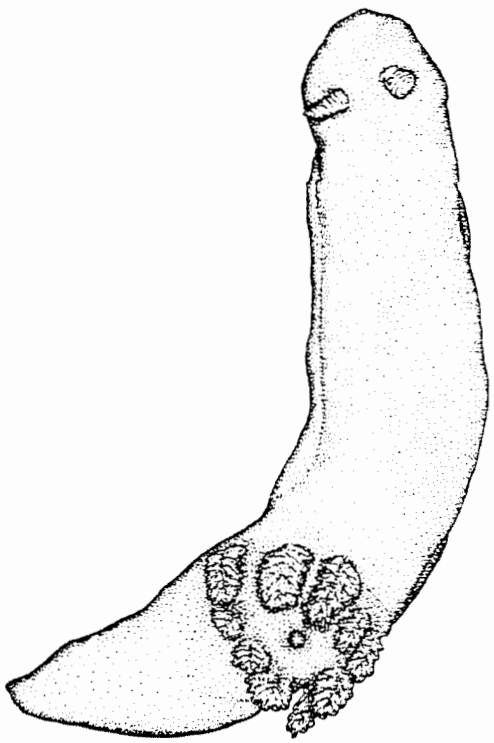

Figure 1.
Gymnodoris inornata (sensu Baba, 1937) from Hong Kong. Animal drawn from colour slide by K.R. Jensen. This species is uniformly orange in colour. Total length of animal was ca. 40 mm.

Characteristics of families:

Phanerobranchia (=Anadoridoidea)

Corambidae : Family thought to be restricted to temperate waters. However, one undescribed species has been recorded from South Africa (Gosliner 1987), and another occurs in southeastern Australia (Rudman 1998a), thus more species are likely to be found. They occur on encrusting bryozoans, and are very well camouflaged. Mantle overhanging; gills and anus posteroventral.

Goniodorididae (=Okeniidae): With reduced mantle skirt and few lateral processes. Rhinophores lamellate. Oral veil with lateral lobes or tentacles. Some species have dorsal keel on tail. Feed on bryozoans or ascidians.

Onchidorididae : With overhanging mantle; usually papillose and spiculose. Rhinophores lamellate, retractable. Most species occur in temperate waters. Gymnodorididae (Fig. 1 and Fig. 10 in Jensen 1998): Most species without mantle skirt. Rhinophores lamellate, non-retractable. Voracious predators of other opisthobranchs. Fig. 1 shows *Gymnodoris inornata (sensu* Baba 1937) from Hong Kong, which may not be identical to *G. inornata* (Bergh, 1880) (Rudman, pers. comm.). This species is uniformly orange in colour and has a circlet of 10-14 branched gills around the anus. It feeds on other dorid nudibranchs (Hughes 1985). Because of the uncertain species identity the exact distribution of this species is uncertain, but it probably has a wide Indo-West Pacific distribution (Rudman & Darvell 1990).

Polyceridae : Mantle skirt much reduced. Oral veil may have tentacular processes. Rhinophores lamellate, retractable. Some species have lateral tentacular processes. Gills tripinnate. Feed on bryozoans and ascidians.

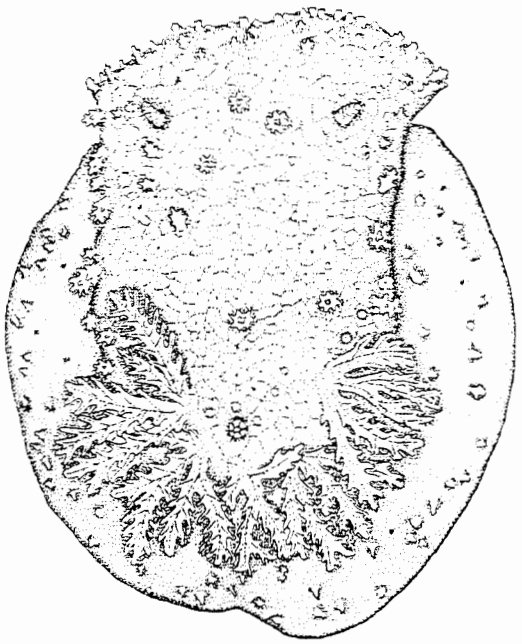

Figure 2. *Kalinga ornata* Alder & Hancock, 1864 from Hong Kong. Animal drawn from colour slide by K.R. Jensen. Total length of animal was ca. 170 mm.

Triophidae (Fig. 2): Sometimes considered a subfamily of Polyceridae (Rudman 1998a). Mantle skirt reduced. Tentacular processes laterally and along oral veil. Oral tentacles are broad lobes. Rhinophores lamellate, retractable. Usually with a dorsal keel on tail, which may be used for swimming. Some species have bioluminescence. Feed on bryozoans. Fig. 2 shows *Kalinga ornata* Alder & Hancock, 1864, which is a very large species (170 mm for the figured specimen). Its body is covered by numerous red tubercles. Along lateral margins are long, branched processes with red and yellow pigmentation; in live animals these processes pulsate. It has a broad oral veil with a row of warty tentacles. There are 6 highly branched gills surrounding the tall, red anal spout. The figured specimen was trawled in Hong Kong in April 1995, but the species has also been collected from a drying fishing net at the beach near RIA3 in Nha Trang, Vietnam during the TMMP training course in taxonomy of marine molluscs (Nov. 1999). It has a wide Indo-West Pacific distribution (Rudman & Darvell 1990).

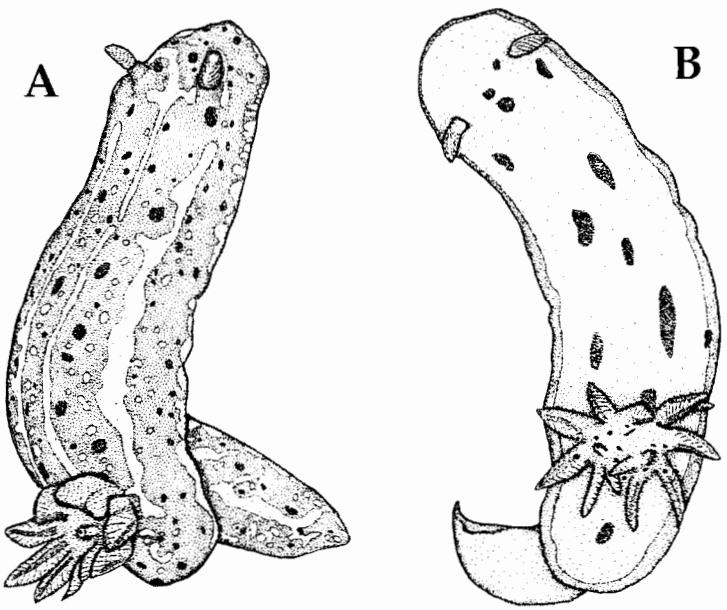

Figure 3.
Family Chromodorididae from Hong Kong drawn from colour slides by K.R. Jensen. A - *Hypselodoris festiva* (Adams, 1861). This species is blue with yellow stripes and red lines on rhinophores and gills. Total length of animal about 30 mm. B - *Chromodoris orientalis* Rudman, 1983. This species is white with yellow-orange margins of mantle, foot, rhinophores and gills; black spots are scattered on mantle. Total length of animal about 30 mm.

Aegeritidae (=Notodoridídae): Spiculose, tuberculate body wall. Rhinophores smooth, retractable. Tuberculate ridge overhanging gills. Feed on calcareous sponges.
Vayssiereidae : Tiny species, no gills, no mantle skirt, and no oral tentacles. Rhinophores smooth, non-retractable. One species feeds on serpulid polychaetes.

Cryptobranchia (=Eudoridoidea)
Hexabranchidae : Monogeneric ("Spanish dancer"). Large species with broad mantle skirt. Each gill has separate pocket.
Chromodorididae (Fig. 3): Mantle skirt usually broad and smooth. Defensive glands arranged in patterns, which are taxonomically important. Usually brightly coloured. Rhinophores lamellate, retractable. Feed on sponges. Indo-Pacific species have been described in a series of papers containing numerous colour pictures (Rudman 1973, 1977, 1982b, 1983, 1984, 1985, 1986a,b,c, 1987, 1988, 1990, 1995; Gosliner 1994, 1996; Gosliner & Behrens 1998a; Gosliner & Johnson 1999; Valdés & Gosliner 1999; Valdés *et al.* 1999). The largest nudibranch family; there may be about 300 species in the genus *Chromodoris* alone (Gosliner & Johnson 1999). Fig. 3A shows *Hypselodoris festiva* (Adams, 1861) from Hong Kong. It has been anatomically described in Baba (1995). It has a blue background colour with yellow stripes and spots arranged in lines; the rhinophores have red lamellae and gill axes have red edges. It may be confused with the similarly coloured species *H. infucata* Rüppell & Leuckart, 1828, and *H. obscura* (Stimpson, 1855). However, these two species have yellow spots, not arranged in lines (Rudman 1977). *H. festiva* has been recorded from Japan and the South China Sea (Baba 1995). Fig. 3B illustrates *Chromodoris orientalis* Rudman, 1983 from Hong Kong. This species is recognized by a yellow-orange mantle border and a number of large, black spots on a white background. The pattern of the black spots varies among specimens. The rhinophores and edges of gills are yellow-orange. The anatomy has been described in Rudman (1983). Small specimens may be confused with another white, dark-spotted species, *C. tumulifera* Collingwood, 1881. However, in this species the spots are actually dark red-purple, and the yellow-orange band along the mantle margin is submarginal with an irregular inner edge (Rudman 1983). Also, *C. orientalis* has been confused with *C. pallescens* Bergh, 1874 (Orr 1981, Morton & Morton 1983), which is now considered a junior synonym of *C. aspersa* (Gould, 1852) (Rudman 1983). *C. orientalis* is only known from Japan and Hong Kong (Rudman & Darvell 1990).
Doridídae : Usually split into a number of separate families (e.g. Aldisidae, Archidoridídae, Discodoridídae, Halgerdidae, Kentrodoridídae, Platydoridídae) (see e.g. Debelius 1996; Fahey & Gosliner 1999; Gosliner & Behrens 1998b; Gosliner & Fahey 1998), but considered one family by Rudman (1998a) and Willan & Brodie (1989). Mantle thick and broad, often tuberculate; some species have caryophyllidia, i.e. specialized, complex papillae with spicules (=minute, crystalline, needle- hook- or disc-shaped structures). Rhinophores lamellate, retractable. Feed on sponges.
Dendrodorididae : Broad mantle skirt, smooth or tuberculate. Rhinophores lamellate, retractable. Gills postero-dorsal, retractable. No radula or jaws. Feed on sponges. Phylogenetic relationships have been discussed in Brodie *et al.* (1997) and Wägele *et al.* (1999).
Phyllidiidae (Fig. 4): Mantle thick, warty, spiculate. Rhinophores lamellate, retractable. Gills simple latero-ventral folds. Anus usually dorsal (ventral in genus *Fryeria*). No radula or jaws. Feed on sponges. The family has been revised recently (Brunckhorst 1993). An identification key to Indo-Pacific species has been just been published (Fahrner & Beck 2000). Fig. 4 shows *Phyllidiella pustulosa* (Cuvier, 1804) from Phuket, Thailand. It is black with black

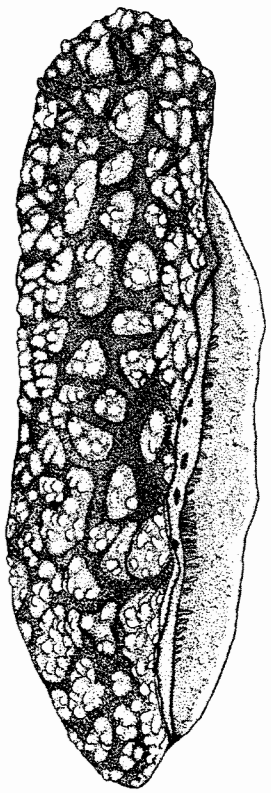

Figure 4. *Phyllidiella pustulosa* (Cuvier, 1804) from Phuket, Thailand. Animal drawn from colour slide by K. R. Jensen. This species is black, with black rhinophores and pink clusters of tubercles. Total length of animal ca. 50 mm.

rhinophores and pink clustered tubercles. Foot dark grey. It has a wide Indo-Pacific distribution (Brunckhorst 1993). The figured specimen was about 50 mm alive.

Actenidiacea
Synonyms: Cladobranchia, Nudibranchia s.s.

The remaining three suborders are sometimes united into one taxon, alternately called Actenidiacea (Wägele 1989), Cladobranchia (Willan 1987) or Nudibranchia *sensu strictu* (Salvini-Plawen & Steiner 1996). This taxon is considered the sister group of the Doridacea, which is then called Ctenidiacea (Wägele 1989) or Anthobranchia (Salvini-Plawen 1980).

Suborder Arminacea

This suborder is the smallest and most heterogeneous nudibranch suborder. Most likely it is not a monophyletic group (Willan 1998). It is sometimes subdivided into two superfamilies, Metarminoidea, comprising the cerata-bearing families, and Euarminoidea, comprising families without cerata. As with the existing doridacean superfamilies, the arminacean superfamily names are not based on existing genus-level taxa, hence cannot be valid. Cerata-bearing arminaceans can be distinguished from aeolids by not having cnidosacs at the tips of the cerata, and by having cerata in front of the rhinophores. No synapomorphic characters have been identified to unite the "superfamily". Hence the families will be listed separately.

Characteristics of families:

Doridomorphidae : Only one species in the tropics; dorid-like appearance, but no gills and lateral anus as well as hard jaws and branched digestive gland indicate arminacean affinity (Willan 1998).

Charcotiidae : One species in South Africa, otherwise Antarctic or subantarctic; no gills, lateral anus, separate male and female genital openings (Willan 1998). This family is considered a possible sister group of the Aeolidiacea by some authors (Wägele 1997).

Madrellidae : Broad mantle with long cerata. Large oral veil, also with cerata. Non-retractile rhinophores with separate stalk and clavus. Anus postero-lateral (Willan 1998). Diet, where known, is bryozoans (Burn 1989).

Zephyrinidae (= Proctonotidae; = Janolidae; =Antiopellidae): Flattened bodies with numerous cerata (extending around the head). Middorsal anus. Distinct oral tentacles. Non-retractile rhinophores, not divided into stalk and clavus. Some species with sensory "caruncle" between bases of rhinophores (Miller & Willan 1986; Willan 1998). These species feed on bryozoans.

Pinufiidae : Monotypic (only one species), *Pinufius rebus;* feeds on *Porites* (Rudman 1981, 1982a).

Arminidae (Fig. 5 and Fig. 5B in Jensen

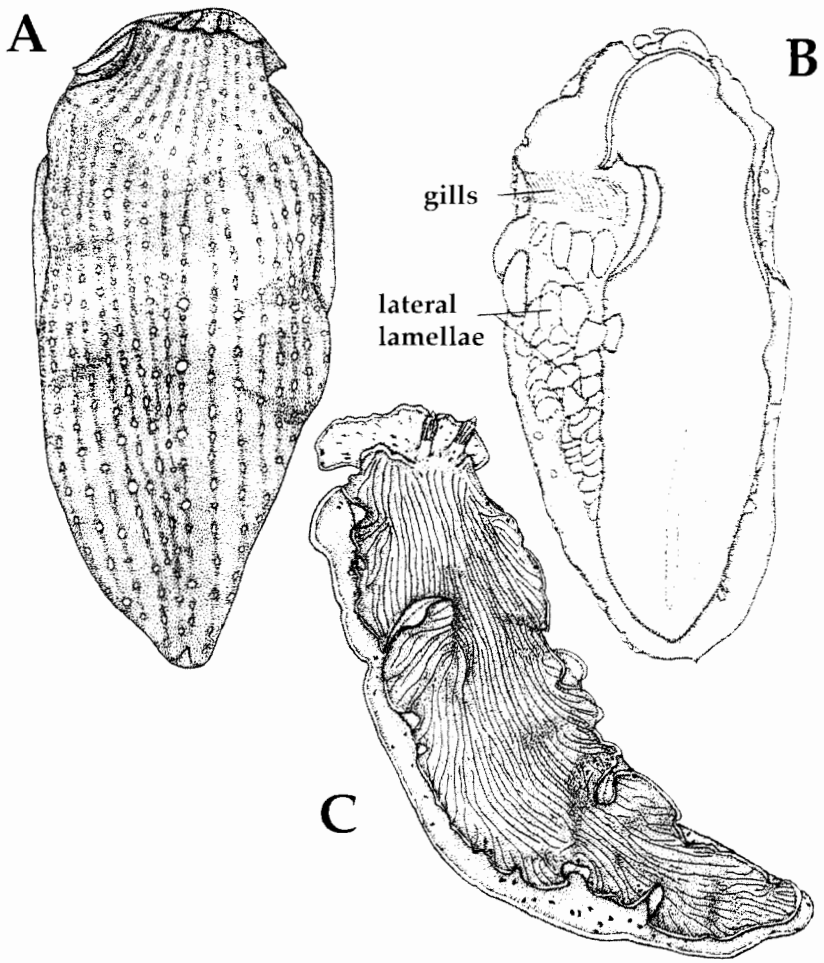

Figure 5. Arminidae from Hong Kong drawn from colour slides by K.R. Jensen. A - *Armina punctulata* Lin, 1990 (from Jensen 1997). B - *Armina variolosa* (Bergh, 1904), ventral view (modified from Jensen 1997). C -*Dermatobranchus tongshaensis* Lin, 1981. Total length of animal ca. 55 mm.

1999): Limaciform bodies. Longitudinally lamellate or warty notum overhanging foot; not covering head. Large oral veil, sometimes with dorsal papillae. Some species have fleshy ridge (caruncle) in front of rhinophores. Rhinophores with vertical lamellae on clavus. Anus lateral. Gills, when present form transverse, anterior row of lamellae on hyponotum. Many species also have longitudinal or diagonal lateral lamellae (also called hyponotal lamellae or subnotal lamellae) on ventral surface of mantle (=hyponotum); these contain branches of the digestive gland. The family is characterised by at least one synapomorphy, the presence of so-called marginal sacs, which are microscopical structures along the mantle rim (Kolb & Wägele 1998). This is the largest family of the suborder (more than 70 species). They feed on octocorals. Phylogeny of the genera has been outlined in Kolb & Wägele (1998). Anatomical descriptions of some Indo-Pacific species can be found in Baba (1976), Miller & Willan (1986) and Jensen (1997). Fig. 5A shows *Armina punctulata* Lin, 1990 from

Hong Kong (from Jensen 1997). This species is dark grey with light grey tubercles arranged in longitudinal rows. It occurs subtidally in black muddy sediment. It appears to be a Hong Kong endemic. Fig. 5B shows the ventral surface of *Armina variolosa* (Bergh, 1904) which is a large, reddish-orange species with white tubercles on the notum. On the ventral surface the anterior gill lamellae and the numerous diagonally arranged hyponotal or lateral lamellae are seen. Also, the posterior foot sole has a conspicuous pedal gland. The specimen was trawled in Hong Kong (Jensen 1997), but occurs also in Japan and Hainan Island. Fig. 5C shows *Dermatobranchus tongshaensis* Lin, 1981 from Hong Kong. The specimen was about 55 mm long alive. It is grey with dark grey to black lamellae dorsally. It has a yellow marginal band on mantle, foot, and head shield. There are some black spots laterally and on head veil. The genus *Dermatobranchus* has neither gills nor hyponotal lamellae (Jensen in press).

Suborder Dendronotacea

This is also a rather heterogeneous group, which most likely is not monophyletic (Thollesson 1999a). Dendronotaceans have latero-dorsal cerata, which may be branched; the cerata contain a branch of the digestive gland, and gills may be attached to the cerata. The bases of the rhinophores are surrounded by conspicuous sheaths, which may have tentacular processes at the rim. The mantle skirt is usually reduced. There is an oral veil, which may bear more or less elaborate processes. They have conspicuous jaws.

Characteristics of families:

Dendronotidae : Cerata highly branched. Oral veil with branched processes. Rhinophore sheaths usually with long, digitiform processes. This family has a northern distribution with only a few species recorded from warm water in Japan (Baba 1949).

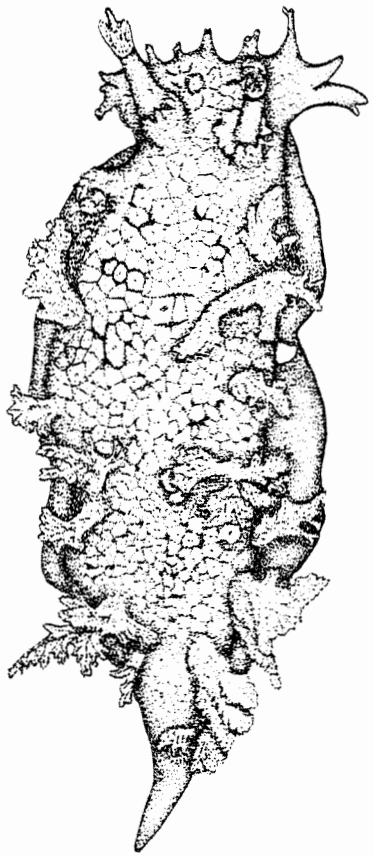

Figure 6. *Marionia echinomuricea* Jensen, 1994 from Hong Kong. Animal drawn from colour slide by K.R. Jensen. This species is grey with a reticulate pattern of reddish-brown lines. Total length of animal ca. 60 mm.

Tritoniidae (Fig. 6): Cerata forming branched gills. Oral veil with tentacular processes. Rhinophore sheaths lobed or with short papillae at edges. Anus and genital opening antero-lateral on right side. Feed on octocorals. Although many species are known from the Indo-Malayan region (Debelius 1996; Gosliner *et al.* 1996), few have been anatomically described. *Marionia echinomuriceae* Jensen 1994 (Fig. 6) was recently described from Hong Kong (Jensen 1994). It is grey with a reticulate pattern of reddish-brown lines. The dorsal surface is

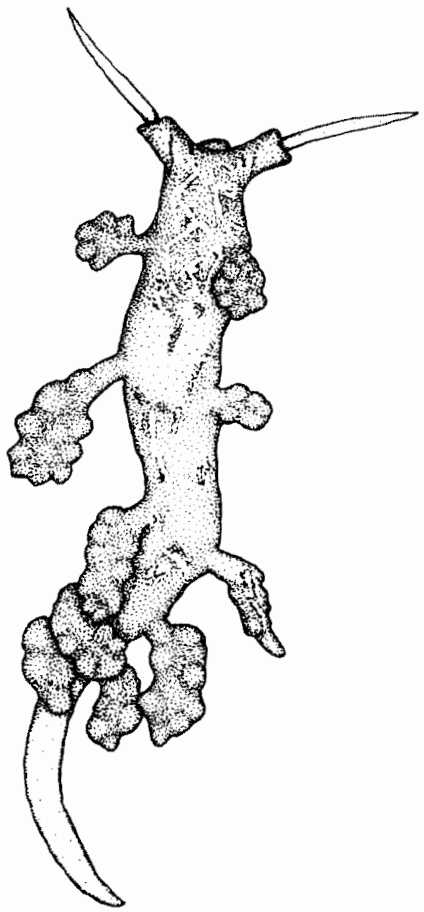

Figure 7.
Doto sp. from Hong Kong. Animal drawn from colour slide by K.R. Jensen. The animal had black mottlings on a transparent background. It was only 3 mm long.

tuberculate; tubercles have green or white centers. Oral veil bilobed with 6-8 processes on each lobe. Ten to 14 pairs of highly branched gills laterally. It feeds on the gorgonian *Echinomuricea indomalaccensis*.
Bornellidae (Fig. 7 in Jensen 1998): Body narrow, cylindrical. Cerata in few clusters, often with small gills at bases. Oral veil forms two highly branched tentacles. Rhinophore sheaths usually with long processes at edges. The anatomy of *Bornella stellifer* (Adams & Reeve in Adams, 1848) from Phuket, Thailand was described by Jensen (1998).

Dotidae (Fig. 7): Small animals with reduced oral veil. Rhinophore sheaths with smooth edges; rhinophores simple. The cerata are more or less tuberculate. Anus between anterior cerata; genital opening antero-lateral. Feed on hydroids. Fig. 7 shows a probably undescribed species of *Doto*, which was collected from hydroids on a floating bamboo pole in Hong Kong. The colour is black mottlings on a transparent background.
Besides these families, a number of rather aberrant, mostly monogeneric families exist: Marianinidae, Hancockiidae, Scyllaeidae, Tethyidae, Phylliroidae, and Lomanotidae.

Suborder Aeolidacea

Nudibranchs with usually slim bodies. Dorsolaterally are more or less cylindrical appendages, cerata, usually containing a branch of the digestive gland. Mid-dorsally is a distinct pericardial hump. The cerata are usually arranged in rows or clusters, with a distinct separation between precardiac (in front of pericardium) and postcardiac (behind pericardium) groups. An important synapomorphy for this suborder is the presence of cnidosacs (structures used for storing functional nematocysts of cnidarian prey) (Wägele 1998). Most species have long, simple oral tentacles. The rhinophores are variably shaped: simple, annulate, warty, lamellate (=perfoliate). There are no rhinophore sheaths, and the rhinophores are non-retractile. The foot often has tentacular processes at anterior corners. The position of the anus was previously used for taxonomic purposes, but this character apparently does not reflect phylogenetic relationships. The Aeolidacea have conspicuous jaws, and usually narrow radulae. The division into families is still debated (Miller 1974; Gosliner & Willan 1991; Rudman 1998c), and molecular data have not helped to elucidate this (Thollesson 1999a). The familial division given here is that used by Rudman (1998c).

Aeolidaceans usually feed on Cnidaria, but some species have highly specialized diets, e.g. fish eggs, gastropod eggs, barnacles.

Characteristics of families:

Flabellinidae : Some species have a distinct mantle edge. The cerata may be in single rows or in clusters. Rhinophore shape variable. Oral tentacles usually long. Foot usually with tentacular corners. Anus pleuroproctic or acleioproctic (Fig. 8). The radula is triserate.

Eubranchidae : Small animals with smooth rhinophores. Oral tentacles short. They have few cerata in single rows; the cerata are usually inflated. Anus acleioproctic (Fig. 8). The radula is triseriate.

Aeolidiidae : Rather big species. The foot is wider than the body. Numerous cerata in rows; sometimes rows are on a common ridge. Oral tentacles long. Rhinophore shape variable. Anus cleioproctic (Fig. 8). The radula is uniseriate.

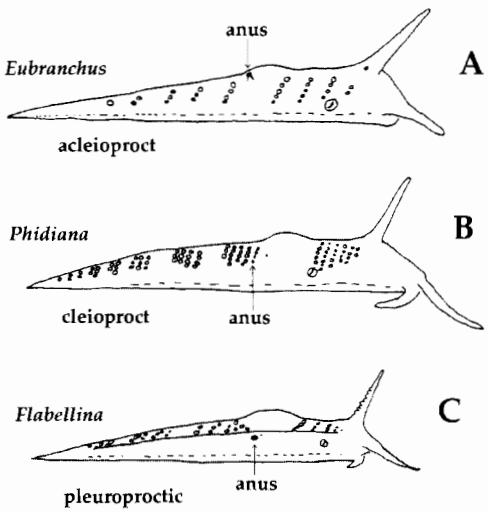

Figure 8. Different positions of anus (and cerata) in the suborder Aeolidacea. A - *Eubranchus* with cerata in rows and acleioproctic anus (=dorsal, between precardiac and postcardiac cerata). B - *Phidiana* with cerata in clusters of rows and cleioproctic anus (=between cerata of first postcardiac cluster). C - *Flabellina* with cerata in clusters and pleuroproctic anus (=lateral, below level of cerata). Modified from various sources.

Figure 9. *Phidiana militaris* (Alder & Hancock, 1864) from Hong Kong. Animal drawn from colour slide by K.R. Jensen. It has a characteristic pattern of red stripes dorsally and laterally; rhinophores, oral and pedal tentacles, cerata and tail have yellow tips. Total length of animal ca. 50 mm.

Glaucidae (Fig. 9 And Fig. 5D in Jensen 1999): This family is sometimes split into a number of separate families, here given subfamilial rank, i.e. Facelininae, Favorininae, Pteraeolidiinae, Glaucinae, Crateninae, Herviellinae. The morphology is highly variable; cerata may be in rows, clusters of rows, or arches. Oral tentacles long. Rhinophore shape variable. Anus usually cleioproctic (Fig. 8). The radula is uniseriate. Fig. 9 shows *Phidiana militaris* (Alder & Hancock, 1864) from Hong Kong. It has a characteristic pattern of red stripes and the rhinophores, oral tentacles, pedal tentacles, cerata, as well as the tail have yellow tips. The cerata are arranged in indistinct clusters. The rhinophores are simple. Previously this species has only been recorded from the Arabian Sea and India

(Debelius 1996). The present record from Hong Kong extends the known distribution range. *P. milleri* Rudman, 1980 from New Zealand and *P. indica* (Bergh, 1896) with a wide Indo-West Pacific distribution, have sometimes been confused with *P. militaris*. However, colour patterns as well as anatomy are different (Rudman 1980).

Embletoniidae : Small animals with a bilobed oral veil; no oral tentacles. The cerata are in a single row. The rhinophores are simple. Anus between 2nd and 3rd cerata. The radula is uniseriate. Some species have occasionally been referred to the Dendronotacea. Some species live interstitially.

Tergipedidae : Small animals with cerata in single oblique rows. The foot corners are rounded. The anus is acleioproctic (Fig. 8).

Fionidae : Monospecific; *Fiona pinnata* cosmopolitan; feeding on floating goose barnacles or siphonophores (Thompson & Brown 1984). Rhinophores and oral tentacles smooth. Cerata irregularly arranged. Anus latero-dorsal. The radula is uniseriate.

ACKNOWLEDGEMENTS

I would like to thank the organizers of the 10th Congress/Workshop of the TMMP for financial support of my participation; also the organizers of the Training Course in mollusc biodiversity in Nha Trang are thanked for the opportunity to collect a few nudibranchs. The Carlsberg Foundation supported my participation in workshops in Hong Kong; the staff of the Swire Institute of Marine Science is thanked for logistic support.

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