

The Systematics and Phylogeny of Phyllidiid Nudibranchs (Doridoidea)

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ABSTRACT. Investigations into the taxonomy, phylogeny, biogeography and ecology of nudibranchs belonging to the family Phyllidiidae Rafinesque are reported. All prior research on the Phyllidiidae is reviewed. There were 74 nominal species as of January, 1992. The literature revealed enormous confusion in the taxonomy of phyllidiids caused primarily from inadequate anatomical study (or none at all) and descriptions of single preserved specimens. Intraspecific variation, particularly its ontogenetic component, is identified as an additional cause of misidentification.

Traditional sources of nudibranch taxonomic characters, such as jaws and radula, are lacking in the Phyllidiidae. Characters used in this study are: general shape and body profile; colour and pattern; morphology of notal tubercles, ridges, and the mantle margin; rhinophoral colour; number of lamellae on each rhinophoral clavus; gills; morphology of foot and foot sole; oral tentacles; anatomy of the alimentary system; anatomy of the reproductive system; penial spine morphology; and sperm ultrastructure.

Six genera are recognised and each is redescribed. Features which clearly demarcate the genera occur principally in the digestive system, and also in the reproductive system and external morphology. A key to genera is provided. A total of 49 valid, Indo-Pacific species is recognised; a full synonymy is given for each species. *Phyllidia* Cuvier remains the largest genus with 15 (including 8 new) species. *Fryeria* Gray is considered a valid genus with six (including 3 new) species. *Phyllidiella* Bergh is reinstated and nine (including 4 new) species are recognised. *Phyllidiopsis* Bergh, the second largest genus, contains 14 (including 6 new) species. *Ceratophyllidia* Eliot appears to contain three (including 2 new) species, however specimens are very rarely collected and further work remains to be done prior to their formal description. The recently described genus *Reticulidia* Brunckhorst contains two species. In all, 22 new species of phyllidiid nudibranchs are described.

Study of anatomy has allowed a phylogenetic hypothesis to be proposed for the first time. *Ceratophyllidia* is the sister group to the remaining genera. *Phyllidia*, *Fryeria* and *Reticulidia* are the most derived genera. The morphology and anatomy of phyllidiids indicates monophyly with dorids. However, the grouping of the Phyllidiidae and Dendrodorididae as Porostomata is

polyphyletic and rejected as homeoplaseous. Differences in foregut anatomy between the two groups support the view that suctorial feeding of sponges has arisen independently in both groups.

Biogeographical distribution of species and ecological observations are reported. As a result of field observations, the sponge foods of several phyllidiid species are reported for the first time. The sponge food and chemical defence compounds of phyllidiid species may also be useful in taxonomic study. *In situ* observations of feeding and study of the functional anatomy of the foregut enabled a description of the method of operation of the feeding apparatus of each genus. The spawn of three species are described for the first time.

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Introduction

Historical Perspective: the Literature Reviewed

Nudibranchs of the family Phyllidiidae Rafinesque, 1814 occur throughout the tropical Indo-Pacific region (Bergh, 1869, 1889, 1905; Eliot, 1910; Risbec, 1929, 1953; Edmunds, 1971, 1972; Rao *et al.*, 1974; Baba & Hamatani, 1975; Orr, 1981; Bertsch & Johnson, 1981; Wu & Romig, 1982; Lin, 1983; Willan & Coleman, 1984) and the Red Sea, (Rüppell & Leuckart, 1830 or 1831; Vayssière, 1906, 1912; White, 1951; Heller & Thompson, 1983; Yonow, 1986). A small number of phyllidiid species are known from the Mediterranean Sea (Aradas, 1847; Pruvot-Fol, 1951, 1952, 1962; Bouchet, 1983; Cattaneo & Barletta, 1984; Brunckhorst & Willan, 1989) and from the tropical Atlantic (Bergh, 1890; Ev. Marcus & Er. Marcus, 1962, 1967; Ev. Marcus, 1977;

Bouchet, 1977; Brunckhorst, 1990b).

The phyllidiid fauna of the Indo-West Pacific has not been examined comprehensively since Bergh's (1869) monograph. Three new generic names and more than 50 new specific names have been introduced since the publication of Bergh's (1869) monograph. The most recent review was that of Pruvot-Fol (1956, 1957a) who discussed most species, but did not differentiate generic features. As at January 1992, the family Phyllidiidae consisted of 74 nominal species belonging to five genera. The largest genus, *Phyllidia* Cuvier, consists of 56 nominal species. *Phyllidiopsis* Bergh has 12 nominal species (including 4 Atlantic Ocean species; Brunckhorst, 1990b). *Fryeria* Gray, *Ceratophyllidia* Eliot and *Reticulidia* Brunckhorst, presently contain three, two and one nominal species respectively.

Radulae and jaws are absent in the Phyllidiidae, whereas most other doridoids possess buccal armature (Macfarland, 1905; Boss, 1982; Willan & Coleman,

1984). Phyllidiids have oral glands closely associated with the muscular pharynx (Bergh, 1869; Eliot, 1904; Ev. Marcus & Er. Marcus, 1962; Wägele, 1985; Brunckhorst, 1989b). The dorsomedian, circumanal gill circling of the dorids has been replaced in the Phyllidiidae by a series of ventrolateral gill leaflets. Modification of the oral glands and the stomach region of the digestive tract has occurred in the Phyllidiidae (Wägele, 1985; Gosliner & Behrens, 1988; Brunckhorst, 1989b, 1990a,b; Brunckhorst & Willan, 1989). These features are regarded as advanced or derived (apomorphic) characters within the Nudibranchia. The reproductive system of phyllidiids corresponds to the triaulic condition of advanced dorids (Bergh, 1869; Wägele, 1985; Brunckhorst, 1989b). Further anatomical comparisons are required, but these features may indicate that the Phyllidiidae should have superfamily status distinct from other dorids (see Eliot, 1903b; Willan & Coleman, 1984).

Systematics

The following account proceeds chronologically with respect to the introduction of taxa. However, for the sake of continuity, more recent works are discussed where they are relevant to a particular name.

The genus *Phyllidia* was first introduced by Cuvier (1797) who did not name any species. Lamarck (1801) described and named *P. varicosa* (type by subsequent designation). This animal was described again and named *P. trilineata* by Cuvier (1804) who, on that occasion, also named three other species, *P. pustulosa*, *P. ocellata* and *P. borbonica*. Blainville (1816) called a specimen of *P. varicosa*, *P. quinquelineata* because it had five dorsal ridges (Blainville, 1826: 99; Bergh, 1869: 500). There is presently some confusion over the status of *P. varicosa* (Yonow, 1986; Brunckhorst, 1989b).

In 1828, Rüppell & Leuckart completed a report on Red Sea opisthobranchs, however this work was not published until 1830 or 1831. Rüppell & Leuckart (1830 or 1831) described one new phyllidiid having a ventral, posterior anus. They misidentified their specimens as *Phyllidia pustulosa* Cuvier and, later, Gray (1853) introduced a new genus, *Fryeria*, for the Rüppell & Leuckart specimens. Bergh (1869) introduced *Fryeria rüppelii* (sic) n.nom. for Rüppell & Leuckart's (1830 or 1831) specimens to avoid confusion with *Phyllidia pustulosa* Cuvier. *Fryeria rueppelii* Bergh and *F. pustulosa* Gray are objective synonyms, being based on the same syntypes. However, O'Donoghue (1929) erroneously listed *Phyllidia pustulosa* Cuvier as the type species of *Fryeria*, because it appeared to be the first described species of *Fryeria* Gray. Yonow (1986) considered *Fryeria* Gray to be a junior synonym of *Phyllidia* Cuvier, and introduced the genus *Reyfriedia* for phyllidiid nudibranchs having a ventral anus situated posteriorly between mantle and foot. Recently,

Brunckhorst *et al.* (1989) have shown that *Fryeria* is nomenclaturally valid because it was deliberately based on Rüppell & Leuckart's specimens not those of Cuvier.

Other workers (Collingwood, 1881; Risbec, 1929, 1956; Pruvot-Fol, 1957a; Baba & Hamatani, 1975) have mentioned species belonging to the genus *Fryeria*, but according to Edmunds (1972) and Yonow (1986), they may be distinct from *Fryeria rueppelii* Bergh, 1869. Edmunds (1972) believed that there could be three sibling species covered by the name *F. rueppelii*.

After Rüppell & Leuckart's (1830 or 1831) descriptions of Red Sea opisthobranchs, Ehrenberg (1831) described *Phyllidia arabica*, also from the Red Sea, and in 1847, Aradas described three new species of *Phyllidia* from the Mediterranean Sea.

A paper on new species of Ceylonese (i.e., Sri Lankan) molluscs by Kelaart (1859) included the description of *Phyllidia zeylanica*. Eliot (1906) discussed some of Kelaart's specimens and considered *P. zeylanica* to be a distinct species, not a synonym of *P. varicosa*, as Bergh (1869) had suggested. The rediscovery of this species enabled Burn (1970) and Rao *et al.* (1974) to prepare redescrptions.

In a historical context, the latter half of the nineteenth century (1869-1905) was dominated by the meticulous work of Bergh. In a monograph specifically on phyllidiids, Bergh (1869) differentiated a new genus, *Phyllidiella*, having an asymmetrical oral tube rather than a symmetrical one as in *Phyllidia* Cuvier (see also Bergh, 1875, 1889, 1890, 1905; Eliot, 1904; Pruvot-Fol, 1956). Bergh (1869) recognised *Phyllidiella pustulosa* (Cuvier) as the first described species of his new genus, and added *P. nobilis*. Bergh (1869, 1875, 1877, 1889, 1890) presented detailed descriptions, with drawings, of new phyllidiid species, whilst also redescrbing others. In most of his works Bergh gave precise measurements of the internal and external characters of single specimens including organ systems, and even the "thorns" (i.e., penial spines) lining the ejaculatory duct in a number of species were illustrated. However, the genus *Phyllidiella* was not recognised by many later authors.

In 1875, Bergh described the genus, *Phyllidiopsis* (type species: *P. Cardinalis*), as a phyllidiid similar to *Doriopsis* Pease, 1860 in the nature of the mantle, oral tentacles and in not possessing a mass of oral glands around the pharynx (see Bergh, 1890, 1892; Eliot, 1903b; Er. Marcus & Ev. Marcus, 1970). Several species belonging to the genus *Phyllidiopsis* have since been described from both the Indo-West Pacific and the Atlantic. Bouchet (1977), in describing a new *Phyllidiopsis*, recognised eleven nominal species. He remarked that many of the earlier descriptions of species belonging to this genus were poor and incomplete.

Eliot (1903a) described another new genus, *Ceratophyllidia*, having "...pear shaped bodies set on stalks..." (Eliot, 1903a: 250). Bergh (1905) and Bouchet (1977) suggested that *Ceratophyllidia* should be referred to *Phyllidiopsis* Bergh, but Gosliner (1987) on re-examining *C. africana* Eliot disagrees. In his descriptions

and partial review, Eliot (1903b, 1904) discussed the taxonomic status of phyllidiid genera and considered *Phyllidiella* Bergh to be an unnecessary synonym of *Phyllidia*. Eliot (1904) also gave a summary of the generic characters of known Phyllidiidae.

A number of works by Baba figure *Phyllidia* species from Japanese waters (Baba, 1930, 1936, 1937, 1949, 1976). Baba (1930) described a new species, *P. tuberculata* (replacement name *P. japonica* Baba 1937), which he subsequently synonymised with *P. ocellata* Cuvier (Baba & Hamatani, 1975). Risbec also described various phyllidiids including new species from Madagascar (Risbec, 1929), New Caledonia (Risbec 1928, 1953), and Vietnam (Risbec, 1956).

Pruvot-Fol (1951, 1952) described two new Mediterranean *Phyllidia*. In her original description of *Phyllidia pulitzeri* from the Mediterranean, Pruvot-Fol (1962) was uncertain whether to place the species in either *Phyllidia* or *Phyllidiopsis*. Wägele (1985) has since shown that placement in the former genus is correct. Wägele (1984, 1985) remarked on the confusion surrounding the taxonomy of the family Phyllidiidae and presented a detailed synopsis of the histology and anatomy of *P. pulitzeri*. Brunckhorst & Willan (1989) have now shown that there is only one biological species of *Phyllidia*, *P. flava* Aradas, known from the Mediterranean Sea.

In her review of the family Phyllidiidae, Pruvot-Fol (1956, 1957a) commented on the necessity for anatomical accounts in descriptions of new species, emphasising the difficulty of relying on external morphology alone. She pointed out that phyllidiids lack buccal armature, a character used to differentiate other dorid nudibranchs (e.g., Rudman, 1983, 1984). She also considered the penial spines described by Bergh (1869, 1875, 1889) to be too similar to characterise individual species (Pruvot-Fol, 1956). Pruvot-Fol (1956, 1957a) reviewed the genera *Phyllidia* Cuvier, *Fryeria* Gray and *Phyllidiopsis* Bergh, omitting *Phyllidiella* Bergh and *Ceratophyllidia* Eliot, apparently considering the latter two genera to be indistinguishable from *Phyllidia* and *Phyllidiopsis* respectively. Since Pruvot-Fol's work many new species, from many parts of the world have been proposed but no review of phyllidiid systematics has been undertaken.

Er. Marcus & Ev. Marcus (1970) described two new *Phyllidia* species from the South Pacific and expressed uncertainty in using the position of the oral glands relative to the oral tube in taxonomic work on the Phyllidiidae (see also Eliot, 1904; Wägele, 1985). The use of foregut anatomy in the taxonomic and phylogenetic study of phyllidiids is discussed in detail in the current work. Bouchet (1983) described *Fryeria bayi*, the second known species of this genus and the first from Mediterranean waters, where he considered this species to be endemic. Yonow (1984a) described two new species of *Phyllidia* from Sri Lanka, the site of Kelaart's first collection of opisthobranchs (Kelaart, 1858, 1859). Her new species were distinguished from other *Phyllidia* by their dorsal markings. Yonow (1986)

considered many previous records of *Phyllidia varicosa* to be *P. arabica* Ehrenberg. Yonow (1986) suggested that *P. arabica* possesses a black longitudinal foot stripe, and that *P. varicosa* does not. In this case, there appear to be very few, if any, records in the literature referring to *P. varicosa* (without a foot stripe). Yonow (1986, 1988) recognised twelve species of *Phyllidia* from the Red Sea and considered seven to be endemic. Gosliner & Behrens (1988) redescribed *Phyllidiopsis cardinalis* Bergh and *Ceratophyllidia africana* Eliot and named a new species from the Pacific coast of North America, *Phyllidiopsis blanca*. Brunckhorst (1989, 1990b) has reassessed some species of *Phyllidia* and *Phyllidiopsis* and (Brunckhorst, 1990a) described a new Indo-West Pacific genus, *Reticulidia*.

Some workers have placed the families Phyllidiidae and Dendrodorididae together within the infraorder Porostomata on account of the lack of buccal armature (see Bergh, 1892; O'Donoghue, 1932; Thompson, 1976; Boss, 1982; Ev. Marcus, 1983; Yonow, 1988). According to Bergh (1875, 1889, 1890, 1892) and Pruvot-Fol (1957a), *Phyllidiopsis* Bergh is close to *Doriopsis* Pease, and intermediate between dorids (?dendrodorids) and *Phyllidia*, in features of the oral tentacles and finely tuberculated mantle. However, Bergh (1892) and Eliot (1903b) remarked that this may be an artificial grouping because of other differences between these two families (in particular, the form and position of gills). Bergh and Eliot also suggested that the ventrolateral gill leaflets of phyllidiids separated them from all dorids except the Corambidae. Todd (1981, 1983) and Thompson & Brown (1984) considered phyllidiids as primitive dorids akin to *Armina* Rafinesque and *Corambe* Bergh, because of their lateral placement of gills. O'Donoghue (1929) remarked that dendrodorids and phyllidiids differed in most characteristics. He considered that the loss of jaws and radula by both groups as a superficial similarity. Willan & Coleman (1984) considered the Phyllidiidae in the suborder Anthobranchia, superfamily Doridoidea and also remarked on the considerable differences between phyllidiids and other dorid families.

Anatomy

Phyllidiids are tough-bodied, oval, dorsoventrally flattened nudibranchs. They have retractile, lamellate rhinophores and coloured tubercles on the mantle. Like dorids, all species have a dorsal anus, except for the genus *Fryeria* Gray which possesses a posteroventral anus which is protrusible (Bergh, 1875). *Phyllidiopsis* Bergh has a uniquely elongate foregut and *Ceratophyllidia* Eliot is distinctive in the possession, of soft, round stalked papillae on the mantle (Bergh, 1869, 1875; Eliot, 1903a,b, 1910; Gosliner, 1987; Gosliner & Behrens, 1988; Brunckhorst, 1990a,b).

Whilst Cuvier (1804) included some drawings of anatomy, Bergh (1869, 1873, 1875) was the earliest worker to provide detailed anatomical descriptions of

phyllidiids. In her review, Pruvot-Fol (1956, 1957a) emphasised the importance of anatomical accounts of new species and gave some details of her dissections.

The genera *Phyllidia*, *Phyllidiopsis* and *Ceratophyllidia* are presently separated from each other by oral gland position, the former has these glands contained within the oral tube, and the latter two genera have oral glands absent or apparently free from the oral tube (Bergh, 1869, 1875; Eliot, 1904). Bergh (1890), Ev. Marcus & Er. Marcus (1962) and Eliot (1903a, 1904) further discussed the foregut anatomy of *Phyllidiopsis*. It is clear, however, that some authors were unsure of the anatomical differences existing between genera (e.g., Pruvot-Fol, 1957a; 1962). Eliot (1903a, 1904) discussed the characters which diagnose genera of the Phyllidiidae and Bergh (1869, 1875) and Eliot (1903a, 1904) suggested that differences in foregut anatomy may be of taxonomic value. Rao *et al.* (1974) described the internal anatomy, including that of the reproductive system of *Phyllidia varicosa* and *P. zeylanica*. Edmunds (1971, 1972) briefly described the mouthparts, gut and genital system of *Phyllidia* species from East African waters.

In summary, the internal anatomy of phyllidiids has received insufficient attention since Bergh's works. Recent authors have relied on external morphology for their descriptions (e.g., Baba, 1930, 1949; Baba & Hamatani, 1975; Thompson, 1980; Heller & Thompson, 1983; Perrone, 1983; Yonow, 1984a, 1986, 1988). However, thorough anatomical work has been published recently. Wägele (1984, 1985) has presented a comprehensive examination of the anatomy of *Phyllidia flava* (as *P. pulitzeri*), with details of the lateral gill leaflets and vascular, reproductive, excretory and digestive systems of this species. Gosliner & Behrens (1988) and Brunckhorst (1989b, 1990a,b) have also elucidated anatomical features of phyllidiid genera.

General Biology

Very little is known about the ecology or life history of phyllidiid nudibranchs. This is partly attributable to the rarity of finding large numbers of phyllidiids together, as well as the difficulties in making prolonged underwater observations and in keeping phyllidiids in aquaria.

Cattaneo (1982) commented on albinism in *Phyllidia* from a submarine cave habitat off the Gulf of Naples, Italy. Willan & Coleman (1984) reporting on four phyllidiids, suggested that these animals seem to prefer caves or the underside of ledges in the clear waters of reefs. However, several phyllidiid species have been observed to be active throughout daylight hours (Bertsch & Johnson, 1981; Johnson & Boucher, 1983; Johnson, 1989; Brunckhorst, 1991) and in Hawaii, Bertsch & Johnson (1981) observed *P. pustulosa* was usually the only nudibranch in areas of abundant live coral.

Few feeding observations have been reported, one of the few being Miller's (1969) record of *Phyllidia nobilis* feeding on a sponge in Fiji. Phyllidiid nudibranchs possess a small mouth (without radula or other buccal hard parts), oral glands and pharyngeal retractor muscles (Bergh, 1869, 1875; Eliot, 1903a; Ev. Marcus & Er. Marcus, 1967; Er. Marcus & Ev. Marcus, 1970; Wägele, 1985). They are now known to be suctorial predators of sponges (Barletta & Melone, 1976; Bertsch & Johnson, 1981; Schulte, 1982; Willan & Coleman, 1984; Macri, 1986). Burreson *et al.* (1975) observed *Phyllidia varicosa* feeding on a creamish sponge belonging to the genus *Hymeniacion*. Barletta & Melone (1976) observed *Phyllidia flava* (as *P. pulitzeri*) feeding on the sponge *Acanthella acuta* Picchetti. Macri (1986) reported *in situ* observations of the same species feeding on *Axinella cannabina* Esper. Macri (1986) also described the mating and egg laying of *P. flava*. Previously, Barletta (1974a) had described the egg laying of this species in captivity. The reproduction and development of *P. varicosa* (= *P. arabica* according to Yonow, 1986) has recently been described by Soliman (1986, 1987).

The ecology of phyllidiid symbionts has received little attention, although copepods belonging to the family Lichomolgidae have been observed attached to the gill leaflets of phyllidiids (Humes & Stock, 1973; Brunckhorst, 1985).

All *Phyllidia* species appear to have a characteristic odour and apparently none has any known predator (Bertsch & Johnson, 1981; Johnson, 1981; Brunckhorst, 1988, 1989a, 1991). Pease (1868) first remarked on the "foetid" smelling secretion of *Phyllidia nigra*. Thompson (1960a, 1960b) brought attention to the acidic secretions of many opisthobranchs, concluding that the position and function of "skin glands" which secrete these compounds, must be defensive in nature. Experiments with *P. varicosa* showed that, when disturbed, it secreted a poisonous mucous capable of killing fish and crustaceans in an aquarium (Johannes, 1963). Burreson *et al.* (1975) and Hagadone *et al.* (1979) described an allonome, 9-Isocyanopupukeanane and its 2-isomer, having a new sesquiterpene skeleton, from *P. varicosa* and its food. Their work demonstrated the molecular basis for the association between this nudibranch and its sponge prey, *Hymeniacion* sp. Schulte (1982) confirmed the isonitrile fraction which is attached to different terpenoid skeletons, is characteristic of the distasteful secretions of six species of *Phyllidia* from the Hawaiian Islands. Cimino *et al.* (1982, 1983) have also shown that the defensive secretions of *P. flava* contain biologically active compounds mainly derived from its sponge prey. These findings led Scheuer (1982: 528) to comment "...Relationships among biota on tropical coral reefs are frequently governed by chemical phenomena". Scheuer (1977, 1982) drew attention to the importance of chemistry or "chemical communication" in marine ecology. Gunthorpe & Cameron (1987) also described the toxic qualities of three *Phyllidia* species (*P. elegans*, *P. nobilis* and *P. ocellata*) from Queensland waters.

In their review, Faulkner & Ghiselin (1983) discussed the evolutionary implications of chemical defence in the ecology of dorid nudibranchs. They suggested that defence chemicals are present in *Phyllidia* and some other dorid nudibranchs, and have been developed over time as a result of adaptation. They also commented on the evolutionary pathways leading to aposematic (i.e., conspicuous and bright) colouration in distasteful dorid nudibranchs, with particular reference to *Phyllidia* species. I consider most contrastingly patterned phyllidiid species to be aposematic (Brunckhorst, 1988, 1989a, 1991). Brunckhorst (1989a) illustrated a dorid mimic of *P. pustulosa*. Edmunds (1987) and Gosliner & Behrens (1990) provide detailed discussions of the role of colour in opisthobranchs.

Nudibranchs belonging to the family Phyllidiidae have generally been found to be widespread in the tropical Indo-West Pacific Ocean (Baba, 1930; Risbec, 1928, 1953, 1956; Edmunds 1971, 1972; Lin, 1983; Willan & Coleman, 1984). *Phyllidia ocellata*, *P. varicosa* and *P. pustulosa* are well known examples which appear to be common throughout the tropical Indo-West Pacific and Red Sea zoogeographic regions (Edmunds, 1971, 1972; Baba & Hamatani, 1975; Wu & Romig, 1982; Lin, 1983; Yonow, 1984a, 1986).

Some species may be endemic to the Mediterranean Sea (Pruvot-Fol, 1951, 1956, 1962; Bouchet, 1983; Brunckhorst & Willan, 1989) and others to the Red Sea (Yonow, 1986). Phyllidiid nudibranchs appear in species lists, with distributional information, compiled by a number of authors (Ev. Marcus & Er. Marcus, 1967; Er. Marcus & Ev. Marcus, 1970; Edmunds, 1971, 1972; Baba & Hamatani, 1975; Ros, 1976b; Cattaneo & Barletta, 1984; Macri, 1986; Brunckhorst, 1989b). Records of Phyllidiidae from Australian waters can be found in Allan (1957), Kenny (1970), Burn (1975) (updated with additional records by Willan & Coleman, 1984), Wells & Slack-Smith (1986) and Brunckhorst (1989b, 1990a,b). Because of past taxonomic confusion, many such lists are unfortunately problematic resources in elucidating geographic distributions.

Currently, the genus *Phyllidiopsis* is known primarily from warm Atlantic waters (Bergh, 1890, 1892; Eliot, 1903a; Ros, 1976b; Ev. Marcus & Er. Marcus, 1962, 1967; Ev. Marcus, 1977; Meyer, 1977; Bouchet, 1977; Thompson, 1980), although a number of species are known from the Indo-West Pacific (Bergh, 1875; Eliot, 1904; Gosliner & Behrens, 1988; Brunckhorst, 1990b). I suggest that the Atlantic species should be placed in a separate genus (Brunckhorst, 1990b; this work).

The description by Bouchet (1983) of *Fryeria bayi*, apparently endemic to the Mediterranean Sea is of interest biogeographically, as *Fryeria* had been considered to be restricted to the Indo-West Pacific (Bergh, 1869, 1875; Edmunds, 1972). *Reticulidia* Brunckhorst (1990a) is currently known from the western Pacific and eastern Indian Oceans and *Ceratophyllidia* Eliot from East Africa and the western Indian Ocean. (Eliot, 1903a, 1910; Gosliner, 1987; Gosliner & Behrens, 1988).

Conclusions

It is clear that many previous descriptions of phyllidiid species have been either incomplete or inadequate. In the past, some new species descriptions have been based on external features, often of single, preserved specimens. There seem to be few defined characters which may assist in the delineation of genera and species. The large number of available names may partially be ascribed to these shortfalls in our knowledge of the Phyllidiidae.

This revision is based on the examination of as much material from around the world as was possible to procure. Very little material from the Atlantic Ocean was available and, therefore, no Atlantic species are redescribed. However, in the context of the present work, study of the original descriptions of the nominal Atlantic species and examination of the type of *Phyllidiopsis berghi* Vayssière, has enabled discussion of the taxonomic status of the group. With consideration given to all the examined material and through the study of the type species (and available type specimens) of each genus, the following account attempts to more adequately define generic characters. With the genera thus established, the species contained in each genus are then described. The species descriptions include a full synonymy, remarks on intraspecific variation, feeding and habitat. New species are also described. Species are compared across genera when external appearances are similar. Finally, phylogenetic considerations and some ecological observations arising from the present study are discussed.

Material and Methods

Collections. More than 1300 specimens of the Phyllidiidae were examined. Approximately half this number were collected by the author and are now deposited in the Australian Museum, Sydney. The remaining material stems, primarily, from the Australian Museum. Further records were provided by a number of friends and colleagues who generously provided specimens and/or colour slides of living animals. Collecting data, details of colour slides and observations on the live animals were entered into a custom designed database using Dbase III⁺ (Ashton Tate Inc., 1986) and these data are summarised at the beginning of each species description. Size of specimens is the crawling length of live specimens, however the size of old type specimens is the preserved length of the specimen. Live size is given in millimetres (mm) if known. Depth of collection is given in metres (m) if known. Abbreviations of locations are: PNG – Papua New Guinea; GBR – Great Barrier Reef, Australia; Qld – Queensland, Australia; WA – Western Australia; NT – Northern Territory, Australia; NSW – New South Wales, Australia. Abbreviations of collectors: DJB – D.J. Brunckhorst; SKB – S.K. Brunckhorst; RCW – R.C. Willan; Carlson-

Hoff – C. Carlson & P.J. Hoff. Other collectors names are given in full. Registration numbers of specimens conserved in museums are included. The following abbreviations are used to denote these Institutions: AM – Australian Museum, Sydney; BMNH – British Museum (Natural History), London; CASIZ – California Academy of Science, San Francisco; MNHN – Muséum National d'Histoire Naturelle, Paris; MV – Museum of Victoria, Melbourne; NTM – Northern Territory Museum, Darwin; USNM – National Museum of Natural History, Smithsonian Institution, Washington D.C.; WAM – Western Australian Museum, Perth; ZMA – Zoölogische Museum, Instituut voor Taxonomische Zoölogy, Universitat van Amsterdam, Netherlands; ZMUC – Zoologisk Museum, København, Denmark. Biogeographic information was collated from the database records and past literature.

The majority of specimens were collected by the author on SCUBA. A small number were found intertidally on reef flats. Specimens were photographed alive, then frozen prior to fixation in 10% seawater, buffered formalin. The foregut and notum of some specimens that had been fixed in Bouin's fluid were sectioned and stained for light microscopy. Staining techniques which were used include; Mayer's haematoxylin-eosin, periodic acid-Schiff (PAS), and alcian blue-kernechtrot (after Luna, 1968; Culling, 1974).

Morphological preparations. Details of external morphology were described from live specimens and photographs of live specimens. Usually, more than ten specimens of each species were dissected (and in some cases, more than 80). Descriptions of internal anatomy refer to preserved specimens. Anatomical features were examined under binocular dissecting microscope and drawings were made with the aid of a camera lucida. Particular attention was given to the alimentary and reproductive systems. Portions of the foregut, notum and gills were prepared (by ultrasonic cleaning, alcohol dehydration, critical point drying, stub mounting and sputter coating) for scanning electron microscopy (SEM). Attempts were made to isolate the armed region of the ejaculatory duct (penis) for SEM studies (alcohol dehydration and air drying before coating). In most cases the distal vas deferens, penial sheath and/or genital aperture had to be cut and the partially everted portion of the penis extracted by hydrostatic pressure or mechanically with fine needles. If the penis was inverted when the animal was preserved, the duct was split open to reveal the penial spines. All photographs, Scanning Electron Micrographs (SEM) and drawings are by the author unless otherwise acknowledged.

Ecology. Ecological observations stem from my field work in southern Papua New Guinea, Guam, southern Thailand and on the Great Barrier Reef, Australia. Additional data were made available by friends or colleagues or were collated from collecting information pertaining to museum specimens. Dr John Hooper (NTM) identified the sponges.

Terminology. Some specific terminology, especially that concerned with the foregut anatomy, are defined here. Some other characteristics of nudibranchs well known from the molluscan literature are not included.

- Foot* – entire ventral locomotory structure including its muscular tissue, nerves and secretory structures.
- Glandular discs* – firm, glandular discs inside the pharyngeal bulb of *Reticulidia* (after Brunckhorst, 1990a).
- Glandular segment of oesophagus* – swollen glandular, posterior part of oesophagus (*Ceratophyllidia* only; see Gosliner & Behrens, 1988; Brunckhorst, 1990b).
- Hyponotum* – surface of underside (ventral) of mantle skirt.
- Mantle* – includes entire dorsal tissue covering (i.e., of notum + hyponotum).
- Notum* – dorsum; dorsal surface of mantle.
- Oesophagus* – foregut tube posterior from the buccal ganglia and leading into the stomach and/or digestive gland mass (after Eliot, 1906; Young, 1969).
- Oesophageal pump* – bulbous, muscular portion of posterior oesophagus (*Phyllidiopsis* only; after Brunckhorst, 1990b).
- Oral tube* – here considered as the anterior most cylindrical tube leading anteriorly from the pharyngeal bulb to the mouth (after Brunckhorst, 1989b, 1990a,b).
- Papillae* – soft “pear-shaped” or mushroom shaped, detachable protuberances of *Ceratophyllidia* (after Eliot, 1903a; Gosliner, 1987; Gosliner & Behrens, 1988).
- Pharyngeal bulb* – swollen, bulbous portion of pharynx (Brunckhorst, 1989b, 1990a,b; possibly homologous to a modified posterior oral tube but not the buccal bulb of radula bearing dorids), usually with muscular, folded tissue wall and possessing oral glands and well-developed retractor muscles (after “bulbus pharyngeus” Bergh, 1869).
- Rhinotubercle* – single tubercle closely associated with each rhinophore; if present one occurs immediately posterior to each rhinophoral pocket (after “rhinophore knoten”, Bergh, 1869, 1889).
- Side of foot* – lateral side of foot below gills, but not in contact with substrate.
- Sole* – flat, ventral part of foot in contact with substrate.
- Sole margin* – outermost edge of foot.
- Tubular pharynx* – cylindrical foregut tube from pharyngeal bulb to buccal ganglia (i.e., anterior from buccal ganglia; after Eliot, 1906; Young, 1969; Brunckhorst, 1990b).
- Tubercle* – tubercles are the hard irregular protuberances of the notum, supported by calcareous, and perhaps (?) chitinous or siliceous spicules (Figs 1, 2D,E).

Species accounts. Complete descriptions of all generic characters and anatomy is given in Review of the Genera (below). Only those features which are specifically distinct or indicate some departure from the described generic characters are included in the

species descriptions. A discussion of any new synonymies follows the synonymy list for each species.

Phyllidiidae Rafinesque, 1814

Type genus. *Phyllidia* Cuvier, 1797.

Review of the Genera: Description of Morphology, Anatomy and Histology

The generic definitions presented here are based on the type species of each genus, but they also take into account all of the species that I have studied. Detailed descriptions of anatomy and morphology are given prior to the reappraisal of specific taxa. Some species display variation in external colour and pattern, but internal anatomical features within genera and species appear to be relatively constant. The characters used in the present study include: general shape and body profile; colour and pattern; morphology of notal tubercles, ridges and the mantle margin; rhinophoral colour; number of lamellae on each rhinophoral clavus; morphology of foot and foot sole; gills; oral tentacles; foregut anatomy; anatomy of midgut and hindgut; anatomy of reproductive system; penial spine morphology; sperm ultrastructure.

Six genera are recognised – *Phyllidia* Cuvier, *Fryeria* Gray, *Phyllidiella* Bergh, *Phyllidiopsis* Bergh, *Ceratophyllidia* Eliot and *Reticulidia* Brunckhorst.

General features. Members of the family Phyllidiidae are tough bodied and generally possess hard notal tubercles (Figs 1, 2D). They are usually adorned in contrasting colours and patterns. Phyllidiids are “dorid-like” nudibranchs in their oval to elongate bodies, retractile lamellate rhinophores (Fig.2A), compact digestive gland mass and triaulic reproductive system. The Phyllidiidae have no jaws or radula and lack the dorsal, circumanal floret of gills which are typical of other dorids. The secondary gills of all phyllidiid nudibranchs are flat and triangular in shape, the longest edge being attached at right angles across the groove which occurs ventrolaterally between the mantle and the foot (Fig.2B). The opposite corner to the attached edge is rounded (Fig.2C). Large and small gill leaflets alternate in a series (from 70 - 150 leaflets) around the entire ventrolateral groove. The gills are interrupted by the mouth, anteriorly, and the reproductive openings on the right hand side (and in *Fryeria* by the anal opening). A posterior, median, dorsal anus is present in all members of the Phyllidiidae except for *Fryeria* (posteroventral). The mantle skirt covers the foot. The oral tentacles usually possess a ventrolateral groove.

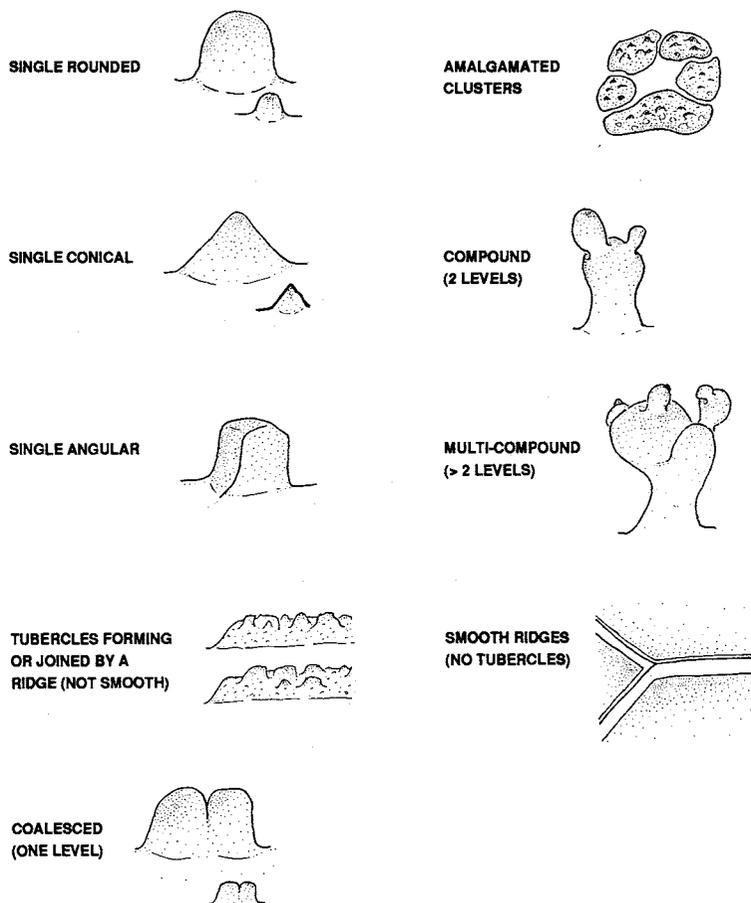


Fig.1. Diagrammatic representations of tubercle morphology and terminology used in this work.

In general shape, phyllidiids tend to be more oval than elongate. The body wall, mantle and foot are highly spiculate. There appear to be two spicule types, calcareous (observed to dissolve in the acidic Bouins Fluid) and siliceous (or ?chitinous; do not dissolve in Bouins; personal observation).

The foregut is highly modified for suctorial feeding on sponges. The posterior portion of the oral tube is expanded into a muscular bulbous region (here termed pharyngeal bulb, see Brunckhorst 1989b, 1990a,b). Two robust retractor muscles insert (either dorsally or posteriorly) onto the pharyngeal bulb and originate from the dorsolateral body wall. Multiple oral glands are associated with the pharyngeal bulb.

The reproductive system of phyllidiids corresponds to the triaulic condition (with 2 allosperm receptacles - bursa copulatrix and receptaculum seminis) of some other doridoids (e.g., chromodorids, see Rudman, 1984).

The vaginal duct of phyllidiids has a common vestibule with the ejaculatory duct. The genital vestibule is lined with folded epithelium which forms longitudinal ridges and canals. Penial spines are usually present in the distal portion of the ejaculatory duct which is eversible. The sperm nucleus of phyllidiids is elongate whereas that of other dorids is short (Healy, personal communication, 1989-1990).

Phyllidia Cuvier, 1797

Phyllidia Cuvier, 1797.-Lamarck, 1801.-Cuvier, 1804a,b.-Gray, 1847, 1853.-Bergh, 1869, 1875, 1892.-Eliot, 1903b, 1904.-Pruvot-Fol, 1956, 1957a.-Er. Marcus & Ev. Marcus, 1970.

Phyllidium Montagu, 1815 (mis-spelling).

Phyllidea Swainson, 1840 (mis-spelling).

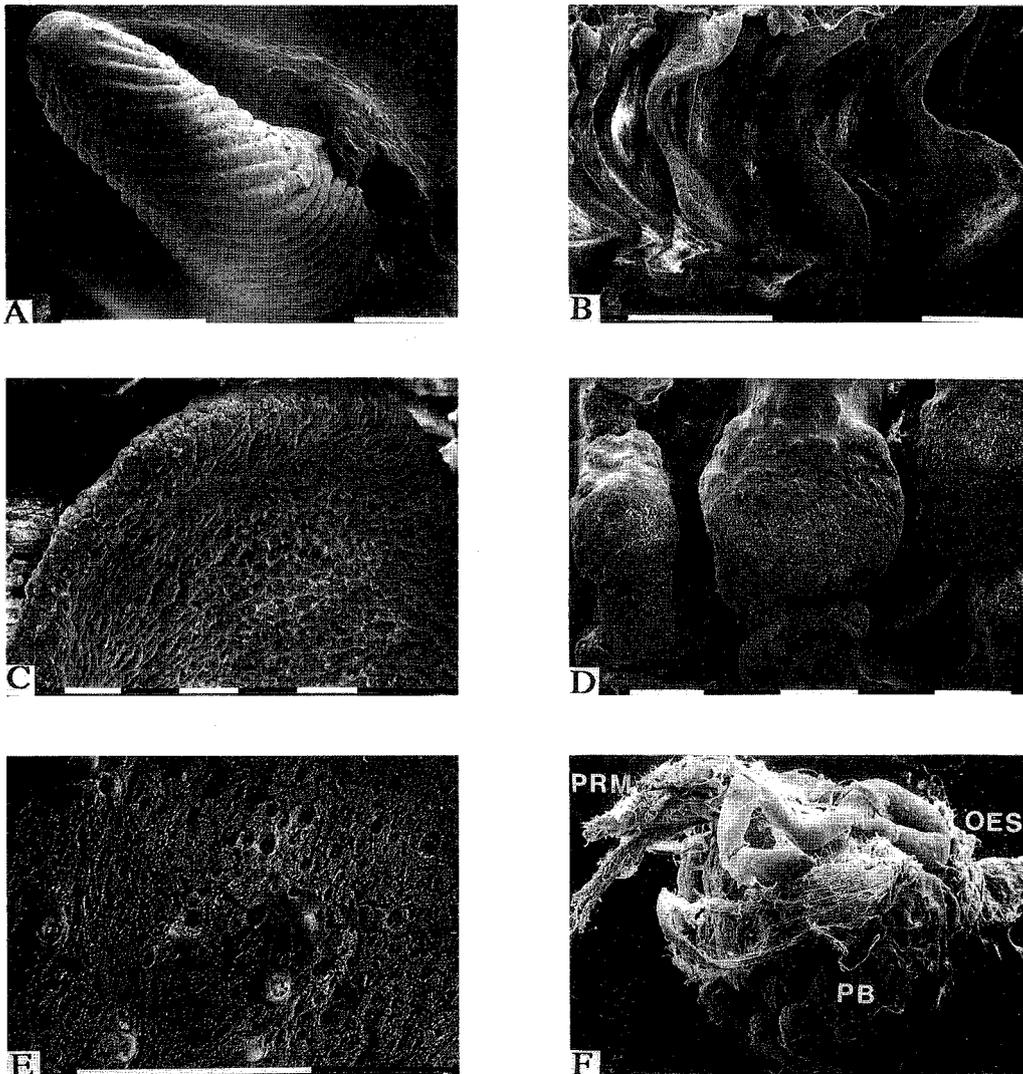


Fig.2. *Phyllidia varicosa*. Scanning Electron Microscope (SEM) photographs showing: A, lamellate rhinophore; B, ventrolateral gill leaflets; C, rounded edge of one gill leaflet; D, tubercles on the median ridges; E, surface of central tubercle (in D) showing spicules and pores; F, foregut region. Abbreviations: OES, oesophagus; PB, pharyngeal bulb; PRM, pharyngeal retractor muscle. A,B,D,F scale = 1 mm; C,E scale = 0.1 mm.

Type species. *Phyllidia varicosa* Lamarck, 1801, by subsequent designation.

External morphology. Species of *Phyllidia* are medium to large, oval-shaped phyllidiids, generally possessing large tubercles on the dorsum (Fig.2D,E). The tubercles may form, or be joined by, longitudinal ridges. Small species usually possess a large number of smaller, simple notal tubercles. Rhinotubercles are present. The rhinophore colour is cream to gold-yellow. The number of lamellae on the rhinophore clavus varies ontogenetically but appears to be a useful specific character in mature specimens (see Fig.3A). The foot sole may possess a longitudinal black stripe. The oral tentacles are separate, finger like protuberances. A groove is present on the ventrolateral surface of each oral tentacle. The mantle margin is broad, entirely

covering the foot. The anus is dorsal and median in position.

Anatomy (Figs 2F, 4, 5). The visceral envelope is a dark grey-black sheet. The mouth leads into a short narrow oral tube which passes into a swollen, musculoglandular pharyngeal bulb. Inside the pharyngeal bulb there is a thick, folded, glandular epithelium having firm cream coloured glandular bodies which often protrude posteroventrally (Figs 2F, 4). These glands correspond with Bergh's (1869, 1905) "short, fingered swellings". They were also figured by Edmunds (1972) as "raised glands" and "glandular knobs". The length of the pharyngeal bulb is equal to its breadth. Two large extrinsic retractor muscles insert posterodorsally onto the pharyngeal bulb and originate from the dorsolateral body wall about one quarter to one third of the length down

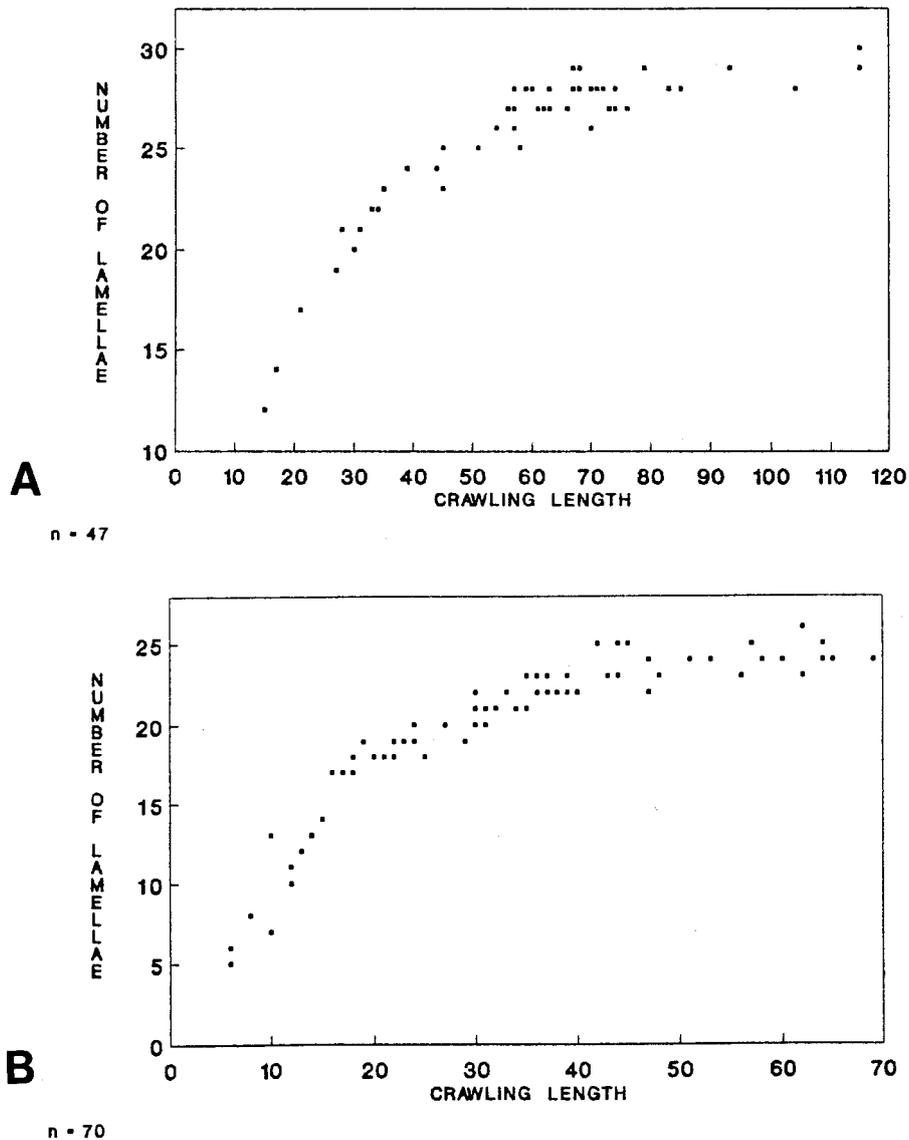


Fig.3. Comparison of number of lamellae on rhinophore clavus in relation to crawling length of specimen: A, *Phyllidia varicosa*; B, *Phyllidiella pustulosa*.

the body. A short, narrow tubular pharynx leaves the pharyngeal bulb posterodorsally. The pharynx narrows slightly and forms a distinctive "S" bend through the central nerve ring. The buccal ganglia occur on the ventrolateral surface of the pharynx, immediately posterior to the central nerve ring (Figs 4, 5). From there, the oesophagus continues back into a large compact digestive gland mass which occupies about two thirds of the body cavity. The tubular pharynx is about twice the length of the oesophagus. There is no distinct separation into a stomach region within the digestive gland mass. Over a length of up to 6 mm the alimentary canal broadens slightly into a thin walled tract. There are several fragile openings into this tract from the surrounding digestive gland (Wägele, 1985; Brunckhorst, 1989b; personal observation). The intestine originates dorsally from the posterior half of the digestive gland mass and passes forward before turning to the right, almost encircling the pericardium, and then straightening to run posteriorly down the right side to open mid-dorsally via the anal papilla (Fig.5).

Sectioned material from the foregut of *Phyllidia varicosa*, *P. coelestis*, *P. elegans* and *P. ocellata* gave positive indications for the staining technique using alcian blue. The folded oral glands (within the pharyngeal bulb) stained blue indicating the presence of weakly acidic, sulphated mucosubstances (OSO₃H groups), and purple, indicating the presence of strongly

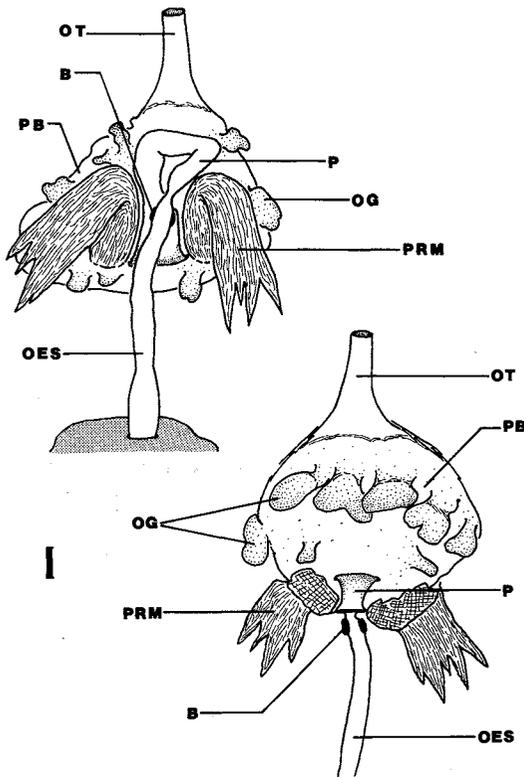


Fig.4. *Phyllidia varicosa*. Generalised dorsal view (upper) and ventral view (lower) of foregut showing glandular bodies partly protruding from pharyngeal bulb. Abbreviations: B, buccal ganglia; OES, oesophagus; OG, oral gland; OT, oral tube; P, pharynx; PB, pharyngeal bulb; PRM, pharyngeal retractor muscle. Scale = 1 mm.

acidic, sulphated mucosubstances (Luna, 1968; Culling, 1974).

The blood gland overlies the oesophagus, central nerve ring and reproductive organs. The excretory system was not completely traced although the position of the renal syrinx is indicated in Figure 5. The renal syrinx links the pericardium with the digestive gland. In some specimens, part of the nephridium was visible beneath the syrinx and intestine.

Reproductive system (Fig.6). In *Phyllidia*, as in all phyllidiids, the ovotestis overlies the anterior portion of the digestive glands. The remainder of the reproductive system occurs in the space between the pharyngeal bulb (anteriorly) and the digestive gland mass (posteriorly) and opens laterally between the mantle and foot on the right side (Fig.5). From the ovotestis the hermaphrodite duct expands into a spherical ampulla. The ampulla is the same size or slightly smaller than the bursa copulatrix

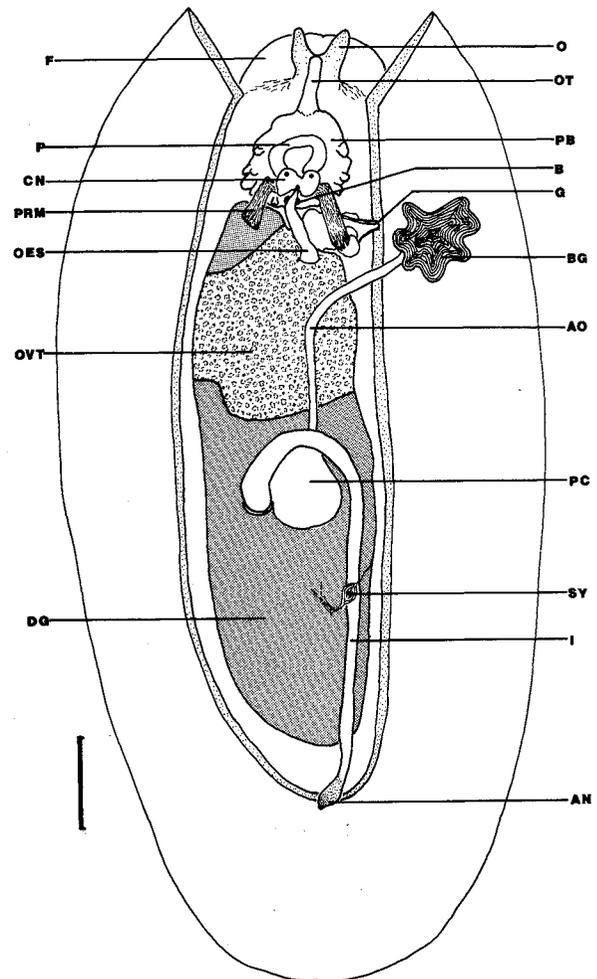


Fig.5. *Phyllidia varicosa*. Generalised dorsal view of anatomy. Abbreviations: AN, anus; AO, aorta; B, buccal ganglia; BG, blood gland; CN, central nerve ring; DG, digestive gland mass; F, foot; G, reproductive openings; I, intestine; O, oral tentacles; OES, oesophagus; OT, anterior oral tube; OVT, ovotestis; P, pharynx; PB, pharyngeal bulb; PRM, pharyngeal retractor muscle; PC, pericardium; SY, syrinx. Scale = 5 mm.

and receptaculum seminis. The prostate (prostatic section of the vas deferens) and oviduct separate immediately at their common departure point from the ampulla (Fig.6). The oviduct is thin walled and convoluted. The prostate is only slightly convoluted and narrows distally into a short vas deferens. The penis is large and bulbous. It is eversible, the distal end possessing rows of spines. In side view, the penial spines have a broad base, are recurved and taper to a fine point. The nidamental gland mass is very large and spherical. The bursa copulatrix and receptaculum seminis are large, rounded, and of equal size (Fig.6). The vaginal duct divides at the base of the bursa (i.e., the bursa has no stalk). Distally, the vaginal duct enters a common vestibule with the penis. The genital aperture is lined with longitudinal ridges of folded epithelium, possibly matching the rows of penial spines.

Remarks. The genus *Phyllidia* Cuvier is distinguishable by a suite of internal and external characters. Externally it has large notal tubercles, cream to gold rhinophores, dorsal anus and two separate digitate oral tentacles. Some features of the reproductive system are characteristic (see Table 2). In particular, the short vas deferens and bulbous ejaculatory duct (penis). The most diagnostic anatomical feature is the morphology of the pharyngeal bulb and its internal "cauliflower-like", firm oral glands which often protrude posteriorly and ventrally from the bulb (Figs 2F, 4). A summary of the proportions of foregut parts is given in Table 1.

With reference to the foregut of *Phyllidia*, Bergh's (1869: 499) "Bulbus pharyngeus symmetricus" requires clarification. The general shape and layout of the foregut is, very approximately, symmetrical. Even when the foregut is retracted, there is no great divergence from

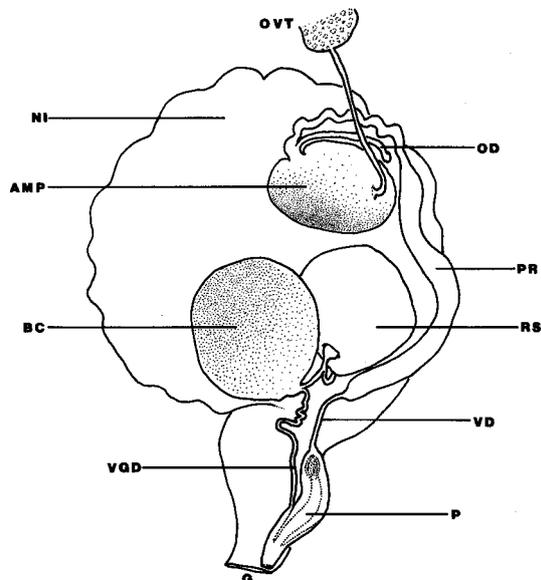


Fig.6. *Phyllidia varicosa*. Reproductive system. Abbreviations: AMP, ampulla; BC, bursa copulatrix; G, reproductive openings; NI, nidamental glands; OD, oviduct; OVT, ovotestis; P, penis; PR, prostatic vas deferens; RS, receptaculum seminis; VD, vas deferens; VGD, vaginal duct. Scale = 1 mm.

this "general symmetry". Bergh (1869) contrasted this with the situation in *Phyllidiella* where the folding of the foregut appeared to result in an "asymmetry" in the general shape of the foregut (in particular, the folding to the left of the pharynx). Although observable in some specimens, I concur with Er. Marcus & Ev. Marcus (1970) in considering foregut symmetry an unreliable feature and therefore little taxonomic weight is given to it in the present work.

There has been confusion over the identity of the type species, *Phyllidia varicosa* Lamarck (see Yonow, 1986). A full discussion of this species is given in the following chapter and, because the holotype cannot be traced, a neotype is designated. This step is necessary to ensure the nomenclatural stability of this species as the primary type for the family Phyllidiidae.

There are 15 species in the genus *Phyllidia*.

Fryeria Gray, 1853

Fryeria Gray, 1853.—Bergh, 1869, 1875, 1889, 1892.—Eliot, 1903b, 1904.—Pruvot-Fol, 1957a.—Er. Marcus & Ev. Marcus, 1970.—Edmunds, 1972.—Bouchet, 1983.—Brunckhorst *et al.*, 1989.—Opinion 1663.

Reyfriedia Yonow, 1986.—García-Gomez, 1987.—Gosliner & Behrens, 1988.—Yonow, 1988.—Yonow & Hayward, 1991.

Type species. *Fryeria rueppelii* Bergh, 1869, by monotypy (Brunckhorst *et al.*, 1989; Opinion 1663).

External morphology. Species of *Fryeria* are medium-sized phyllidiids, oval in shape and possessing a broad mantle skirt. Large tubercles are single, rounded and often yellow capped. Between the tubercles, medially, there may be low longitudinal ridges. In the absence of large tubercles, the dorsum is rough with many tiny spiculate bumps. Rhinotubercles are present. The rhinophores are generally creamish to yellow in colour. As in *Phyllidia*, the number of lamellae on the rhinophoral clavus appears to be constant (within a narrow range) for each species. Two separate, short, conical oral tentacles occur ventrally at the mouth. The oral tentacles bear lateral grooves. The gill series is interrupted by the anal opening at a posterior, ventral position. The anus or rectum is protrusible (Bergh, 1875, pl.16, fig.8; personal observation, 1988, 1989). There are no distinctive markings on the foot sole.

Anatomy (Figs 7, 8, 9A). There is a dark visceral envelope. Anteriorly, a long oral tube leads from the mouth into the pharyngeal bulb. The pharyngeal bulb has the same form as *Phyllidia*, but it is smaller and broader, its breadth being about one and a half times its length. Firm, cream coloured glandular bodies occur within the pharyngeal bulb. These oral glands protrude posteriorly from the bulb (Fig.9A) and were figured by Bergh (1875, pl.16, fig.5). Two large extrinsic retractor muscles insert posterodorsally onto the pharyngeal bulb, one on either side of the tubular pharynx (Fig.7). These

muscles originate from the dorsolateral body wall one quarter to one third of the length down the body. A short, tubular pharynx arises posterodorsally from the pharyngeal bulb and curves up in the usual "S" bend, narrowing slightly as it passes through the central nerve ring. The buccal ganglia occur on the ventrolateral surface of the pharynx immediately posterior to the central nerve ring. The oesophagus is longer than the pharynx (Table 2) and leads posteriorly into the digestive gland mass. Within the compact digestive glands there are many openings to the alimentary tract, but there is no distinct stomach region. The intestine originates dorsally from the posterior half of the digestive gland mass and passes to the right around the pericardium before running posteriorly along the right, ventrolateral side of the digestive glands (Fig.7). The anus opens ventrally and the protrusible rectum possesses short retractor muscles which originate from the body wall around the anal opening.

The aorta runs forward from the median placed heart. A blood gland overlies the region of the pharynx and central nervous system (Fig.7).

Reproductive system (Fig.8). The reproductive

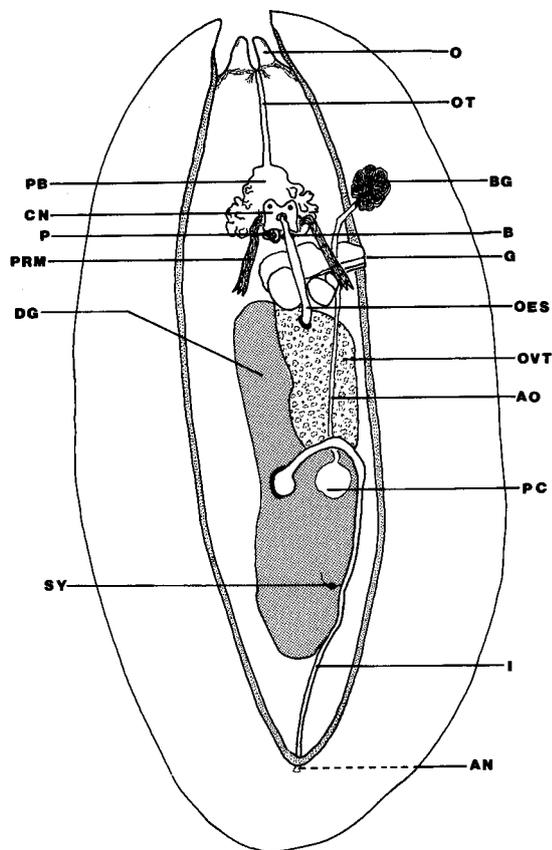


Fig.7. *Fryeria rueppelii*. Generalised dorsal view of anatomy. Abbreviations: AN, anus; AO, aorta; B, buccal ganglia; BG, blood gland; CN, central nerve ring; DG, digestive gland mass; G, reproductive openings; I, intestine; O, oral tentacles; OES, oesophagus; OT, anterior oral tube; OVT, ovotestis; P, pharynx; PB, pharyngeal bulb; PC, pericardium; PRM, pharyngeal retractor muscle; SY, syrxinx. Scale = 5 mm.

system is situated in the space between the pharyngeal bulb and the digestive gland mass, and opens laterally between mantle and foot on the right side (Fig.7). The ovotestis overlies the anterior part of the digestive glands. A hermaphrodite duct leads from the ovotestis to a very large ampulla (3 times the size of the bursa copulatrix; Fig.8). The prostate (prostatic vas deferens) and oviduct separate from a common opening at the base of the ampulla. The prostate is broad and relatively straight (i.e., not convoluted). It narrows distally into the long vas deferens, before expanding slightly into the muscular ejaculatory duct. The penis is short and straight. Rows of recurved spines are present at the distal end of the penis.

From the ampulla, the short, narrow oviduct passes into the spherical nidamental gland mass. The elongate ovate bursa copulatrix is darker than the more rounded receptaculum seminis. The bursa has a short, broad extension from its base where the vaginal duct divides (but is not stalked as in *Ceratophyllidia*; Fig.18). Distally, the vaginal duct enters a contiguous aperture with the penis.

Remarks. The genus *Fryeria* has been diagnosed on the basis of its most easily observed external feature, a ventral anus. A few workers have questioned the validity of the genus because it seemed to be based on this single, possibly variable character (Gosliner & Behrens, 1988; Burn, personal communication, 1987). Indeed Gosliner & Behrens (1988) had one specimen of *Phyllidiopsis blanca* with a ventrally placed anus. This individual also seems to have been unusual in other respects and of the many specimens of *P. blanca* which have subsequently been examined, none has had a ventral anus (Gosliner, personal communication, 1989). Nevertheless, these observations are valuable, and when

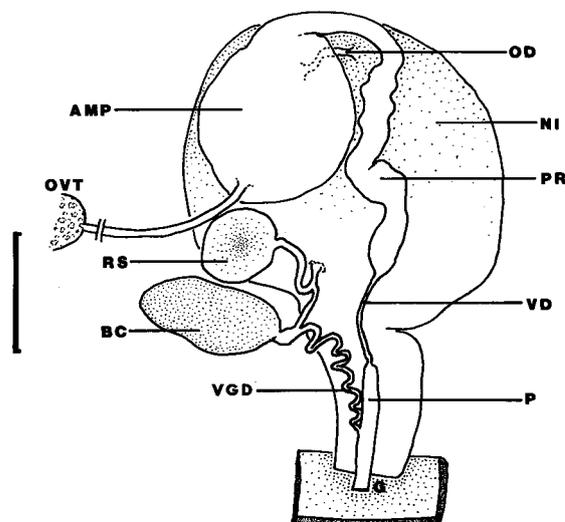


Fig.8. *Fryeria rueppelii*. Reproductive system. Abbreviations: AMP, ampulla; BC, bursa copulatrix; G, reproductive openings; NI, nidamental glands; OD, oviduct; OVT, ovotestis; P, penis; PR, prostatic vas deferens; RS, receptaculum seminis; VD, vas deferens; VGD, vaginal duct. Scale = 1 mm.

further such ?mutant individuals of any taxa become available, insights into the phylogeny of this group may be gained.

The present study supports *Fryeria* as a valid genus in its possession of a number of distinct features. The morphology of the pharyngeal bulb and associated glands are similar to *Phyllidia*. However, in *Fryeria* the pharyngeal bulb is smaller and broader, the oral tube longer, the pharynx shorter, and the oesophagus longer when compared to *Phyllidia* (Table 1). The oral glands of *Fryeria* appear to be concentrated posterodorsally (Fig.9A), rather than ventrally in the pharyngeal bulb (see also Bergh, 1875). The intestine of *Fryeria* runs ventrolaterally (not dorsally across the digestive glands). The ventral anus is protrusible. The rectum has retractor muscles associated with it. There are also differences in the reproductive system, in particular the very large ampulla and short straight penis in *Fryeria* (Table 2). These features appear to be consistent in the species I have studied.

Recently there has been confusion over the application of the name *Fryeria* Gray for this genus. The following account is summarised from Brunckhorst *et al.* (1989). Yonow (1986) wrongly considered that Gray had designated *P. pustulosa* Cuvier as the type species, and therefore considered *Fryeria* to be a junior synonym of *Phyllidia*. Yunow introduced *Reyfriedia* [with "type species *R. ruppelii* (Bergh, 1869)"] as a replacement name for *Fryeria* (Yonow, 1986: 1418). Brunckhorst *et al.* (1989) have now shown that Gray (1853) intentionally used the specimens misidentified by Ruppell & Leuckart

(1830 or 1831) as "*Phyllidia pustulosa* (Cuv.)" as the basis for his new genus, *Fryeria*, because they had a ventral anus (ICZN, 1985, Art.11, Deliberate use of Misidentification). Their specimens differed in external morphology from *P. pustulosa* Cuvier, 1804 (Ruppell & Leuckart, 1830 or 1831: 36, pl.11, fig.1a,b; Brunckhorst *et al.*, 1989). Gray (1853:221) listed only one species, *pustulosa* Ruppell & Leuckart, in his new genus *Fryeria*. Therefore *Fryeria pustulosa* Gray, 1853 is the type species by indication (type by monotypy) (ICZN, 1985, Art.68d). Bergh (1869) recognised, however, that Gray's action meant there were two phyllidiids with the same specific epithet, and introduced *Fryeria ruppelii* as a replacement name for both *Phyllidia pustulosa* Ruppell & Leuckart and *Fryeria pustulosa* Gray to differentiate that taxon from *Phyllidia pustulosa* Cuvier. Although Bergh's replacement name has no validity under the Code, it has received wide acceptance in the literature over the past century (Brunckhorst *et al.*, 1989; Brunckhorst & Rudman, 1990). We recommended that previous type fixations for *Fryeria* Gray be set aside by the Commission and the specific name *pustulosa* Gray, 1853 (as published in the binomen *Fryeria pustulosa*) be suppressed. Brunckhorst *et al.* (1989) and Brunckhorst & Rudman (1990) further argued that for nomenclatural stability and to prevent similar confusion in the future, the currently accepted name, *Fryeria ruppelii* Bergh, 1869 be placed on the Official List of Specific Names in Zoology under the corrected spelling *rueppelii*, as the specific name for the type species of *Fryeria* Gray, 1853. *Reyfriedia* Yonow is a synonym of *Fryeria* Gray. This

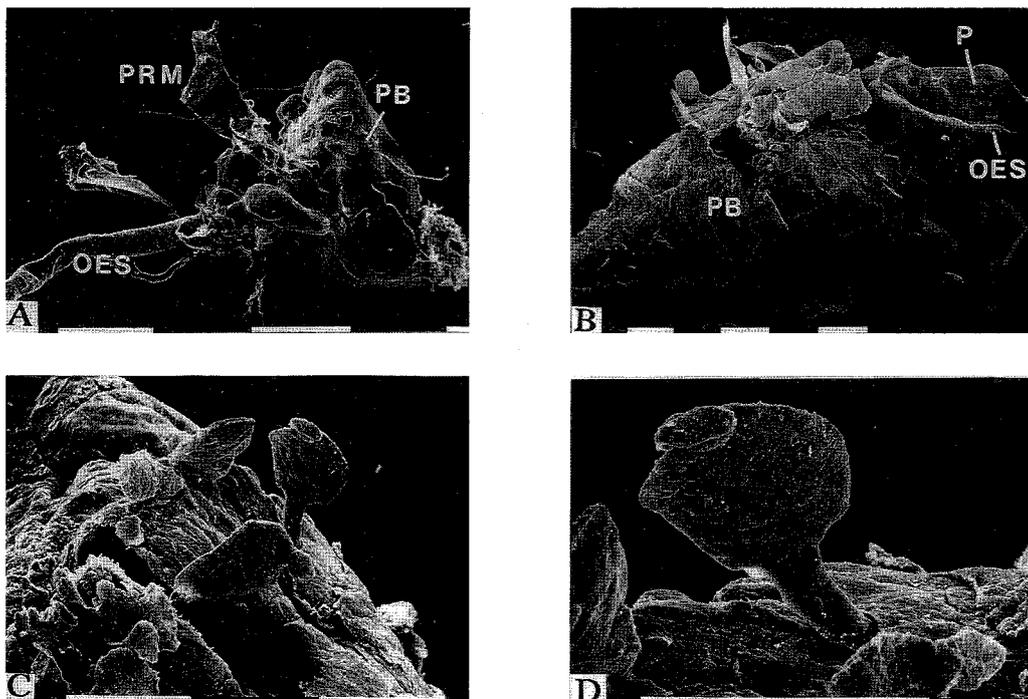


Fig.9. Scanning Electron Micrographs (SEM) of characteristic features of the foregut, prepared using critical point drying technique: A, *Fryeria rueppelii*, lateral view of foregut. Abbreviations: PB, pharyngeal bulb, PRM, pharyngeal retractor muscles, OES, oesophagus; B, *Phyllidiella pustulosa*, lateral view of foregut. Abbreviations: PB, pharyngeal bulb covered by oral glands, P, pharynx, OES, oesophagus; C,D, *Phyllidiella pustulosa*, individual oral glands showing duct entering pharyngeal bulb. Scale = 1 mm.

conclusion was endorsed by the ruling of the International Commission in Opinion 1663 (1992).

I concur with Edmunds (1972) in considering *Fryeria* to contain a number of Indo-West Pacific species and in the present work I recognise six species.

Phyllidiella Bergh, 1869

Phyllidiella Bergh, 1869.—Bergh, 1875, 1892, 1905.—Eliot, 1903b, 1904.—Er. Marcus, 1965.—Er. Marcus & Ev. Marcus, 1970.—Burn, 1970.

Type species. *Phyllidia pustulosa* Cuvier, 1804, here designated.

External morphology. Species of *Phyllidiella* are medium sized, generally oval shaped phyllidiids. Form and arrangement of notal tubercles is variable. Tubercles may be single, compound, coalesced into groups, or amalgamated into ridges. The colours of the dorsum generally include black and pink. Yellow pigmentation is absent in living specimens. The anal opening is dorsal and median in position. The rhinophores are predominantly black, but some species may possess a second colour (white to

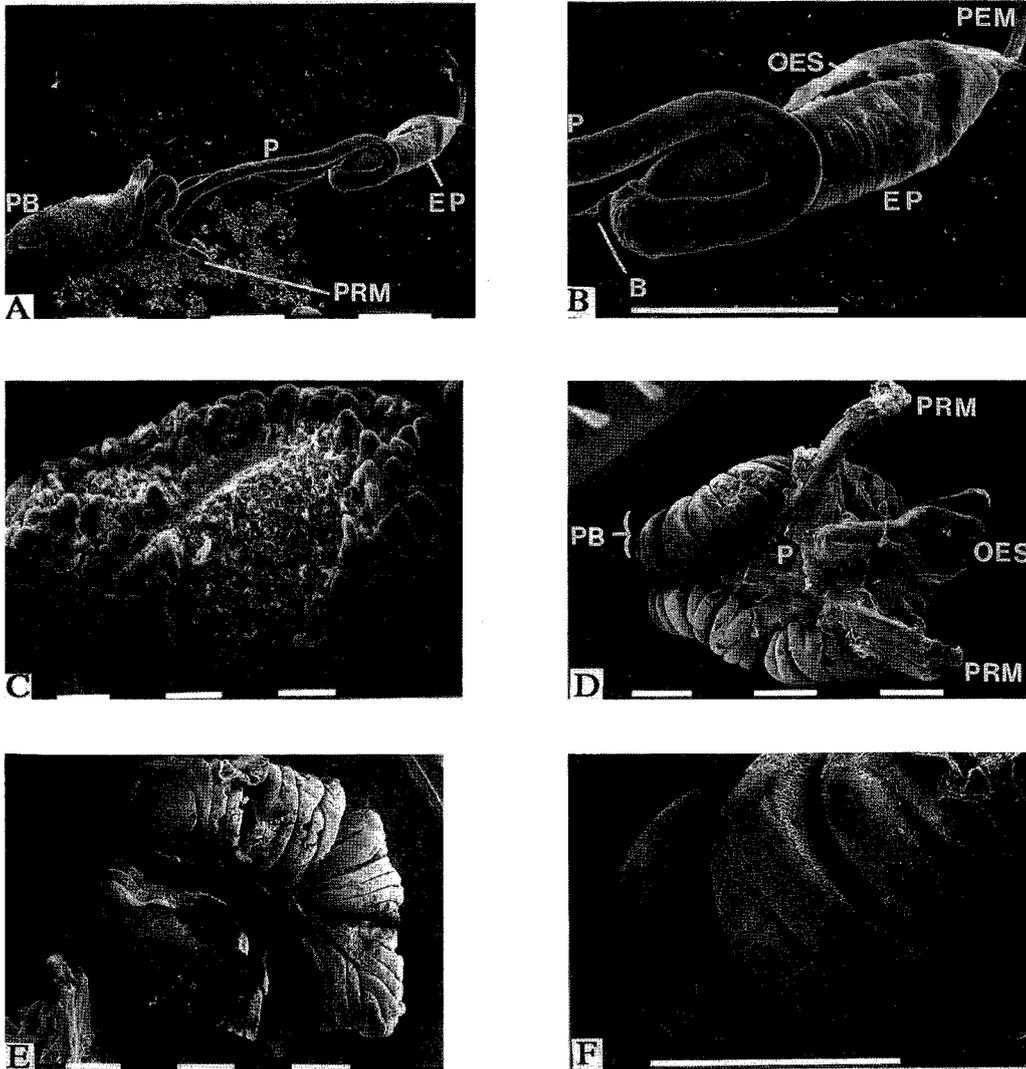


Fig.10. Scanning Electron Micrographs (SEM) of characteristic features of the foregut, prepared using critical point drying technique: A, *Phyllidiopsis cardinalis*, dorsolateral view of foregut. Abbreviations: EP, muscular oesophageal segment, P, tubular pharynx, PB, pharyngeal bulb, PRM, pharyngeal retractor muscles; B, *Phyllidiopsis cardinalis*, muscular oesophageal segment. Abbreviations: B, buccal ganglia, EP, muscular oesophageal segment, P, tubular pharynx, PEM, posterior oesophageal retractor muscle, OES, oesophagus; C, *Phyllidiopsis cardinalis*, pharyngeal bulb showing enveloping, minute oral glands (scraped away in centre); D, *Reticulidia halgerda*, dorsal view of foregut. Abbreviations: P, pharynx, PB, pharyngeal bulb (tissue envelope removed), PRM, pharyngeal retractor muscle, OES, oesophagus; E, *Reticulidia halgerda*, ventral view of pharyngeal bulb (slightly damaged) showing glandular discs; F, *Reticulidia halgerda*, glandular discs. A,B,D,E,F scale = 1 mm; C scale = 0.1 mm.

pink) towards the base of the rhinophore. The number of lamellae on the rhinophoral clavus varies ontogenetically but appears to be a useful specific character in mature specimens (Fig.7b). Rhinotubercles are absent. The foot is whitish to grey in colour and the sole lacks distinctive markings. The oral tentacles are separate, they have a broad base and are triangular in shape. Each oral tentacle possesses a ventrolateral groove.

Anatomy (Figs 9B-D, 11-14). The visceral envelope is pitch black in colour. A second black envelope or sheet occurs around the anterior part of the pharyngeal bulb. The oral tube is of moderate length (i.e., longer than in *Phyllidia*, but shorter than in *Fryeria* or *Phyllidiopsis*), and it gradually dilates into a large,

elongate, folded, muscular pharyngeal bulb. The length of the pharyngeal bulb is at least twice its breadth. A huge mass of pale pink to white oral glands overlies the pharyngeal bulb (Figs 9B, 11, 12). Individual glands are soft, flattened and leaf-like in shape (Figs 9C-D, 12). These glands are "free" from the pharyngeal bulb, in that their only connection is via a narrow duct (Fig.9D) (i.e., the glands are not internal or closely attached to the pharyngeal bulb). Two long retractor muscles insert onto the pharyngeal bulb posterolaterally and originate from the dorsal body wall at least half way down the body length. The initially broad, thick pharynx leaves the pharyngeal bulb posteriorly. The long pharynx commonly loops to the left before twisting to the right where it narrows into a more tubular form (Figs 11, 12), and then passes to the central nerve ring [This may be the "asymmetry" to which Bergh (1869, 1875, 1892) referred]. Anteriorly, the pharynx passes upwards through the central nerve ring. The buccal ganglia are situated on the ventrolateral surface of the distal part of the pharynx. The narrow oesophagus leads posteriorly into the digestive gland mass where there is no distinct stomach region. In *Phyllidiella*, the length

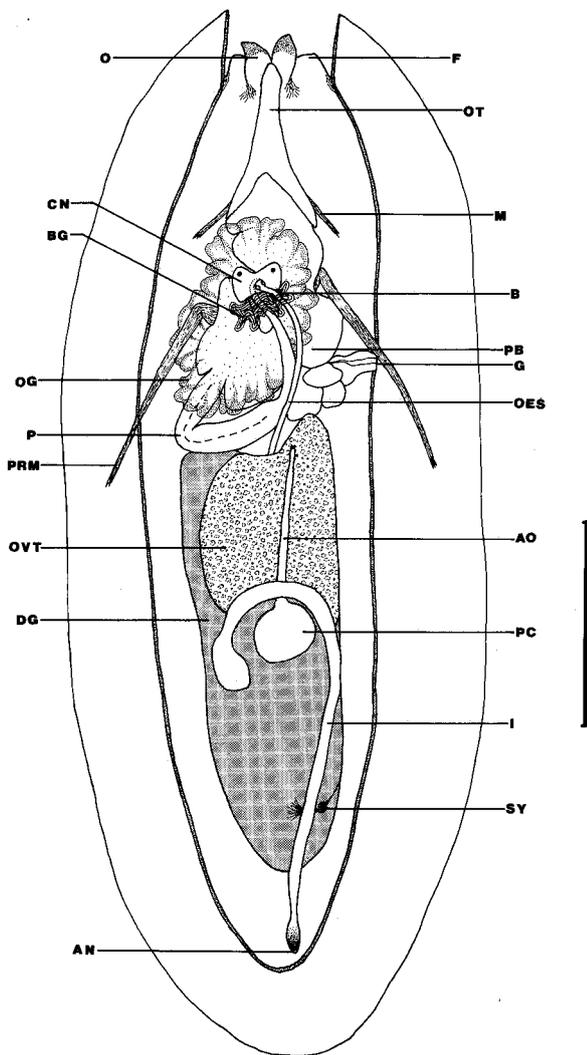


Fig.11. *Phyllidiella pustulosa*. Generalised dorsal view of anatomy. Abbreviations: AN, anus; AO, aorta; B, buccal ganglia; BG, blood gland; CN, central nerve ring; DG, digestive gland mass; F, foot; G, reproductive openings; I, intestine; M, muscle; O, oral tentacles; OES, oesophagus; OG, oral glands; OT, anterior oral tube; OVT, ovotestis; P, pharynx; PB, pharyngeal bulb; PRM, pharyngeal retractor muscle; PC, pericardium; SY, syrinx. Scale = 10 mm.

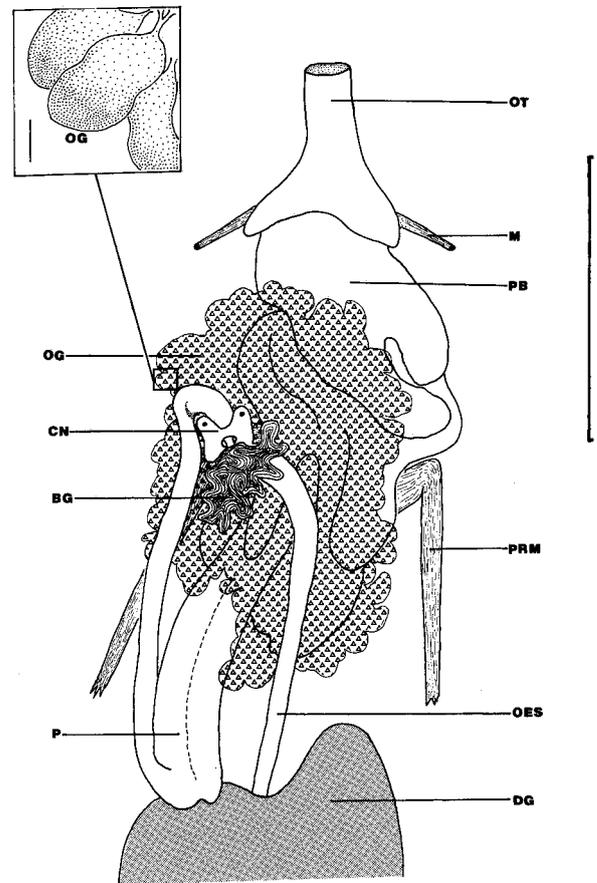


Fig.12. *Phyllidiella pustulosa*. Generalised dorsal view of foregut. Abbreviations: BG, blood gland; CN, central nerve ring; DG, digestive gland mass; M, muscle; OES, oesophagus; OG, oral glands; OT, anterior oral tube; P, pharynx; PB, pharyngeal bulb; PRM, pharyngeal retractor muscle. Scale = 5 mm. Inset scale = 0.5 mm.

of the pharynx is twice that of the oesophagus. The intestine leaves the compact digestive glands dorsally, circles forward and to the right around the pericardium, then straightens to run posteriorly down the dorsal surface of the digestive gland mass to a dorsal anal opening. Immediately prior to the anus the intestinal wall thickens into a muscular rectum. In most species of *Phyllidiella* the rectum has grey-black pigmentation (Fig.12).

The pericardium communicates with the anterior part of the body via a large aorta. Finer vessels connect the large, dorsal blood gland to the aorta. Transverse sections of the foregut of *Phyllidiella pustulosa* gave a weak positive indication with alcian blue stain. The PAS test for muco-polysaccharide based secretions was negative. These results suggest that the oral glands of *Phyllidiella* have a somewhat different secretion to that of *Phyllidia*.

Reproductive system (Fig.13). The hermaphrodite duct leads from the ovotestis (Fig.12) to an oval ampulla. A short oviduct and long prostatic vas deferens arise separately from the ampulla. The sinuous prostate narrows distally into a narrow vas deferens which leads into the short, narrow ejaculatory duct. The penis possesses rows of narrow recurved spines, each has a somewhat irregular surface. The oval nidamental gland mass is generally pale yellow in colour and it has a convoluted appearance (Fig.13). The dark bursa copulatrix is smaller than the translucent, brownish receptaculum seminis. The vaginal duct divides at the base of the bursa (i.e., the bursa has no stalk). The vaginal duct enters a common vestibule with the penis.

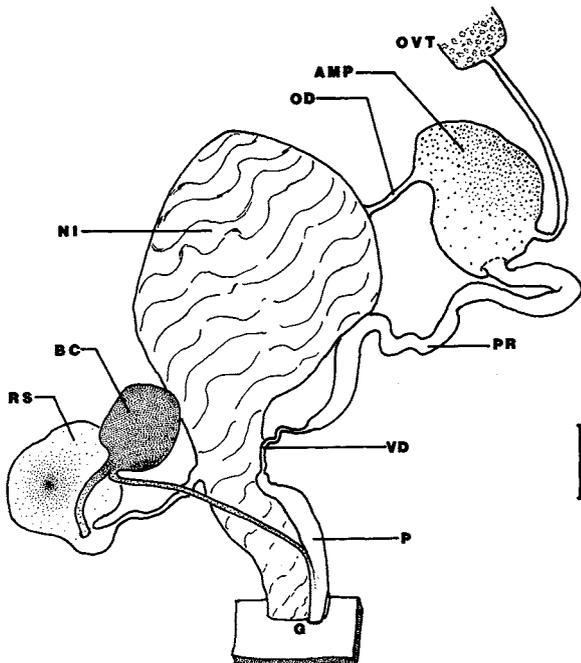


Fig.13. *Phyllidiella pustulosa*. Unravalled reproductive system. Abbreviations: AMP, ampulla; BC, bursa copulatrix; G, reproductive openings; NI, nidamental glands; OD, oviduct; OVT, ovotestis; P, penis; PR, prostatic vas deferens; RS, receptaculum seminis; VD, vas deferens. Scale = 1 mm.

The small penis is quite narrow. Longitudinal ridges of folded epithelium line the vaginal aperture possibly matching the rows of penial spines (Fig.28C).

Remarks. Some authors have recognised *Phyllidiella* as at least subgenerically distinct from *Phyllidia* (Eliot, 1904; Lin & Si, 1965; Er. Marcus, 1965; Er. Marcus & Ev. Marcus, 1970; Burn, 1970; Lin *et al.*, 1986). I believe the genus *Phyllidiella* Bergh, 1869 should be reintroduced because it encompasses a group of species which have particular and unique modifications to the foregut. Some external features also appear to be distinct. Nevertheless, confirmation of generic placement is best made by examination of the foregut. Internally, *Phyllidiella* has a large, elongate pharyngeal bulb possessing remarkably long retractor muscles and a mass of leaf-like oral glands external to the pharyngeal bulb. In the reproductive system the oviduct and long prostatic vas deferens arise separately from the ampulla (cf. *Phyllidia* in which there is a common opening prior to division). *Phyllidiella* displays characteristic differences in its morphology and anatomy when compared to other genera (Tables 1 & 2). I have observed a considerable range of variation in the form of notal tubercles of living and preserved specimens belonging to *Phyllidiella*. Occasionally live specimens (in particular *Phyllidiella pustulosa*) appear greenish in colour underwater, however they invariably photograph (flash or natural lighting) a pinkish colour (personal observation, 1986-1989). The reason for this phenomenon is may be related to colour absorption underwater and the pigments derived from the specimen's food, or caused by structural colours (rather than pigments). I have not observed this phenomenon in other genera.

Bergh (1869) introduced *Phyllidiella* for Cuvier's (1804) *Phyllidia pustulosa* and *Phyllidiella nobilis* Bergh, 1869. I will later show that these two specific names are synonyms. Bergh (1869) confused the specific identity of *Phyllidiella nigra* (Hasselt) and *Phyllidiella pustulosa* (Cuvier), and introduced *Phyllidiella nobilis* for his specimens of *P. pustulosa*. His concept of the genus *Phyllidiella* appears to have been quite clear, however, and all these species possess the generic characters described above. Bergh (1869, 1875, 1892) always listed "*Phyllidiella pustulosa* (Cuvier)" as the first described species of this genus, and therefore I designate *Phyllidia pustulosa* Cuvier 1804 herein as the type species of *Phyllidiella*. There are nine species in the genus *Phyllidiella*.

Phyllidiopsis Bergh, 1875

Phyllidiopsis Bergh, 1875.—Bergh, 1889, 1890, 1892.—Eliot, 1903b, 1904.—Ev. Marcus & Er. Marcus, 1962.—Pruvot-Fol, 1954, 1956, 1957a.—Gosliner & Behrens, 1988.—Brunckhorst, 1990b.

Type species. *Phyllidiopsis cardinalis* Bergh, 1875, by monotypy.

External morphology. Species of *Phyllidiopsis* are small to medium sized phyllidiids, oval to elongate in shape. Most species are quite flattened, however a few species have a high profile. Morphology of the dorsum is variable. Some species have large compound and/or coalesced tubercles, whereas a number of others are relatively smooth with small, simple tubercles and/or low ridges. Rhinotubercles are absent. Species of *Phyllidiopsis* display a wide range of colours externally (e.g., olive, purple, pink, red, brown, yellow, blue, black and white). However, in contrast to *Phyllidiella* there is little intraspecific variation externally in *Phyllidiopsis*. The rhinophores may be bicoloured. The number of lamellae on the rhinophore clavus is specific (within a limited range) for mature specimens. The foot sole lacks distinctive markings, but is variable in colour between species. The oral tentacles are broad and fused together to form a squarish shape. The fused oral tentacles have a groove on each lateral margin and

they may possess a small median indentation anteriorly (Fig.14).

Anatomy (Figs 10A-C, 14, 15). The viscera are encased in a dark envelope. The mouth opens beneath and between the fused oral tentacles. From the mouth a soft, folded, concertina-like, oral tube leads back to the thickened pharyngeal bulb. The pharyngeal bulb has thick musculoglandular tissue walls and it can be partially invaginated to allow the long, tubular pharynx to evert through it (Figs 10A, 14). The exterior of the pharyngeal bulb appears to be quite smooth and devoid of oral glands (Gosliner & Behrens, 1988), however SEM studies show that the surface of the bulb is completely enveloped by tightly packed, minute, oral glands (Brunckhorst, 1990b; Fig.10C). Individual glandular bodies measured 0.05-0.1 mm in diameter. The length of the pharyngeal bulb is three to four times its breadth. The tubular pharynx leaves the posterior of the pharyngeal bulb. At this point, two, narrow, elongate retractor muscles insert onto the posterior of the bulb, one on either side of the tubular pharynx. The retractor muscles are pulled into the pharyngeal bulb when the pharynx is everted. These muscles originate from the dorsolateral body wall. The tubular pharynx passes directly through the central nerve ring and runs dorsally over the digestive gland mass (Fig.14).

Overlying the foregut region is the blood gland which connects to the aorta by a short duct passing near the pharyngeal bulb on the right side. The buccal and gastro-oesophageal ganglia are situated far posteriorly at the end of the tubular pharynx. These ganglia have long connectives running forward to the central nerve ring. Behind the buccal ganglia, the oesophagus broadens into a short, swollen, muscular segment here termed the oesophageal pump (it is thick walled with much circular muscle; Fig.10B). The oesophagus then narrows, immediately turning to the right in a 'U' before entering the digestive gland mass dorsally. The tubular pharynx is about three times the length of the oesophagus. At the base of the 'U' where the oesophagus turns sharply, a long retractor muscle arises. This muscle passes under the intestine and down the midline to its origin on the extreme posterior body wall. Some species (including *P. cardinalis*) have a definite stomach region within the digestive glands while a distinct stomach is lacking in others. The intestine arises dorsally in the usual position, encircles the pericardium to the right, and then straightens to run posteriorly to the dorsal anal opening.

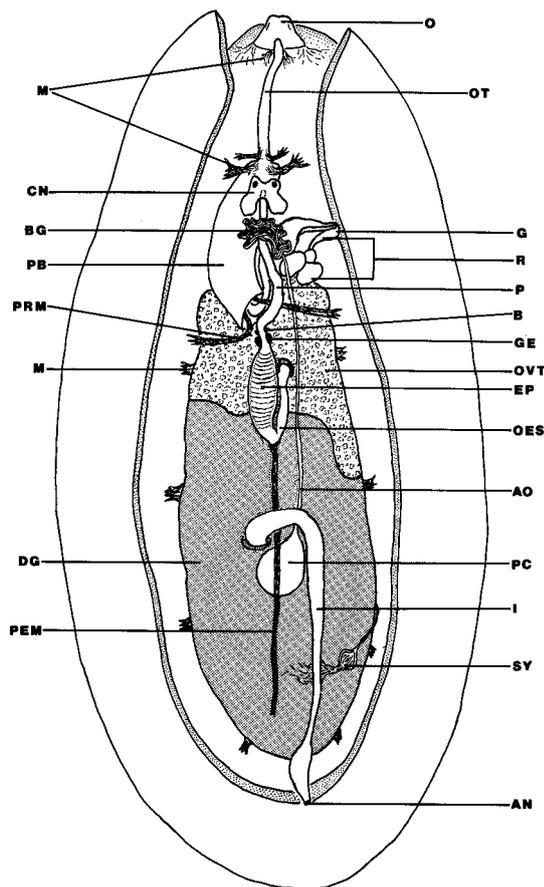


Fig.14. *Phyllidiopsis cardinalis*. Generalised dorsal view of anatomy. Abbreviations: AN, anus; AO, aorta; B, buccal ganglia; BG, blood gland; CN, central nerve ring; DG, digestive gland mass; EP, muscular segment of oesophagus ('oesophageal pump'); G, reproductive openings; GE, gastro-oesophageal ganglia; I, intestine; M, muscle; O, oral tentacles; OES, oesophagus; OT, anterior oral tube; OVT, ovotestis; P, tubular pharynx; PB, pharyngeal bulb; PC, pericardium; PEM, posterior oesophageal retractor muscle; PRM, pharyngeal retractor muscle; R, reproductive system; SY, syrinx. Scale = 5 mm.

Reproductive system (Fig.15). As in other phyllidiids, a whitish ovotestis overlies the anterior part of the digestive glands. The ovotestis is connected to the ampulla by the hermaphrodite duct. *In situ*, the vaginal duct and its two vesicles lie to the right of the nidamental gland mass. The oval ampulla is similar in size and shape to the bursa copulatrix. The oviduct and prostate divide at a common point, directly from the base of the ampulla (Fig.15). The prostatic vas

deferens is generally convoluted and in some species it may be bound together by connective tissue (see Brunckhorst, 1990b). A short distal vas deferens leads from the prostate into an elongate penis which is armed with spines at its distal, eversible end. The recurved penial spines possess a very broad base and taper gently to a point. The nidamental gland mass is elongate and oval in shape, and generally cream to yellowish in colour. The semitransparent receptaculum seminis is slightly smaller than the darker bursa copulatrix. The bursa is not stalked. The vaginal duct divides immediately at the base of the bursa. Distally, the vaginal duct enters a common vestibule with the penis.

Remarks. *Phyllidiopsis cardinalis* Bergh, 1875 is the type species of this relatively large genus (14 species are recognised from the tropical Indo-West Pacific in the present work) which is characterised by a number of features. These include: the fused oral tentacles; the elongate pharyngeal bulb (now shown to possess an external covering of tiny oral glands, see Fig.10C); the long tubular pharynx; the oesophagus having a swollen muscular segment; the dorsomedian entrance of the oesophagus into the digestive gland mass; the anterior foregut muscles; and the long posterior oesophageal retractor muscle (Bergh, 1875, 1889; Gosliner & Behrens, 1988; Brunckhorst, 1990a,b; present work). The relative proportions of the foregut components and the reproductive system in

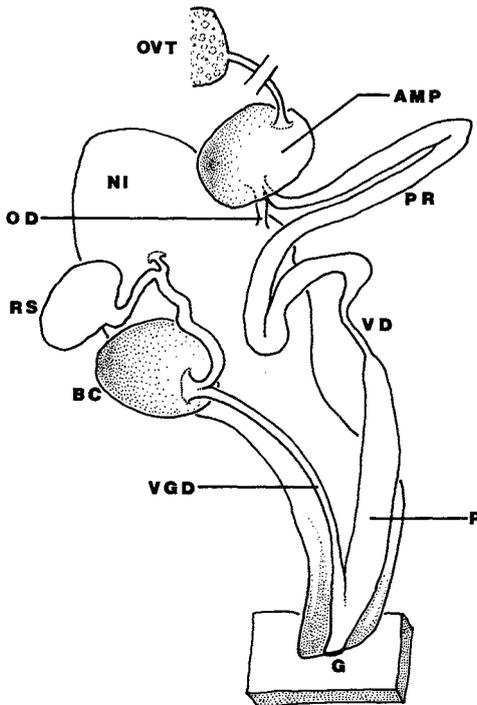


Fig.15. *Phyllidiopsis cardinalis*. Reproductive system. Abbreviations: AMP, ampulla; BC, bursa copulatrix; G, reproductive openings; NI, nidamental glands; OD, oviduct; OVT, ovotestis; P, penis; PR, prostatic vas deferens; RS, receptaculum seminis; VD, vas deferens; VGD, vaginal duct. Scale = 1 mm.

Phyllidiopsis contrast with those of the other genera (Tables 1, 2).

All the tropical Indo-West Pacific species of *Phyllidiopsis* possess retractor muscles associated with the anterior and posterior regions of the foregut (Bergh, 1875; Gosliner & Behrens, 1988, Brunckhorst, 1990a,b; present work). However, species described from the Atlantic Ocean (and *P. blanca* Gosliner & Behrens, 1988, from the Pacific coast of North America) lack similar muscles of the foregut and have a glandular segment (not muscular) on the posterior oesophagus (Bergh, 1890; Meyer, 1977; Bouchet, 1977; Thompson, 1980; Gosliner & Behrens, 1988). Vayssière (1902) appears to have figured a posterior oesophageal retractor muscle for *P. berghi* (syntype is in MNHN), however that species lacked anterior retractor muscles and the swollen oesophageal segment was glandular. The Atlantic *Phyllidiopsis* species group and the Indo-West Pacific *Phyllidiopsis* species group may be of Tethyan origin. *Phyllidiopsis berghi* and *P. blanca* are quite similar morphologically (personal observation) and they may be an example of cognate species living on both sides of Central America. Differences in the anatomy suggest that the Atlantic species should be contained in a separate genus. A review of the Atlantic species is needed to confirm their anatomy and hence taxonomy.

Ceratophyllidia Eliot, 1903

Ceratophyllidia Eliot, 1903a.–Eliot 1903b, 1904, 1910.–Gosliner, 1987.–Gosliner & Behrens, 1988.

Type species. *Ceratophyllidia africana* Eliot, 1903, by original designation.

External morphology. Species of *Ceratophyllidia* are oval shaped, small to medium sized phyllidiids. The dorsum bears numerous, soft, stalked papillae. Animals are able to autotomise the papillae (Gosliner & Behrens, 1988). The papillae may possess minute, dark pigment spots dorsally. The notum is spiculate and may have widely scattered tiny tubercles and dark spots (Fig.16). *Ceratophyllidia* species are cream to white or pale grey in colour. The lamellate rhinophores are whitish. Rhinotubercles are absent. The anus opens dorsally. Ventrally, the foot and gills are usually the same pale colour as the rest of the body. The oral tentacles are partially fused medially and each has a ventrolateral groove. The foot sole is devoid of markings.

Anatomy (Fig.17). The oral tube is short and rapidly expands into a musculoglandular pharyngeal bulb. The surface of the pharyngeal bulb is smooth and devoid of glands. The length of the pharyngeal bulb is one and a half times its breadth. Two large oral glands (ptyaline) are present behind the pharyngeal bulb (Fig.17). The

long ducts arising from the two oral glands empty into the posterior of the pharyngeal bulb at the point where the pharynx leaves. The pharynx and the long ducts of the two oral glands can evaginate through the pharyngeal bulb. Two pairs of retractor muscles, each coalesced at their point of insertion (Fig.17) arise posterolaterally on the pharyngeal bulb. These muscles attach to the dorsolateral body wall approximately one third of the way down the body length. The long pharynx leaves the pharyngeal bulb posteriorly, bends upwards in a long sinuous curve, and passes through the central nerve ring.

The buccal ganglia occur on the side of the pharynx posterior to the central nerve ring. A long oesophagus continues posteriorly over the digestive glands. There is a swollen, glandular oesophageal segment prior to its narrowing to enter the digestive gland mass dorsally (Fig.17). A stomach is present within the digestive gland mass. The intestine arises posterodorsally, and in the usual manner circles to the right around the pericardium before straightening to run further posteriorly to the dorsal anal opening. A blood gland (removed in Fig.17) overlies the anterior part of the foregut. An aorta runs anteriorly from the heart in the posteromedian pericardium.

Reproductive system (Fig.18). A hermaphrodite duct connects the ovotestis to the large rounded

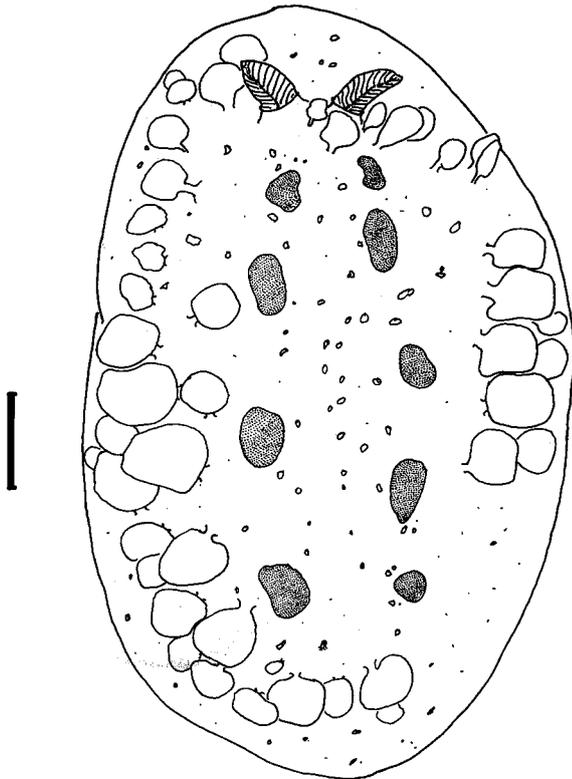


Fig.16. *Ceratophyllidia* (sp.1). Dorsal view of 8 mm specimen (5 m depth, Bile Bay, Guam, leg. C. Carlson & P. Hoff, 19 June 1975). Some papillae have been lost from the notum. Scale = 1 mm.

ampulla. The oviduct and prostatic vas deferens divide at their common exit point from the ampulla (Fig.18). The prostate is long and convoluted. There is no distinct narrowing of the prostate distally into a vas deferens. The penis is short and narrow. Penial spines appear to be absent (Gosliner & Behrens, 1988). I was not able to isolate them. The nidamental gland is flattened and oval in shape (Fig.18). The receptaculum seminis and bursa copulatrix are similar in size and oval in shape. The long vaginal duct divides distally from the bursa copulatrix (i.e., the bursa has a distinct stalk; Fig.18). The distal end of the vaginal duct enters a common vestibule with the penis.

Remarks. There are a number of features which characterise the genus *Ceratophyllidia*. The soft papillae of the dorsum and the partially fused oral tentacles are unique externally. The alimentary system is also distinctive in its possession of two large ptyaline

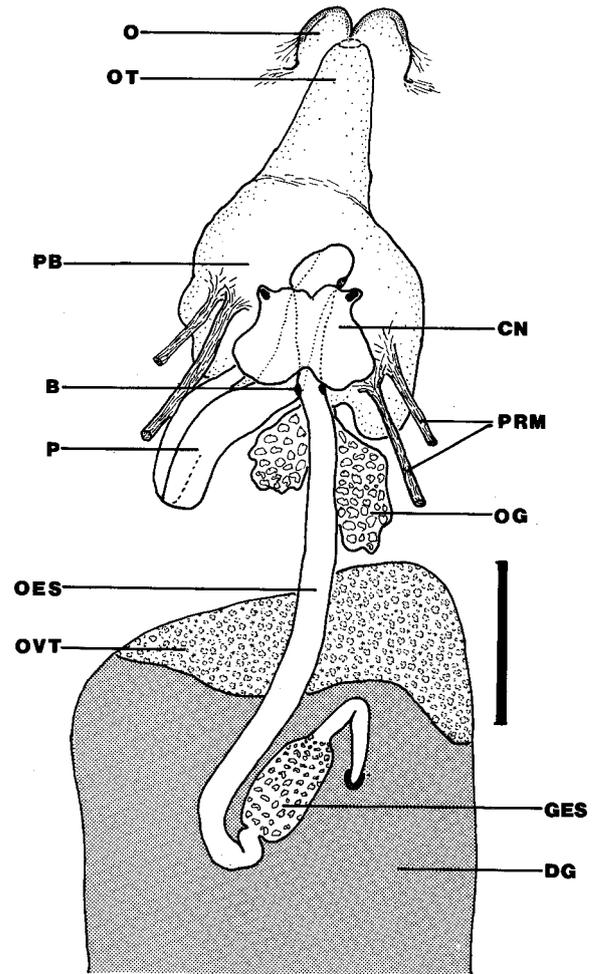


Fig.17. *Ceratophyllidia africana*. Generalised dorsal view of alimentary system. Abbreviations: B, buccal ganglia; CN, central nerve ring; DG, digestive gland mass; GES, glandular oesophageal segment; O, oral tentacles; OES, oesophagus; OG, oral glands (ptyaline); OT, anterior oral tube; OVT, ovotestis; P, tubular pharynx; PB, pharyngeal bulb; PRM, pharyngeal retractor muscle. Scale = 1 mm.

glands with long ducts, the long pharynx and long oesophagus, and the glandular oesophageal segment (Table 1). The bursa copulatrix has a long stalk (Fig.18; Table 2).

Eliot (1903b) had first suggested that *Phyllidiopsis papilligera* Bergh, 1890 should be considered the type for a new genus which he (previously) called *Ceratophyllidia* (Eliot, 1903a). Confusion over the identity of the type species could arise due to the closeness of the publication dates of these two works of Eliot. The former report by Eliot (1903b), referring to *P. papilligera*, was received by the series editor (J.S. Gardiner) in June 1902 (footnote: p.540), however it was not published until sometime between July and November 1903 (some bibliographies incorrectly refer to this paper as 1906; the original clearly states 1903 as the year of publication of Vol.2, pt.1). Nevertheless, Eliot's (1903a) description of *Ceratophyllidia africana* as a new genus and species correctly stands as the type by original designation [ICZN, 1985, Art. 68 (a)(i)]. The present work confirms and strengthens the recent validation of the genus by Gosliner (1987), and Gosliner & Behrens (1988). There are three species in the genus *Ceratophyllidia*.

Reticulidia Brunckhorst, 1990

Type species. *Reticulidia halgerda* Brunckhorst & Burn, 1990 (in Brunckhorst, 1990a), by original designation.

External morphology. Species of *Reticulidia* are oval to elongate, medium sized phyllidiids. Animals are brightly and graphically patterned. The body wall is spiculose, but notal tubercles are completely absent. The notum bears a reticulate network of smooth, sharp ridges dorsally. A narrow base gives

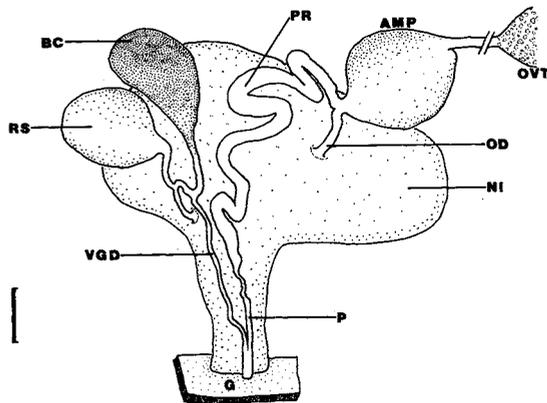


Fig.18. *Ceratophyllidia africana*. Reproductive system (partly after Gosliner & Behrens, 1988). Abbreviations: AMP, ampulla; BC, bursa copulatrix; G, reproductive openings; NI, nidamental glands; OD, oviduct; OVT, ovotestis; P, penis; PR, prostatic vas deferens; RS, receptaculum seminis; VGD, vaginal duct. Scale = 1 mm.

the ridges a sharp appearance (triangular in section) like ribbons standing on edge. The ridges are not supported by spicules (confirmed by sectioned material). The main colours are black and orange. The rhinophores are orange and the number of lamellae on the clavus appears to be species specific (Brunckhorst, 1990a). Rhinotubercles are absent. The dorsal median anus opens posteriorly on the crest of a ridge. Ventrally, *Reticulidia* species are yellow-orange in colour. The gills and reproductive apertures are as in *Phyllidia*. The oral tentacles are separate, long and cylindrical in living specimens (but variable in the preserved state through shrinkage and contraction).

Anatomy (Figs 10D-F, 19, 20). The tissue envelope which surrounds the viscera is translucent yellowish in colour. The mouth, which opens between the oral tentacles and foot, leads into the oral tube. The oral tube is relatively short (but longer than in *Phyllidia*), formed by transparent whitish tissue, and it rapidly expands to envelope the pharyngeal bulb (Fig.19). The pharyngeal

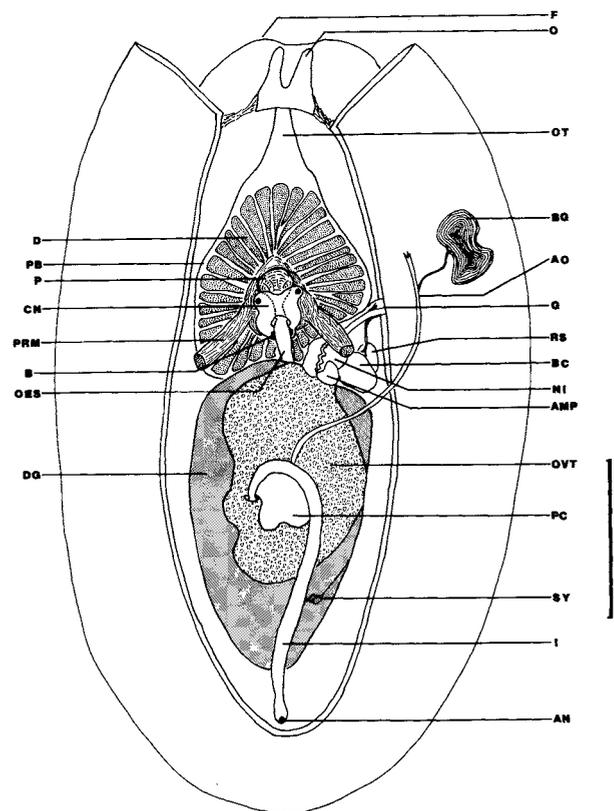


Fig.19. *Reticulidia halgerda*. Generalised dorsal view of anatomy. Abbreviations: AMP, ampulla; AN, anus; AO, aorta; B, buccal ganglia; BC, bursa copulatrix; BG, blood gland; CN, central nerve ring; D, glandular disc; DG, digestive gland mass; F, foot; G, reproductive openings; I, intestine; NI, nidamental gland; O, oral tentacles; OES, oesophagus; OT, anterior oral tube; OVT, ovotestis; P, muscular pharynx; PB, pharyngeal bulb; PC, pericardium; PRM, pharyngeal retractor muscle; RS, receptaculum seminis; SY, syrinx. Scale = 5 mm.

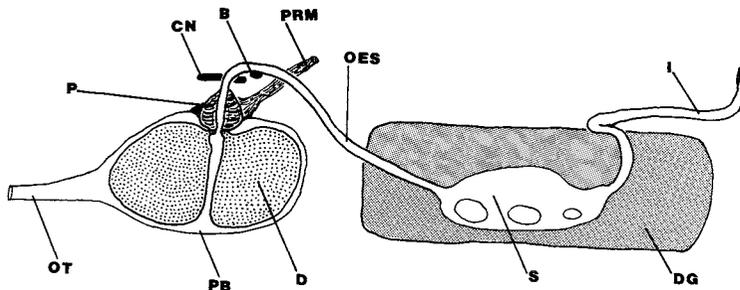


Fig.20. *Reticulidia halgerda*. Diagrammatic sagittal view of alimentary system. Abbreviations: B, buccal ganglia; CN, central nerve ring; D, glandular disc; DG, digestive gland mass; I, intestine; OES, oesophagus; OT, anterior oral tube; P, muscular pharynx; PB, pharyngeal bulb; PRM, pharyngeal retractor muscle; S, stomach.

bulb is very broad; the ratio of its length to breadth being 1:1. There are no oral glands associated with the outside of the pharyngeal bulb. Internally, a number of smooth discs consisting of dense, glandular tissue stand on end in a closely packed circle uninterrupted by the opening of the oral tube into the pharyngeal bulb (Figs 10D-F, 19). In preserved material the glandular discs were pale orange in colour. In the type species, *R. halgerda*, the number of discs within the pharyngeal bulb varied between 39 and 48 in five specimens examined.

Each disc is attached, dorsally, to the anterior edge of the opening to the pharynx. The short, muscular pharynx leaves the centre of the pharyngeal bulb, dorsally (Figs 10D, 19, 20). In the centre of the pharyngeal bulb there is a small cavity beneath the opening of the pharynx and surrounding this cavity are the radially encircling discs (Fig.20). There is no other tube or duct passing through the pharyngeal bulb from oral tube to pharynx (i.e., the pharyngeal bulb is a highly modified posterior portion of the oral tube). The translucent tissue envelope closely surrounds the glandular discs like a closely fitting garment. On the external, dorsal surface of the pharyngeal bulb, muscle tissue surrounds the base of the pharynx and from this, two large retractor muscles arise (Fig.19). The pharyngeal retractor muscles originate from the dorsolateral body wall about one third of the way down the body length. The pharynx in *Reticulidia* is very short. Where it leaves the pharyngeal bulb, the pharynx is initially broad and muscular (Figs 19, 20). It quickly narrows, passes through the central nerve ring, and turns posteriorly. The buccal ganglia occur on the ventrolateral surface of the pharynx, immediately posterior to the central nerve ring. The oesophagus is also very short and it runs posteriorly into the anterior of the digestive gland mass which occupies about half of the body cavity. Within the digestive gland mass the alimentary tract expands into a stomach region. The stomach has a thin tissue wall. On each side of the stomach are two or three large openings to the digestive glands (Fig.20). The intestine leaves dorsally from the

digestive gland mass, circles around the pericardium to the right and passes posteriorly to the dorsal anal opening.

A blood gland (moved to the right in Fig.19) overlies the central nerve ring and foregut region. It is connected to the anterior part of the aorta by at least one fine vessel. The excretory system connects with the heart via the syrinx which is situated to the right of the pericardium (Fig.19).

Reproductive system (Fig.21). The ovotestis overlies the anterior part of the digestive gland mass (Fig.19). The hermaphrodite duct connects with the spherical to oval ampulla. The oviduct and a short proximal vas deferens (leading into the prostatic vas deferens) divide at the base of the ampulla. The prostate is convoluted and, without narrowing, leads directly into the long muscular ejaculatory duct (Fig.21). The penis is eversible and

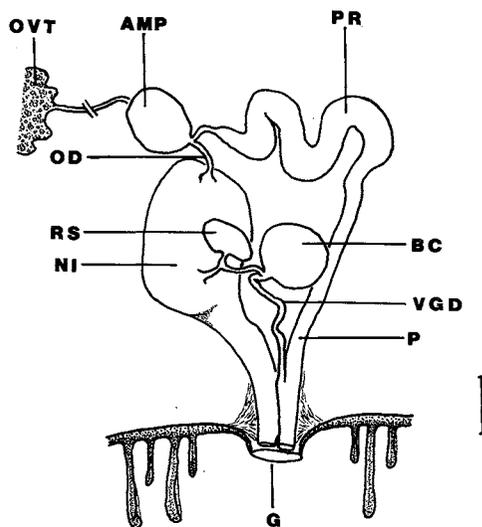


Fig.21. *Reticulidia halgerda*. Unravalled reproductive system showing external opening and gill leaflets. Abbreviations: AMP, ampulla; BC, bursa copulatrix; G, reproductive openings; NI, nidamental glands; OD, oviduct; OVT, ovotestis; P, penis; PR, prostatic vas deferens; RS, receptaculum seminis; VGD, vaginal duct. Scale = 1 mm.

armed with rows of narrow, recurved, chitinous spines at its distal end. The penial spines have some pitting and furrows on their broad base. Apparently unique to *Reticulidia* is the presence of 'paired spines' (i.e., 2 spines arising from a single base; see Brunckhorst, 1990a). The ratio of single to paired spines was approximately 10:1. Individual spines in a pair may be of equal or unequal length. The nidamental gland mass is elongate-ovate in shape and generally pale yellow-orange in colour. The bursa copulatrix is spherical and of similar size to the ampulla. The receptaculum is smaller and oval in shape.

The vaginal duct divides immediately on leaving the bursa (i.e., the bursa is not stalked). Distally, the vaginal duct enters a common vestibule with the penis. The epithelium lining the entrance to the genital aperture forms longitudinal ridges, possibly matching the rows of penial spines.

Remarks. The genus *Reticulidia* Brunckhorst, 1990 is markedly different externally and internally from all five genera described above. *Reticulidia* is peculiar in the possession of radially arranged, glandular discs within the pharyngeal bulb, and in

Table 1. Comparison of the alimentary system of phyllidiid genera.

Genus	Pharyngeal bulb (PB) length: breadth	Pharynx length : Oesophagus length	Position pharynx leaves pharyngeal bulb	Stomach	Oral tube length	Anus
<i>Phyllidia</i>	1-1.5:1 (large PB)	2:1	posterodorsal	absent	short	dorsal
<i>Fryeria</i>	1:1.5 (small PB)	1:1.5	posterodorsal	absent	long	ventral protrusible
<i>Phyllidiella</i>	2:1 (PB very large)	2:1	posterior (ant. pharynx dilated)	absent	moderate	dorsal
<i>Phyllidiopsis</i>	3-4:1 (PB elongate)	3:1	posterior	present in some spp.	long (concertina like)	dorsal
<i>Ceratophyllidia</i>	1.5:1 (PB conical)	1:1 (both long)	posterior	present	short	dorsal
<i>Reticulidia</i>	1:1 (PB large, round)	1:1 (both short)	dorsal	present	moderate (dilates around PB)	dorsal

Table 2. Comparison of the morphology of reproductive organs of phyllidiid genera.

Genus	Nidamental glands	Receptaculum seminis (RS) vs. Bursa copulatrix (BC)	Penis	Bursa stalked	other features
<i>Phyllidia</i>	very large, spherical	both large rounded equal in size	bulbous; armed	no	vas deferens short
<i>Fryeria</i>	small spherical	BC ovate; similar in size	short narrow; armed	no, or very short	very large ampulla; vas deferens long
<i>Phyllidiella</i>	ovate	RS irregular-ovate; BC smaller	short narrow; armed	no	ducts from ampulla are separate
<i>Phyllidiopsis</i>	elongate ovate	both ovate; RS smaller	elongate; armed	no	vaginal duct long
<i>Ceratophyllidia</i>	flattened ovate	both small, similar in size; ovate	short narrow; ?unarmed	yes, long	vaginal duct long
<i>Reticulidia</i>	small ovate	BC large, rounded; RS smaller, ovate	elongate; armed	no	no narrowing of prostatic vas deferens prior to penis

having smooth reticulate ridges on the notum (tubercles are absent). The large, broad pharyngeal bulb with its internal glandular discs and very short, dorsally exiting pharynx are quite different to the foregut of *Phyllidia*. A generalised comparison of the

foregut of *Phyllidia*, *Phyllidiopsis* and *Reticulidia* is given in Figure 22. Other differences in anatomy are summarised in Tables 1 and 2. Two species are known to belong to *Reticulidia* (Brunckhorst, 1990a; present work).

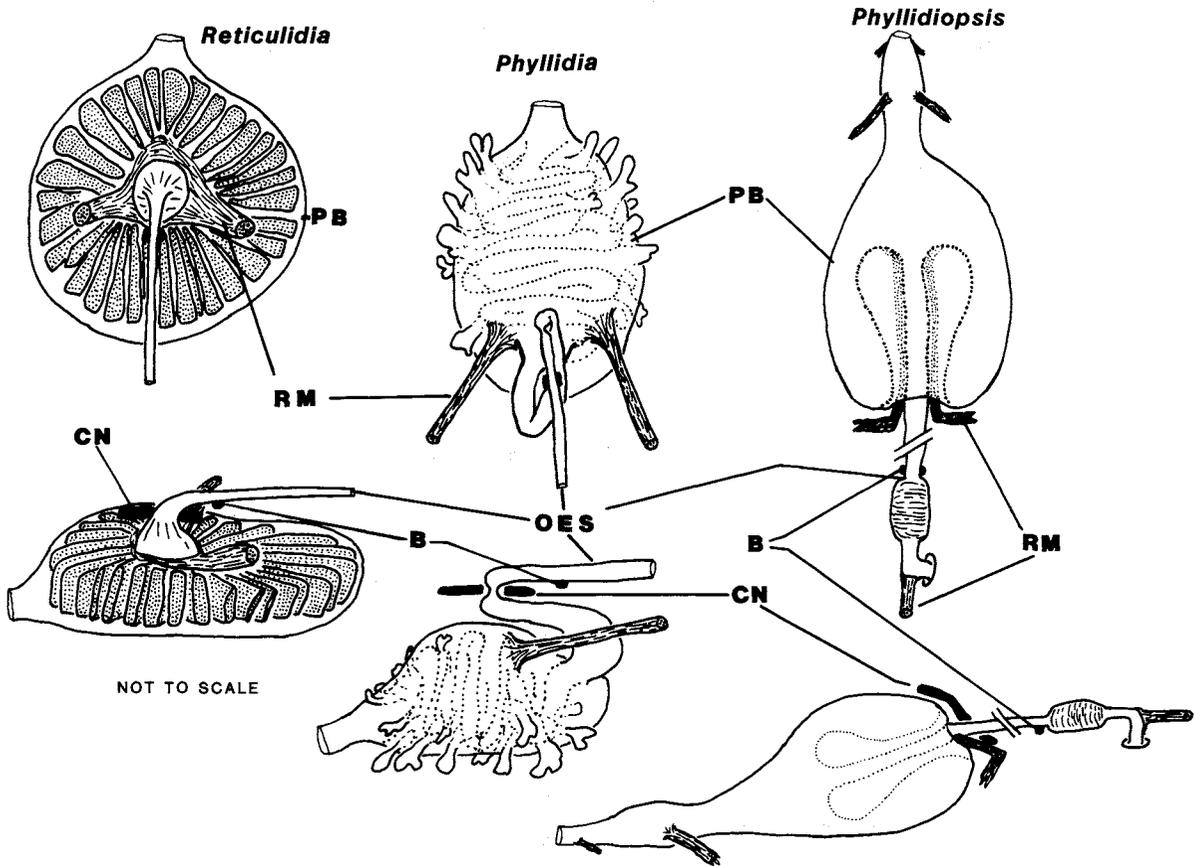


Fig.22. Schematic dorsal (upper) and lateral (lower) representations of the foregut and associated musculature (in particular the pharyngeal bulb) of *Reticulidia halgerda*, *Phyllidia varicosa* and *Phyllidiopsis cardinalis*. Abbreviations: B-buccal ganglia; CN, central nerve ring; OES, oesophagus; PB, pharyngeal bulb; RM, retractor muscle.

Key to Phyllidiid Genera

1. Oral tentacles partially or completely fused; foregut elongate (elongate pharyngeal bulb and long tubular pharynx) 2
- Oral tentacles separate, digitate; foregut not elongate (broad pharyngeal bulb & pharynx short)..... 3

2. Dorsum with stalked papillae; oral tentacles partially fused; 2 large, free salivary/ptyaline glands; glandular oesophageal segment; oesophageal retractor muscle absent *Ceratophyllidia*
- Dorsum tuberculate; oral tentacles completely fused; minute oral glands enveloping pharyngeal bulb; muscular oesophageal segment; oesophageal retractor muscle present *Phyllidiopsis*

3. Rhinophores not black; multiple oral glands within pharyngeal bulb; pharyngeal bulb short, pharyngeal retractor muscles short.....4
- Rhinophores black; multiple oral glands external to pharyngeal bulb; pharyngeal bulb large; pharynx broad, oesophagus tubular; pharyngeal retractor muscles long*Phyllidiella*
4. Rhinophores cream to yellow; rhinotubercles present; dorsum tuberculate; oral glands 'cauliflower' like (may protrude from pharyngeal bulb)5
- Rhinophores orange; rhinotubercles absent; dorsum has smooth network of ridges, no tubercles; radially arranged glandular discs within pharyngeal bulb; very short pharynx exits pharyngeal bulb dorsally*Reticulidia*
5. Tubercles single, rounded; pharyngeal bulb broader than long; intestine runs ventrolaterally; anus ventral and protrusible; ampulla large; penis short and straight*Fryeria*
- Large tubercles usually compound, or forming ridges; large pharyngeal bulb, slightly longer than broad; intestine runs dorsally; anus dorsal, non-protrusible; ampulla small; penis bulbous*Phyllidia*

Phyllidia Cuvier, 1797

Phyllidia varicosa Lamarck

Figs 2A-F, 3A, 4-6, 23A-B, 24A-D, Pl.1A-D

Phyllidia varicosa Lamarck, 1801: 66.—Cuvier, 1804a: 268.—Oken, 1815: 286.—Blainville, 1816: 26.—Blainville, 1826: 99.—Gray, 1847: 168.—Bergh, 1869: 360-433, 499-504, pl.14-18a.—Bergh, 1875: 661.—Eliot, 1903b: 562.—Eliot, 1904: 281.—Basedow & Hedley, 1905: 145.—Bergh, 1905: 180-181, pl.17, fig.8.—Eliot, 1908: 120.—Eliot, 1910: 435.—Vayssière, 1912: 84.—Pruvot-Fol, 1933: 95.—Baba, 1936: 42-43, fig.25.—White, 1951: 252.—Dawydoff, 1952: 111.—Pruvot-Fol, 1956: 61, fig.1.—Pruvot-Fol, 1957a: 105.—Johannes, 1963: 104-105.—Lin & Si, 1965: 7.—Er. Marcus, 1965: 277.—Miller, 1969: 545, fig.187.—Lim & Chou, 1970: 135, pl.16, fig.b.—Edmunds, 1971: 388-389, fig.23.—Edmunds, 1972: 75-77, fig.1.—Rao *et al.*, 1974: 119-121, fig.2a-b.—Baba, 1975: 257, fig.1.—Baba & Hamatani, 1975: 174, fig.1.—Burn, 1975: 516.—Burrison *et al.*, 1975: 4763.—Lin, 1975: 141-154, pl.2, fig.9.—Hagadone *et al.*, 1979: 2484-2494.—Bertsch & Johnson, 1981: 74-75.—Orr, 1981: 59.—Wu & Romig, 1982: 149-153, figs 1,2.—Heller & Thompson, 1983: 339-341, fig.8a-g.—Johnson & Boucher, 1983: 282.—Lin, 1983: 152, pl.1, fig.9.—Willan & Coleman, 1984: 42, 53, pl.131.—Yonow, 1984a: 227, figs 7c, 8c-e.—Lin *et al.*, 1986: 129.—Soliman, 1986: 255-260, pls 1-15.—Yonow, 1986: 1415.—Karuso, 1987: 35-36.—Tan *et al.*, 1987: 75-76, fig.3.—Coleman, 1989: 46.—Johnson, 1989: 3,5.—Brunckhorst, 1989b: 43,44.—Lin, 1990: 135.—Gosliner & Behrens, 1990: pl.11B (top).

Phyllidia trilineata Cuvier, 1804a: 268, pl.A, figs 1-6.—Cuvier, 1804b: 277.—Oken, 1815: 268.—Blainville, 1826: 99.—Quoy & Gaimard, 1824: 419-420, pl.87, figs 7-10.—Quoy &

Gaimard, 1832: 292-293, pl.21, fig.25.—Gray, 1850-1854: pl.312, figs 3, 4, 6a-b, 7.—Gray, 1853: 220.—Gray, 1857: 216.—Dawydoff, 1952: 111.

Phyllidia borbonica Cuvier, 1804b: 277 (n.syn.).

Phyllidia quinquelineata Blainville, 1816: 52.—Blainville, 1826: 99 (n.syn.).

Phyllidia arabica Ehrenbergh, 1831 (pages unnumbered).—Bergh, 1869: 434-438, 504-506.—Yonow, 1986: 1403-1405, figs 10a-c.—Yonow, 1988: 143, pl.1.—Yonow & Hayward, 1991: 18, 19, figs 11A,B, 12F.

Phyllidia fasciolata Bergh, 1869: 507-508.—Pruvot-Fol, 1956: 63 (n.syn.).

Phyllidia varicosa var. *quadrilineata* Bergh, 1905: 181, pl.12, figs 41, 42 (n.syn.).

Phyllidia honloni Risbec, 1956: 22-24, figs 71-75, 79-81.—Lim & Chou, 1970: 134, pl.17, fig.b.—Lin, 1983: 152, pl.1, fig.6.—Lin, 1990: 137 (n.syn.).

Phyllidia verrucosa (sic).—Marsh *et al.*, 1986: 95, fig.70 (error pro. *Phyllidia varicosa* Lamarck, 1801) (non *Phyllidia verrucosa* Hasselt, 1824).

Phyllidia sp.—Yonow, 1986: 1415, fig.6b.—Yonow, 1988: 149, fig.3c.

Comments on synonymy. *Phyllidia varicosa* Lamarck and *Phyllidia trilineata* Cuvier are objective synonyms in that they have the same type specimen. The same specimen was used by Cuvier (1797) to establish the genus. *Phyllidia varicosa* was the first phyllidiid species to be described. On the basis of a single specimen (originating from Réunion Island), Cuvier (1797) introduced the genus *Phyllidia* but he did not name a species. Lamarck (1801) introduced the specific name *varicosa* for Cuvier's specimen, which Cuvier (1804a) himself later called *P. trilineata*. A number of

early authors described specimens of this species under these or other names (e.g., Blainville, 1816, 1826; Quoy & Gaimard, 1824, 1832; Ehrenbergh, 1831; Bergh, 1869). All these early specimens had three to five dorsal longitudinal ridges, however the foot sole was not described in every case. *Phyllidia varicosa* must be a common species to have been frequently and widely collected in those early days. In my own experience, I have found it to be one of the most common phyllidiids encountered, both intertidally and subtidally.

Contrary to previous synonymies, Yonow (1986) considered *P. arabica* Ehrenberg as a separate species in its possession of a foot stripe, and further considered that *P. varicosa* lacked a foot stripe. Yonow (1986) had no example of a specimen with the latter condition, but based her decision on Cuvier's (1804) description and figure of *P. trilineata*. Cuvier did not describe *P. trilineata* in detail, stating that *P. varicosa* Lamarck should be known as *P. trilineata* Cuvier (1804:268). Cuvier's drawing gave no indication of a foot stripe, however, only part of the ventral side of the animal was illustrated (and that rather indistinctly). It is likely that Cuvier's preserved specimen had lost the black pigment of the stripe on its foot sole. *Phyllidia arabica* Ehrenberg and *P. varicosa* Lamarck both have a longitudinal foot stripe (which is often faded in preserved specimens). Bergh examined the holotype of *P. arabica* and considered it to be "very close" to *P. varicosa*, probably the same species (Bergh, 1869: 360-438, 499-506). The results of extensive field work throughout the Indo-West Pacific Ocean have shown that this species (having 3-6 blue grey ridges, yellow capped tubercles and a black stripe on the foot sole) is indeed, common (personal communications, 1987-1989; P. Bouchet, C. Bryce, T. Gosliner, S. Johnson, W. Rudman, R. Willan; personal observation, 1985-1991). Furthermore, there has been no collection of a similar species with no foot stripe (*sensu* Yonow, 1986). The species described here must, therefore, be attributed to *P. varicosa* Lamarck, 1801. This species has been well documented and illustrated by many authors in the present century.

It is clear that the species described here is that originally intended by Lamarck and Cuvier. Unfortunately the holotype (Cuvier's specimen) is lost (Bouchet, *in litt.*, 1988). Owing to its importance as the primary type for the genus *Phyllidia* and for the family Phyllidiidae, and with the priority for nomenclatural stability uppermost,

a neotype is here designated. The preserved specimen (43 mm) is illustrated in Figure 23. It originates from the type locality, Réunion Island, in the western Indian Ocean and is deposited in MNHN, Paris. The holotype of *P. borbonica* Cuvier is a large specimen of *P. varicosa*. The *P. varicosa* var. *quadrilineata* of Bergh and the *P. quinquelineata* of Blainville were specimens of *P. varicosa* with four and five dorsal, longitudinal ridges, respectively. *Phyllidia arabica* is identical to *P. varicosa* (Bergh, 1869: 409-506; see comments below). Five out of the nine syntypes of *P. honloni* and Risbec's figures also match *P. varicosa*. *Phyllidia fasciolata* is a colour variation of *P. varicosa*; Pruvot-Fol also considered it a synonym of the latter species. The *P. verrucosa* of Marsh *et al.* (1986) is a mis-spelling; the animal depicted in their colour photograph is *P. varicosa*. The description of *Phyllidia* sp. by Yonow (1986, 1988) is consistent with *P. varicosa*.

Types. *Phyllidia varicosa* Lamarck (= *P. trilineata* Cuvier). Holotype lost; neotype here designated (43 mm preserved length) in MNHN; preserved specimen figured here in Figure 23 (this specimen comes from the type locality, Réunion Island, and was collected from 5-20 m depth, Cape le Houssaye, St Paul, Réunion by J. Drivas and M. Jay in 1989). *Phyllidia borbonica* Cuvier. Holotype (63 mm preserved length) in MNHN, not figured.

Phyllidia quinquelineata Blainville. Holotype lost (described as "the same as *P. trilineata* Cuvier, but with five longitudinal ridges"; Blainville 1826: 99).

Phyllidia arabica Ehrenbergh. Holotype not located in Frankfurt Museum (possibly destroyed in World War II); Bergh (1869: 504-506) examined it.

Phyllidia fasciolata Bergh. Probably no holotype; mentioned in footnote by Bergh 1869: 507-508 in reference to *P. varicosa* and *P. arabica*.

Phyllidia honloni Risbec. Lectotype (61 mm preserved length) in MNHN, number E34203, ?figured by Risbec 1956: figs 71-75, 79-81; 4 paralectotypes, (preserved lengths - E34202, 43 mm; E34204, 57 mm; E34205, 60 mm) in MNHN are also *P. varicosa*; 4 other smaller syntypes are actually *P. coelestis* (see comments under *P. coelestis*).

Material examined. *Western Pacific Ocean* - 5 specimens (43 mm MNHN E34202, 61 mm MNHN E34203, 57 mm MNHN E34204, 60 mm MNHN E34205, 60 mm MNHN E34599), Vietnam, ?Risbec, ?1956; 93 mm specimen (AM C142667), Apo Island, Philippines, 32 m depth, May 1983, B.E. Picton; 83 mm specimen (AM C141838, Rove Caves,

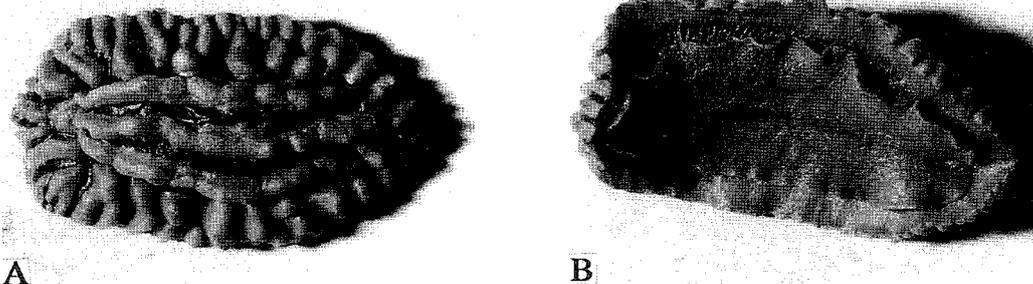


Fig. 23. *Phyllidia varicosa* Lamarck, 1801. Neotype specimen (43 mm) from type locality, Réunion, western Indian Ocean. A, dorsal view; B, ventral view, note black midline stripe on foot sole.

Solomon Islands, 3 m depth, 2 Nov. 1983, I. Knight; 50 mm specimen, Uepi Island, Solomon Islands, 9 m depth, 24 May 1987, P. Chapman-Smith; 70 mm specimen (MV F64047), Noumea, 1964, R. Catala; 43 & 61 mm specimens (BMNH 1845.12.12.10-11), Philippines, 1840? Cumming; 104 & 95 mm specimens (AM C162718), Sponge Mound, Apra Harbour, Guam, 22 m depth, 5 July 1988, DJB & SKB; 1 specimen, Kabira, Japan, 7 May 1979, K. Kitao photo.

Eastern Australia – 30 mm specimen (AM C162722), Orontes Reef, Port Essington, NT, 13 m depth, 10 Aug. 1986, RCW; 70 mm specimen (AM C168912), Flat Rock, off North Stradbroke Island, Qld, 18 m depth, 18 July 1980, M. Ready; 67 mm specimen (AM C168909), Henderson Rock, Moreton Island, Qld, 30 m depth, 17 Apr. 1981, M. Ready; 68 mm specimen (AM C162725), Cook Island, North NSW, 7 m depth, 11 Aug. 1985, J. Short; 90 mm specimen, Duncan Bay, Norfolk Island, 12 m depth, 1 Sept. 1991, K. Whysall.

Great Barrier Reef – 69 mm specimen, Wistari Reef, 24 m depth, 5 Sept. 1983, RCW; 1 specimen, Pioneer Bay, Orpheus Island, 20 July 1982, N. Yonow, photo; 70 mm specimen, Davies Reef, 1 Nov. 1986, A. Ghisotti; 50 mm specimen (MV), Eagle Cay, 5 m depth, 7 Nov. 1975, N. Coleman; 74 mm specimen (MV F54952), Pennys' Bay, Orpheus Island, 1 June 1968, N. Coleman; 74 mm specimen (MV F54952), Orpheus Island, Townsville, 1-3 m depth, 1 June 1968, N. Coleman; 60 mm specimen, Lady Musgrave Island, 15 m depth, 1 Aug. 1989, C. Buchanan.

Papua New Guinea – 48 mm specimen, Milne Bay, 20 m depth, 1 Apr. 1983, R. Vanderloos; 8 mm specimen (MV F54957), Horseshoe Reef, 10 m depth, 1 Aug. 1980, N. Coleman; 34 mm specimen (AM C162723), patch off Lion Island, 14 m depth, 17 June 1988, SKB & DJB; 62 mm specimen (AM C162724), patch off Lion Island, 10 m depth, 17 June 1988, DJB & SKB; 4 specimens (115, 72, 68, 57 mm, AM C162719), patch off Lion Island, 18 m depth, 20 June 1988, DJB & SKB; 37 mm specimen, patch off Lion Island, 18 m depth, 24 June 1988, DJB & SKB.

Madang – 27 mm specimen (AM C168910), Anemone Reef, 11 m depth, 10 Jan. 1988, RCW; 73 mm specimen, Bombes Reef, Madang, 10-18 m depth, 11 Jan. 1988, RCW; 7 specimens (71, 115, 76, 74, 70, 67, 66 mm) Barracuda Point, 15 m depth, 13 Jan. 1988, RCW; 63 & 58 mm specimens, Magic Pass, 15-22 m depth, 14 Jan. 1988, RCW; 17 specimens (93, 67, 65, 64, 62, 61, 58, 57, 55, 50, 45, 39, 38, 29, 27, 25, 15 mm in AM), 5-18 m depth, Madang lagoon, Feb. 1988, RCW; 51 mm specimen, Barracuda Point, 15 m depth, 17 Jan. 1988, RCW; 3 specimens (45, 44, 33 mm), Sek Island, 15 m depth, 18 Jan. 1988, RCW; 40 mm specimen, Magic Passage, 18 m depth, 18 Jan. 1988, RCW; 31 mm specimen, Barracuda Point, 5-21 m depth, 23 Jan. 1988 RCW; 10 specimens (60, 33, 88, 41, 48, 56, 15, 38, 21, 79 mm), slope off Madang Resort, 9-18 m depth, 1 Feb. 1988, RCW; 28 mm specimen, Christmas Bay, 6-30 m depth, 10 Feb. 1988, RCW; 1 specimen, The Quarry, 6-30 m depth, 11 Feb. 1988, RCW; 1 specimen, Banana Reef, 6-30 m depth, 15 Feb. 1988, RCW; 85 & 60 mm specimens, off Country Club, 15 m depth, 18 Feb. 1988, RCW; 17 mm specimen, Barracuda Point, 20 m depth, 20 Feb. 1988, RCW.

Indian Ocean – 1 specimen, Sri Lanka, N. Yonow, ?1980; 1 specimen, Bandos Island, Maldives, 26 m depth, 21 Apr. 1985, P. Chapman-Smith; 54 mm specimen (AM C154745), Sodwana Bay, South Africa, July 1976, R.E. Stobbs; 63 mm specimen (MNHN), leg?, ?1790-1800.

Réunion – neotype (43 mm, MNHN), 5-20 m depth, 1989, M. Jay; 50 mm specimen, 1-20 m depth, 1987, M. Jay; 5 specimens (30, 44, 59, 72, 56 mm, AM C168914), 5-20 m

depth, 1989, M. Jay; 32 mm specimen, 6 m depth, 1989, M. Jay.

Western Australia – 3 specimens (63, 35, 59 mm, AM C168908), Dampier Archipelago, 0-8 m depth, 21 May 1987, D. Johnson; 61 mm specimen (WAM 2206-84), Scott Reef, 8-18 m depth, 7 Nov. 1984, C. Bryce & F. Wells; 57 mm specimen (WAM457-89), Kendrew Island, 27 Oct. 1974, COT Survey; 45 & 56 mm specimens (WAM 476-86), Ashmore Reef, 18 Sept. 1986, F. Wells; 45 & 56 mm specimens (WAM 476-86), Ashmore Reef, 0 m depth, 18 Sept. 1986, F. Wells; 61 mm specimen (WAM 2206-84), Scott Reef, 8-18 m depth, 7 Nov. 1984, C. Bryce & F. Wells; 57 & 39 mm specimens (AM C140633), Mermaid Reef, 12 Oct. 1982, G. Saveracker.

Thailand – 58 mm specimen (AM C162721), Phi Phi Island, 4-10 m depth, 25 Nov. 1989, DJB; 3 specimens (30-70 mm, AM C168913), Phi Phi Island, 10 m depth, 25 Nov. 1989, local divers; 81 mm specimen (AM C162720), Phi Phi Island, 5 m depth, 26 Nov. 1989, DJB; 39 mm specimen (AM C168911), Phuket Island, 5-20 m depth, 5 July 1989, RCW.

Red Sea – 60 mm specimen, Shadwan North, Red Sea, 25 Sept. 1989, M. Ilan.

External morphology (Figs 2A-E, 23, Pl.1B-D). Live specimens ranged in length from 8-115 mm and mean size was 57 mm. *Phyllidia varicosa* is elongate-ovate in shape. Its basic colours are black, blue-grey and yellow. The rhinophores are yellow and rounded at the apex. Specimens greater than 60 mm in length (alive) possess 27-30 lamellae on the rhinophoral clavus (Fig.3A). The notum of *Phyllidia varicosa* has many conical or angular, sometimes compound tubercles with blue-grey to pale grey bases and yellow apices. There may be from three to six, longitudinal, blue-grey to pale grey ridges joining the median tubercles. The ridges may be broken or continuous. A central ridge is always present. On either side of the central ridge, the next two ridges run posteriorly from the rhinotubercles (Pl.1B-C). Towards the margins of the notum there are usually numerous, short, transverse ridges interspersed by black rays. The underside of the notum is cross hatched. The foot and gills are grey. The foot sole always possesses a median black longitudinal stripe (which may be broken; Pl.1D). The grey oral tentacles are tipped in pale yellow.

Anatomy (Figs 4-6, 24A-D). The anatomy is typical for the genus *Phyllidia*. *Phyllidia varicosa* has no distinctive markings on the foregut. In general, the reproductive system is cream to yellowish in colour but the bursa copulatrix and ampulla are tan-brown. Individual penial spines are small (6-8 μ m in vertical height). The base of the spine is broad (7-8 μ m in length; Fig.24A-B,D). The posterior end of the base of each spine are coalesced with that of the next spine in the row. The dorsal surface of the spine is almost straight to its apex (Fig.24C).

Distribution. *Phyllidia varicosa* is a common species, known from throughout the Indo-West

Pacific Oceans including the central Pacific and the Red Sea.

Remarks. *Phyllidia varicosa* is a large species that can be distinguished by its relatively numerous (3-6), longitudinal, tuberculate notal ridges. The ridge and bases of the tubercles are blue-grey in colour. Tubercles are capped in yellow. The foot sole possesses a black longitudinal foot stripe. The rhinophoral clavus possesses 27-30 lamellae. *Phyllidia tula* has a longitudinal black stripe on its foot, but the foot is very dark grey and the notum possesses single rounded tubercles and is without ridges. *Phyllidia coelestis* is a smaller species which has neither a foot stripe nor a median ridge. It is more oval in shape and possesses 19-26 lamellae on the rhinophoral clavus. The morphology of its penial spines also differs (Brunckhorst, 1989b; compare Figs 24D, 25B).

Phyllidia tula Er. Marcus & Ev. Marcus

Figs 24E-F, 25A, Pl.1E

Phyllidia tula Er. Marcus & Ev. Marcus, 1970: 172, figs 43-47.—Brunckhorst, 1989a: 7 (colour photograph).

Type. *Phyllidia tula* Er. Marcus & Ev. Marcus. Lectotype here designated as larger syntype (approximately 80 mm preserved length, specimen twisted in "U" shape in preserved state) USNM 576439; figured by Er. Marcus & Ev. Marcus, 1970: fig 43; paralectotype (second syntype, approximately 55 mm preserved length, contracted and flattened) USNM 576439.

Material examined. *Western Pacific Ocean – Micronesia* – 80 & 55 mm specimens (USNM 57639), Ellice Islands, 1 Dec. 1965, R.L. Sixberry.

Guam – 59 mm specimen, Bile Bay, 15 m depth, 15 Mar.

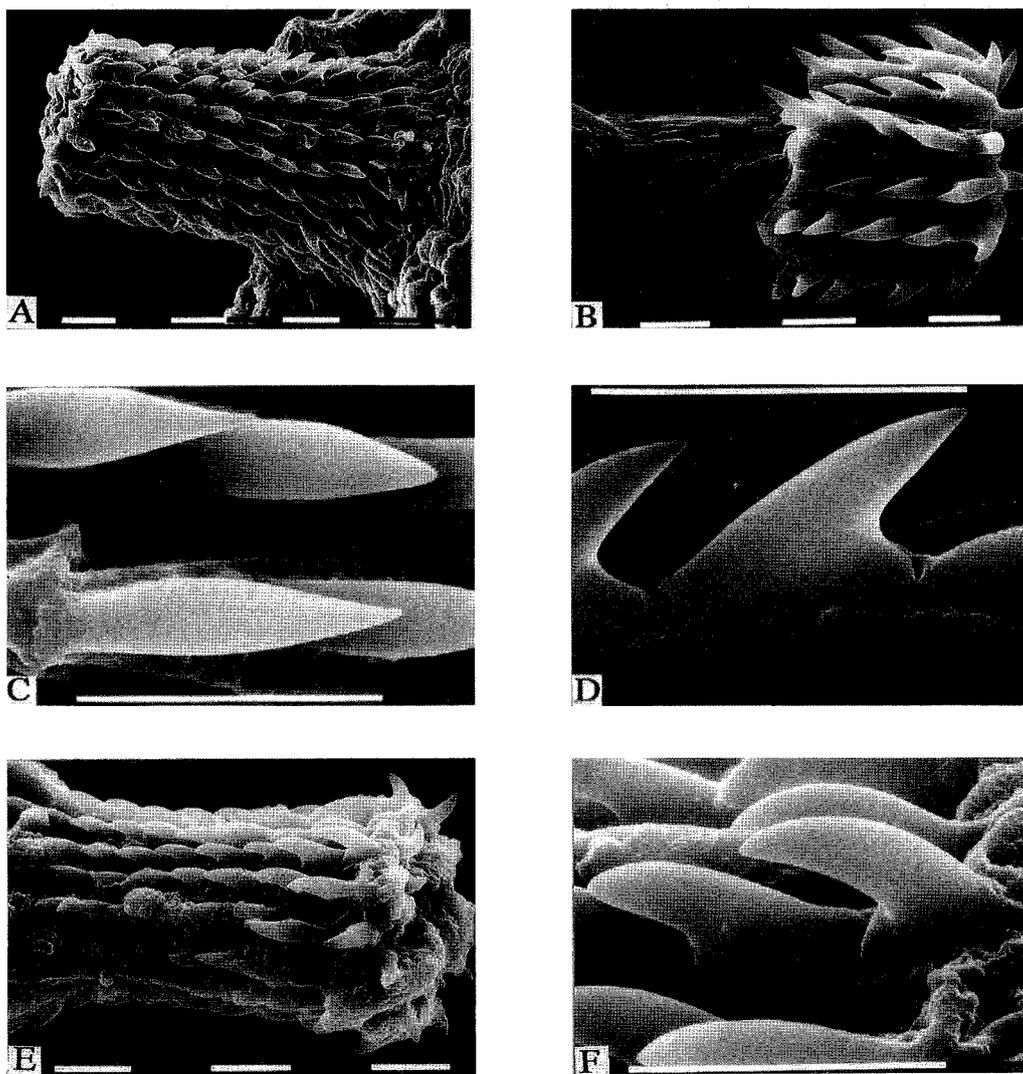


Fig. 24. A, *Phyllidia varicosa*. SEM of everted penis; B, *Phyllidia varicosa*. SEM of partially everted penis. C, *Phyllidia varicosa*. SEM of two rows of penial spines; D, *Phyllidia varicosa*. SEM of penial spine, lateral view; E, *Phyllidia tula*. SEM of everted penis; F, *Phyllidia tula*. SEM of penial spines, lateral view. Scales = 10 μ m.

1969, Carlson-Hoff; 76 mm specimen, Bile Bay, 3 m depth, 28 June 1970, Carlson-Hoff; 46 & 53 mm specimens (AM C162715), Bile Bay, 6 m depth, 27 June 1988, DJB & SKB; 51 & 52 mm specimens (AM C162717), Bile Bay, 14 m depth, 30 June 1988, DJB & SKB; 86 mm specimen (AM C162716), Bile Bay, 10 m depth, 2 July 1988, DJB & SKB; 71 & 65 mm specimens (AM C162713), Annae Island, 9 m depth, 5 July 1988, DJB & SKB; 55 mm specimen (AM C162712), Bile Bay, 4 m depth, 9 July 1988, DJB & SKB; 65 mm specimen (AM C162714), Bile Bay, 10 m depth, 15 July 1988, DJB & SKB; 45 & 54 mm specimens (AM C168906), Bile Bay, 5 m depth, 14 Feb. 1988, Carlson-Hoff; 48 mm specimen (AM C168907), Bile Bay, 16 m depth, 15 Mar. 1969, Carlson-Hoff.

External morphology (Fig.25A, Pl.1E). Live specimens ranged in length from 45-86 mm and mean size was 59 mm. The basic colours of the animal are black (the mantle background) and pale yellow (the tubercles). A large, elongate *Phyllidia*, *P. tula* possesses numerous simple, rounded tubercles on its dorsum. Though the tubercles never form ridges, they may coalesce at their bases. Tubercles are largest centrally (Fig.25A) and progressively decrease in size towards the margins (i.e., large median tubercles, smaller lateral and tiny marginal tubercles) (Pl.1E). These tubercles are yellow and have pale bases. Some tubercles are entirely yellow. The rhinophores are gold coloured and their clavus possesses 20-24 lamellae in larger specimens (50-86 mm). Ventrally, the foot, gills and hyponotum are dark grey. The foot sole has a black, median longitudinal stripe. The foot stripe is always present, but is not always distinct because of the dark grey colouration of the foot. The oral tentacles are quite long, triangular and pointed. They are also dark grey, but the tips are bright yellow.

Anatomy. Typical for the genus *Phyllidia*. The foregut has characteristic markings. One or two longitudinal black lines occur on the dorsal side of the oral tube. The intestine is very broad where it arises from the digestive gland mass (cf. *P. coelestis*, *P. varicosa*).

The reproductive system matches that described earlier for *Phyllidia*. The bursa copulatrix is brown and has a dark tissue envelope. The penis also has a black tissue envelope. The prostatic vas deferens is short and straight (i.e., not convoluted); distally it narrows to become a long duct leading into the penis. The oviduct leading from the ampulla divides just prior to entering the nidamental gland mass. It is black in the region of its division. Penial spines are stout, and curve smoothly to their apex (Fig.24E). Individual spines measure 5-8 m in vertical height and 4-5 μ m across the base (Fig.24F).

Distribution. *Phyllidia tula* is known only from Micronesia (Er. Marcus & Ev. Marcus, 1970; present work). It appears to be restricted in its distribution and has not been found elsewhere in the western Pacific Ocean despite intensive collecting.

Remarks. The distinctive features of *P. tula* include:

its numerous, yellow, rounded tubercles which are isolated or coalesced only at their base and do not form ridges (as occur in *P. varicosa* and *P. coelestis*); a gradation in tubercle size from the central area to the marginal edge of the mantle; a dark grey ventral surface, except for the black stripe on the foot sole and the yellow tips of the oral tentacles; and oral tentacles which are triangular in shape with pointed ends rather than rounded as occur in *P. varicosa* and *P. coelestis*. Internally, *P. tula* has black longitudinal markings on the foregut (*P. coelestis* has transverse markings; *P. varicosa* has none). A feature of the reproductive system in *P. tula* not observed in any other species is the division of the oviduct just prior to its entry to the nidamental gland mass. The penial spines of *P. tula* are broader and more cylindrical than those of *P. varicosa*.

Phyllidia coelestis Bergh, 1905

Fig.25B, Pl.1F-H

- Phyllidia coelestis* Bergh, 1905: 182, pl.3, fig.16.—Eliot, 1906: 673.—Pruvot-Fol, 1956: 64.—Pruvot-Fol, 1957a: 106.—Kenny, 1970: 91.—Burn, 1975: 516.—Coleman, 1981: 157, pl.472.—Lin, 1983: 152, pl.1, fig.5.—Willan & Coleman, 1984: 53.—Lin *et al.*, 1986: 85.—Brunckhorst, 1989b: 35-45, figs 1-4.—Coleman, 1989: 49.—Lin, 1990: 137.—Gosliner & Behrens, 1990: pl.11 B (left).
- Phyllidia nobilis*.—Farran, 1905: 345, pl.3, figs 16,17 (non *Phyllidiella nobilis* Bergh, 1869).
- Phyllidia elegans*.—Edmunds, 1972: 82, fig.4b (non *Phyllidia elegans* Bergh, 1869).
- Phyllidia picta* Pruvot-Fol, 1957a: 110-111, figs 5-12.—Burn, 1975: 516 (n.syn.).
- Phyllidia alia* Yonow, 1984a: 224, figs 6c-d, 7a, 8f-g.
- Phyllidia varicosa*.—Gosliner, 1987: 90, pl.152 (non *Phyllidia varicosa* Lamarck, 1801).

Comments on synonymy. Bergh (1905) described *Phyllidia coelestis* from a 32 mm specimen collected on a reef-flat near Salayer, Indonesia, during the "Siboga" expedition. He also published a colour drawing of the living animal (Bergh, 1905: pl.3, fig.16). The holotype of *P. coelestis* was partially dissected by Bergh, but remains recognisable. The above synonymy follows that of Brunckhorst (1989b). I have recently examined the holotype of *Phyllidia picta* and found it to be *P. coelestis*. Risbec (1956) misidentified four of his "*P. honloni*" specimens; they are *P. coelestis*. The syntype figured by Risbec, however, is *P. varicosa* (see comments under *P. varicosa*). Coleman (1989) has recently published a colour photograph of *P. coelestis*.

Types. *Phyllidia coelestis* Bergh. Holotype (33 mm preserved length; partially dissected and notum intact) ZMA Moll.3.05.022; figured by Bergh, 1905: pl.3, fig.16 (Indonesia).

Phyllidia picta Pruvot-Fol. Holotype (12 mm preserved length) BMNH 1854.7.19.91; figured by Pruvot-Fol, 1957a: figs 5-12.

Phyllidia alia Yonow. Holotype (22 mm preserved length)

BMNH 198310 W/1, figured by Yonow, 1984a: fig.6c. Paratype (30 mm preserved length) BMNH 198310 W/2.

Phyllidia honloni Risbec. Four syntypes (preserved lengths - E34207, 32 mm; E34888, 24 mm; E34212, 40 mm; E34258, 51 mm) MNHN; not figured by Risbec, 1956.

Material examined. *Western Pacific Ocean* - 33 mm specimen (ZMA Moll. 3.05.022), Indonesia, ?1890-1900 Siboga Expedition; 12 mm specimen (BMNH 1854.7.19.91), Java, ?1850 collector unknown; 4 specimens (32 mm, MNHN E34207, 51 mm, MNHN E34258, 24 mm, MNHN E34888,

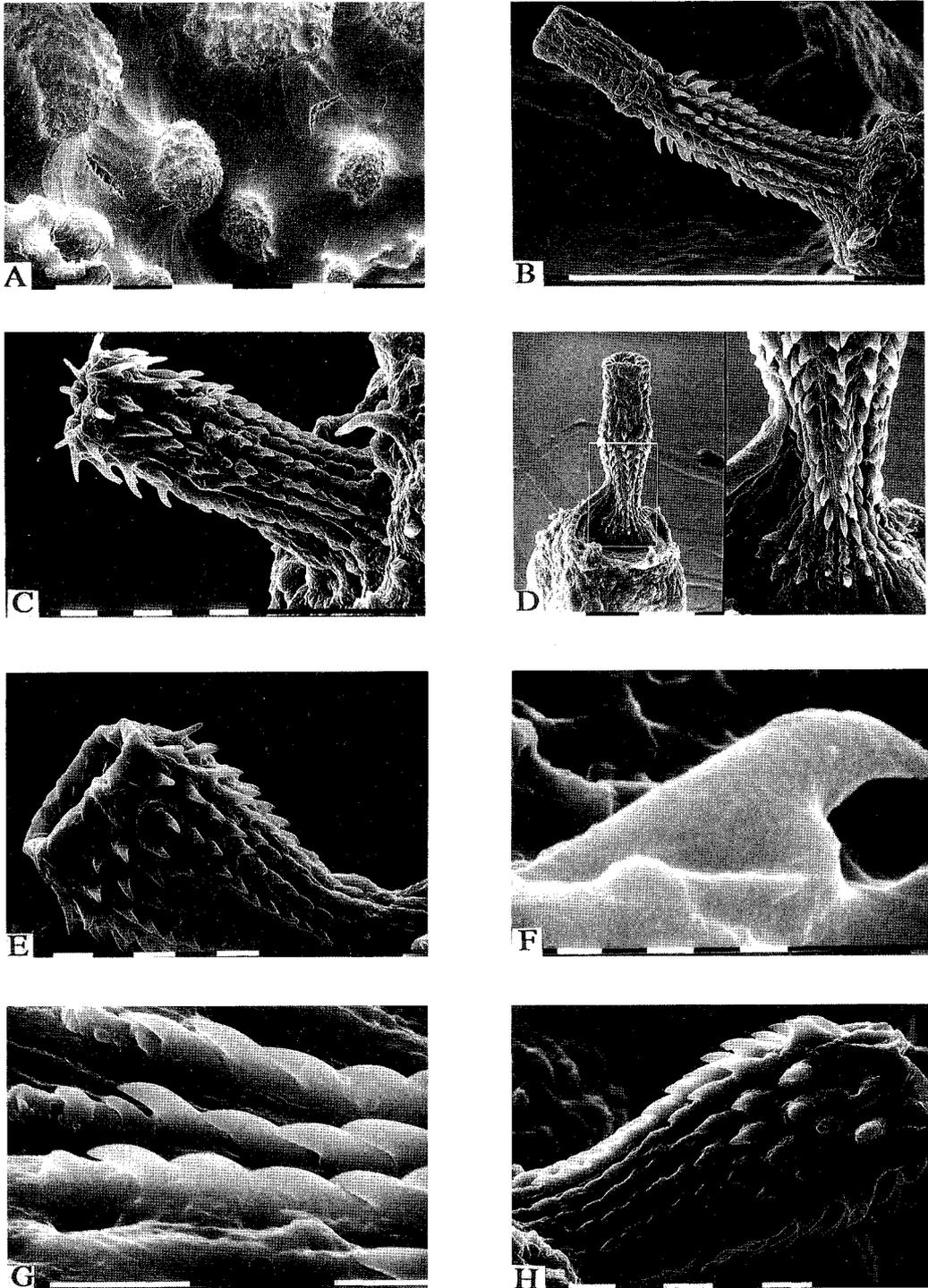


Fig.25. A, *Phyllidia tula*. SEM of median notal tubercles (notum slightly damaged), scale = 1 mm; B, *Phyllidia coelestis*. SEM of completely everted penis showing distal portion without spines, scale = 0.1 mm; C, *Phyllidia elegans*. SEM of everted penis, scale = 10 μ m; D, *Phyllidia ocellata*. SEM of everted penis. scale = 50 μ m; E, *Phyllidia ocellata*. SEM of everted penis, scale = 10 μ m; F, *Phyllidia carlsonhoffi* n.sp. SEM of a single penial spine, scale = 1 μ m; G, *Phyllidia willani* n.sp. SEM of rows of penial spines, scale = 10 μ m; H, *Phyllidia babai* n.sp. SEM of everted penis, scale = 10 μ m.

40 mm, MNHN E34212) ?Risbec, 1956; 1 specimen, Cagli, Fiji, 25 May 1986, G. Brodie; 1 specimen, Makaluva Channel, Fiji, 5 Aug. 1986, G. Brodie; 1 specimen, Suva Reef, Fiji, 25 Feb. 1986, G. Brodie; 13 mm specimen, Nukubuca, Laucala Bay, Fiji, 1 m depth, 9 July 1987, RCW; 31 mm specimen (AM C168782), Fiji, Yonow; 55 & 60 mm specimens (AM C168790), Orontes Reef Point, Essington, NT, 13 m depth, 10 Aug. 1986, RCW; 48 mm specimen (AM C153599), Darwin Harbour, NT, 8 m depth, 24 June 1987, W. Rudman; 35 mm specimen, Thursday Island, Torres Strait, 2 m depth, 16 June 1985, DJB; 1 specimen (AM C168781), Uepi Island, Solomon Islands, 16-20 m depth, 24 May 1987, P.Chapman-Smith; 27 & 41 mm specimens (AM C142660), Negros Island, Philippines, 20 m depth, 3 Mar. 1983, B.E. Picton.

Eastern Australia - Great Barrier Reef - 1 specimen, Orpheus Island, 8 m depth, 8 Nov. 1986, R. Cattaneo; 1 specimen, Phantom Channel, Orpheus Island, 8 m depth, 8 Nov. 1986, G. Caferio; 1 specimen, Orpheus Island, 6 Nov. 1986, R. Cattaneo; 28 & 32 mm specimens (AM C168783), Pelorous Island, Townsville, 10-15 m depth, 20 Mar. 1982, M. Ready; 1 specimen (AM C138123), Pelorous Island, 15 m depth, 10 Apr. 1983, R. King; 1 specimen (AM C138743), Pelorous Island, 1 June 1983, W. Rudman; 1 specimen, Pandora Reef, 4 m depth, 1 Dec. 1984, DJB; 37 mm specimen (AM C162646), Linnet Reef, 10 m depth, 15 Oct. 1986, DJB; 32 mm specimen (AM C168784), Linnet Reef, 10 m depth, 15 Oct. 1986, DJB; 15 mm specimen (AM C168798), Tydeman Reef, 12 m depth, 17 Oct. 1986, DJB; 33 mm specimen (AM C168786), Wistari Reef, 12 m depth, 1 Dec. 1987, DJB; 49 mm specimen (AM C168799), Batt Reef, Cairns, 12 m depth, 17 Jan. 1987, DJB; 52 mm specimen (AM C168785), Heron Reef, 1 m depth, 5 Sept. 1983, RCW; 45 mm specimen, Pandora Reef, 4 m depth, 1 Dec. 1984, DJB; 50 mm specimen, Heron Island, 0-1 m depth, 5 Sept. 1983, RCW; 1 specimen (MV), Heron Island, 8 m depth, 23 July 1973, N. Coleman; 30 mm specimen (MV), off Mackay, 1 July 1977, I. Kirwen; 35 mm specimen (AM C168796), Lizard Island, 3-4 m depth, 8 Oct. 1982, RCW; 19 mm specimen (AM C168797), Lizard Island, 6-10 m depth, 30 Sept. 1982, RCW; 32 mm specimen, Watsons Bay, Lizard Island, 3-5 m depth, 8 Oct. 1982, RCW.

Papua New Guinea - 1 specimen, Milne Bay, 1 Apr. 1983, R. Vanderloos; 27 mm specimen (AM C162647), patch off Lion Island, 12 m depth, 17 June 1988, DJB & SKB; 30 mm specimen (AM C162648), patch off Lion Island, 4 m depth, 18 June 1988, DJB & SKB; 32 mm specimen, patch off Lion Island, 9 m depth, 18 June 1988, DJB & SKB; 39 mm specimen (AM C168787), patch off Lion Island, 18 m depth, 20 June 1988, DJB & SKB; 20 mm specimen (AM C168791), Horseshoe Reef, 18-24 m depth, 21 June 1988, DJB & SKB; 38.5 mm specimen (AM C168795), Loloata Island, 8 m depth, 23 June 1988, DJB & SKB; 1 specimen, Milne Bay, 1 July 1982, R. Vanderloos; 39 mm specimen, Lion Island, 3 m depth, 18 Apr. 1984, Carlson-Hoff; 13.5 mm specimen, Lion Island, 3 m depth, 18 Apr. 1984, Carlson-Hoff; 45 mm specimen, Sunken Barrier Reef, 30 m depth, 20 Apr. 1984, Carlson-Hoff.

Madang - 22 mm specimen (AM C168789), Anemone Reef, 11 m depth, 10 Jan. 1988, RCW; 3 specimens, Magic Pass, 15-22 m depth, 14 Jan. 1988, RCW; 9.5 mm specimen (AM C168788), Barracuda Point, 9 m depth, 14 Jan. 1988, RCW; 18 mm specimen (AM C168792), Madang Lighthouse, 15-35 m depth, 15 Jan. 1988, RCW; 1 specimen, Barracuda Point, 15 m depth, 17 Jan. 1988, RCW; 11 mm specimen, Planet Rock, 12-20 m depth, 19 Jan. 1988, RCW; 16.5 mm specimen, Madang Lighthouse, 7-8 m depth, 22 Jan. 1988,

RCW; 1 specimen, Kranket Island, 3-20 m depth, 24 Jan. 1988, RCW; 1 specimen, The Pinnacle, 6-30 m depth, 25 Jan. 1988, RCW; 2 specimens, 'Hole In Wall', 9-15 m depth, 27 Jan. 1988, RCW; 9 mm specimen, The Chimney, 7-28 m depth, 30 Jan. 1988, RCW; 1 specimen, Wreck-'USS Boston', 15-35 m depth, 31 Jan. 1988, RCW; 28 mm specimen, Kranket Wall, 10-25 m depth, 4 Feb. 1988, RCW; 1 specimen, Kranket Wall, 10-25 m depth, 4 Feb. 1988, RCW; 1 specimen, The Quarry, 6-30 m depth, 11 Feb. 1988, RCW; 4 specimens, Banana Reef, 6-30 m depth, 15 Feb. 1988, RCW; 41 mm specimen (AM C168800), Planet Rock, 6-30 m depth, 16 Feb. 1988, RCW; 45 mm specimen, Banana Reef, 6-30 m depth, 18 Feb. 1988, RCW.

Indian Ocean - 22 mm specimen (BMNH 198310 W/1), Koduwakatimalai Bay, Sri Lanka, 1 m depth, 3 Aug. 1981, N. Yonow; 30 mm specimen (BMNH 198310 W/2), Koduwakatimalai Bay, Sri Lanka, 4 m depth, 7 Aug. 1981, N. Yonow; 20 mm specimen, Réunion Island, 1-20 m depth, 1987, M. Jay.

Western Australia - 31 mm specimen (WAM 240-88), north-west of Buffon Island, 23 July 1988, F. Wells, C. Bryce; 39 mm specimen (WAM 239-88), north-west of Buffon Island, 23 July 1988, F. Wells, C. Bryce; 34 & 29.5 mm specimens (WAM 210-88), Robray Reef, 15 July 1988, F. Wells, C. Bryce; 46 mm specimen (WAM 171-87), Roly Rock, Dampier, 3 Apr. 1987, F. Wells, C. Bryce; 47 mm specimen (WAM 458-89), Kendrew Island, 11 May 1973, COT Survey; 41 mm specimen (WAM 1048-85), 'Yardie Ck.', 28 May 1981, Slacksmith, Bryce; 35 mm specimen, Dampier Archipelago, 0-8 m depth, 22 Apr. 1987, D. Johnson.

Thailand - 55 mm specimen (AM C162649), Phi Phi Island, 1 m depth, 24 Nov. 1989, DJB; 5 specimens (16, 15, 29, 25, 34 mm, AM C168793), Phi Phi Island, 4-16 m depth, 25 Nov. 1989, DJB; 36 & 17 mm specimens (AM C168794), Phuket Island, 5-20 m depth, 7 July 1989, RCW.

External morphology (Pl.1F-H). Live specimens ranged in length from 9-60 mm and mean size was 33 mm. *Phyllidia coelestis* is broad and oval in shape. The basic colours of *P. coelestis* are blue to grey-blue, black and yellow. The notum has three black longitudinal bands; two of these bands run laterally, each on the outside of two, mediolateral, blue-grey ridges which have tubercles capped in yellow. The ridges, which may be interrupted in some specimens, originate anteriorly behind each rhinophore and converge posteriorly in the region of the anus. Two tall, narrow, gold-capped rhinotubercles are present, one immediately behind each rhinophore. The rhinotubercles are separate from the two ridges. Two to four isolated, large, yellow capped tubercles arise from the median black band; however, these are never joined as a midline ridge. There are always two isolated tubercles in the midline, one immediately anterior to, and the other immediately posterior to, the rhinophores (Pl.1F-G). The rhinophores are yellow in colour and each clavus possesses 19-26 lamellae. Around the mantle margin is a broad blue-grey band with small tubercles, the larger ones of which may be yellow capped. Sometimes, meanderings of black encroach into this blue-grey margin. The foot is grey and has no distinctive markings on its sole (Pl.1H).

The pattern of juveniles appears to be simpler with

less variation in the two ridges. These ridges are not interrupted in juveniles, and thus form a distinctive "Y" shape on the dorsum. The oral tentacles are pale grey in colour.

Anatomy. The alimentary and reproductive systems conform to those of *Phyllidia* as described in and Brunckhorst (1989b).

Internally, the single, most significant diagnostic feature of *P. coelestis* is the presence of two transverse, dark bands on the dorsal surface of the foregut. One occurs at the junction of the oral tentacles and the oral tube, and the other occurs on the anterior section of the pharyngeal bulb (Brunckhorst, 1989b). The pharyngeal bulb is quite broad in *P. coelestis*.

The oviduct in *P. coelestis* is thin walled and very convoluted. The receptaculum seminis is translucent and the bursa copulatrix yellow-brown in colour. Distally, the slightly bulbous end of the penis is armed with 14-16 longitudinal rows of spines separated by channels (Fig.25B). Individual spines arise from a relatively narrow, rounded base, are curved, and taper to a fine point facing back towards the vas deferens. The extreme tip of the penis is devoid of spines. In a 33 mm specimen, the distal spineless segment of the penis measured 40 μm , the spinose region measured 76 μm , and an individual spine was approximately 5-7 μm in vertical height (Brunckhorst, 1989b).

Distribution. *Phyllidia coelestis* is relatively common on tropical reefs throughout the Indo-West Pacific Ocean. It is now known from the western Pacific Ocean, South China Sea, Timor Sea and across the Indian Ocean to South Africa (Brunckhorst, 1989b).

Remarks. *Phyllidia coelestis* can be distinguished from other similar-looking phyllidiids by colour and pattern: in particular the "Y" shape of the blue-grey dorsal ridges; the yellow-capped mid-dorsal tubercles (which never form a median ridge as in *P. varicosa*); the evenly tuberculate, broad, blue-grey mantle margin; and the uniformly grey foot without a dark stripe. Internal characters reinforcing specific determination include the two transverse black bands on the foregut and penial spine morphology. Scanning electron micrographs show that the penial spines of *P. coelestis* differ in size and shape from those of *P. varicosa*. Those of *P. varicosa* are broad based, relatively straight and taper evenly to their apex (Fig.24D), whereas those of *P. coelestis* are curved, have a smaller, rounded base which narrows immediately resulting in a slimmer "stem" to the spine (Fig.25B; Brunckhorst, 1989b).

Phyllidia elegans Bergh

Fig.25C, Pl.2A-B

Phyllidia elegans Bergh, 1869: 439-454, 506-507, pls 18b,19.-
Eliot, 1903b: 562.-Dawydoff, 1952: 111.-Pruvot-Fol, 1956:

64-65, fig.4.-Allan, 1957: 5.-Lim & Chou, 1970: 134, pl.17, fig.c.-Burn, 1975: 516.-Lin, 1983: 152, pl.1, fig.1.-
Willan & Coleman, 1984: 53.-Tan *et al.*, 1987: 76, fig.5.-
Coleman, 1989: 48.-Lin, 1990: 135.-Wells *et al.*, 1990: 74, pl.68.

Phyllidia multifaria Yonow, 1986: 1408-1409, figs 4, 11b-h.-
Yonow, 1988: 146, pl.4 (n.syn.).

Comments on synonymy. Yonow's (1986) *P. multifaria* is here considered to fall well within the range of ontogenetic and individual variation I have observed for *P. elegans* (e.g., compare Pl.2A & 2B). Yonow (1988) and Coleman (1989) include colour photographs.

Types. *Phyllidia elegans* Bergh. Holotype (27 mm preserved length; partially dissected, but notum intact) ZMUC; figured by Bergh (1869: pl.18b) (Indonesia).

Phyllidia multifaria Yonow. Holotype, (25 mm preserved length) BMNH 1985.207/1; figured by Yonow 1986: fig.11e.

Material examined. *Western Pacific Ocean* - 27 mm specimen (1862-3 ZMUC), Indonesia, Semper; 1 specimen, Treasure Island, Fiji, 18 Oct. 1985, G. Brodie; 50 mm specimen, Uepi Island, Solomon Islands, 9 m depth, 24 May 1987, P. Chapman-Smith; 32 mm specimen (AM C168801), Uepi Island, Solomon Islands, 16-20 m depth, 24 May 1987, P. Chapman-Smith; 44 mm specimen (AM C168803), South Taiwan, 15 m depth, 20 Dec. 1984, Ms Shuw-ing Lou; 16 mm specimen (AM C168810), Enewetok Atoll, 6-10 m depth, 31 Aug. 1983, S. Johnson.

Guam - 29 mm specimen, Bile Bay, 14 m depth, 11 July 1970, Carlson-Hoff; 26 mm specimen (AM C162658), Bile Bay, 14 m depth, 29 June 1988, DJB & SKB; 23 mm specimen (AM C162659), Bile Bay, 5 m depth, 1 July 1988, DJB & SKB; 25 mm specimen (AM C168808), Asan Bay, 9 m depth, 9 July 1988, DJB & SKB; 18 mm specimen (AM C168805), Bile Bay, 10 m depth, 15 July 1988, DJB & SKB; 21 mm specimen (AM C168809), Bile Bay, 4 m depth, 1 July 1987, Carlson-Hoff; 1 specimen (AM C168812), Bile Bay, 8 m depth, 21 June 1987, Carlson-Hoff; 1 specimen (AM C168813), Bile Bay, 9 m depth, 12 July 1988, DJB; 21 mm specimen, Bile Bay, 4 m depth, 29 June 1988, DJB; 32 mm specimen (AM C168811), Bile Bay, 1 m depth, 17 Sept. 1971, Carlson-Hoff.

Eastern Australia - 45 mm specimen (AM C162652), Flinders Reef, south-east Qld, 10 m depth, 26 May 1987, DJB; 1 specimen (AM C95071), reef off Cardwell, north Qld, ?collector; 52 mm specimen (AM C168804), Flinders Reef, south Qld, 10 m depth, 31 Mar. 1984, RCW; 1 specimen (AM C114850), off Cape York, 16-18 m depth, 18 Feb. 1979, D. Hoese.

Great Barrier Reef - 1 specimen, Wheeler Reef, 17 Nov. 1986, R. Cattaneo; 1 specimen, Wheeler Reef, 10 m depth, 17 Nov. 1986, R. Cattaneo; 53 mm specimen (AM C95071), Yamacutta Reef, 6 m depth, 23 July 1974, D. Young; 15 mm specimen (AM C162650), Macgillivray Reef, Lizard Island, 14 m depth, 18 Oct. 1986, DJB; 30 mm specimen (AM C162651), Heron Reef, 6 m depth, 27 Nov. 1987, DJB; 46 mm specimen, Wistari Reef, 22 m depth, 7 July 1981, RCW; 53 mm specimen (AM C162654), Wistari Reef, 10 m depth, 1 Dec. 1987, DJB; 63 mm specimen (AM C162655), Wistari Reef, 6 m depth, 29 Nov. 1987, DJB; 40 mm specimen, Wistari Reef, 12 m depth, 2 Dec. 1987, DJB; 44 mm specimen (AM C162653), Wistari, 12 m depth, 2 Dec. 1987, DJB; 24

mm specimen (AM C168807), Heron Island, 20 Oct. 1989, A. Flower & L. Newman.

Papua New Guinea – 23 & 26 mm specimens (AM C162656), patch off Lion Island, 10 m depth, 17 June 1988, DJB & SKB; 26 mm specimen (AM C162656), patch off Lion Island, 10-17 June 1988, DJB & SKB; 35 mm specimen (AM C162657), patch off Lion Island, 16 m depth, 18 June 1988, DJB & SKB; 33 mm specimen (AM C168802), Horseshoe Reef, 18-24 m depth, 21 June 1988, DJB & SKB; 1 specimen, Milne Bay, 1 Apr. 1983, R. Vanderloos.

Madang – 45 mm specimen, The Pinnacle, 20 m depth, 11 Jan. 1988, RCW; 41 mm specimen, The Chimney, 15-30 m depth, 17 Jan. 1988, RCW; 32 mm specimen, The Pinnacle, 6-30 m depth, 25 Jan. 1988, RCW; 1 specimen, The Pinnacle, 5-46 m depth, 8 Feb. 1988, RCW; 1 specimen, Christmas Bay, 6-30 m depth, 10 Feb. 1988, RCW; 1 specimen, The Quarry, 6-30 m depth, 11 Feb. 1988, RCW; 1 specimen, Planet Rock, 6-30 m depth, 16 Feb. 1988, RCW; 36 mm specimen (AM C168814), 18-30 m depth, 1 Feb. 1988, RCW; 2 specimens (AM C168816), 18-30 m depth, 1 Feb. 1988, RCW; 1 specimen (AM C168815), Fiji, 1 July 1987, RCW; 1 specimen, The Pinnacle, 20 m depth, 11 Jan. 1988, RCW; 46 mm specimen, Magic Passage, 18 m depth, 18 Jan. 1988, RCW; 60 mm specimen, Rasch Passage, 15 m depth, 19 Jan. 1988, RCW; 5 specimens, Planet Rock, 6-30 m depth, 16 Feb. 1988, RCW.

Indian Ocean – 5 specimens (AM C168801), St Paul, Réunion Island, 1989, M. Jay; 14, 19 & 38 mm specimens (AM C162660), Phi Phi Island, southern Thailand, 16 m depth, 28 Nov. 1989, DJB; 35 mm specimen (AM C162661), Phi Phi Island, southern Thailand, 18 m depth, 2 Dec. 1989, DJB.

Western Australia – 42 mm specimen (WAM 66-87), Roly Rocks, 5 m depth, 31 Mar. 1987, F. Wells & C. Bryce; 47 mm specimen, Roly Rocks, 5 m depth, 31 Mar. 1987, F. Wells & C. Bryce; 1 specimen (WAM 605-86), Christmas Island, 1986, F. Wells; 1 specimen (WAM 2420-84), Scott Reef, 1984, C. Bryce; 1 specimen (WAM), Scott Reef, ?collector; 1 specimen (MV), Coral Bay, southern WA, 9 m depth, 1 Aug. 1979, I. Kirwen.

Red Sea – 25 mm specimen (BMNH 1985.207/1), Jezarat Seba, 10-15 m depth, 23 June 1983, N. Yonow; 35 mm specimen (BMNH 1985.207/2), 10-15 m depth, 7 Aug. 1983, N. Yonow; 25 mm specimen, Abington Reef, 10-15 m depth, 1983, N. Yonow; 30 & 35 mm specimens, 10-15 m depth, 1983, N. Yonow; 3 specimens, ?Red Sea, 1983, ?N. Yonow.

External morphology (Pl.2A-B). Live specimens ranged in length from 14-63 mm and mean size was 35 mm. The basic colours of *Phyllidia elegans* are black, pink and yellow. The background of the dorsum is black and the notal tubercles are pink and often capped in yellow. However some specimens may have only one or a few yellow-capped tubercles. The pink base of each rhinotubercle spreads out around its respective rhinophoral opening. The notal tubercles often appear to line up, medially and if coalesced may form irregular broken ridges (however these seem to be quite variable). In larger animals tubercles tend to remain isolated but their bases may merge. The more densely packed, smaller tubercles around the mantle edge have black rays running between them to the edge of the mantle. The rhinophores are yellow and possess 18-22 lamellae on their clavus (in specimens greater than 40 mm).

Ventrally, the hyponotum is pale grey and cross hatched, and the oral tentacles are pale, finger like with rounded yellow tips. The foot is usually cream to pale grey in colour and it possesses a black line on the lateral side of the foot, just below the grey gills. The sole has a median longitudinal, black stripe.

Anatomy. Typical for the genus *Phyllidia*. There is a single black band encircling the pharyngeal bulb where the oral tube leaves it.

The reproductive system is mostly white in colour; the receptaculum seminis is yellow and translucent; the bursa copulatrix is brownish.

Rows of penial spines are present at the distal end of the penis (Fig.25C). Individual spines are approximately 10 µm in vertical height and are smooth and recurved like those of *P. coelestis*.

Distribution. *Phyllidia elegans* is now known from coral reef regions throughout the western Pacific and Indian Oceans including the Red Sea.

Phyllidia elegans has been collected from Guam and Enewetok but not, to my knowledge from Hawaii.

Remarks. The present study indicates that *P. elegans* displays some ontogenetic and individual variation in the arrangement of notal tubercles. However, the colouration and markings of *P. elegans* serve to clearly distinguish it from its conspecifics. These features include: the pink tubercles which are often capped in yellow; the pale yellow tipped oral tentacles; the pale foot which has a median longitudinal black line on the sole and black lines on its sides; and internally, the black band encircling the junction of pharyngeal bulb and oral tube. *Phyllidia varicosa* and *P. tula* both have a black line on the foot sole, but neither has pink colouration nor black lines on the sides of the foot. Most species of *Phyllidiella* have pink tubercles but their foregut morphology is very different, and none has yellow colouration or dark ventral markings.

Phyllidia flava Aradas

Pl.2C

- Phyllidia papillosa* Aradas, 1847: 120.–Brunckhorst & Willan, 1989: 205-214.
Phyllidia flava Aradas, 1847: 121.–Brunckhorst & Willan, 1989: 205-214, figs 1,2.
Phyllidia rolandiae Pruvot-Fol, 1951: 37-38, fig.19.–Pruvot-Fol, 1954: 328, fig.129a-f.–Pruvot-Fol, 1956: 69, fig.8.
Phyllidia aurata Pruvot-Fol, 1952: 408-411, figs 1-7.–Pruvot-Fol, 1956: 70, fig.9.–Perrone, 1985: 102.
Phyllidia pulitzeri Pruvot-Fol, 1962: 566-569, figs 1-6, pl.1.–Barletta, 1974a: 25-32.–Barletta, 1974b: 1-4.–Barletta & Melone, 1976: 218.–Ros, 1980: 181-183.–Cattaneo, 1982: 376-377.–Cimino *et al.*, 1982: 472.–Schmekel & Portmann, 1982: 139.–Wägele, 1984: 246-251.–Macri, 1985: 33-36.–Perrone, 1985: 102.–Wägele, 1985: 63-79, figs 1-7.–Macri, 1986: 3-5.–Karuso, 1987: 36.–Wägele & Schminke, 1987:

4, figs 23, 29.—Wägele, 1988: 48, fig.3.
Phyllidia sp.—Perrone, 1983: 177-178, figs 1-5.

Comments on synonymy. The above synonymy follows Brunckhorst & Willan (1989). In their review, Brunckhorst & Willan (1989) discuss the taxonomic status of this species choosing *P. flava* as the senior synonym for the four other available names (above). Acting as first revisors, Brunckhorst & Willan considered the description of *P. flava* to be more complete than that of *P. papillosa*. *Phyllidia depressa* Aradas was considered unrecognisable. A neotype for *P. flava* was designated in order to fix it and *P. pulitzeri* as objective synonyms (Brunckhorst & Willan, 1989).

Types. *Phyllidia papillosa* Aradas. Holotype untraceable.
Phyllidia flava Aradas. Holotype untraceable (Sicily). Neotype (20 mm preserved length) MNHN, designated by Brunckhorst & Willan, 1989: fig.1.

Phyllidia aurata Pruvot-Fol. Holotype (18 mm preserved length) MNHN; figured by Pruvot-Fol, 1953: fig.1.

Phyllidia rolandiae Pruvot-Fol. Holotype lost.

Phyllidia pulitzeri Pruvot-Fol. Holotype lost. Neotype (20 mm preserved length) MNHN, designated by Wägele, 1985: 65; figured by Brunckhorst & Willan, 1989: fig.1.

Material examined. *Mediterranean Sea* – 20 mm specimen (MNHN), Xlendi, Gozo, Malta, 5-30 m depth, 1 May 1983, Heike Wägele; 1 specimen, Zaffino Cave, Italy, 6 m depth, 1 May 1979, R. Cattaneo; 1 specimen, Zaffino Cave, Italy 6 m depth, 1 June 1982, R. Cattaneo; 19 mm specimen (AM C168817), Portofino-Aurora, Italy, 20 m depth, 8 Jan. 1981, R. Cattaneo; 1 specimen, Zaffino Cave, Italy, 6 m depth, 1 May 1978, R. Cattaneo; 17 mm specimen (AM C162662), Xlendi, Malta, 8 m depth, 28 Mar. 1983, H. Wägele; 19 mm specimen (AM C162663), Cape Zafferano, Sicily, 1985, M. Chemello; 21 mm specimen (AM C162664), Portofino, Italy 20 m depth, 24 Jan. 1981, R. Cattaneo; 27 mm specimen (AM C162665), Monaco, Italy, 20 m depth, 9 July 1980, G. Barletta.

External morphology (Pl.2C). *Phyllidia flava* is a relatively small species of *Phyllidia* (the largest specimen examined was 27 mm preserved length). This species does not have any black pigmentation and is therefore unique in the genus *Phyllidia*. In life, the colour of the notum, hyponotum, and foot is (golden) yellow. Many tubercles are yellow in colour though some notal tubercles are coloured white. There are two types of notal tubercles. The larger, broader, rounded ones are white. Interspersed between these are smaller, conical yellow ones (see Wägele, 1985; Brunckhorst & Willan, 1989: fig.1). However, the distinction between tubercle types is difficult to discern in the preserved animals (see Wägele, 1985 and Brunckhorst & Willan, 1989 for discussion of preservation artefacts). The rhinophores are yellow. The mantle possesses a skeletal network formed from massed, lanceolate spicules (Perrone, 1983; personal observation). These spicules also support the notal tubercles.

Anatomy. Typical for the genus *Phyllidia*. The viscera and reproductive system are all yellow in colour.

Minute penial spines (approximately 3-4 µm in vertical height) were observed under the light microscope but were not isolated for SEM studies.

Distribution. *Phyllidia flava* is known only from the Mediterranean Sea and is the only species of *Phyllidia* recognised from there. For records, see Wägele (1985) and Brunckhorst & Willan (1989).

Remarks. Wägele (1984, 1985) gave a detailed description of the anatomy and histology of this species. *Phyllidia flava* is bright yellow with contrasting large white tubercles. Smaller tubercles are yellow. As *Phyllidia flava* lacks black pigmentation it is easily distinguished from all of its conspecifics. *Phyllidia ocellata* is the only other species with a gold background colour to the dorsum that sometimes has white capped tubercles. However *P. ocellata* is a large species which has black, often circular, regions on the dorsum. Ventrally, *P. ocellata* is coloured grey.

Phyllidia ocellata Cuvier

Fig.25D-E, Pls 2D-H, 3A

Phyllidia ocellata Cuvier, 1804a: 269, pl.a, fig.7.—Cuvier, 1804b: 277.—Oken, 1815: 286.—Gray, 1850-1854: 312, fig.8.—Gray, 1853: 220.—Gray, 1857: 216.—Bergh, 1869: 508-509.—Pruvot-Fol, 1956: 62-63, fig.2.—Baba, 1965: 182, fig.585.—Burn, 1970: 39-41.—Nishimura & Suzuki, 1971: 140, pl.51, fig.5.—Edmunds, 1972: 77-79, fig.2.—Baba, 1975: 259, fig.6.—Baba & Hamatani, 1975: 176-178, fig.4.—Burn, 1975: 516.—Coleman, 1981: 157, pl.473.—Willan & Coleman, 1984: 42, pl.130.—Brunckhorst, 1985: 49, 51.—Tan *et al.*, 1987: 76, fig.4.—Coleman, 1989: 47.

Phyllidiopsis carinata Eliot, 1910: 435-436, pl.25, figs 8, 9, 12.

Phyllidia multituberculata Boettger, 1918: 129-130, pl.8, figs 4a-c.—O'Donoghue, 1932: 164-165.—Yonow & Hayward, 1991: 21, figs 10F, 13C.

Phyllidia tuberculata Baba, 1930: 117-118, pl.4, fig.1a-d (non *Phyllidia tuberculata* Risbec, 1928).

Phyllidia japonica Baba, 1937: 310 (n.nom. pro. *P. tuberculata* Baba, 1930).—Baba, 1949: 71-72, 156-157, pl.29, fig.108.—Baba, 1960: 112, pl.55, fig.14.—Lim & Chou, 1970: 134, pl.16, fig.c.

Phyllidia baccata Pruvot-Fol, 1957a: 111-113, figs 13-21, pl.1 (n.syn.).

Phyllidia ocellata undula Yonow, 1986: 1411-1413, figs 5, 12a,b.—Yonow, 1988: 146, pl.5 (n.syn.).

Comments on synonymy. Pruvot-Fol's (1956) *P. baccata* is included in the synonymy of *P. ocellata* as her description and figures clearly match the present species.

The taxon which Yonow (1986) referred to as *P. ocellata undula* has now been collected in the Indian Ocean (Réunion Island and western Australia) and the western Pacific Ocean (Great Barrier Reef, Australia and Papua New Guinea) (present work), and therefore the *P. ocellata undula* form is not endemic to the Red

Sea. Its colouration is here considered to fall within the extremely wide range of pattern observed in *P. ocellata* specimens examined in the present work (Pls 2D-H, 3A). There are no anatomical differences.

Types. *Phyllidia ocellata* Cuvier. Lectotype here designated (approximately 35 mm preserved length) MNHN; ?figured by Cuvier, 1804a: fig.7 (Timor).

Phyllidiopsis carinata Eliot. Holotype (20 mm preserved length) BMNH 1919.9.16.8; figured by Eliot, 1910: pl.25, figs 8, 9, 12.

Phyllidia multituberculata Boettger. Holotype not located.

Phyllidia tuberculata Baba (= *P. japonica* Baba). Holotype not located; notes and drawings of original specimen were kindly made available to me by Dr K. Baba (*in litt.*, 1987, 1989).

Phyllidia baccata Pruvot-Fol. Holotype should be in MNHN, but not located (was dissected by Pruvot-Fol); figured by Pruvot-Fol, 1956: pl.1, figs 13-21.

Phyllidia ocellata undula Yonow. Holotype (18 mm preserved length) BMNH 1985.208/1, figured by Yonow 1986: figs 5a,b, 12b; paratype (40 mm preserved length) BMNH 1985.208/2.

Material examined. *Western Pacific Ocean* – 1 specimen (MNHN), Timor, ?1790-1800 Baudin, Timor Expedition; 1 specimen, Sagami Bay, Japan, 1949, K. Baba; 25 mm specimen, Echizen Coast, Japan, 8 Aug. 1976, K. Baba; 40 mm specimen, Sado, Japan, 3 Sept. 1969, Dr Usuki; 50 mm specimen, Echizen-Cho, Japan, 8 Aug. 1976, Takaoka Club; 1 specimen, Sagami Bay, Japan, 3 Sept. 1969, K. Baba; 1 specimen, Pacific Harbour, Fiji, 11 Jan. 1986, Gibbons; 35 mm specimen, Treasure Island, Fiji, 23 Nov. 1985, G. Brodie; 50 mm specimen, Suruga Bay, Japan, 15 Dec. 1976, Tokai University; 50 mm specimen, Fiji, 1 July 1987, RCW; 2 specimens, Lelepa Island, Vanuatu, 20 m depth, 1 Dec. 1985, L. Thornton; 60 mm specimen, Isle Of Pines, New Caledonia, 23 m depth, 1 Sept. 1988, P. Chapman-Smith; 1 specimen (AM C132455), 'Reef' in Coral Sea, 5-6 m depth, 8 Dec. 1981, D. Young.

Eastern Australia – 57 mm specimen (AM C153239), Split Solitary Island, north NSW, 20 m depth, 1 May 1987, C. Buchanan; 16 mm specimen (AM C168845), Old Woman Island, Mooloolaba, Qld, 14 m depth, 22 Aug. 1987, DJB; 28 mm specimen, Flat Rock, north-east of Point Lookout, 22 m depth, 7 Apr. 1981, RCW; 38 mm specimen (AM C162694), Inner Gneering Shoal, south-east Qld, 15 m depth, 10 July 1982, RCW; 1 specimen (MV), Lord Howe Island, 13 m depth, 27 Nov. 1979, N. Coleman; 38 mm specimen, Inner Gneering Shoals, south-east Qld, 16 m depth, 10 July 1982, RCW; 45 mm specimen, The Crack, Norfolk Island, 15 m depth, 1 June 1991, K. Whysall.

Great Barrier Reef – 1 specimen, north-west of Orpheus Island, Ingham, 10 m depth, 8 Nov. 1986, R. Cattaneo; 60 mm specimen, Magnetic Island, Townsville, 8-10 m depth, 1985, G. & J. Kelly; 1 specimen, Cape Cleveland, Townsville, 6-10 m depth, 1985, G. & J. Kelly; 46 mm specimen (AM C168844), Bare Islet, AIMS, north Qld, 5 m depth, 8 Aug. 1986, DJB; 1 specimen (MV), Tryon Island, 16 m depth, 1 July 1969, R. Burn; 1 specimen (MV), Heron Island, 13 m depth, 17 July 1973, N. Coleman; 1 specimen (AM C95070), Yamacutta Reef, 28 July 1974, I. Loch; 1 specimen (MV), Swains Reefs complex, 15 Sept. 1974, N. Coleman; 1 specimen (MV), Heron Island, J. Booth; 3 specimens (44, 64, 28 mm, AM C162693), Bare Islet, AIMS, Townsville, 8 m

depth, 18 Sept. 1986, DJB; 36 mm specimen (AM C162698), Tydemann Reef, PCB, 12 m depth, 17 Oct. 1986, DJB; 70 mm specimen, Low Isles, north Qld, 0-1 m depth, 1 Aug. 1988, A. Page; 45 mm specimen (AM C168902), Two Isles Reef, off Cooktown, 12 m depth, 14 Oct. 1986, DJB; 37 & 51 mm specimens (AM C168903), Wistari Reef, 10 m depth, 12 Nov. 1980, RCW; 40 mm specimen, Lady Musgrave Island, 18 m depth, 1 Aug. 1989, C. Buchanan; 50 mm specimen, Cape Cleveland, Townsville, 6-10 m depth, 1985, G. & J. Kelly.

Papua New Guinea – 43 mm specimen, Milne Bay, 1 Aug. 1982, R. Vanderloos; 44 mm specimen (AM C162696), patch off Lion Island, 4 m depth, 17 June 1988, DJB & SKB; 39 & 37 mm specimens (AM C162697), patch off Lion Island, 18 m depth, 20 June 1988, DJB & SKB; 39 mm specimen, patch off Lion Island, 18 m depth, 24 June 1988, DJB & SKB; 1 specimen (AM C136921), Normanby Island, 1 Dec. 1981, N. Coleman.

Madang – 42 mm specimen (AM C168847), MV Coral Queen, 15-33 m depth, 13 Jan. 1988, RCW; 30 mm specimen (AM C168846), Madang Lighthouse, 7-8 m depth, 22 Jan. 1988, RCW; 53 mm specimen (AM C162695), Magic Passage, 18 m depth, 18 Jan. 1988, RCW; 43 mm specimen, The Chimney, 7-28 m depth, 30 Jan. 1988, RCW; 3 specimens (45, 36, 62 mm, AM C168847), 5-28 m depth, 1 Feb. 1988, RCW; 30 mm specimen, under Madang Lighthouse, 7-8 m depth, 22 Jan. 1988, RCW.

Indian Ocean – 40 mm specimen (BMNH 1985.208/2), Tongue Island, Red Sea, 15 m depth, 19 June 1983, N. Yonow; 18 mm specimen (BMNH 1985.208/1), Tongue Island, Red Sea, 20 m depth, 19 June 1983, N. Yonow; 44 mm specimen (BMNH), Tongue Island, Red Sea, 19 June 1983, N. Yonow; 30, 28 & 15 mm specimens, (AM C168905), Réunion Island, 5-20 m depth, 1989, M. Jay; 50, 45 & 40 mm specimens (MNHN), Réunion Island, 1-20 m depth, 1987, M. Jay.

Thailand – 30 & 39 mm specimen (AM C162699), Phi Phi Island, 7-15 m depth, 25 Nov. 1989, DJB; 35 & 38 mm specimen (AM C162700), Phi Phi Island, 16 m depth, 27 Nov. 1989, DJB; 35 mm specimen (AM C162701), Phi Phi Island, 27 Nov. 1989, DJB; 32 & 26 mm specimen (AM C162702), Phi Phi Island, 16 m depth, 1 Dec. 1989, DJB; 33 mm specimen (AM C162703), Phi Phi Island, 18 m depth, 2 Dec. 1989, DJB; 45 mm specimen (AM C162704), Phi Phi Island, 12 m depth, 4 Dec. 1989, DJB; 36 & 33 mm specimen (AM C162705), Phi Phi Island, 16 m depth, 5 Dec. 1989, DJB; 5 specimens (21, 22, 29, 32, 33 mm, AM C168904), Phi Phi Island, 16 m depth, 28 Nov. 1989, DJB & SKB.

Western Australia – 40 mm specimen (WAM), Rottneest Island, 6 Dec. 1984, C. Bryce; 1 specimen (WAM 347-85), Shark Bay, 1985, C. Bryce; 29 mm specimen (WAM 347-85), Shark Bay, 7-12 m depth, 17 Mar. 1986, F. Wells & C. Bryce; 51 mm specimen (AM C140563), north-north-east of Port Hedland, 38-40 m depth, 25 Oct. 1983, B.W. Jenkins; 1 specimen (WAM 70-64), Beagle Island, 63 m depth, 1 Apr. 1959, W. & W. Poole; 39 mm specimen (WAM 245-88), Lucas Island, 24 July 1988, C. Bryce & F. Wells; 36 mm specimen (WAM 1088-85), Dirk Hartog Island, 3-6 m depth, 4 May 1981, S. Slack-Smith; 42 mm specimen (WAM 301-85), Shark Bay, 7 m depth, 15 Mar. 1986, F. Wells & C. Bryce; 55 mm specimen (AM C140597), Kingston Reef, Rottneest Island, 10 m depth, 11 Sept. 1982, G. Saveracker.

External morphology (Pls 2D-H, 3A). Live specimens ranged in length from 16-70 mm and the mean was 39 mm. The primary colours of *P. ocellata* are black, white and gold. The ventral surface is grey.

The dorsum has a gold background and black areas (typically rings) bordered with white. The rounded or conical tubercles are usually isolated and may be gold, or white in colour. Their surface is often irregular because of the underlying matrix of supporting spicules.

Tubercles may be compound in some specimens, but generally they do not coalesce into continuous ridges. Often the median tubercles appear to line up longitudinally, almost joining as a ridge.

The rhinophores are gold in colour and their clavus possess 27-30 lamellae each (42-70 mm specimens).

Ventrally, the cross-hatched hyponotum, gills and foot are grey. The foot sole is paler towards the margin and lacks any distinctive markings. The finger like oral tentacles are gold at their rounded ends.

Anatomy. Typical for the genus *Phyllidia*. In live specimens the digestive glands are orange-red in colour (yellow to orange in the preserved state). The oral tube is almost transparent. The foregut lacks markings. At the posterior end of the intestine, the rectum or anal papilla has dark grey to black pigmentation.

The reproductive organs are generally all pale cream in colour. The receptaculum seminis is translucent. A short (10-15 μm), distal section of the everted penis is devoid of spines. The everted spinous region has a constricted area at its base (Fig.25D). The penial spines (Fig.25E) have a short base, and are narrow and slightly recurved. Individual spines were approximately 5-7 μm in vertical height.

Distribution. *Phyllidia ocellata* is a common phyllidiid throughout the tropical Indo-West Pacific Ocean, including the Red Sea.

Remarks. *Phyllidia ocellata* is easily recognised in the common form as described by Cuvier (1804). The most typical dorsal pattern consists of four to ten black rings bordered in white, each with a central gold or white tubercle. There is little ontogenetic variation in external pattern (i.e., juveniles resemble adults), however considerable individual variation in dorsal pattern occurs in this species. From the basic pattern described, there appear to be numerous related and irregular patterns where the black areas expand and/or meander across the dorsum (Pls 2D-H, 3A). One of these forms was described as "*P. ocellata undula*" by Yonow (1986). The "*undula*" form is intermediate in this respect. Some specimens collected in southern Thailand had a dorsum with a mostly black background and yellow tubercles, but little or no white. The first specimen (33 mm live length) was found mating, *in situ* (16 m depth) with a more "typical" specimen (36 mm live length) (Pl.3A). A third specimen (39 mm) had white borders around some tubercles in the black region (personal observation, 1989).

Phyllidia ocellata can be separated from other predominantly gold-yellow *Phyllidia* species. It appears

to be closest in colour to *P. flava*, but *P. flava* does not have any black pigmentation. *Phyllidia varicosa*, *P. tula* and *P. coelestis* have yellow capped tubercles, but all have blue-grey pigmentation and the former two have a black stripe on the foot sole. *Phyllidia coelestis* has transverse black bars on the foregut and a blue-grey mantle margin.

Phyllidia zebrina Baba

Pl.3B

Phyllidia zebrina Baba, 1976: 5-8, figs 1, 2.

Type. *Phyllidia zebrina* Baba. Holotype (14 mm preserved length) in His Majesty's Marine Biological Laboratory, figured by Baba, 1976: figs 1, 2; this work, Plate 3B.

Material examined. 14 mm specimen, Amadaiba, Japan, 60 m depth, 13 Feb. 1956, His Majesty's Biological Laboratory.

External morphology (Pl.3B). Photographs and notes on this species were kindly made available by Dr K. Baba (*in litt.* 1987, 1989). The dorsum of *P. zebrina* is cream to pale yellow in colour and has a number of short, fine, transverse black lines (brown in the preserved state). These black lines terminate before the mantle edge. Many minute, rounded tubercles arise from the notum giving it a rough appearance. The rhinophores are cream to pale yellow in colour. The anus opens dorsally on a tubercle.

Ventrally, *P. zebrina* is cream coloured. In the holotype the foregut was partly protruding from the mouth and the oral tentacles were not visible.

Anatomy. The anatomy of *P. zebrina* is not known. It is probably the same as that of *Phyllidia*. However the protrusion of part of the foregut through the mouth and the apparent absence of separate oral tentacles (Baba, 1976: 7), suggests that the species may belong in the genus *Phyllidiopsis*. Details of the reproductive system are not known.

Distribution. The holotype of *P. zebrina* was collected from a depth of 60 m in Sagami Bay, Japan. There are no other records to my knowledge.

Remarks. *Phyllidia zebrina* is a distinct species, distinguished by its cream to pale yellow dorsum with very small tubercles and fine black lines. Unlike *P. varicosa* and *P. coelestis*, there are no dorsal ridges. *Phyllidia flava* is yellow, but it completely lacks any black pigmentation. *Phyllidia ocellata* and *P. loricata* have large black rings or spots, not fine black lines like those of *P. zebrina*. Examination of further specimens is essential to elucidate the anatomy and to confirm its generic placement.

Phyllidia exquisita n.sp.

Pl.3C

Type. Holotype here designated (22 mm live length) AM C159472 (viscera intact, notum with single incision); the remaining eight specimens (see material) are designated paratypes.

Material examined. *Western Pacific Ocean* – holotype (22 mm, AM C159472), Wistari reef, GBR, 24 m depth, 29 Nov. 1987, DJB; juvenile specimen (AM C168768), Wistari Reef (west side), GBR, 14 m depth, 19 Aug. 1981, M. Ready; 1 specimen (MV), Tryon Island, GBR, 1972, I. Marrow; 11 mm specimen, Lion Island, PNG, 3 m depth, 18 Apr. 1984, Carlson-Hoff; 12 mm specimen, Motupore, PNG, 3 m depth, 17 Apr. 1984, Carlson-Hoff; 1 specimen (MV), Horseshoe Reef, PNG, 10 m depth, 1 Aug. 1980, N. Coleman; 1 specimen, "Joske's", Fiji, 20 July 1986, G. Brodie; 23 mm specimen (AM C159473), Kwajalein Atoll, Marshall Island, 1983, S. Johnson; 30 mm specimen (AM), Turtle Arch, Norfolk Island, 21 m depth, 1 Nov. 1992, K. Whysall.

Indian Ocean – 15 mm specimen (AM C159474), Phi Phi Island, southern Thailand, 16 m depth, 1 Dec. 1989, DJB.

External morphology (Pl.3C). Live specimens ranged in length from 10-23 mm. *Phyllidia exquisita* is a small species with white, black and yellow colouration. The notum possesses simple, rounded tubercles arranged in more or less longitudinal rows but neither joined by, nor forming ridges. The tubercles take on the colour of their immediate background (i.e., white or black). Tubercles in a white area are capped in yellow. The dorsal pattern is characteristic and appears to show little intraspecific variation. The rhinophores are yellow in colour and each clavus possesses 17-20 lamellae. Centrally, there is a short, longitudinal black line. This line is joined at either end by transverse black lines. Short black radial lines occur marginally and their presence has the effect of highlighting the two white, longitudinal rows of tubercles (Pl.3C). These white areas may be interrupted by a black transverse line. The mantle margin is edged in yellow. The ventral surfaces are white. The foot sole has no characteristic markings, and the oral tentacles are short and conical in ventral view.

Anatomy. Typical for the genus *Phyllidia*. The 22 mm specimen appeared to be mature. In the preserved state the nidamental gland mass is large and cream in colour. The ampulla and bursa copulatrix are also large and cream to yellow in colour. The translucent to white receptaculum seminis is slightly smaller than the bursa. Penial spines were small (less than 5 µm), and could not be isolated for further elucidation by SEM.

Distribution. *Phyllidia exquisita* is presently known from the central and western Pacific Ocean and the north-eastern Indian Ocean (Thailand).

Remarks. *Phyllidia exquisita* is a relatively small species characterised by the possession of white background colour with black lines, two median longitudinal areas of white on either side of the central tubercles, small, simple rounded tubercles which occur in definite rows (but do not form ridges), yellow edge to the mantle margin, and white colouration ventrally.

The present species does not possess the orange-yellow background colouration or the pattern found in *P. ocellata*. It is most similar to *P. willani* n.sp. and *P. babai* n.sp. in the possession of a white background colour and black markings (this work). Both those species are much larger. *Phyllidia willani* n.sp. also differs from *P. exquisita* in having black swirls (Pl.3F), large and small tubercles, a characteristic granular appearance to the notum, and grey colouration ventrally. *Phyllidia babai* n.sp. has black rings (rather than lines) and larger tubercles (Pl.4A). These features are illustrated in the photographs of the living representatives of the three species.

Phyllidia exquisita has 17-20 lamellae (20 mm specimen) on the rhinophoral clavus. In comparison, *P. willani* n.sp. has 16-19 lamellae (43 mm specimen), and *P. babai* has 21-24 lamellae (39 mm specimen) on each rhinophoral clavus. As a juvenile of a species would have proportionally fewer lamellae than an adult (e.g., Fig.3), it is unlikely that *P. exquisita* could be a juvenile of *P. willani* n.sp. (given that specimens of the latter species have the same or fewer lamellae on the rhinophoral clavus).

Etymology. The exquisite and fine patterns of this species are the basis for its name.

Phyllidia carlsonhoffi n.sp.

Fig.25F, Pl.3D

Type. Holotype here designated (27 mm live length) AM C159479; the remaining 35 specimens are designated paratypes.

Material examined. *Western Pacific Ocean* – 32 mm specimen, Makaluva Channel, Fiji, 22 Jan. 1984, G. Brodie; 8 mm specimen, Suva, Fiji, 9 July 1987, RCW; 23 mm specimen, Nukubuko Reef, Laucala Bay, Fiji, 9 July 1987, RCW; 25 mm specimen, Nukulouko (Laucala Bay, Fiji), 9 July 1987, RCW; 29 & 35 mm specimens (AM C168771), Suva Reef, Fiji, 1 July 1987, RCW/Brodie.

Papua New Guinea – Madang – holotype (27 mm, AM C159479), Bombes Reef, 12 m depth, 16 Jan. 1988, RCW; 19 mm specimen, Barracuda Point, 9 m depth, 8 Feb. 1988, RCW; 13 mm specimen, Rasch Passage, 15-33 m depth, 12 Jan. 1988, RCW; 60 mm specimen, Bombes Reef, 15 m depth, 13 Jan. 1988, RCW; 58 mm specimen, Banana Reef, 6-30 m depth, 18 Feb. 1988, RCW; 55 mm specimen, Banana Reef, 6-30 m depth, 18 Feb. 1988, RCW; 46 mm specimen, Rasch Passage, 18 m depth, 19 Feb. 1988, RCW; 68 mm specimen (AM C168770), Madang Lagoon, 5-20 m depth, 18 Feb. 1988, RCW; 55 mm specimen (AM C168770), Madang Lagoon, 5-20 m depth, 18 Feb. 1988, RCW.

Micronesia – 43 & 16 mm specimens (AM C159481), Ponape-Pakin, 14 m depth, 21 Aug. 1985, Carlson-Hoff; 4 specimens (40, 38, 26, 12 mm, AM C159541), Ponape (Mwahnd Pass), 18 m depth, 16 Oct. 1987, Carlson-Hoff; 3 specimens, Truk, 1988, University of Guam Marine Laboratory; 27 & 46 mm specimens (AM C159482), Choptop Reef, Enewetok Atoll, 6 m depth, 15 June 1981, S. Johnson.

Guam – 23 mm specimen, Bile Bay, 8 m depth, 21 June 1987, Carlson-Hoff; 22 mm specimen, Bile Bay, 14 m depth, 15 Mar. 1969, Carlson-Hoff; 33 mm specimen, Bile Bay, 12 m depth, 27 Nov. 1971, Carlson-Hoff; 60 mm specimen (AM C168769), Bile Bay, 10 m depth, 21 June 1987, Carlson-Hoff; 43.5 mm specimen (AM C159480), Bile Bay, 7 m depth, 3 July 1988, DJB & SKB; 47 mm specimen (AM C159484), Bile Bay, 10 m depth, 15 July 1988, DJB & SKB; 60 mm specimen (AM C159483), Bile Bay, 5 m depth, 20 Mar. 1988, Carlson-Hoff; 35 mm specimen, Bile Bay, 12 m depth, 6 Feb. 1974, Carlson-Hoff; 65 mm specimen (AM C159540), Bile Bay, 13 m depth, 2 June 1974, Carlson-Hoff.

External morphology (Pl.3D). Live specimens ranged in length from 8-68 mm and mean size was 36 mm. *Phyllidia carlsonhoffi* has a black background colour with cream tubercles which are capped in yellow. The notal tubercles are broad based but do not form ridges. Large conical, tubercles alternate with very small rounded ones (Pl.3D). The central notal tubercles in this species are relatively tall, attaining a height of 7 mm in some specimens. The rhinophoral pockets occur on the anterior surface of the base of the sharply defined rhinotubercles. There are no tubercles immediately anterior to each rhinophoral pocket. There is, however, a single tubercle situated in the midline anterior to the rhinophores (but not immediately adjacent to the rhinophoral pocket). The rhinophores are yellow in colour and their clavus possess 23-26 lamellae each (40-65 mm specimens).

Ventrally, the hyponotum is grey with a darker grey hatched pattern. The foot and gills are pale grey. The foot sole has a median longitudinal black line. The oral tentacles are very long (2.5-3 mm) and cylindrical, with rounded extremities tipped in bright yellow.

Anatomy. Typical for the genus *Phyllidia*. The pharyngeal bulb is orange-brown in preserved specimens. The oral tube is cream and possesses an indistinct transverse, grey band on its posterior dorsal surface. Posteriorly, the oesophagus expands slightly before entering the digestive gland mass. The intestine is relatively narrow.

In the preserved state the reproductive system is mostly yellow in colour. The receptaculum seminis is translucent. The prostatic vas deferens is quite short and narrow. The penis is silver-white and relatively long. Individual penial spines are very small (4-6 μm in vertical height); they have a very broad base (5 μm) and short curved stem tapering to a rounded apex (Fig.25F).

Distribution. At present *Phyllidia carlsonhoffi* is known from the western Pacific Ocean (Micronesia, Papua New Guinea and Fiji).

Remarks. *Phyllidia carlsonhoffi* is characterised by alternating large conical and small rounded tubercles (not joined as ridges), long, rounded oral tentacles, and a median black line on the foot sole. Internally, the posterior, dorsal oral tube swells slightly as it enters the digestive gland mass. In the preserved state the viscera tend to be darker coloured (brown-orange) than those of other *Phyllidia* species (usually cream). *Phyllidia varicosa*, *P. elegans* and *P. tula* each have a median black line on the foot sole. *Phyllidia varicosa* and *P. elegans* possess notal ridges and compound tubercles (*P. carlsonhoffi* has neither) and are blue-grey and pink respectively. *Phyllidia tula* appears to be similar to *P. carlsonhoffi*, but differs in a number of features. Ventrally, *P. tula* is always dark grey whereas *P. carlsonhoffi* is paler in colour. The oral tentacles are triangular in *P. tula*, whereas they are long and cylindrical in *P. carlsonhoffi*. Dorsally, *P. tula* is more tuberculate with a graduated series of tubercles which decreases in size from very large in the centre to tiny and closely packed at the margin. The tubercles of *P. carlsonhoffi* are evenly spaced with alternating large and small tubercles. *Phyllidia madangensis* n.sp. is very similar to *P. carlsonhoffi* dorsally, however the former lacks alternating smaller tubercles, its larger tubercles are sparsely scattered, and it lacks markings on both the foot sole.

Some internal differences are also apparent. In particular, *P. tula* has longitudinal black lines on the oral tube. In comparison, *P. carlsonhoffi* has a grey band around the posterior of the oral tube (*P. madangensis* lacks foregut markings). The penis of *P. tula* is bulbous (as is typical in *Phyllidia*), whereas that of *P. carlsonhoffi* is slender.

Etymology. This species is named in honour of Mr Clay Carlson and Dr Patty-Jo Hoff.

Phyllidia madangensis n.sp.

Pl.3E

Phyllidia sp.–Gosliner & Behrens, 1990: pl.9H (colour illustration).

Type. Holotype here designated (26 mm live length) AM C162802; the remaining six specimens are designated paratypes.

Material examined. *Western Pacific Ocean* – holotype specimen (26 mm, AM C162802), Barracuda Point, Madang, 15 m depth, 13 Jan. 1988, RCW; 38 mm specimen (AM C168772), Barracuda Point, Madang, 15 m depth, 13 Jan. 1988, RCW; 43 mm specimen, Madang Lagoon, PNG, 18m depth, 8 Feb. 1988, RCW; 13 mm specimen, Bile Bay, Guam, 5 m depth, 8 Dec. 1973, Carlson-Hoff; 48 mm specimen, Bile Bay, Guam, 15 m depth, 15 Mar. 1969, Carlson-Hoff; 70 mm specimen, Lelepa Island, Vanuatu, 20 m depth, 1 Dec. 1985, L. Thornton; 60 mm specimen, Guadalcanal, Solomon Islands, 1 Apr. 1983, I. Knight.

External morphology (Pl.3E). Live specimens ranged in length from 13-60 mm. The dorsum of *Phyllidia madangensis* has a black background and very sparsely scattered tubercles. The rounded tubercles have granular white-grey sides and are capped in bright yellow. Typically, four large, isolated tubercles arise medially. Tubercles are more numerous towards the margins, but even there, they are still isolated and widely spaced (Pl.3E). The rhinophores are gold and their clavus possess 17-20 lamellae (in specimens greater than 38 mm in length). The rhinotubercles are tall and occur immediately posterior, and slightly lateral to each rhinophoral pocket. Immediately in front of, and slightly medial, to each rhinophoral pocket there is a low, rounded tubercle (Pl.3E).

Ventrally, the foot is dark grey with a pale grey margin. There is no median black line on the sole. The anterior edge of the foot is indented slightly and cream to pale yellow in colour. Anteriorly, the triangular oral tentacles are cream in colour.

Anatomy. Typical for the genus *Phyllidia*. In the preserved state the foregut and digestive gland mass are cream in colour and without darker markings. The reproductive system is pale yellow in colour except for the translucent white receptaculum seminis. The penis is white and slightly bulbous as in most *Phyllidia* species. The penial spines of this species were observed under dissecting microscope but they could not be isolated for SEM examination.

Distribution. *Phyllidia madangensis* is currently known from the tropical western Pacific Ocean (Guam, Vanuatu, Solomon Islands and Papua New Guinea).

Remarks. *Phyllidia madangensis* is characterised by having few, sparsely scattered notal tubercles and no dark stripe on the foot sole. Rhinotubercles occur in all *Phyllidia* species, but the presence of a small tubercle immediately in front of each rhinophoral pocket appears to be unique to *Phyllidia madangensis*. Although similar to *P. carlsonhoffi*, *P. varicosa* and *P. tula*, the present species has neither a black line on the foot sole nor markings on the foregut as have the other three species. *Phyllidia madangensis* also has relatively fewer lamellae (17-20) on the rhinophoral clavus when compared to equivalent sized specimens of *P. carlsonhoffi*, *P. varicosa* and *P. tula*.

Etymology. The species is named for its type locality, Madang Lagoon, Papua New Guinea.

***Phyllidia willani* n.sp.**

Fig.25G, Pl.3F

Phyllidia sp. 2.—Tan *et al.*, 1987: 76, fig.7 (colour illustration).
Phyllidia sp.—Gosliner & Behrens, 1990: pl.9G (colour illustration).

Type. Holotype here designated (36 mm live length) AM C159511; the remaining seven specimens are designated paratypes.

Material examined. *Western Pacific Ocean* — 40 mm specimen (AM C142616), Mactan Island, Philippines, 32 m depth, 27 Mar. 1983, B.E. Picton.

Papua New Guinea – Madang — holotype (36 mm, AM C159511), Anemone Reef, 11 m depth, 10 Jan. 1988, RCW; 1 specimen, Barracuda Point, 5 m depth, 13 Jan. 1988, RCW; 43 mm specimen (AM C159512), Madang Lighthouse, 15-35 m depth, 15 Jan. 1988, RCW; 30 mm specimen, Madang Lighthouse, 7-8 m depth, 22 Jan. 1988, RCW; 25 mm specimen (AM C159513), Madang Lagoon, 6-30 m depth, 15 Jan. 1988, RCW; 32 & 50 mm specimens, Madang Lagoon, 6-30 m depth, 15 Jan. 1988, RCW.

External morphology (Pl.3F). Live specimens ranged in length from 23-50 mm. *Phyllidia willani* is more oval than elongate in shape. The dorsum has a very pale lemon-yellow background with minute dots of white pigment which impart an overall granular appearance (Pl.3F). The distinctive pale granular pattern covers the whole mantle region. The notal tubercles have the same granular appearance and are single and rounded. Medially, there are four large tubercles arranged as though at the corners of a diamond. The large tubercles are capped in pale yellow and have minute, low tubercles encircling their bases. Numerous other smaller tubercles are scattered over the notum. Laterally, there are two longitudinal swirls of black (Pl.3F). Small patches of black may also occur on the dorsum. The rhinophores are gold in colour and their clavus possess 16-18 lamellae each (specimens greater than 36 mm).

The hyponotum is pale, cross-hatched and it may have black patches showing through from the dorsum. The foot sole is pale cream in colour. The side of the foot is grey. Anteriorly, the foot is indented and the oral tentacles are long, cylindrical and pale cream-yellow in colour.

Anatomy. Typical for the genus *Phyllidia*. In preserved specimens the digestive gland mass is brown-orange in colour. The foregut is paler and it does not have dark markings. The anal papilla/rectum is pale yellow. The reproductive system is very pale cream to translucent in *Phyllidia willani* and hence the two sperm receptacles are difficult to differentiate without tracing the very fine vaginal duct.

Rows of smooth, sharply pointed and recurved penial spines (4-6 μ m in length) occur in this species (Fig.25G). The penial spines are closely packed, almost overlapping and their bases are fused anteriorly and posteriorly within a row.

Distribution. *Phyllidia willani* is presently known from the South China Sea (Tan *et al.*, 1987), the Philippines and Papua New Guinea.

Remarks. Distinguishing features of *Phyllidia willani* include the pale granular background colouration, the

two laterally positioned longitudinal black swirls, the four median notal tubercles, the pale coloured foot and oral tentacles, orange digestive gland mass, pale yellow rectum, and small fine penial spines.

Phyllidia willani is most similar to *P. ocellata* and *P. babai* n.sp. In contrast to *P. willani*, the dorsum of *P. ocellata* is gold with black areas bordered in white and coloured tubercles which arise from the black areas. *P. ocellata* has a grey foot and grey oral tentacles with yellow tips (both pale cream in *P. willani*). The anal papilla/rectum of *P. ocellata* is dark grey to black (pale yellow in *P. willani*). Mature specimens of *P. willani* have 16-18 lamellae on the rhinophoral clavus whereas those of *P. ocellata* have 27-30 lamellae. The penial spines of *P. willani* are fewer and more sharply recurved than those of *P. ocellata*. The dorsum of *P. babai* n.sp. has a white background and the mantle margin is bordered in yellow. In contrast, *P. willani* has a pale granular dorsum and no contrasting coloured edge to the mantle. The small species, *P. exquisita*, has white, black and yellow colouration. However, it differs from the present species in its possession of a yellow mantle margin, numerous rows of single tubercles, longitudinal and transverse black lines, and two lateral bands of white. Although *P. willani* is a larger species, it has fewer lamellae on the rhinophoral clavus than has the smaller *P. exquisita*.

Etymology. This species is named in honour of Dr R.C. Willan.

***Phyllidia babai* n.sp.**

Fig.25H, Pls 3G-H, 4A

Type. Holotype here designated (37 mm live length) AM C162730; the remaining 14 specimens are designated paratypes.

Material examined. *Western Pacific Ocean – Great Barrier Reef* – 25 mm specimen (AM C94073), Broadhurst Reef, Townsville, 14 m depth, 4 Oct. 1973, I. Loch; 36 mm specimen (AM C162727), Two Isles, 12 m depth, 14 Oct. 1986, DJB; 65 mm specimen (AM C162726), Wistari Reef, 10 m depth, 29 Dec. 1988, L. Newman; 43 mm specimen (AM C132255), North Point Reef, Lizard Island, 18 m depth, 20 Nov. 1981, J. Gates.

Papua New Guinea – holotype (37 mm, AM C162730), patch off Lion Island, 18 m depth, 20 June 1988, DJB & SKB; 29 & 32 mm specimens (AM C162732), patch off Lion Island, 12 m depth, 17 June 1988, DJB & SKB; 3 specimens (25, 34, 26 mm, AM C162731), patch off Lion Island, 18 m depth, 18 June 1988, DJB & SKB; 3 specimens (34, 38, 30 mm, AM C162729), patch off Lion Island, 18 m depth, 20 June 1988, DJB & SKB; 39 mm specimen (AM C168921), reef patch off Lion Island, 18 m depth, 24 June 1988, DJB; 26 mm specimen (AM C162733), Horseshoe Reef, 18-24 m depth, 21 June 1988, DJB & SKB; 31 mm specimen (AM C162728), Horseshoe Reef, 14 m depth, 22 June 1988, DJB & SKB; 27 mm specimen, Sunken Barrier Reef, 12 m depth, 20 Apr. 1984, Carlson-Hoff.

External morphology (Pls 3G-H, 4A). Live specimens ranged in length from 25-65 mm and mean size was 34 mm. *Phyllidia babai* is predominantly pale cream to white in colour. Laterally, the notum has six to eight black rings encircling simple conical tubercles (Pls 3G, 4A). The tubercles are cream to white with white caps and occur in longitudinal rows. The central row of tubercles may be joined by a broken ridge. There is a fine yellow edge to the mantle margin (Pls 3G, 4A). Central tubercles may be yellow capped in large specimens, but are usually white. The rim of the rhinophoral pocket is bordered in white. The rhinophores are yellow and their clavus possess 21-24 lamellae each (specimens greater than 28 mm).

The hyponotum is white to pale grey and has a cross hatched pattern. The foot is pale cream to white and has no other markings. The oral tentacles are white with yellow tips and are pointed at their apex (*cf.* rounded). The ventrolateral grooves on the oral tentacles of this species are long (extending from the base to the tip).

Anatomy. Typical for the genus *Phyllidia*. In the preserved state the oral tube is white and without markings. The anal papilla/rectum is pale grey. The reproductive system is pale cream except for the ampulla which is brownish yellow, and the receptaculum seminis which is translucent. The ampulla, receptaculum seminis and bursa copulatrix are all of similar size. Rows of penial spines are present. Individual penial spines (8-10 μ m in vertical height) have a very broad base and are triangular in general shape (Fig.25H). The spines are only slightly recurved at their apex.

Distribution. *Phyllidia babai* is known from north-eastern Australia (Great Barrier Reef) and Papua New Guinea. Future collecting will probably reveal a wider distribution.

Remarks. *Phyllidia babai* is closest to *P. ocellata*, but the two are distinct species. The characteristic features of *P. babai* include: the very pale yellow to cream dorsum; black rings with a central, white, conical tubercle; the fine yellow edge to the mantle; rhinophoral clavus possessing 21-24 lamellae; the rim of the rhinophoral pocket edged in white; pale cream-white ventral colouration; white pointed oral tentacles tipped in yellow with long lateral grooves; the grey rectum/anal papilla; and penial spines which are broad based and triangular in shape. In contrast, *P. ocellata* possesses, a bright gold coloured dorsum with black patches bordered in white, and gold or white rounded tubercles, no contrasting colour on the mantle edge or rim of the rhinophoral pockets, 27-30 lamellae to the rhinophoral clavus, dark grey ventral colouration, dark grey oral tentacles with rounded ends tipped in yellow and short lateral grooves, dark pigmentation on the rectum/anal papilla, and recurved penial spines which are small, narrow and have a short base.

Phyllidia exquisita and *P. willani* are similar to the present species as they all have pale background

colouration. *Phyllidia exquisita* has a yellow mantle margin but possesses longitudinal black and white areas and rounded tubercles. Unlike *P. babai*, *P. willani* has a granular, pale yellow dorsum with black lateral swirls and no yellow on the mantle margin.

Etymology. This species is named in honour of Dr K. Baba.

Phyllidia goslineri n.sp.

Pl.4B

Type. Holotype here designated (14 mm live length) AM C162760 (partially dissected by dorsal incision).

Material examined. Holotype (14 mm, AM C162760), Planet Rock, Madang, Papua New Guinea, 12-20 m depth, 19 Jan. 1988, T.M. Gosliner.

External morphology (Pl.4B). The basic colours of *Phyllidia goslineri* are cream and brown. The background colour of the dorsum is cream to pale brown (although the notum is semitransparent and the bright red digestive gland mass shows through medially). Irregularly shaped, tan blotches occur over the entire dorsum. There are also innumerable, minute, dark brown spots evenly spaced over the entire dorsum (Pl.4B). Notal tubercles are very small and rounded, and they possess the colouration of their immediate background. The anal opening occurs on a slightly larger, rounded cream tubercle. The cream coloured rhinophores are somewhat club shaped and their clavus possess (16-17) broad lamellae.

Ventrally, the foot and digitate oral tentacles are cream in colour. The bright red digestive gland mass was visible through the median part of the foot in the live specimen. The hyponotum is semitransparent and pale brown-cream in colour. The surface of the hyponotum is cross hatched and possesses four fine encircling ridges.

Anatomy. Typical for the genus *Phyllidia*. After preservation, the foregut including the digestive gland mass was pale brown (bright red in the live specimen).

In the preserved specimen, the reproductive system appeared to be well developed and the specimen mature. The nidamental gland mass and prostatic vas deferens were yellow, the ampulla silver-cream and the sperm receptacles were of similar size and cream in colour. Penial spines were examined under the light microscope but they could not be cleared of tissue for SEM examination. Individual spines appeared to be short, very slender (approximately 3-5 µm in length) and slightly recurved.

Distribution. The single specimen was collected by Dr T.M. Gosliner in Madang, Papua New Guinea.

Remarks. The specimen representing this new species is accompanied by colour photographs and field notes on the live specimen by Dr R.C. Willan and Dr Gosliner. There is no hesitation in consideration of the present species as new and distinct from all other described *Phyllidia* species. *Phyllidia goslineri* has characteristic colouration consisting of a translucent cream notum with irregular brown (tan) coloured blotches and numerous minute, dark brown dots. The club shaped rhinophores, foot and oral tentacles are all cream in colour.

Most *Phyllidia* species have yellow rhinophores, however the present species and *P. scottjohnsoni* n.sp. have cream rhinophores. *Phyllidia scottjohnsoni* n.sp. differs considerably from *Phyllidia goslineri* in having an opaque cream-white dorsum, and large, black spots and no brown pigmentation. *Phyllidiopsis loricata* has large, black to dark brown spots but its alimentary system is quite different to that of *Phyllidia goslineri*. *Phyllidia scottjohnsoni* and *Phyllidiopsis loricata* have pointed rhinophores whereas in *Phyllidia goslineri* they are club shaped. To my knowledge, there are no other *Phyllidia* species with brown colouration.

Etymology. This species is named in honour of Dr T.M. Gosliner.

Phyllidia polkadotsa n.sp.

Pl.4C

"Yellow-black *Phyllidia*" Bertsch & Johnson, 1981: 76 (lower photo).

Type. Holotype here designated (25 mm live length) AM C162778; the remaining two specimens are designated paratypes.

Material examined. Holotype (25 mm, AM C162778), Makua, Oahu, Hawaii, 6-10 m depth, 19 Sept. 1979, S. Johnson; 15 mm specimen (AM C162779), Pupukea, Oahu, Hawaii 12 m depth, 19 Sept. 1979, S. Johnson; 13 mm specimen, Makua, Oahu, Hawaii, 8 m depth, 8 Feb. 1985, S. Johnson.

External morphology (Pl.4C). Live specimens ranged in length from 15-25 mm. *Phyllidia polkadotsa* is golden yellow in colour with black spots on its dorsum. Both dorsally and ventrally, the background colour is gold (whitish in the preserved state). There are numerous (greater than 10), large, round, black spots on the dorsum. The notal tubercles are small, single and rounded, and they are evenly distributed. There are three, low, median longitudinal ridges. The tubercles and ridges have the colouration of their immediate background. The rhinophores are gold in colour and each clavus possesses 11-13 lamellae. Ventrally, the hyponotum is golden with the black spots showing through where they occur. The gills, foot and triangular shaped oral

tentacles are also gold in colour.

Anatomy. Typical for the genus *Phyllidia*. The reproductive system appeared to be mature in the larger specimen. The prostatic vas deferens was long (approximately 3 mm) with a long and narrow distal vas deferens running into a relatively elongate penis. Penial spines were not isolated for SEM examination.

Distribution. *Phyllidia polkadotsa* is presently known only from Hawaii (Johnson, *in litt.*, 1989).

Remarks. *Phyllidia polkadotsa* is distinctively patterned. The dorsum is gold with black spots. Ventrally, it is coloured gold. The notal tubercles are low and rounded and there are three low, median longitudinal ridges. The male reproductive organs are elongate compared to other *Phyllidia* species.

The Mediterranean *Phyllidia flava* is gold but it has relatively larger tubercles capped in white and it lacks black pigmentation.

Phyllidiopsis loricata possesses black spots but has a pale cream to white background colour.

Phyllidia polkadotsa does not have any white pigmentation whereas *P. ocellata* often has black rings, bordered in white, and with a central gold or white tubercle. *Phyllidia ocellata* differs particularly from *P. polkadotsa* in having grey ventral colouration, many more fine lamellae (27-30) on the rhinophoral clavus and the absence of three, low, dorsal longitudinal ridges.

Etymology. The name refers to the flamboyant, dorsal pattern of black polka dots on a golden yellow background.

Phyllidia scottjohnsoni n.sp.

Pl.4D

Phyllidia loricata.—Bergh, 1905: 182, pl.17, figs 9,10 (non *Phyllidia loricata* Bergh, 1873).

Comments on synonymy. Bergh's (1905) reference to this species was probably a misidentification. His figure of a broad specimen with mid-dorsal spots appears to be closer to the present species.

Type. Holotype here designated (14 mm live length) AM C162783; the remaining six specimens are designated paratypes.

Material examined. Holotype (14 mm, AM C162783), Pupukea, Hawaii, 15 m depth, 8 July 1985, S. Johnson; 14 & 15 mm specimen, Haleiwa, Hawaii, 15 m depth, 23 Aug. 1985, S. Johnson; 19 & 26 mm specimen, Kure Atoll, Hawaii, 8 m depth, 1 Aug. 1985, S. Johnson; 25 mm specimen (MV F54947), Mandora, Darwin, NT, 1 m depth, 21 Nov. 1972, N. Coleman; 7 mm specimen, Bile Bay, Guam, 1 m depth, 22 June 1975, Carlson-Hoff.

External morphology (Pl.4D). Live specimens ranged in size from 6.5-25 mm. The dorsum of *Phyllidia scottjohnsoni* has a white coloured background and six to ten, large black spots. Small black dots may occur around the mantle edge. *Phyllidia scottjohnsoni* is oval in shape and flattened dorsoventrally. Many tiny, irregular tubercles are scattered on the dorsum. Medially, the tubercles may form up to five indistinct, broken, low ridges. The short, cream coloured rhinophores bear seven to nine broad lamellae on the clavus (specimens greater than 15 mm). Ventrally, the hyponotum (except beneath the black spots), gills, foot and pointed oral tentacles are white to cream in colour.

Anatomy. Typical for the genus *Phyllidia*. All the viscera and reproductive organs are white in colour. Penial spines were observed through the tissue of the inverted penis of one specimen, but they could not be isolated for SEM examination.

Distribution. *Phyllidia scottjohnsoni* is known from the central and western Pacific Ocean and as far east as Darwin (Timor Sea).

Remarks. *Phyllidia scottjohnsoni* can be distinguished by its white background with black spots, small tubercles and cream to white rhinophores. *Phyllidia ocellata* generally has black rings around its tubercles but it has a gold background colour and gold rhinophores. *Phyllidia scottjohnsoni* appears to be a small species in comparison to *P. ocellata*, *P. tula*, *P. varicosa* and *P. elegans*. *Phyllidiopsis loricata* (Bergh) is superficially similar to *Phyllidia scottjohnsoni*, however the former species has a different alimentary system, is more elongate and it lacks black spots in the mid-dorsal region. *Phyllidia scottjohnsoni* has fewer (7-9) lamellae on the rhinophoral clavus than *Phyllidiopsis loricata* (16-19 fine lamellae). *Phyllidia scottjohnsoni* is flattened dorsoventrally to a greater extent than most other *Phyllidia* species.

Etymology. The species is named in honour of Scott Johnson who provided material of this and other species, from the central Pacific.

Fryeria Gray, 1853

Fryeria rueppelii Bergh

Figs 7, 8, 9A, Pl.4E

Phyllidia pustulosa.—Rüppell & Leuckart, 1830 or 1831: 36, pl.11, fig.1a-b (non *P. pustulosa* Cuvier, 1804).

Fryeria pustulosa Gray, 1853: 221.—Gray, 1850-1854: pl.312, fig.5-5a.—Vayssièrè, 1912: 87 (see Brunckhorst *et al.*, 1989; Opinion 1663, 1992 for suppression of name).

Fryeria rüppelii Bergh, 1869: 514-515.—Bergh, 1875: 663-669, pl.16, figs 5-9.

Phyllidiella pustulosa.—Eales, 1938: 110-111 (non *P. pustulosa*

Cuvier, 1804).

Reyffria rueppelii (Bergh).—Yonow, 1986: 1418-1420, 1424, figs 9, 12f-j.—Yonow, 1988: 149, pl.8.

Fryeria rueppelii (correction of spelling).—Brunckhorst *et al.*, 1989: 161-164.—Brunckhorst & Rudman, 1990: 189-190.

Comments on synonymy. Edmunds (1972: 86) noted that many references to *F. rueppelii* Bergh also included other, undescribed, Indo-West Pacific species belonging to the same genus. The synonymy given above contains references to *F. rueppelii sensu stricto*. References to other specimens attributed to *F. rueppelii* (with variable spellings of the specific epithet) actually refer to three other Indo-West Pacific species and these are described in the following sections. *Fryeria rueppelii* Bergh 1869 is considered the name for the type species of *Fryeria* Gray (Brunckhorst *et al.*, 1989; Opinion 1663, 1992). *Fryeria pustulosa* Gray is an objective synonym of *F. rueppelii* Bergh as both were based on Rüppell & Leuckart's (1830 or 1831) specimens which were misidentified as *Phyllidia pustulosa* Cuvier.

The correct spelling of the specific epithet for the present species is *rueppelii* (Brunckhorst *et al.*, 1989).

Type. *Fryeria pustulosa* Gray and *F. rueppelii* Bergh. Lectotype, here selected (larger syntype, 43 mm preserved length) BMNH 1989155; figured by Rüppell & Leuckart, 1830 or 1831: pl.11, fig.1a-b; paralectotype (smaller syntype, 38 mm preserved length) BMNH 1989155.

Material examined. *Indian Ocean – Red Sea – 38 & 42 mm specimen* (BMNH 1989.155), 1820s?, Rüppell & Leuckart; 2 specimens (BMNH Acc.no. 2337), N. Yonow; 27 mm specimen (BMNH 1987.069), Tongue Island, 16 June 1983, N. Yonow; 1 specimen (BMNH 1987.069), Zubair Island, 10 m depth, 25 June 1983, N. Yonow; 20 mm specimen (BMNH 1987.069), Zubair Island, 10 m depth, 18 June 1983, N. Yonow; 28 mm specimen (BMNH 1987.069), north of Creek, Jeddah, 17 Jan. 1983, N. Yonow; 24 mm specimen, Tawilla, Gulf of Suez, 25 Sept. 1989, M. Ilan.

External morphology (Pl.4E). Live specimens ranged in length from 7-42 mm. *Fryeria rueppelii* has a broad ovate shape. The background colouration of the dorsum is dark blue to black. The mantle margin is edged in yellow-orange. The large, isolated, central tubercles are oval and rounded in profile; their broad bases are white, and their apices are yellow-orange. In preserved specimens, three, low, broken, black ridges are present in a longitudinal median position. These ridges, however, are indistinct in live specimens. White semicircles, usually with smaller yellow-orange capped tubercles, occur around the mantle margin. The rhinotubercles are tall, sharply defined, and their apex is yellow-orange. The rhinophores are yellow-orange and each clavus possesses 15-17 lamellae (specimens greater than 20 mm in length).

The oral tentacles are conical and their lateral grooves are short. The ventral surface is grey except for the edge of the mantle and the tips of the oral tentacles which

are both yellow-orange. The gills are a darker shade of grey.

Anatomy. The present species is the type for the genus *Fryeria* (Figs 7, 8, 9A). The foregut region lacks characteristic markings. On leaving the digestive gland mass, the intestine immediately tapers to a narrow tube. The protrusible anal papilla is grey. In the present species, the prostatic vas deferens is very broad and the ampulla is very large (approximately 4 times the size of the bursa copulatrix). The penis is narrow and relatively short (less than 1 mm). Penial spines were not isolated.

Distribution. *Fryeria rueppelii* appears to be restricted to the Red Sea (Yonow, 1986; present work). Previous reports of this species from other Indo-West Pacific locations are attributable to different species (Edmunds, 1972; present work).

Remarks. External features which distinguish *F. rueppelii* from other species of *Fryeria* include its white and yellow-orange tubercles, white marginal semicircles, and, in particular, the yellow-orange edge to the mantle. In contrast, *F. bayi* is white to cream in colour with fine, pale brown markings.

Of the new species described in this work, *F. guamensis* resembles *F. rueppelii*. However, *F. guamensis* n.sp. differs in having paler yellow colouration, numerous small tubercles around the mantle margin, and in lacking white semicircles or yellow-orange colouration on the mantle edge. Internally, the ampulla and prostate of *F. guamensis* n.sp. are much smaller than those of *F. rueppelii*. The anal papilla of *F. guamensis* n.sp. is white-cream (grey in *F. rueppelii*).

Fryeria bayi Bouchet

Pl.5D

Fryeria bayi Bouchet, 1983: 65-68, figs 1-2.—Cattaneo & Barletta, 1984: 208.—Garcia-Gomez, 1987: 200.

Type. *Fryeria bayi* Bouchet. Holotype (8 mm preserved length) MNHN; figured by Bouchet, 1983: 66, fig.1.

Material examined. 2 specimens, 6 mm & 8 mm (MNHN), Punta Bianca, Corsica, Mediterranean Sea, 38 m depth, 1 Sept. 1981, P. Bouchet.

External morphology (Pl.5D). The two preserved specimens measured 8 mm and 6 mm respectively. *Fryeria bayi* is a small, ovate species. The dorsal background colouration is white to pale cream, and it has a mottled pattern of pale brown. The notum is relatively smooth. The tubercles are numerous, evenly dispersed, minute in size, and low and rounded in profile. The rhinophores are white to pale cream and

each clavus possesses three very oblique lamellae. The edge of each rhinophoral pocket is slightly raised as a low sheath. Ventrally, the foot sole is white to pale cream. The oral tentacles have rounded (as opposed to pointed) extremities.

Anatomy. Typical for the genus *Fryeria* (Bouchet, 1983). At the posterior end of the oesophagus the gut expands into a large "pre-intestinal sac" (Bouchet, 1983: 67) (? stomach) which lies on the dorsal surface of the digestive gland mass. The reproductive system of this species was not examined by myself. Bouchet (1983) reported that the reproductive system was immature in an 8 mm specimen.

Distribution. *Fryeria bayi* is endemic to the Mediterranean Sea (Bouchet, 1983; Garcia-Gomez, 1987). It is the only species of *Fryeria*, and only the second phyllidiid species known from that Sea (Brunckhorst & Willan, 1989).

Remarks. The pale cream dorsum with its fine, pale brown, mottled pattern sets *F. bayi* apart from all other *Fryeria* species. The dorsal intestinal sac is also unique to this species.

Fryeria rueppelii, *F. guamensis* n.sp., *F. menindie* n.sp. and *F. marindica* (Yonow & Hayward) all have a black background, gold-yellow capped tubercles and gold rhinophores (pale cream in *F. bayi*). *Fryeria larryi* is closer to *F. bayi*, but it has yellow colouration (no brown pigmentation) and is not mottled. In contrast, *F. larryi* possesses a few red, transverse lines which occur laterally.

Fryeria marindica (Yonow & Hayward)

Pl.5B-C

Fryeria rüppelii.—Bergh, 1889: 862-865, pl.84, figs 19-22.—Eliot, 1903b: 563.—Edmunds, 1972: 84-86, fig.4a (non *Fryeria rueppelii* Bergh, 1869).

Fryeria pustulosa.—Risbec, 1929: 45-49, figs 1-9 (non *Fryeria pustulosa* Gray, 1853).

Reyfria ruppelii (Bergh).—Wells *et al.*, 1990: 75, pl.70 (non *Fryeria rueppelii* Bergh, 1869).

Reyfria marindica Yonow & Hayward, 1991: 23, 26, figs 10C,D, 13E.

Comments on synonymy. The descriptions and illustrations provided by the above authors do not correspond with the features of *F. rueppelii* Bergh, 1869 (see Rüppell & Leuckart, 1830 or 1831: pl.11, fig.1a-b; present work, Pl.4E).

Edmunds (1972: 84-85) has already noted some differences and listed the present species as the second of "three distinct forms confused under the name "*Fryeria rüppelii*" (Edmunds 1972: 86). The original description (Yonow & Hayward, 1991) is sketchy and did not include examination of anatomy, and is

apparently based on a single preserved specimen, however the type locality is unclear as the illustrated specimen is marked as Maldivian in origin.

Type. *Reyfria marindica* Yonow & Hayward. Holotype (25 mm), BMNH 1986.231, Grand Bay, Mauritius; however the illustrated specimen is apparently from the Maldives (Yonow & Hayward, 1991: fig.13E).

Material examined. *Indian Ocean* – 27 & 30 mm specimens (AM C126508), Christmas Island, 15 Nov. 1980, Tong & McDonald; 30 mm specimen (WAM 558-86), Christmas Island, 1986, C. Bryce/F. Wells; 22, 25 & 26 mm specimens (AM C168922), Réunion, 5-20 m depth, 1989, M. Jay.

Thailand – 25 mm specimen (AM C162796), Phi Phi Island, 27 Nov. 1989, DJB; 13, 24 & 26 mm specimens (AM C162794), Phi Phi Island, 16 m depth, 27 Nov. 1989, DJB; 13 mm specimen (AM C162800), Phi Phi Island, 8-10 m depth, 28 Nov. 1989, DJB; 22 mm specimen (AM C162795), Phi Phi Island, 16 m depth, 28 Nov. 1989, DJB; 16 & 36 mm specimens (AM C162797), Phi Phi Island, 16 m depth, 1 Dec. 1989, DJB; 12 mm specimen (AM C162798), Phi Phi Island, 12 m depth, 2 Dec. 1989, DJB.

Western Australia – 35 mm specimen (AM C162799), Dampier Archipelago, 0-8 m depth, 21 May 1987, D. Johnson; 1 specimen (MV), Kendrew Island, 5 Nov. 1971, N. Coleman; 38 mm specimen (MV F54949), Kendrew Island, 16 Oct. 1972, N. Coleman; 40 mm specimen (MV F54949), Kendrew Island Reef, 14 Oct. 1972, N. Coleman; 28 mm specimen (MV F54948), Murion Island Channel, 21 Aug. 1972, N. Coleman.

External morphology (Pl.5B-C). Live specimens I examined ranged in length from 12-40 mm and the mean size was 24 mm. *Fryeria marindica* is elongate-ovate in shape and it possesses black, blue and yellow colouration. The predominant colour of the dorsum is pale blue-grey. These blue-grey areas have an angular shape and occur mediolaterally to the margins. Many black rays or stripes run laterally to the margins through the blue-grey areas (Pl.5B-C). There are two longitudinal black bands running on either side of a single median longitudinal ridge. The ridge may be interrupted in some specimens. The median longitudinal ridge is blue-grey in colour and it joins with coalesced tubercles, the larger ones of which are capped in yellow. The other notal tubercles are low and isolated, and rounded in shape (the larger ones are capped in yellow). The rhinotubercles are small and possess rounded yellow apices. The rhinophores are gold and each clavus bears 20-23 lamellae (specimens greater than 24 mm in length). The ventral surfaces are grey. The foot sole lacks other markings. The oral tentacles are cylindrical and rounded anteriorly.

Anatomy. Typical for the genus *Fryeria*. The foregut is predominantly pale cream, however the pharyngeal bulb has a dark band anteriorly. The oesophagus is slightly dilated before it enters the digestive gland mass. The intestine runs posteriolaterally down the right side to the posterior ventral anal opening. The protrusible anal papilla is grey.

In preserved specimens the ampulla was yellow-brown. The receptaculum seminis was semi-translucent, and the rest of the reproductive organs were cream. The bursa copulatrix had an elongate, pyriform shape. The penial spines were small (less than 6 μm), and they could not be isolated for further elucidation by SEM.

Distribution. *Fryeria marindica* is presently known from coral reefs in the Indian Ocean from northern Western Australia to eastern Africa (Eliot, 1903b; Edmunds, 1972).

Remarks. The genus *Reyfria* Yonow is a junior synonym of *Fryeria* Gray (see prior discussion; Brunckhorst *et al.*, 1989; Brunckhorst & Rudman, 1990; Opinion 1663). Distinctive features of *F. marindica* include its elongate shape, small round tubercles, a single median blue ridge with yellow capped tubercles, mediolateral to marginal blue areas (angular in shape) with many black rays running laterally to the mantle edge, 20-23 lamellae on each rhinophoral clavus, grey ventral colouration and grey anal papilla.

Fryeria marindica has already been compared to other *Fryeria* species in the preceding descriptions. It appears to be closest to *F. menindie* which is found in the western Pacific Ocean. However, *F. menindie* is more oval in shape, possesses large, broad based tubercles which are gold capped and tall rhinotubercles. For specimens of similar size, *F. menindie* possesses fewer lamellae on each rhinophoral clavus, has three low, mid-dorsal ridges (*F. marindica* has one) and blue crescentic areas on the mantle margin. Ventrally, *F. menindie* is paler and it has an anterior indentation on the foot. Internally, the foregut of *F. menindie* is white whereas that of *F. marindica* is cream with a dark band. Further study of the penial spines of *F. marindica* would be useful, however individual spines appeared to be smaller than those of *F. menindie*.

Fryeria guamensis n.sp.

Fig.26A, Pl.4F

Fryeria rüppelli.—Er. Marcus, 1965: 279 (non *Fryeria rueppelii* Bergh, 1869).

Fryeria sp.—Karus, 1987: 36.

Comments on synonymy. The specimens from the Caroline Islands listed by Er. Marcus (1965) appears to belong to the present species.

Type. Holotype here designated (24 mm live length) AM C162764; the remaining eight specimens are designated paratypes.

Material examined. *Western Pacific Ocean – Micronesia – Guam* – holotype (24 mm, AM C162764), Bile Bay, 10 Aug. 1987, Carlson-Hoff; 25 & 29 mm specimen (AM C162765), Bile Bay, 21 m depth, 20 Aug. 1987, Carlson-Hoff;

32 mm specimen, Sella Bay, 29 July 1970, Carlson-Hoff; 27 mm specimen (AM C162766), Bile Bay, 27 June 1988, DJB & SKB; 47 mm specimen (AM C162767), Bile Bay, 28 June 1988, DJB & SKB; 21 mm specimen (AM C162768), Bile Bay, 11 July 1988, DJB & SKB; 8 mm specimen (AM C162768), Bile Bay, 11 July 1988, DJB & SKB; 19 mm specimen (AM C162769), Bile Bay, 1-6 m depth, 1 June 1988, K. Jensen.

External morphology (Pl.4F). Live specimens ranged in length from 7-47 mm. *Fryeria guamensis* has an elongate body. The background colour of the dorsum is black, the tubercles have white to pale grey bases and they are capped in pale yellow. The notum possesses many discrete rounded tubercles. The larger mid-dorsal tubercles are arranged in an alternating series consisting of one central, and two mediolateral tubercles. Smaller, lateral tubercles occur outside this mid-dorsal area, and many minute, isolated tubercles occur around the mantle margin (Pl.4F). The rhinotubercles are low and rounded. The rhinophores are gold in colour and each clavus possesses 18-20 lamellae (specimens greater than 22 mm).

The ventral surface of *F. guamensis* is dark grey. The marginal notal tubercles are visible on the hyponotum as small pale spots. The margin of the foot sole is pale grey. The digitate oral tentacles are dark grey-black with pale yellow tips.

Anatomy. Typical for the genus *Fryeria*. In the preserved state there is a very dark visceral envelope over three quarters of the body cavity, however anteriorly, this envelope is pale and translucent. The foregut and digestive gland mass are pale cream to white. The reproductive organs are cream to white. The penis is narrow and relatively long (approximately 1.5-2 mm). The penial spines are large (12-15 μm in vertical height, Fig.26A) and they have a broad triangular base (8 μm in width). The distal half of the spine is slender and curves to a pointed apex.

Distribution. *Fryeria guamensis* is presently known from Micronesia (Er. Marcus, 1965; present work).

Remarks. *Fryeria guamensis* is characterised by: the alternating series of large mid-dorsal tubercles; the numerous, minute, isolated tubercles around the mantle margin; rounded tubercles which are capped in pale yellow; low rhinotubercles; and very dark oral tentacles with pale yellow tips. Internal features which distinguish *F. guamensis* include the pale viscera and the pale, translucent anterior region of the visceral envelope (dark in other species of *Fryeria*).

Fryeria guamensis is easily separated from congeners such as *F. rueppelii*, *F. menindie* n.sp. and *F. marindica* because it has neither a semicircular pattern nor black rays extending to the mantle edge. *Fryeria rueppelii* has a yellow orange edge to the mantle margin. *Fryeria guamensis* also lacks the low ridges of the other three species and it has no broad white areas (as in *F.*

rueppelii), or blue colouration (as in *F. menindie* n.sp. and *F. marindica*) on the dorsum. For similar sized specimens, *F. guamensis* has a greater number of lamellae on the rhinophoral clavus than *F. rueppelii*, but fewer than *F. marindica*. The penial spines of *F. guamensis* are large (12-15 μm) and have a broad triangular base, whereas those of *F. menindie* n.sp. are smaller (8-10 μm) and have a rounded base. Penial spine morphology is not known for the other *Fryeria* species.

Etymology. The present species is named for its type locality, Guam.

Fryeria larryi n.sp.

Pl.4G

Type. Holotype here designated (6 mm live length) AM C169367.

Material examined. Holotype (6 mm, AM C169367), Bile Bay, Guam, 8 m depth, 22 Sept. 1973, Carlson-Hoff.

External morphology (Pl.4G). Adult size of *F. larryi* is unknown. The background colour of the dorsum is yellow. There are several (7 on the holotype) isolated, narrow red lines running transversely on the mantle margin (Pl.4G). The notal tubercles are minute and rounded, and are evenly distributed over the dorsum. The rhinotubercles are small and similar in shape to the other notal tubercles. The rhinophores possess the same yellow colouration as the dorsum (i.e., not gold). Each rhinophoral clavus possesses 8-10 lamellae. Ventrally, the hyponotum, foot, gills and oral tentacles are yellow and there are no contrasting markings. In the preserved state, the oral tentacles were short and almost square. The posterior, ventral anal opening is large.

Anatomy. The single specimen was not dissected. The ventrally placed anus indicates that this species belongs in the genus *Fryeria*.

Distribution. *Fryeria larryi* is presently known from Guam.

Remarks. *Fryeria larryi* is distinctive and can be recognised easily by its yellow colouration and the red, transverse markings on the notum. It is the only species of *Fryeria* with yellow ventral colouration. No other species of *Fryeria* has yellow gills. The anus in other *Fryeria* species is very small and often difficult to observe without a microscope, but that of *F. larryi* appears to be large.

The only other *Fryeria* species which does not possess black pigmentation is *F. bayi*. *Fryeria bayi* is also a small species, but it is cream-white in colour with a brownish mottled pattern, and it has white rhinophores with three very oblique lamellae. These features clearly separate *F. bayi* from *F. larryi*. *Phyllidia zebrina* is superficially similar to the present species, however it possesses a pale cream colouration with brownish markings, larger tubercles (minute in *Fryeria larryi*) and a dorsal anus.

Etymology. This species is named for my father, Larry.

Fryeria menindie n.sp.

Fig.26B, Pls 4G, 5A

Fryeria rüppelii.—Pruvot-Fol, 1957a: 114-115, pl.1, figs 2-3 (non *Fryeria rueppelii* Bergh, 1869).

Fryeria rüppelii.—Baba, 1975: 260, figs 7, 8 (non *Fryeria rueppelii* Bergh, 1869).

Fryeria rueppelii.—Baba & Hamatani, 1975: 178-179, fig.5 (non *Fryeria rueppelii*, Bergh, 1869).

Fryeria ruppelii.—Burn, 1975: 516.—Coleman, 1981: 157-158, pls 474, 475.—Willan & Coleman, 1984: 42, pl.132.—Tan *et al.*, 1987: 75, fig.1.—Gosliner & Behrens, 1990: pl.11B (lower right) (non *Fryeria rueppelii* Bergh, 1869).

Fryeria pustulosa.—Risbec, 1953: 13-15 (non *Fryeria pustulosa* Gray, 1853).

Comments on synonymy. The above synonymy refers to specimens which have been misidentified as *Fryeria rueppelii* Bergh. In all cases the specimens can be identified as the present species from the illustrations and descriptions provided by the authors.

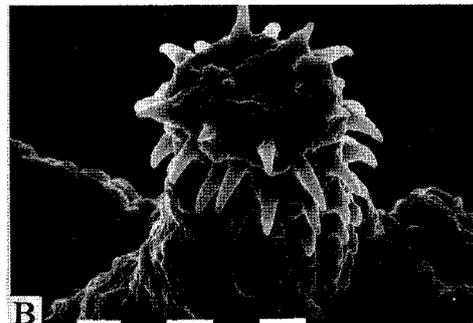
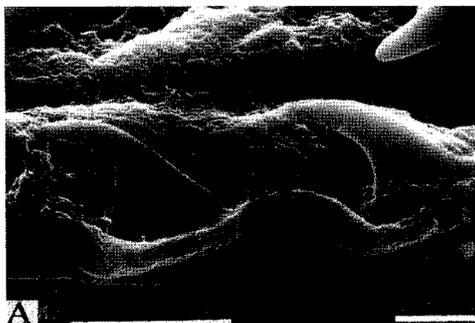


Fig.26. A, *Fryeria guamensis* n.sp. SEM of penial spines; B, *Fryeria menindie* n.sp. SEM of everted penis. Scales = 10 μm .

Type. Holotype here designated (33 mm live length) AM C140054; the remaining 22 specimens are designated paratypes.

Material examined. *Western Pacific Ocean* – 34 mm specimen (AM C154741), Beneegi, Solomon Islands, 1975, J. Settle; 33 mm specimen (AM C141839), Ruaniu-to Wreck, Solomon Islands, 1984, I. Knight; 35 mm specimen, Seto, Kii, Japan, 19 Sept. 1967, Araga-Harris; 19 mm specimen, Suva area, Viti Levu, Fiji, 1 July 1987, RCW; 26 mm specimen, Nukubuko Reef, Laucala Bay, Fiji, 9 July 1987, RCW; 24 mm specimen (AM C162790), Laucala Bay, Fiji, 14 July 1986, G. Brodie; 26 mm specimen (AM C162790), Fiji, 1 July 1986, G. Brodie; 18 mm specimen, Hyatt, Fiji, 7 Jan. 1984, Yonow photo; 1 specimen, Sabato Point, Tutuba Island Vanuatu, 4 Aug. 1976, RCW; 3 specimen, "Pres.Coolidge", Vanuatu, 33-42 m depth, 5 Aug. 1976, RCW; 45 mm specimen, Sail Rock, Norfolk Island, 21 m depth, 1 Aug. 1991, K. Whysall.

Papua New Guinea – 29 mm specimen (AM C162787), The Pinnacle, Madang, 6-30 m depth, 25 Jan. 1988, RCW; 19 mm specimen (AM C162789), Anemone Reef, Madang, 11 m depth, 10 Jan. 1988, RCW; 14 mm specimen (AM C162791), patch off Lion Island, 10 m depth, 17 June 1988, DJB & SKB; 25 mm specimen (AM C162793), patch off Lion Island, 18 m depth, 20 June 1988, DJB & SKB; 21 mm specimen (AM C162788), Horseshoe Reef, 18-24 m depth, 21 June 1988, DJB & SKB; 31 mm specimen (MV F54966), Horseshoe Reef, 20 m depth, 1 Aug. 1980, N. Coleman; 35 mm specimen (ZMUC), Indonesia-PNG, ?1870s, ?Semper.

Eastern Australia – Great Barrier Reef – holotype (33 mm, AM C140054), Pelorus Island, Ingham, north Qld, 10 m depth, 8 Nov. 1983, R. King; 1 specimen (AM C132250), Horseshoe Reef, 17 Nov. 1981, J. Gates; 19 mm specimen (AM C162792), Tydemann Reef, 10 m depth, 17 Oct. 1986, DJB; 1 specimen (MV), Heron Island, 10 m depth, 27 July 1973, N. Coleman.

External morphology (Pls 4G, 5A). Live specimens ranged in length from 14-45 mm and mean size was 27 mm. *Fryeria menindie* is oval and possesses black, blue and gold colouration. The background colour of the dorsum is black. Single, isolated tubercles occur on the notum. Individual tubercles have a broad blue base which gives them a conical shape, and their apex is rounded and gold in colour. Within the median region of the notum, single tubercles alternate in position (i.e., 1 median, 2 mediolateral; see Pls 4G, 5A). Three, low, longitudinal black ridges occur mid-dorsally; these are interrupted by the large, median isolated tubercles (the tubercles do not join as a ridge). The ridges are difficult to see on live specimens, but are easier to discern on preserved material. Wide, crescentic, blue areas, often with one or two gold capped tubercles, occur around the mantle margins. The blue pigmentation of each crescent extends to the mantle edge (i.e., the mantle rim is not coloured yellow). Between each crescentic area there is a black ray which extends to the edge of the mantle. The rhinotubercles are tall and narrow, they are blue with gold apices. The rhinophores are gold in colour and each rhinophoral clavus bears 17-20 lamellae (specimens greater than 22 mm in length).

Ventrally, the foot and gills are pale grey. The hyponotum is pale grey and its margins are cross hatched

with fine, darker grey lines. The conical oral tentacles are entirely grey. The foot sole is uniformly pale grey. The anterior end of the foot, below the mouth, appeared to be notched (i.e., indented) in both live and preserved material. There is darker grey pigmentation around the posterior, ventral anal opening.

Anatomy. Typical for the genus *Fryeria*. The oral tube of *F. menindie* is white and does not possess markings. The intestine runs ventrolaterally to its posterior anal opening. The protrusible anal papilla is pale grey to white in colour. In the preserved state the reproductive system is white to cream. The ampulla is elongate, ovate, and almost bilobed. It enters the nidamental gland mass directly (i.e., there is no short external duct). The prostatic vas deferens (prostate) is long and folded; distally it narrows to a long duct which in turn becomes a slender penis. The penial spines (Fig.26B) of *F. menindie* have a broad base from which they taper to a point which is usually recurved as a hook. Individual spines measure approximately 8-10 μm in vertical height.

Distribution. *Fryeria menindie* is known from the western Pacific Ocean (see synonymy above), and it appears to be restricted to this area. The specimen illustrated by Willan & Coleman (1984: 43) was from northern Western Australia. This record would appear to represent the extreme western edge of the range for this species. Its occurrence there could be explained by the northern Australian/Timor Sea connection between the Indian and Pacific Oceans. All other *Fryeria* specimens that I have collected or examined from the eastern Indian Ocean belong to *F. marindica*. *Fryeria menindie* has not been recorded from the central Pacific region (i.e., Micronesia, Marshall Islands, Hawaii or Tahiti).

Remarks. External features distinguishing *F. menindie* from its congeners include the broad blue bases to its isolated, large tubercles (gold capped), the three narrow, black median ridges and pale grey colouration ventrally (the tips of the oral tentacles are also grey). Some of the differences between *F. menindie* and other *Fryeria* species can be seen in Plates 4E-G, 5A-D. *Fryeria menindie* resembles *F. rueppelii*, *F. guamensis* and *F. marindica*. *Fryeria menindie* and *F. rueppelii* are oval in shape whereas *F. guamensis* and *F. marindica* are elongate. *Fryeria rueppelii* has crescentic areas on its margin, however these are white (as are the bases of the tubercles; blue in *F. menindie*). The mantle margin of *F. rueppelii* is edged in yellow-orange whereas there is no such contrasting colouration to the mantle edge in *F. menindie*. *Fryeria marindica* also has blue and gold colouration, but does not possess the crescent shaped areas around the margin. The blue areas of *F. marindica* are elongate and angular. *Fryeria marindica* possesses a single midline longitudinal ridge (*F. menindie* has three ridges) of coalesced tubercles. *Fryeria marindica* has many black rays running between its blue

tubercular areas. *Fryeria guamensis* has pale yellow capped tubercles (gold in *F. menindie*), lacks blue colouration and has neither crescentic areas nor black rays extending laterally to the mantle margins. The penial spines of *F. guamensis* are large with a triangular base whereas those of *F. menindie* are smaller and possess a rounded base.

Etymology. "Menindie" is one Australian aboriginal word for the yolk of an egg. Here it refers to the appearance of the dorsal tubercles which have rounded yellow apices.

Phyllidiella Bergh, 1869

Phyllidiella pustulosa (Cuvier)

Figs 3B, 9B-D, 11-13, 27, 28A-C, Pl.5E-F

- Phyllidia pustulosa* Cuvier, 1804a: 268, pl.a, fig.8.—Cuvier, 1804b: 277.—Oken, 1815: 286.—Gray, 1847: 168.—Eliot, 1904: 283.—Baba, 1949: 156-157, pl.29, fig.107.—Kenny, 1960: 227.—Er. Marcus, 1965: 278.—Miller, 1969: 545.—Kenny, 1970: 91.—Lim & Chou, 1970: 134, pl.17, fig.d.—Baba, 1975: 257, figs 2-5.—Baba & Hamatani, 1975: 175-176, figs 2, 3.—Burn, 1975: 516.—Heller & Thompson, 1983: 342-344, fig.9a-k.—Johnson & Boucher, 1983: 282.—Yonow, 1986: 1413-1414, fig.12c-d.—Karuso, 1987: 36.—Tan *et al.*, 1987: 75, fig.2.—Yonow, 1988: 147, pl.6.—Brunckhorst, 1989a: 7.—Burn, 1989: 771, pl.53, fig.6.—Johnson, 1989: 3.
- Phyllidia verrucosa* Hasselt, 1824: 244.—Bergh, 1887: 313, pl.6, fig.7 (n.syn.).
- Phyllidia albonigra* Quoy & Gaimard, 1832: 291-292, pl.21, figs 26-27.—Gray, 1850-1854, pl.312, fig.2.—Gray, 1857: 216.—Bergh, 1869: 512.—Pruvot-Fol, 1956: 66-67, fig.5-3 (n.syn.).
- Phyllidiella nobilis* Bergh, 1869: 485-492, 512-513, pl.24b.—Bergh, 1875: 661-662.—Bergh, 1889: 860-862, pl.84, figs 11-18.—Bergh, 1902: 194-195, pl.2, fig.15.—Bergh, 1905: 184, pl.3, fig.17 (n.syn.).
- Phyllidia spectabilis* Collingwood, 1881: 136-137, pl.10, figs 19-23.
- Fryeria variabilis* Collingwood, 1881: 137, pl.10, figs 24-28.—Risbec, 1956: 24, fig.85.—Er. Marcus & Ev. Marcus, 1970: 173-174, figs 50-52 (n.syn.).
- Phyllidia rotunda* Eliot, 1904: 282-283.—Lim & Chou, 1970: 134, pl.17, fig.a.—Lin, 1983: 152, pl.1, fig.7 (n.syn.).
- Fryeria pustulosa* (Cuvier).—Haas, 1920: 140.—Pruvot-Fol, 1933: 95.—O'Donoghue, 1929: 732 (non *Fryeria pustulosa* Gray, 1853).
- Phyllidia nobilis* (Bergh).—Risbec, 1928: 58.—Baba, 1936: 41-42, fig.24.—Dawydoff, 1952: 111.—Risbec, 1953: 12.—Pruvot-Fol, 1956: 66, fig.5i,ii.—Risbec, 1956: 25, figs 76-78.—Er. Marcus, 1965: 278.—Miller, 1969: 545.—Baba, 1975: 258-259.—Lin, 1983: 152, pl.1, fig.4.—Willan & Coleman, 1984: 42, pl.131.—Lin *et al.*, 1986: 86.—Coleman, 1989: 47.—Gosliner & Behrens, 1990, pl.11A (lower).—Yonow & Hayward, 1991: 21, fig.11F-H. (n.syn.).
- Phyllidia variabilis* (Collingwood).—Risbec, 1956: 24 (n.syn.).
- Phyllidia varians* Pruvot-Fol, 1956: 68 (mis-spelling pro. *Fryeria variabilis* Collingwood, 1881) (n.syn.).
- Phyllidia melanocera* Yonow, 1986: 1406-1407, figs 2, 10f-

i.—Yonow, 1988: 145, pl.3 (n.syn.).

Phyllidia sp.—Orr, 1981: 60.

Phyllidia sp. ("olympic phyllidia").—Coleman, 1989: 48.

Comments on synonymy. The majority of references to this species have used the names *Phyllidia pustulosa* Cuvier or *Phyllidia nobilis* (Bergh). Bergh (1869) introduced the genus *Phyllidiella*, but failed to realise his specimens belonged to *P. pustulosa*, instead describing them as a new species, *Phyllidiella nobilis*. The type specimens of *Phyllidia pustulosa* and *Phyllidia nobilis* are almost identical. They are illustrated in Figure 27A and B respectively. Study of the descriptions and illustrations of Hasselt's (1824) *Phyllidia verrucosa* and Bergh's (1887) redescription of it shows that it is the present species. The specimens described and illustrated as *Phyllidia spectabilis* (Collingwood, 1881) also belong to the present species. The figured syntype of *Phyllidia albonigra* matches *Phyllidiella pustulosa* (personal observation) and this was confirmed by examination of Quoy & Gaimard's (1832) colour plate. Many of the previous misidentifications are attributable to typological descriptions of single, preserved specimens. The majority of phyllidiid species that I have studied show little ontogenetic variation in dorsal pattern (i.e., juveniles resemble adults). *Phyllidiella pustulosa* is an exception and the considerable ontogenetic variation in its dorsal pattern has led to confusion. This is exemplified by Yonow's (1986, 1988) specimens of *Phyllidia melanocera* which are juvenile *Phyllidiella pustulosa*. Her specimens of *P. melanocera* ranged in size from 17-24 mm and those of *P. pustulosa* measured 33-55 mm (Yonow, 1986: 1406, 1413). Heller & Thompson (1983: 342-344) recognised and described the juvenile and adult pattern (three median clusters of tubercles), in their Red Sea specimens.

Types. *Phyllidia pustulosa* Cuvier. Lectotype here selected (only surviving syntype; approximately 35 mm preserved length) MNHN; figured by Cuvier, 1804a: pl.A, fig.8; and this work, Figure 27A.

Phyllidia verrucosa Hasselt. Holotype presumed lost; could not be located in Leyden Museum (see Bergh, 1887: 313); illustrated by Bergh, 1887: pl.6, fig.7.

Phyllidia albonigra Quoy & Gaimard. Lectotype here selected (syntype; approximately 25-30 mm contracted, preserved length) MNHN; figured by Quoy & Gaimard, 1832: pl.21, figs 26, 27.

Phyllidiella nobilis Bergh. Holotype (28 mm preserved length) ZMUC; figured by Bergh, 1869, pl.246; and this work, Figure 27B; dissected paratype (33 mm preserved length) ZMUC.

Phyllidia spectabilis Collingwood. Holotype presumed lost; could not be located in BMNH.

Fryeria variabilis Collingwood. Holotype presumed lost; could not be located in BMNH.

Phyllidia rotunda Eliot. Holotype presumed lost; could not be located in BMNH.

Phyllidia melanocera Yonow. Holotype (24 mm live length) BMNH 1985206/1; figured by Yonow, 1986: figs 2B, 10F.

Material examined. *Western Pacific Ocean* – lectotype

(MNHN), Timor Expedition 1790-1800?, Baudin - Timor; 30 mm specimen (MNHN), Tonga, ?1828-1829, Quoy & Gaimard; 28 & 33 mm specimen (ZMUC), Indonesia, ?1860-1863, Semper; 1 specimen, Uepi Island, Solomon Islands, 6 m depth, 24 May 1987, P. Chapman-Smith; 1 specimen (AM C154742), Toy-oran, Central Philippines, ?collector; 1 specimen (AM C154743), Banacon Island, Philippines, ? collector; 35 mm specimen, Yonehara Reef, Japan, 5 May 1978, Mr Kitao; 40 mm specimen (AM C162689), Sesoko Island Okinawa, Japan, 2 m depth, 17 Aug. 1989, J. Keesing; 1 specimen (MV), Herald Cay, Coral Sea, 1 Nov. 1964, R. Burn; 1 specimen, Meyer Island, Kermadec Island Group, 9 m depth, 1984, P. Chapman-Smith; 1 specimen (MV), E. Bremer Island, Gove, 7 m depth, 1 Nov. 1976, DAS; 38 & 16 mm specimens (AM C168837), Orontes Reef, NT, 13 m depth, 10 Aug. 1986, RCW.

Eastern Australia - 1 specimen (MV N144), Potter Point, Sydney, 30 m depth, A. Healy; 48 mm specimen (AM C162672), Flinders Reef, south-east Qld, 14 m depth, 12 Nov. 1982, RCW; 23 & 34 mm specimens (AM C168824), Flinders Reef, south-east Qld, 9 m depth, 26 May 1987, DJB; 60 mm specimen (AM C162679), Old Woman Island, south-east Qld, 14 m depth, 22 Aug. 1987, DJB; 39 mm & 44 mm specimens (AM C168831), Shag Rock, south-east Qld, 11 m depth, 16 Sept. 1980, RCW; 43 mm specimen (AM C162673), Flat Rock, south-east Qld, 10 m depth, 25 Oct. 1988, O. Kelly; 60 mm specimen, Inner Gneering Shoals, south-east Qld, 18 m depth, 22 Aug. 1987, DJB; 34 mm specimen, Old Woman Island, Mooloolaba, Qld, 12 m depth, 22 Aug. 1987, DJB; 1 specimen, Split Solitary Island, Coffs Harbour, 18 m depth, 1985, C. Buchanan; 1 specimen (MV), Julian Rocks, north NSW, R. Burn; 1 specimen (MV), Norfolk Island, 18 m depth, 1976, J.E. Watson; 1 specimen (MV), Norfolk Island, 20 m depth, 1 Sept. 1976, J.E. Watson; 4 specimens (55, 30, 25, 17 mm) Norfolk Island, 12-15 m depth, May-June, 1991, K. Whysall.

Great Barrier Reef - 47 mm specimen (AM C168835), Lizard Island, north Qld, 10 m depth, 5 Oct. 1982, RCW; 1 specimen (AM C154744), Lizard Island, north Qld, ?collector; 47 mm specimen, Lizard Island, 3 m depth, 19 Aug. 1975, RCW; 52 mm specimen, Lizard Island, 3 m depth, 19 Aug. 1975, RCW; 1 specimen (AM C168841), Watsons Bay, Lizard Island Qld, 4 m depth, 4 Oct. 1982, RCW; 29 mm specimen (AM C162671), Two Isles, north of Cooktown, Qld, 12 m depth, 14 Oct. 1986, DJB; 26 mm specimen (AM C162674), Two Isles, north of Cooktown, Qld, 14 Oct. 1986, DJB; 12 & 16 mm specimens (AM C168821), Batt Reef, Cairns, 12 m depth, 17 Jan. 1987, DJB; 14 mm specimen (MV F545950), Pennys' Bay, Orpheus Island, 1 June 1968, N. Coleman; 1 specimen (AM C168842), north-west side of Orpheus Island Qld, 17 May 1982, M. Reedy; 9 m depth, 25 Nov. 1987, DJB; 20 mm specimen, Pelorous Island, 10 m depth, 24 Mar. 1982, RCW; 2 specimens (AM C168840), Horseshoe Reef, Swains reefs, 11 m depth, 9 July 1986, S. Monks & A. Marshall; 1 specimen, Cleveland Bay, Townsville, 6-10 m depth, 1985, G. Kelly; 1 specimen, Brittomart Reef, Cardwell, 6 m depth, 1 Nov. 1984, DJB; 1 specimen, John Brewer Reef, 12 m depth, 10 Nov. 1986, R. Cattaneo; 1 specimen, Bowl Reef, 10 m depth, 18 Nov. 1986, R. Cattaneo; 1 specimen, Davies Reef, 1 Nov. 1986, R. Cattaneo; 1 specimen, Davies Reef, 8 m depth, 11 Nov. 1986, R. Cattaneo; 1 specimen, Rib Reef, Townsville, 12 m depth, 13 May 1986, DJB; 1 specimen (AM C168820), Bare Islet, AIMS, Townsville, Qld, 10 m depth, 18 Sept. 1986, DJB; 5 specimens (32, 39, 26, 31, 35 mm, AM C162686), Heron Island, 45 mm specimen (AM C162927), Heron Island, 6 m depth, 27 Nov. 1987, DJB; 69 mm specimen (AM C168825), Heron Reef, 8 m depth, 30 Nov. 1987, DJB;

1 specimen (MV), Heron Island, 10 m depth, 25 Nov. 1974, N. Coleman; 6-12 m depth, 27 June 1989, DJB; 22 mm specimen (AM C168838), Heron Island, 20 Oct. 1989, Flower & Newman; 31 mm specimen, Heron Island, 12 m depth, 1 Sept. 1983 RCW; 12, 17 & 34 mm specimens (AM C168822), Heron Island, 10 m depth, 28 Nov. 1987, DJB; 33 mm specimen (AM C162678), Heron Island, 10 m depth, 28 Nov. 1987, DJB; 64 mm specimen (AM C168823), Heron Island, 6 m depth, 24 Nov. 1987, DJB; 31 mm specimen (AM C162680), Heron Island, 9 m depth, 26 Nov. 1987, DJB; 40.5 & 44 mm specimens (AM C162680), Heron Island, 9 m depth, 26 Nov. 1987, DJB; 27 mm specimen (AM C168825), Wistari Reef, 24 m depth, 30 Nov. 1987, DJB; 3 specimens (34, 40, 24 mm, AM C162670), Wistari Reef, 10-14 m depth, 1 Dec. 1987, DJB; 44 mm specimen (AM C162675), Wistari Reef, 14-16 m depth, 2 Dec. 1987, DJB; 9 specimens (45, 39, 44, 45, 28, 25, 30, 54, 30 mm, AM C162687), Wistari Reef, 12-16 m depth, 2 Dec. 1987, DJB; 52 & 53 mm specimens (AM C162677), Wistari Reef, 6-20 m depth, 29 Nov. 1987, DJB; 16, 19 & 23 mm specimens (AM C168823), Wistari Reef, 30 mm specimen, Lady Musgrave Island, 15 m depth, 1 Aug. 1989, C. Buchanan.

Micronesia - 6 specimens (37, 28, 25, 32, 27, 24 mm, AM C162683), Bile Bay, 6 m depth, 27 June 1988, DJB & SKB; 3 specimens (24, 22, 35 mm, AM C162682), Bile Bay, 18 m depth, 29 June 1988, DJB & SKB; 43 & 38 mm specimens, Bile Bay, 4 m depth, 1 July 1988, DJB & SKB; 44 mm specimen, Bile Bay, 5 m depth, 1 July 1988, DJB & SKB; 1 specimen (AM C168828), Bile Bay, 4 m depth, 9 July 1988, DJB & SKB; 22 & 34 mm specimens (AM C168829), Bile Bay, 10 m depth, 15 July 1988, DJB & SKB; 31 & 37 mm specimens (AM C168826), Bile Bay, 4 m depth, 5 July 1987, Carlson-Hoff; 36 mm specimen, Bile Bay, 10 m depth, 2 July 1988, DJB & SKB; 35 mm specimen (AM C168827), Bile Bay, 3 m depth, 10 Sept. 1987, Carlson-Hoff; 29 mm specimen, Bile Bay, 8 m depth, 28 June 1970, Carlson-Hoff; 1 specimen (AM C168843), Bile Bay, 3 m depth, 1988, K. Jensen; 56 & 65 mm specimens (AM C162684), Sponge Mound, Apra Harbour, 22 m depth, 5 July 1988, DJB & SKB; 4 specimens (43, 52, 30, 38 mm), Sponge Mound, Apra Harbour, 22 m depth, 5 July 1988, DJB & SKB; 62 & 39 mm specimens (AM C162685), Annae Island, 9 m depth, 5 July 1988, DJB & SKB; 30 mm specimen, Cocos-Merizo, 6 m depth, 2 Aug. 1970, Carlson-Hoff; 17 & 27 mm specimens, Anae Island, 11 m depth, 18 Nov. 1987, Carlson-Hoff; 1 specimen, Achugao Point, 9 m depth, 6 Feb. 1971, Carlson-Hoff; 1 specimen, 1970, Carlson-Hoff; 30.2 mm specimen, Cocos Island, 6 m depth, 2 Aug. 1970, Carlson-Hoff; 42 mm specimen, Bird Island, Saipan, 30 May 1981, Carlson-Hoff; 37 & 25 mm specimens (AM C168830), Ponape, 12 m depth, 16 Oct. 1987, Carlson-Hoff; 4 specimens (21, 15, 22, 9 mm, AM C168839), Enewetok Atoll, Marshall Island, 20 June 1982, S. Johnson.

Papua New Guinea - 42 & 25 mm specimens, Motupore Island, 9 m depth, 16 June 1988, SKB; 11 specimens (17, 18, 10, 32, 26, 18, 18, 14, 15, 21, 22 mm, AM C168832), patch off Lion Island, 8-14 m depth, 17 June 1988, DJB & SKB; 21 & 22 mm specimens (AM C168832), patch off Lion Island; 8-14 m depth, 17 June 1988, DJB & SKB; 36 mm specimen, patch off Lion Island, 16 m depth, 18 June 1988, DJB & SKB; 6 specimens (64, 36, 44, 34.5, 13, 25 mm, AM C168833), patch off Lion Island, 12-15 m depth, 18 June 1988, DJB & SKB; 7 specimens (19, 28, 39, 30, 42, 29, 47 mm, AM C162681), patch off Lion Island, 18 m depth, 20 June 1988, DJB & SKB; 20 & 25 mm specimens (AM C162676), Loloata Island, 8 m depth, 23 June 1988, DJB & SKB; 30

mm specimen, Horseshoe Reef, 18-24 m depth, 21 June 1988, DJB & SKB; 7 specimens (30, 30, 23, 11, 17, 34, 25 mm specimen AM C168834), Horseshoe Reef, 6-18 m depth, 21 June 1988, DJB; 14 mm specimen, Barrier Reef, 10 m depth, 20 Apr. 1984, Carlson-Hoff; 16 mm specimen, Lion Island, 3 m depth, 18 Apr. 1984, Carlson-Hoff; 15 mm specimen, Barrier Reef, 12 m depth, 20 Apr. 1984, Carlson-Hoff.

Madang – 15 mm specimen, Rasch Passage, 15-33 m depth, 12 Jan. 1988, RCW; 34 mm specimen, Madang Lighthouse, 15-35 m depth, 15 Jan. 1988, RCW; 9 mm specimen, Bombes Reef, 12 m depth, 16 Jan. 1988, RCW; 20 mm specimen, 'The Quarry', 0-15 m depth, 21 Jan. 1988, RCW; 1 specimen, Wreck-'USS Boston', 15-35 m depth, 31 Jan. 1988, RCW; 2 specimens, Jais Aber Wharf, 4-9 m depth, 12 Jan. 1988, RCW; 4 specimens, Barracuda Point, 15 m depth, 13 Jan. 1988, RCW; 29 & 17 mm specimens, 1 Feb. 1988, RCW; 1 specimen, Magic Pass, 15-22 m depth, 14 Jan. 1988, RCW; 2 specimens, The Chimney, 15-30 m depth, 17 Jan. 1988, RCW; 7 specimens, Sek Island, 15 m depth, 18 Jan. 1988, RCW; 6 specimens, Planet Rock, 12-20 m depth, 19 Jan. 1988, RCW; 3 specimens, Rasch Passage, 15 m depth, 19 Jan. 1988, RCW; 42 mm specimen, The Chimney, 15-30 m depth, 17 Jan. 1988, RCW; 40 mm specimen, Rasch Passage, 15-33 m depth, 12 Jan. 1988, RCW; 25 mm specimen, Magic Passage, 18 m depth, 18 Jan. 1988, RCW; 6 specimens, Barracuda Point, 5-21 m depth, 23 Jan. 1988, RCW; 3 specimens, 'Hole In Wall', 9-15 m depth, 27 Jan. 1988, RCW; 2 specimens, Christmas Bay, 6-30 m depth, 10 Feb. 1988, RCW; 5 specimens, Barracuda Point, 8-25 m depth, 14 Feb. 1988, RCW; 2 specimens, Barracuda Point, 20 m depth, 20 Feb. 1988, RCW; 16 specimens, slope off Madang Resort, 9-18 m depth, 1 Feb. 1988, RCW; 7 specimens, Kranket Wall, 10-25 m depth, 4 Feb. 1988, RCW; 5 specimens, Christmas Bay, 10-20 m depth, 5 Feb. 1988, RCW; 7 specimens, The Pinnacle, 20 m depth, 11 Jan. 1988, RCW; 25 mm specimen, Banana Reef, 6-30 m depth, 18 Feb. 1988, RCW; 16 mm specimen, Banana Reef, 6-30 m depth, 18 Feb. 1988, RCW; 1 specimen (WAM 439-87), 1987, F. Wells; 1 specimen (WAM 377-87), 1987, F. Wells; 25 mm specimen, Anemone Reef, 11 m depth, 10 Jan. 1988, RCW.

Fiji – 20 mm specimen, Treasure Island, 18 Oct. 1985, G. Brodie; 1 specimen, Treasure Island, 18 Oct. 1985, G. Brodie; 20 mm specimen, Suva, 1 July 1987, RCW; 22 mm specimen, Suva, 1 July 1987, RCW; 1 specimen, Treasure Island, 5 Feb. 1986, G. Brodie; 3 specimens (15, 15, 27 mm), Suva Vicinity, 1 July 1987, RCW; 1 specimen, Suva Reef (Ctss), 17 Apr. 1985, G. Brodie; 18 mm specimen, Nukubuca Reef, 9 July 1987, RCW; 40 & 55 mm specimens, Toberua, 2 Jan. 1984, G. Brodie; 14 mm specimen, Hyatt, Fiji, 7 Jan. 1984, G. Brodie.

Indian Ocean – 31 mm specimen (AM C162688), Chinamans Hat Island, SA, 6 m depth, 24 Nov. 1985, A.R. Davis.

Red Sea – 1 specimen, Shaab, 15 m depth, 30 June 1983, N. Yonow; 1 specimen (BMNH Acc.no. 2337), 10 m depth, 9 July 1983, N. Yonow; 1 specimen (BMNH Acc. No.2337), Shib Ammar, 17 m depth, 1983, N. Yonow; 5 specimens, N. Yonow; 45 mm specimen, Shadwan North, 25 Sept. 1989, M. Ilan.

Thailand – 34 & 14 mm specimens (AM C162690), Phi Phi Island, 4-15 m depth, 25 Nov. 1989, DJB; 37 mm specimen (AM C162691), Phi Phi Island, 5 m depth, 26 Nov. 1989, DJB; 5 specimens (51, 39, 48, 42, 40 mm, AM C162692), Phi Phi Island, 16 m depth, 27 Nov. 1989, DJB; 35 mm specimen (AM C162801), Phuket Island, 5-20 m depth, 7 July 1989, RCW.

Western Australia – 1 specimen (AM C168819), Dampier

Archipeligo, north WA, 0-8 m depth, 21 May 1987, D. Johnson; 1 specimen (MV), Bundegi Reef, 3 m depth, 5 July 1972, N. Coleman; 1 specimen (MV), Sorrento Reef, Perth, 6 m depth, 27 Feb. 1971, N. Coleman; 1 specimen (MV), Sorrento Reef, Perth, 5 m depth, 18 Mar. 1971, N. Coleman; 37.5 mm specimen (WAM 345-85), Monkey Rock, 7-12 m depth, 17 Mar. 1986, F. Wells & C. Bryce; 43 mm specimen (WAM 1068-85), Coral Bay, 5 June 1981, S. Slack-Smith & C. Bryce; 19.5 mm specimen (WAM 422-86), Ashmore Reef, 8 m depth, 13 Sept. 1986, F. Wells & C. Bryce; 22 mm specimen (WAM 1047-85), North-West Cape, 24 May 1980, S. Slack-Smith & C. Bryce; 1 specimen (WAM 455-86), Ashmore Reef, north WA, 1986 ?collector; 1 specimen (WAM 1068-85), North West Cape, north WA, 1985, ?collector; 1 specimen (WAM 2429-84), Scott Reef, north WA, 1984, ?collector; 1 specimen (WAM), Ashmore Reef, north WA; 1 specimen (WAM 2203-84), Scott Reef, north WA; 38.5 & 34 mm specimens (WAM 2667-84), Scott Reef, north WA, 16 Nov. 1984, F. Wells & C. Bryce; 1 specimen (MV), Coral Bay, south WA, 1 Aug. 1979, WA Museum.

External morphology (Fig.27, Pl.5E-F). Live animals ranged in length from 8-69 mm and mean size was 30 mm. *Phyllidiella pustulosa* is an elongate, ovate species with pink tubercles on a black notum. In the median area of the notum, tubercles are usually clustered in three groups with the black dorsum showing between individual tubercles, or tubercles are amalgamated together within these groups so that little or no black is visible between tubercles (Fig.1). The mantle margin is edged in pale pink. This feature is obvious in small to medium sized animals but the pink edging becomes narrower in large specimens or it may be interrupted by black. The tubercles of specimens photographed in natural light or with camera strobe lighting always appear pink. Underwater, tubercles of some individuals appear greyish or green to the human eye. The following *in situ* observations show incontrovertibly that these individuals belong to the present species: greenish specimen (47 mm, AM C162681) observed mating with pink specimen (42 mm, AM C162681), 20 June 1988, 18 m depth, patch reef off Lion Island, PNG; grey-green specimen (36 mm) observed mating with bright pink specimen (44 mm), 18 June 1988, 15 m depth, patch reef off Lion Island, PNG; greenish specimen (38 mm) observed mating with pink specimen (43 mm), 1 July 1988, 4 m depth, Bile Bay, Guam.

The basic pattern of notal tubercles is similar in juveniles and adults. Juveniles have tubercles grouped in amalgamated clusters around the perimeter of the dorsum and three large pink clusters of tubercles in the midline (1 anteriorly around the rhinophores, 1 centrally, 1 posteriorly; Pl.5E). As an animal grows, individual tubercles or a few tubercles separate from the amalgamation and spread out, and the black background colouration appears between. With increasing body size, the distance between these tubercles increases. In large animals, the tubercles are entirely distinct from the original mass, however, the pattern of three main clusters is always present (see Pl.5E-F). Individual tubercles are small, of irregular shape with a rounded apex (rarely angular) and may be compound. The rhinophores are

black and each rhinophoral clavus possesses 22-26 lamellae (specimens greater than 35 mm; Fig.3b). The anal opening occurs far posteriorly. Ventrally, the edge of the hyponotum is pale pink. The rest of the hyponotum is dark grey and cross hatched. The oral tentacles are grey, and broad and triangular in shape. Their tips are rounded and black. Each oral tentacle slants away from the other rather than lying in parallel, and each has a very short lateral groove. The oral tentacles are usually quite distorted in the preserved state. The gills are dark grey. The foot sole is dark grey medially, becoming

lighter towards the margins.

Anatomy. The present species is the type for the genus *Phyllidiella* Bergh. Diagnostic features include the very large pharyngeal bulb that, when retracted, is bunched tightly and unevenly in a semi-concertina fashion. The buccal bulb is often distorted asymmetrically (Fig.12). The pharyngeal bulb is capable of eversion from the mouth for a distance of one third to one half of the body length (personal observation). The mass of oral gland leaflets (Fig.12) is pale pink. The pharyngeal

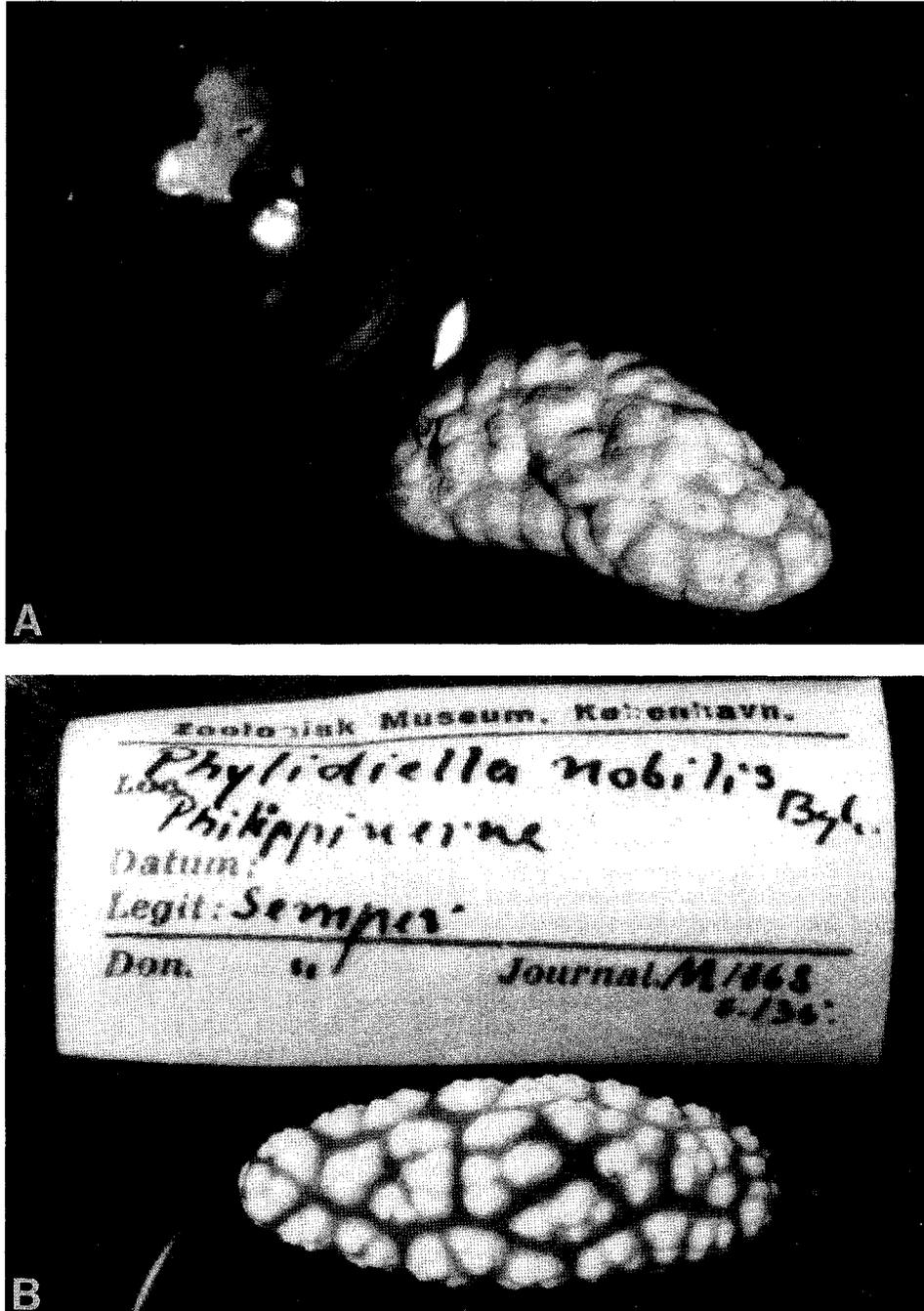


Fig.27. A, *Phyllidiella pustulosa* (Cuvier). Figured syntype (35 mm) here selected as lectotype (MNHN); B, *Phyllidiella nobilis* Bergh. Holotype (28 mm, ZMUC).

retractor muscles are slim and sinuous. The anal papilla is slightly bulbous and covered with dark grey tissue. Black tissue encapsulates the bursa copulatrix and

penis. The receptaculum seminis is brownish. The vas deferens is white; the ampulla may be cream to brown. Penial spines were very difficult to isolate, in spite of

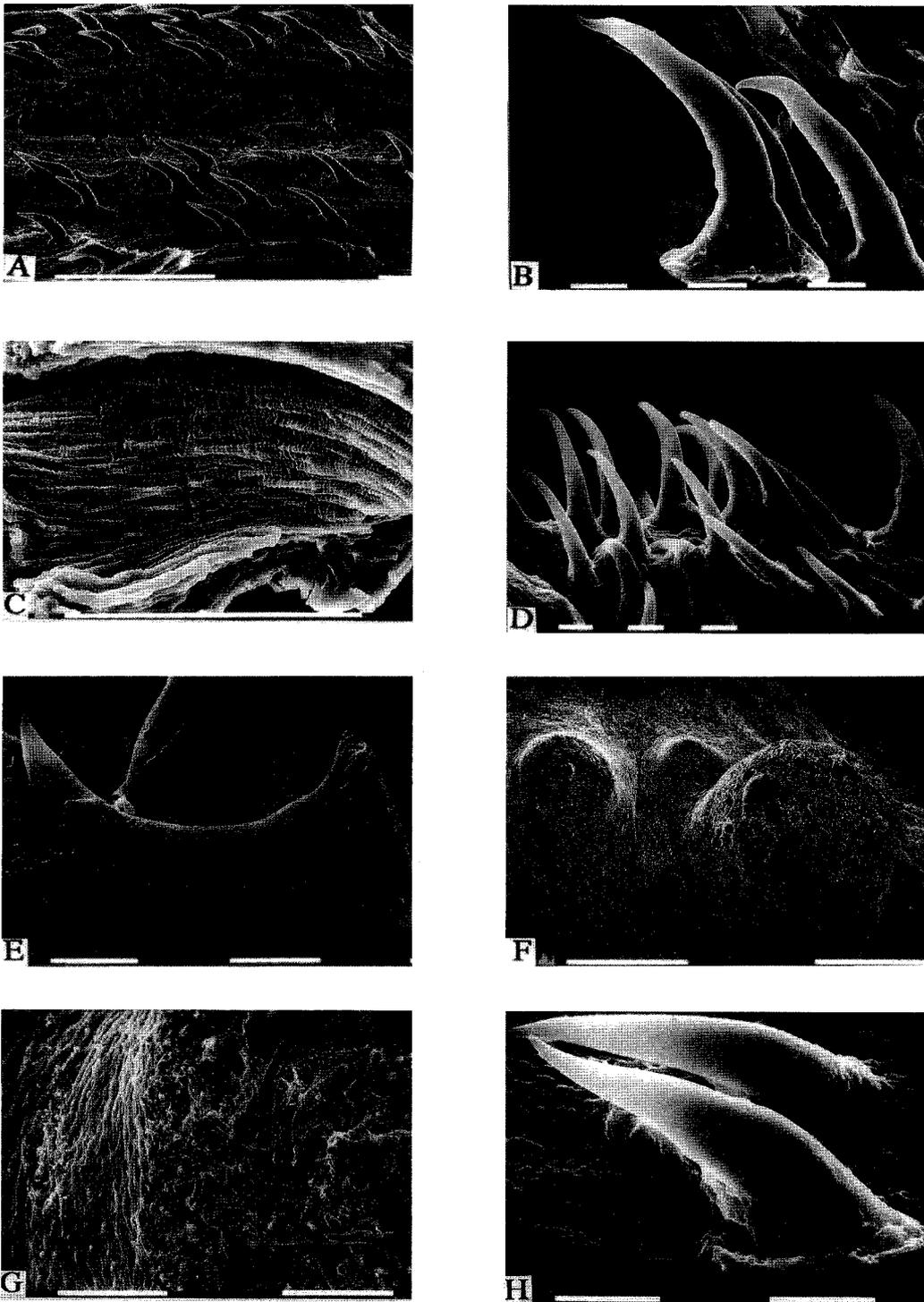


Fig. 28. A, *Phyllidiella pustulosa*. SEM of penial spines, scale = 0.1 mm; B, *Phyllidiella pustulosa*. SEM of penial spines, scale = 10 µm; C, *Phyllidiella pustulosa*. SEM of epithelial lining of vaginal aperture, scale = 0.1 mm; D, *Phyllidiella nigra*. SEM of penial spines, scale = 10 µm; E, *Phyllidiella nigra*. SEM of a single penial spine, scale = 10 µm; F, *Phyllidiella cooraburrama* n.sp. SEM of notal tubercles, scale = 1 mm; G, *Phyllidiella cooraburrama* n.sp. SEM of notal tubercle showing spicules and pore openings, scale = 0.1 mm; H, *Phyllidiella cooraburrama* n.sp. SEM of penial spines, scale = 10 µm.

their very large size (up to 50 μm in length). Individual spines (Fig.28A-B) have a rounded base, a relatively uneven surface, irregular shape (appearing twisted in extreme cases), are slightly recurved, and taper to a fine point. The longitudinal ridges of folded epithelium lining the vagina in this species are illustrated in Figure 28C.

Distribution. *Phyllidiella pustulosa* is one of the most common nudibranchs throughout the tropical Indo-West Pacific. In Australia, it has been recorded as far south as Coffs Harbour (New South Wales), Shark Bay (Western Australia) and South Australia (Burn, 1989; present work).

Remarks. *Phyllidiella pustulosa* changes in appearance as it grows. However, diagnostic features recognisable at any stage include the three median clusters of pink tubercles. The tubercles are in a cluster which is amalgamated in juveniles and separated in large animals (Pl.5E-F). The intensity of pink colouration (and green-grey tones) are possibly related to diet and time since feeding (personal observation). Other distinguishing characters are the pale pink edge to the mantle, the broad, triangular, black tipped oral tentacles and the rhinophoral clavus possessing 22-26 lamellae (specimens greater than 35 mm). Internal features include the very large pharyngeal bulb (apparently the largest of any *Phyllidiella* species), pale pink oral glands, dark grey anal papilla, and the large, irregularly shaped penial spines. *Phyllidiella pustulosa* is closest in appearance to *P. annulata*, *P. zeylanica* and *Phyllidiella granulatus* n.sp. *Phyllidiella annulata* differs in having many pink rings with low angular tubercles (Pl.5G-H), in lacking a pale edge to the mantle, in the possession of 17-20 lamellae on each rhinophoral clavus (specimens greater than 23 mm), and smaller, smooth penial spines (10-15 μm). *Phyllidiella zeylanica* has pink compound tubercles which are coalesced into longitudinal ridges (i.e., not clusters), black longitudinal lines, and the anal opening partially encircled by pink tubercles. *Phyllidiella zeylanica* is pale grey ventrally, has 20-23 lamellae on each rhinophoral clavus (specimens greater than 30 mm), and its penial spines are smaller (approximately 30 μm), with a broad base and gradually tapered. *Phyllidiella granulatus* n.sp. has three median groups of tubercles but differs from *P. pustulosa* in that the tubercles are acute, multi-compound and white with grey bases and intermediate granular grey areas, a granular grey mantle edge, 17-20 lamellae on each rhinophoral clavus and minute penial spines (less than 10 μm).

Phyllidiella annulata (Gray)

Pl.5G-H

Phyllidia annulata Gray, 1853: 220.-Gray, 1857: 216.-Bergh, 1869: 509.-Er. Marcus & Ev. Marcus, 1970: 172-173, figs 48, 49.-Carlson & Hoff, 1973: 6 (colour illustration).

Phyllidia meandrina Pruvot-Fol, 1957a: 113-114, figs 22-26 (n.syn.).

Phyllidia sudanensis Heller & Thompson, 1983: 342, fig.8j.-Yonow, 1986: 1415, fig.6a (n.syn.).

Comments on synonymy. Pruvot-Fol's (1957a) specimens of *Phyllidia meandrina* match the present species. Heller & Thompson (1983) sectioned the single specimen of *P. sudanensis*, however their illustration and brief description corresponds with *Phyllidiella annulata*.

Types. *Phyllidia annulata* Gray. Holotype presumed lost; could not be located in BMNH.

Phyllidia meandrina Pruvot-Fol. Holotype (20 mm preserved length) BMNH 1887.6.7.10; figured by Pruvot-Fol, 1957a: figs 22-26.

Phyllidia sudanensis Heller & Thompson. Holotype destroyed (sectioned by authors); figured by Heller & Thompson, 1983: fig.8j.

Material examined. *Western Pacific Ocean* - 20 mm specimen (BMNH 1887.6.7.10), 'Java', 1860-80?, collector unknown; 25 mm specimen, Fiji, 1987, G. Brodie.

Guam - 1 specimen, Gun Beach, 15 Jan. 1970, Carlson-Hoff; 31 mm specimen, Bile Bay, 5 m depth, 21 June 1987, Carlson-Hoff; 23 & 22 mm specimens (AM C159520), Bile Bay, 6 m depth, 27 June 1988, DJB & SKB; 28 mm specimen, Bile Bay, 3 m depth, 28 June 1988, DJB & SKB AM C159521; 23 mm specimen (AM C159522), Bile Bay, 18 m depth, 29 June 1988, DJB & SKB; 26 mm specimen (AM C159519), Bile Bay, 5 m depth, 1 July 1988, DJB & SKB; 25 mm specimen (AM C159523), Bile Bay, 7 m depth, 3 July 1988, DJB & SKB; 31 & 26 mm specimens (AM C159524), Asan Bay, 9 m depth, 9 July 1988, DJB & SKB; 28 mm specimen (AM C159525), Bile Bay, 3 m depth, 21 Mar. 19/88, Carlson-Hoff; 19 mm specimen (AM C159527), Bile Bay, 3 m depth, 29 Apr. 1988, Carlson-Hoff; 27 mm specimen (AM C159526), Bile Bay, 5 m depth, 4 Mar. 19/88, Carlson-Hoff.

Indian Ocean - 30 mm specimen Réunion Island, Indian Ocean, 1-20 m depth, 1987, M. Jay.

External morphology (Pl.5G-H). Live specimens ranged in length from 19-31 mm in length. *Phyllidiella annulata* is oval in shape. It has a black dorsum with four to fourteen pink rings (white in the preserved state). Small, low notal tubercles with angular sides and rounded apices occur in the pink rings. There is no central tubercle to each ring, only the black background of the dorsum. Minute, isolated, rounded, pink tubercles may occur around the large median rings and around the mantle margin. There is no continuous pink edge to the mantle. Juveniles resemble adults in their dorsal pattern. The rhinophores are black and each rhinophoral clavus possesses 17-20 lamellae (specimens greater than 23 mm). Ventrally, colouration is primarily grey. The hyponotum has some darker cross hatching. The oral tentacles are grey with black tips, and they are black on the lateral margins. The lateral grooves of the oral tentacles are long. The foot sole is dark grey with a broad, pale grey median band, and a

pale marginal edge.

Anatomy. The present species possesses the characteristics of the genus *Phyllidiella*. The pharyngeal bulb of *P. annulata* is conical and relatively small. The reproductive organs are cream in colour except for the bursa copulatrix which is brown to dark grey. The prostatic vas deferens is long and slender. Penial spines were not isolated for SEM studies, however under light microscope they appear to be small (about 10-15 µm), smooth and recurved.

Distribution. *Phyllidiella annulata* is presently known from the Red Sea, tropical Indian Ocean and central-western Pacific Ocean.

Remarks. *Phyllidiella annulata* (Gray) has a distinctive dorsal pattern consisting of numerous pink rings (with small, low tubercles) on a black background. Characteristic internal features include the relatively small pharyngeal bulb, the long slender prostatic section of the vas deferens, and the small penial spines. My records show that *P. annulata* attains a smaller size (approximately half) than *P. pustulosa*. *Phyllidiella annulata* lacks compound tubercles (as in *P. pustulosa* and *P. zeylanica*), tubercular clusters (*P. pustulosa*), and ridges of tubercles (*P. zeylanica*). The dorsal rings on Gray's (1853) preserved specimens had faded to white by the time he examined them. His specimens could not have been *Phyllidia ocellata* which has successive rings or "eye spots" with a central tubercle in each. *Phyllidia ocellata* also differs in having yellow colouration and different foregut anatomy.

Phyllidiella nigra (Hasselt)

Fig.28D-E, Pl.6B

- Phyllidia nigra* Hasselt, 1824: 244.—Bergh, 1887: 313, pl.6, fig.6.—Pruvot-Fol, 1956: 67 (non *Phyllidia nigra* Pease, 1868).
Phyllidiella pustulosa.—Bergh, 1869: 455-484, 510-512, pls 20-24a.—Bergh, 1902: 195.—Bergh, 1905: 183 (non *Phyllidia pustulosa* Cuvier, 1804).
Phyllidia pustulosa.—Baba, 1936: 40-41, pl.3, fig.1.—Lin & Si, 1965: 15, pl.3, fig.1.—Lin *et al.*, 1986: 86 (non *Phyllidia pustulosa* Cuvier, 1804).
Phyllidia serenei Risbec, 1956: 24-25, figs 82-84, 86-89.—Lim & Chou, 1970: 135, pl.16, fig.d.—Lin, 1983: 152, pl.1, fig.8.—Lin, 1990: 137 (n.syn.).
Phyllidia bataviae Pruvot-Fol, 1957a: 107-109, figs 27-34 (n.syn.).
Phyllidia nobilis.—Kenny, 1970: 91 (non *Phyllidiella nobilis* Bergh, 1869).

Comments on synonymy. Hasselt's (1824) original description of *Phyllidiella nigra* was brief, but Bergh's (1887) redescription and publication of Hasselt's original drawings clearly characterise this species. The living specimen was drawn by Maurevert and Bik under van

Hasselt's direction (Bergh, 1887: 304-305). Bergh (1869) misidentified his own specimens of *P. nigra*, referring them to *P. pustulosa* (Cuvier). Later (Bergh, 1887) suggested that *P. nigra* was close to, or a variant of *P. pustulosa* (Cuvier). My examination of Bergh's (1869) specimens (as *P. pustulosa*), those of Risbec (1956) (as *P. serenei*), and those of Pruvot-Fol (1957a) (as *P. bataviae*) confirm that they all belong to one species. Risbec's numerous syntypes of *P. serenei* include specimens of *P. pustulosa* as well as specimens of the present species (personal observation) However, his illustrations (Risbec, 1956, figs 82-84, 86-89) are of specimens belonging to *Phyllidiella nigra* (Hasselt). As neither *P. serenei* nor *P. bataviae* have been widely or consistently used, and to avoid confusion in the future, a lectotype is selected for *P. serenei* Risbec and the same specimen is designated as neotype of *P. nigra* Hasselt. By this action, both names become objective synonyms.

Types. *Phyllidia nigra* Hasselt. Holotype presumed lost, could not be located in Leyden Museum (see Bergh 1887); figured by Bergh 1887; pl.6, fig 6; Neotype here designated (approximately 30 mm, contracted, preserved state) MNHN E34210 (= lectotype for *P. serenei* Risbec).

Phyllidia serenei Risbec. Lectotype here selected (approximately 30 mm, contracted, preserved state) MNHN E34210; paralectotypes (remaining syntypes; 20-40 mm preserved length, very contracted) MNHN, numbers E34208, E34209, E34211; ?figured by Risbec, 1956: figs 82-84, 86-89.

Phyllidia batavia Pruvot-Fol. Lectotype here selected (27 mm preserved length) ZMA Moll. 3.57.001; figured by Pruvot-Fol 1957a: figs 27-34; paralectotype (remaining syntype; 28 mm preserved length) ZMA Moll. 3.57.002.

Material examined. *Western Pacific Ocean* – 1 specimen (MNHN E34210), Vietnam, ?1956, ?Risbec; 1 specimen (MNHN E34208), Vietnam, ?1956, ?Risbec; 1 specimen (MNHN E34209), Vietnam, ?1956, ?Risbec; 1 specimen (MNHN E34211), Vietnam, ?1956, ?Risbec; 27 mm specimen (ZMA Moll.3.57.001), Batavia Bay, Java, 1909; 28 mm specimen (ZMA Moll.3.57.002), Batavia Bay, Java, 1909; 32 & 33 mm specimens (MV F54956), Bunday Reef, Philippines, 9 Nov. 1979, C.C. Lu; 30 mm specimen (MV F54955), Bunday Reef, Philippines, 10 Nov. 1979, C.C. Lu; 35 mm specimen (AM C154742), Bohol Island, Philippines 4 m depth, 27 Feb. 1976, C. Short; 32 mm specimen (AM C154743), Banacon Island, Cent. Philippines, 4 m depth, 2 Mar. 1976, C. Short.
Eastern Australia – Great Barrier Reef – 45 mm specimen, Lizard Island, north Qld, 1 m depth, 4 Oct. 1982, RCW; 2 specimens (45 & 45 mm, AM C162710(1) & (2)), Lizard Island, 0 m depth, 4 Oct. 1982, R. Burn; 1 specimen (MV), Low Isles, 2 m depth, 1954, R. Burn; 58 mm specimen (MV 54953), Pennys' Bay, Orpheus Island, 1 June 1968, N. Coleman; 39 mm specimen (AM C162711), Orpheus Island, Townsville, 0 m depth, 23 Mar. 1982, A. Martin.

Micronesia – 38 mm specimen, Bile Bay, Guam, Carlson-Hoff; 43 mm specimen, Palau, 31 Dec. 1981, Carlson-Hoff; 63 mm specimen (AM C162709), Pohnpei, 23 Aug. 1985, C. Birkeland.

Papua New Guinea – 1 specimen (AM), Bat Island, 2 Sept. 1945, R.C. Swan; 38 mm specimen, Lion Island, 3 m depth, 18 Apr. 1984, Carlson-Hoff.

Madang – 40 mm specimen (AM C162706), Banana Reef, 6-30 m depth, 18 Feb. 1988, RCW; 22 mm specimen, Banana Reef, 6-30 m depth, 18 Feb. 1988, RCW; 50 mm specimen, Kranket Island, 3-20 m depth, 24 Jan. 1988, RCW.

Indian Ocean – 3 specimens (28.5, 44, 43.5 mm, WAM 402-86), West Island, Ashmore Reef, 11 Sept. 1986, F.Wells; 26 mm specimen (AM C162708), Phi Phi Island, southern Thailand, 5 m depth, 26 Nov. 1989, DJB; 40 mm specimen (AM C162707), Phi Phi Island, southern Thailand, 0 m depth, 29 Nov. 1989, DJB; 1 specimen (MNHN), Benthedi, Red Sea.

External morphology (Pl.6B). Live specimens ranged in length from 22-63 mm and mean size was 36 mm. *Phyllidiella nigra* is broad and oval in shape, and convex dorsoventrally (*cf.* flattened). Dorsal colouration consists of a black background and dark pink to red tubercles. The notal tubercles are most commonly single and isolated (although occasionally two or three coalesce), have black bases and, their sides and apices are dark pink to red. They are evenly distributed over the dorsum. Individual tubercles are quite tall (up to 3 mm high) with relatively straight sides and a rounded summit. Tubercles around the mantle margin are smaller. There is no continuous pale edge to the mantle. The pitch black rhinophores are rounded apically and each rhinophoral clavus possesses 19-21 lamellae (specimens greater than 30 mm).

Ventrally, the hyponotum and gills are dark grey. The foot sole is uniformly grey. The sides of the foot have a darker grey band. The oral tentacles are broad, black and cylindrical with rounded tips.

Anatomy. Typical for the genus *Phyllidiella*. The anterior portion of the foregut is black. The pharyngeal bulb is quite broad when retracted. The intestine is also broad and it has black longitudinal striations on its surface. The reproductive organs are cream in colour except for the bursa copulatrix which is orange-brown. The prostatic vas deferens is long. The penis is short and slightly bulbous. The penial spines are large (35-40 µm in vertical height) and have a broad pitted base and a long slender stem with a rough surface (Fig.28D-E). The spines stand upright, are gently recurved distally, and their tip is slightly hooked.

Distribution. *Phyllidiella nigra* is usually encountered on intertidal reef areas. It is known from throughout the Indo-west Pacific region. It appears to be less common in the eastern Indian Ocean.

Remarks. *Phyllidiella nigra* is easily distinguished from conspecifics by its tall, rounded, dark pink to red tubercles which are evenly distributed (not clustered) over the dorsum. The bases of these tubercles are black. Other characteristic features include: the entirely black, rounded oral tentacles; the black anterior part of the foregut; the broad, black, striated intestine; and the large, upright, broad based penial spines which have a hooked apex.

Phyllidiella pustulosa and *P. annulata* differ from *P.*

nigra in the arrangement of the tubercles, in the number of lamellae on the rhinophoral clavus, and in the morphology of the penial spines. *Phyllidiella nigra* is superficially similar to *Phyllidiella cooraburrama* n.sp., but the latter possesses fewer, very large multicomound, pale pink tubercles with broad, pale pink bases, and pale pink rims to the rhinophoral openings. Furthermore, *P. cooraburrama* n.sp. possesses more lamellae (22-24) on the rhinophoral clavus (38-49 mm specimens) and its penial spines are smaller, recurve from a broad base but straighten distally (penial spines upright and hooked apically in *P. nigra*).

Phyllidiella rosans (Bergh)

Pl.6C-D

Phyllidia nigra Pease, 1868: 80, pl.9, fig.5 (non *Phyllidia nigra* Hasselt, 1824).

Phyllidia rosans Bergh, 1873: 67-72, pl.9, figs 1-4, pl.10, figs 1-18.–Bertsch, 1988: 25.–?Karuso, 1987: 36.

Phyllidia bourgini Risbec, 1928: 57-58, fig.3, pl.1.–Risbec, 1953: 12 (n.syn.).

Phyllidia soria Er. Marcus & Ev. Marcus, 1970: 174-175, figs 53, 54 (n.syn.).

Phyllidiopsis cf. striata–Edmunds, 1972: 83, figs 3d,g (non *Phyllidiopsis striata* Bergh, 1889).

Phyllidia mediocris Yonow & Hayward, 1991: 20-21, figs 11C-E, 13A (n.syn.).

Comments on synonymy. Andrew Garrett collected this species in Tahiti and apparently sent material to both Bergh and Pease. Pease (1868) first described this species, however the specific name he chose, *nigra*, had been used previously by Hasselt (1824) for a different species. Therefore this species must be known by the next available name, *P. rosans* Bergh. The holotype of *P. soria* Er. & Ev. Marcus matches this species. Edmunds' (1972) figure also matches *P. rosans*. The identity of *Phyllidia bourgini* Risbec (1928) is most probably the present species even though the longitudinal ridges of Risbec's specimen were interrupted. I have observed this condition in other specimens (also reported by S. Johnson, *in litt.*). *Phyllidia mediocris* Yonow & Hayward clearly matches the present species, as does their holotype; in fact their drawing (Fig.11C) is not unlike the specimens figured by Pease and Bergh. As in some other species studied in the present work the number of ridges can vary, probably with ontogeny.

Types. *Phyllidia nigra* Pease. Holotype could not be located; it is not clear whether Pease had a specimen or only Garrett's notes and drawings; figured by Pease, 1868: pl.9, fig.5).

Phyllidia rosans Bergh. Holotype destroyed (dissected by Bergh); figured by Bergh, 1873: pl.9, figs 1-4, pl.10, figs 1-18.

Phyllidia bourgini Risbec. Holotype not located in MNHN, figured by Risbec, 1928: fig.3, pl.1.

Phyllidia soria Er. Marcus & Ev. Marcus. Holotype (20

mm preserved length) USNM 576008 (partially dissected); figured by Er. Marcus & Ev. Marcus, 1970: figs 53, 54.

Phyllidia mediocris Yonow & Hayward. Holotype (18 mm preserved length) BMNH 1986.232, the Morne, Mauritius.

Material examined. 28 mm specimen, Bandos Island, Maldives, 30 m depth, 1 Apr. 1985, P. Chapman-Smith; 18 mm specimen (AM C162669), Pupukea, Oahu, Hawaii, 12 m depth, 29 June 1983, S. Johnson; 24 mm specimen, Pupukea, Oahu, Hawaii, 12 m depth, 9 May 1979, S. Johnson; 18 mm preserved specimen (BMNH 1986.232), the Morne, Mauritius, collected subtidally, 18 Oct. 1985, M. Frederic; 34 & 35 mm specimens Réunion Island, Indian Ocean, 1-20 m depth, 1987, M. Jay; 5 specimens (30, 25, 20, 19, 16 mm, AM C168818), Réunion Island, Indian Ocean, 5-20 m depth, 1989, M. Jay.

External morphology (Pl.6C-D). Live specimens ranged in length from 18-35 mm. *Phyllidiella rosans* is oval in shape and possesses a black dorsum with numerous, longitudinal, pink ridges. There are 6-9 rounded, longitudinal ridges which are relatively smooth apart from some minute tubercular mounds on the lateral edges of the dorsum (Pl.6D). These dorsal ridges may be interrupted in some individuals (Pl.6C). Two isolated, rounded pink tubercles usually occur in the midline, far posteriorly. The anus opens at the apex of one of these posterior tubercles. The edge of the mantle is pink. The stalk of the rhinophores is pale pink. Each rhinophoral clavus possesses 12-15 black lamellae (specimens greater than 30 mm). Ventrally, the pale grey to white oral tentacles are long and possess rounded apices. The foot and gills are pale grey. The pale foot sole has numerous tiny, dark grey spots.

Anatomy. Typical for the genus *Phyllidiella*. The foregut is cream. The pharyngeal bulb is conical in shape and relatively small compared to other species. The anal papilla is pale pink to white. The reproductive system is cream except for the bursa copulatrix which is dark grey to black. The prostatic vas deferens is broad and convoluted proximally and then narrows as a long tube leading to the ejaculatory duct. The spines lining the penis were examined under the light microscope. Individual spines measure approximately 30-40 µm in height, are stout with a broad, smooth rounded base, and have a slightly recurved (i.e., relatively upright) stem.

Distribution. *Phyllidiella rosans* is now known from Tahiti (Pease, 1868; Bergh, 1873), Hawaii (S. Johnson, *in litt.*), the western Pacific Ocean (Risbec, 1928; Er. Marcus & Ev. Marcus, 1970) and the Indian Ocean (East Africa - Edmunds, 1972; Maldives and Réunion).

Remarks. *Phyllidiella rosans* is distinguished by its numerous, longitudinal, rounded pink ridges, pink margin and black rhinophores which have a pink stalk. Ventrally, *P. rosans* is pale grey. Diagnostic internal features are the relatively small pharyngeal bulb, pale pink rectum and dark bursa copulatrix.

The longitudinal notal ridges of the present species

distinguish it from the three species of *Phyllidiella* described above and also the new species described below. The only other species of *Phyllidiella* which possesses longitudinal ridges and a pale foot is *P. zeylanica*. However, that species differs from *P. rosans* in the very uneven, irregular nature of the notal ridges which are formed from the coalesced bases of compound tubercles (see Pl.6E-G). Eliot (1906) also made this distinction. Furthermore, the foot of *P. zeylanica* is whitish and its gills and oral tentacles are dark grey (pale in *P. rosans*). Each rhinophoral clavus possesses 20-23 lamellae in *P. zeylanica* (specimens greater than 30 mm), but only 12-15 in *P. rosans* (specimens greater than 30 mm). Other differences include the dark anal papilla and very broad triangular penial spines of *P. zeylanica*.

Phyllidiella zeylanica (Kelaart)

Pl.6E-G

Phyllidia zeylanica Kelaart, 1859: 494.-Eliot, 1906: 674, pl.42, fig.10.-Pruvot-Fol, 1956: 67-68.-Narayanan, 1968: 205, figs 14, 15.-Burn, 1970: 37-40.-Rao *et al.*, 1974: 121-123, figs 2c-e.-Yonow & Hayward, 1991: 23, fig.13D.

Phyllidia zeylanicus.-Kelaart, 1883: 108 (mis-spelling pro. *zeylanica* Kelaart, 1859).

Phyllidia ceylanica.-Bergh, 1869: 509-510 (mis-spelling pro. *zeylanica* Kelaart, 1859).

Phyllidia nobilis.-Eliot, 1904: 282, pl.16, fig.1.-Edmunds, 1972: 79-82, figs 3a-c,e-f,h (non *Phyllidiella nobilis* Bergh, 1869).

Phyllidia varicosa.-Farran, 1905: 345.-Risbec, 1929: 49-52, figs 6a-b, 7b, 8a-b (non *Phyllidia varicosa* Lamarck, 1801)

Phyllidia catena Pruvot-Fol, 1956: 70-72, figs 6-7 (n.syn.).

Phyllidia seriata Pruvot-Fol, 1957a: 109-110, figs 1-4 (n.syn.).

Phyllidia empelia Yonow, 1984a: 223-4, figs 6a,b, 7b, 8a,b (n.syn.).

Phyllidia meandrina.-Yonow & Hayward, 1991: 21, figs 10E, 13B (non *Phyllidia meandrina* Pruvot-Fol, 1957)

Phyllidia sp. 1.-Gosliner, 1987: 90, pl.153.

Phyllidia honloni.-Wells *et al.*, 1990: 74, pl.69 (non *Phyllidia honloni* Risbec, 1956).

Comments on synonymy. *Phyllidiella zeylanica* is not a rare species, but apparently it has been rarely identified in the past. Study of the original descriptions and examination of the type specimens of *Phyllidia catena* Pruvot-Fol, *P. seriata* Pruvot-Fol and *P. empelia* Yonow, confirmed that these taxa belong in the synonymy of *Phyllidiella zeylanica*. Yonow (1984a) described *P. empelia* as possessing grey tubercles, however this was the colour in the preserved state as her slide shows the live animal has pink tubercular ridges. Gosliner (1987: pl.153) provided a colour illustration of a live specimen of this species. Yonow & Hayward (1991) misidentified a mature specimen of this species as *Phyllidia meandrina* Pruvot-Fol, and illustrated a juvenile specimen (as *zeylanica*), which illustrated, quite well, the ontogenetic separation of ridges and tubercles which occurs with growth.

Types. *Phyllidia zeylanica* Kelaart. Holotype lost (Kelaart's original drawing in Hancock Museum at Newcastle-on-Tyne; see Eliot, 1906; Burn, 1970) figured by Eliot, 1906: pl.42, fig.10.

Phyllidia catena Pruvot-Fol. Possible holotype (figured syntype; 37 mm preserved length) MNHN, figured by Pruvot-Fol, 1956: figs 6, 7.

Phyllidia seriata Pruvot-Fol. Holotype (27 mm preserved length; dissected) BMNH 1956.1.27.1, figured by Pruvot-Fol, 1957a: figs 1-4.

Phyllidia empelia Yonow. Holotype (20 mm preserved length) BMNH 19839 W/1, figured by Yonow, 1984a: fig.6 a-b; paratype (26 mm preserved length) BMNH 19839 W/2.

Material examined. *Western Pacific Ocean* – 37 mm specimen (MNHN), ?Mayotte/Java, 1909; 27mm specimen (BMNH 1956.1.27.1), ?Java, 1909.

Indian Ocean – 20 & 26 mm specimens (BMNH 19839 W/1 and W/2), Sri Lanka, ?2-5 m depth, 1983, N. Yonow; 1 specimen, Seychelles, N. Yonow; 4 specimens (33, 26, 22, 15 mm, AM C169012), Réunion, 5-20 m depth, 1989, M. Jay; 10 mm specimen, Réunion, 1-20 m depth, 1987, M. Jay; 15 specimens (24, 27, 28, 29, 30, 30, 31, 32, 33, 35, 37, 38, 40, 41, 43 mm, ZMUC), Indonesia, ?1862, Semper.

Thailand – 17 mm specimen, Phi Phi Island, 3 m depth, 24 Nov. 1989, DJB; 45 mm specimen (AM C162738), Phi Phi Island, 1 m depth, 24 Nov. 1989, DJB; 8 mm specimen, Phi Phi Island, 4-10 m depth, 25 Nov. 1989, DJB; 8 specimens (56, 59, 42, 26, 24, 17, 22, 23 mm, AM C162741), Phi Phi Island, 4-10 m depth, 25 Nov. 1989, DJB; 4 specimens (14, 14, 15, 17 mm, AM C162737), Phi Phi Island, 7-15 m depth, 25 Nov. 1989, DJB; 15 & 40 mm (AM C162740), Phi Phi Island, 8 m depth, 25 Nov. 1989, DJB; 35 mm specimen (AM C162736), Phi Phi Island, 5 m depth, 26 Nov. 1989, DJB; 6 specimens (5, 20, 22, 23, 29, 32 mm, AM C162734), Phi Phi Island, 16 m depth, 27 Nov. 1989, DJB; 6 specimens (13, 19, 21, 36, 38, 44 mm, AM C162735), Phi Phi Island, 9 m depth, 27 Nov. 1989, DJB; 3 specimens (14, 34, 37 mm, AM C162739), Phi Phi Island, 16 m depth, 1 Dec. 1989, DJB; 20 & 30 mm specimens (AM C169013), Phuket, 1988, University of Guam Marine Laboratory; 5 specimens (27, 29, 33, 42, 60 mm, AM C168926), Phuket Island, 5-20 m depth, 7 July 1989, RCW.

External morphology (Pl.6E-G). Live specimens ranged in length from 5-60 mm and mean size was 26 mm. *Phyllidiella zeylanica* is elongate-ovate in shape. Its dorsal colouration consists of a black background and irregular tuberculate pink ridges. Up to nine longitudinal ridges (broken or interrupted) may occur. The ridges usually curve and join, anteriorly and posteriorly. There is generally a group of tubercles encircling or just behind the anal opening. The median ridges may separate into two longitudinal groups. The notal tubercles are compound and coalesce forming ridges. Individual tubercles have a pink base and apex, are usually conical in shape but may be rounded. The mantle edge is very narrow, smooth and pink. The margin has a narrow ridge of tiny tubercles. Juveniles possess one or two, narrow, encircling ridges of mostly rounded tubercles around the mantle margin and a single large, elongate, amalgamated mass of tubercles medially. With increasing size, this median mass of tubercles

separates into numerous longitudinal ridges (Pl.6F). The ridges may curve together in some specimens (see Gosliner, 1987: pl.153). The rhinophores are black and each clavus possesses 20-23 lamellae (specimens greater than 30 mm).

Ventrally, there is some grey cross-hatching on the hyponotum. The gills are grey. The oral tentacles are black anteriorly, grey posteriorly, triangular in shape, and the lateral grooves are very deep. The foot sole is white.

Anatomy. Typical for the genus *Phyllidiella*. The foregut is pale and elongate, and the pharyngeal bulb is relatively narrow (i.e., width is about twice the length). The pharyngeal retractor muscles are thick and robust. One 37 mm specimen (AM C162739) was observed *in situ* (16 m depth, Phi Phi Island, 48 km south-east of Phuket, Thailand, 1 Dec. 1989), with its whitish oral tube extended for a distance of approximately one third of its body length into its food sponge. Most of the reproductive system is yellow. The ampulla and bursa copulatrix are small and brownish. The receptaculum seminis is smaller and whitish. Penial spines were not isolated for SEM, however under the light microscope they appear to be short (less than 10 µm) and smooth, with a very broad, triangular base and slightly hooked apex.

Distribution. This species appears to be restricted to the tropical Indian Ocean where it occurs from eastern Africa to Java (above synonymy). It seems that *P. zeylanica* is not as rare as previously thought (Kelaart, 1859, 1883; Burn, 1970; Rao *et al.*, 1974; Yonow, 1984a). Indeed, my field observations in southern Thailand indicate that *P. zeylanica* may be more common than *P. pustulosa* in the Indian Ocean. However, *P. zeylanica* is not known from the tropical Pacific Ocean where *P. pustulosa* is very common.

Remarks. *Phyllidiella zeylanica* is characterised by its numerous, very tuberculate, pink ridges which curve to join anteriorly and posteriorly (but may be interrupted), its pale foot sole, and its dark triangular oral tentacles. Distinguishing internal features are the pale foregut, the pharyngeal bulb which is not as broad as in other species, and the small seminal vesicles.

The present species differs from *P. pustulosa* which does not possess ridges, and from *P. rosans* which possesses relatively smooth rounded ridges (very tuberculate in *P. zeylanica*). For specimens of similar size, the rhinophoral clavus of *P. zeylanica* possesses fewer lamellae than *P. rosans*. The penial spines of *P. zeylanica* also differ from those of the latter two species in shape and size.

On the basis of the dorsal ridges, Bergh (1869) suggested that *P. zeylanica* may be the same as *Phyllidia varicosa* Lamarck, however the latter species has blue and gold colouration, a black line on the foot sole, and its foregut is different.

Phyllidiella cooraburrama n.sp.

Fig.28F-H, Pl.6H

Type. Holotype here designated (38 mm live length) AM C159477, Plate 6H; the remaining specimens are designated paratypes.

Material examined. Holotype specimen (38 mm, AM C159477), Bare Islet, AIMS, Townsville, 5 m depth, 8 Aug. 1986, DJB; 49 mm specimen (AM C159478), Bare Islet, AIMS, Townsville, 5 m depth, 18 Sept. 1986, DJB; 1 specimen, Fiji, 1987, G. Brodie; 44 mm specimen, Ponape, 16 Oct. 1987, Carlson-Hoff.

External morphology (Fig.28F-G, Pl.6H). Live specimens ranged in length from 38-49 mm. *Phyllidiella cooraburrama* is oval in shape. Its notum possesses a black background and pale pink tubercles. The notal tubercles originate from a broad, pale pink base, but then rise vertically. The tubercles are multicomponent with generally flattish apices (Fig.28F-G), but have a fine, porcelain-like texture. Thus, tubercles are very large and very high (Pl.6H). They are irregularly and widely scattered instead of forming patterns, clusters, ridges or groups. Around the mantle margin, the tubercles tend to be lower and smaller. There is no pale edge to the mantle. The rhinophores are black and each clavus possesses 22-24 lamellae (specimens greater than 38 mm).

Ventrally, the hyponotum is grey and the gills are pale grey. The foot sole is white. The oral tentacles are short and broad with rounded tips which are mottled with dark pigment.

Anatomy. Typical for the genus *Phyllidiella*. The foregut and digestive gland mass are pale whitish-pink. In general, the reproductive system is cream in colour. The ampulla and bursa copulatrix are similar in size (relatively large). The former is brownish-yellow, the latter yellow with a dark grey tissue envelope. The receptaculum seminis is cream and much smaller than the bursa. The penial spines are large and stout (about 30 µm in length), but do not possess an expanded base. The spines recurve immediately from their base then straighten distally where they taper to a point (Fig.28H).

Distribution. *Phyllidiella cooraburrama* is presently known from inshore reef areas in Ponape, Fiji, and the Great Barrier Reef, Australia.

Remarks. *Phyllidiella cooraburrama* is a particularly striking nudibranch. It is distinguished by its extremely large, isolated, notal tubercles which have a very broad pink base, are steep sided, tall and multicomponent with flattish (sometimes rounded) apices (Pl.6H). Other characteristic features include the broad oral tentacles, white foot sole, pale white-pink alimentary system, dark pigmentation of the bursa and vaginal duct, and the stout penial spines. In the field, *P. cooraburrama* is easily

separated from its pink congeners by the form of its large tubercles, *P. pustulosa* has grouped clusters of low tubercles, *P. annulata* has rings of pink with low angular tubercles, *P. nigra* has single rounded red-pink tubercles, *P. rosans* has low, rounded, smooth, straight ridges, and *P. zeylanica* has highly tuberculate ridges which join together anteriorly and posteriorly. *Phyllidiella granulatus* is superficially similar to *P. cooraburrama*, but differs in having smaller conical or acute white tubercles on a granular grey background. Some details of the anatomy of *P. cooraburrama* also differ from these species (e.g., the pale white-pink alimentary tract, large bursa and stout penial spines which straighten distally).

Etymology. "Cooraburrama" is one Aboriginal word for the bunyip, a mythical water monster of Australia.

Phyllidiella granulatus n.sp.

Fig.29A-B, Pl.7A

Type. Holotype here designated (23 mm live length) AM C159486; the remaining specimens are designated paratypes.

Material examined. *Western Pacific Ocean* – 35 mm specimen (AM C154744), Lizard Island, 10-15 m depth, 5 June 1979, I. Loch.

Guam – holotype specimen (23 mm, AM C159486), Bile Bay, 7 m depth, 1 July 1988, DJB & SKB; 20 mm specimen (AM C159485), Bile Bay, 18 m depth, 29 June 1988, DJB & SKB; 29 mm specimen (AM C159484), Bile Bay, 18 m depth, 29 June 1988, DJB & SKB; 30 mm specimen (AM C159487), Bile Bay, 6 m depth, 11 July 1988, DJB & SKB; 20 mm specimen (AM C159488), Bile Bay, 9 m depth, 13 July 1988, DJB; 24 & 11 mm specimens (AM C159489), Bile Bay, 12 m depth, 11 July 1988, DJB; 38 mm specimen, Agana, 24 m depth, 30 Dec. 1969, Carlson-Hoff; 17 & 27 mm specimens (AM C159545), Ana'e Island, 11 m depth, 18 Nov. 1987, Carlson-Hoff.

External morphology (Fig 29A-B, Pl.7A). Live specimens ranged in size from 11-40 mm and mean size was 26 mm. *Phyllidiella granulatus* is oval in shape. Its background colouration is granular, grey (to pale grey). Medially, three encircling irregular black bands partition the pale background colour into two or three large patches (Pl.7A). The black bands extend in front of the rhinophores, and behind the anal opening. White tubercles arise from the pale notal areas. The tubercles are conical and usually occur singly. The median tubercles are tall, acute and may be compound (Fig.29A; Pl.7A). The dorsal pattern was similar throughout the size range studied. The black rhinophores are slightly recurved posteriorly and pointed apically. Each rhinophoral clavus possesses 17-20 broad lamellae (specimens greater than 20 mm).

Ventrally, the hyponotum is grey. The gills are dark grey. The foot sole is pale grey with granular white dots.

The oral tentacles are conical, pointed apically, white ventrally, and black tipped dorsally.

Anatomy. Typical for the genus *Phyllidiella*. The

foregut is white and the oral glands are cream. The digestive gland mass is bright orange in live specimens and it fades to yellowish in the preserved state. The reproductive system is grey to cream. The seminal

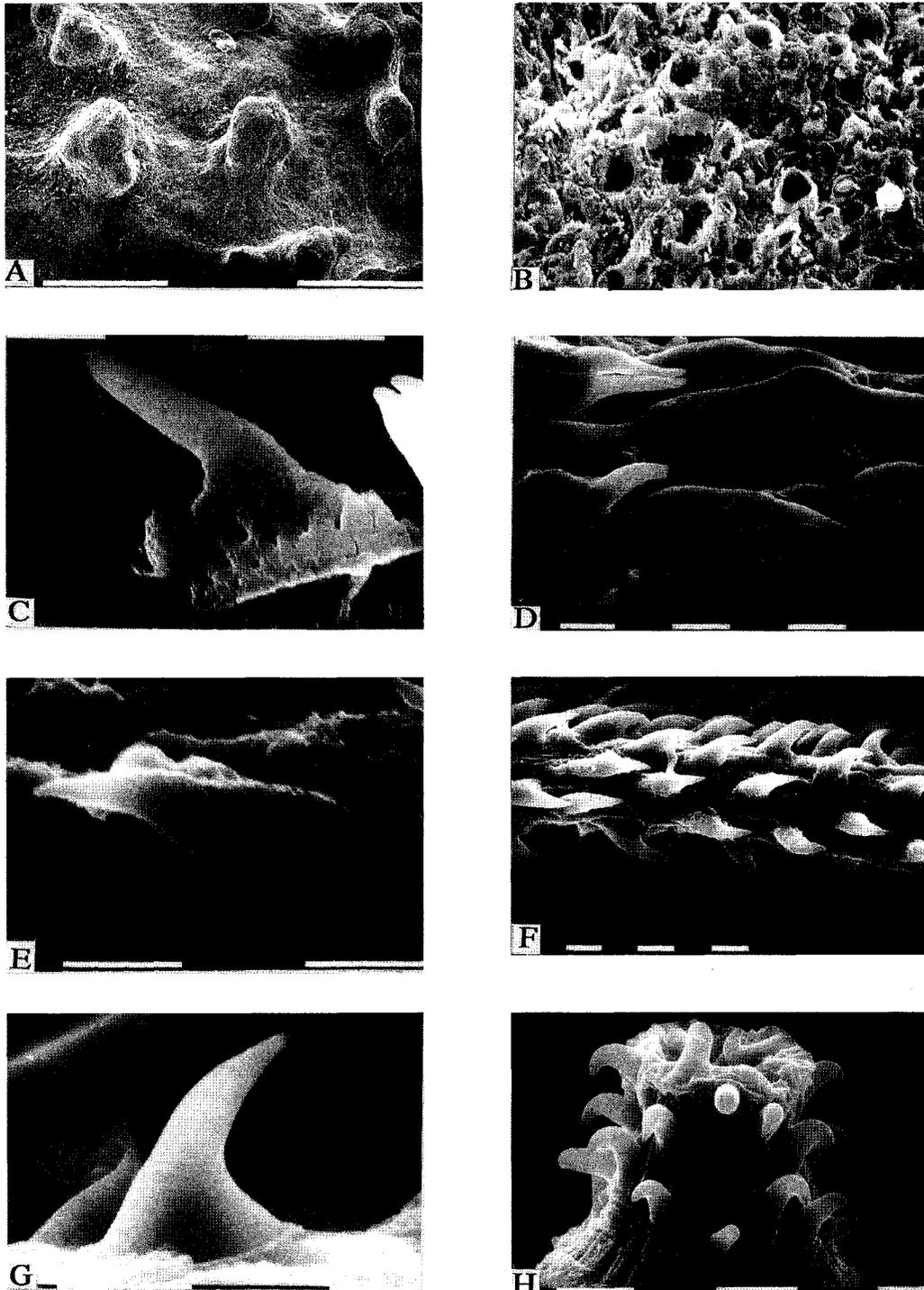


Fig.29. A, *Phyllidiella granulatus* n.sp. SEM of notal tubercles, scale = 1 mm; B, *Phyllidiella granulatus* n.sp. SEM of notum showing pores which may secrete mucous containing "defence" chemicals; C, *Phyllidiella lizae* n.sp. SEM of a single penial spine; D, *Phyllidiella rudmani* n.sp. SEM of penial spines; E, *Phyllidiopsis kremphi*. SEM of a single penial spine; F, *Phyllidiopsis shireenae*. SEM of part of everted penis; G, *Phyllidiopsis shireenae*. SEM of a single penial spine; H, *Phyllidiopsis striata*. SEM of partially everted penis. B-H scale = 10 µm.

vesicles are also grey. The penial spines are small (less than 10 μm in vertical height) and slightly recurved. They could not be isolated for SEM examination.

Distribution. This species is presently known from the tropical western Pacific Ocean (Micronesia to the Great Barrier Reef, Australia).

Remarks. The distinguishing external features of *P. granulatus* are the grey background with conical and acute compound white tubercles, and the circular black bands medially. The granular white pattern on the grey foot sole of live specimens is also characteristic. The bright orange food sponge of this species is probably responsible for the colour of the digestive gland mass. *Phyllidiella granulatus* possesses fewer lamellae on the rhinophoral clavus than most other species of *Phyllidiella*, except *P. rosans*.

The present species shows little similarity to others. *Phyllidiella pustulosa* has three clusters of tubercles which vary ontogenetically in their state of amalgamation, the background colour is black and the tubercles are pink (white tubercles in *P. granulatus*). *Phyllidiella pustulosa* is further separated by its pink foregut and digestive gland mass (which is never orange as in the present species), its large penial spines and grey ventral colouration. *Phyllidiella cooraburrama* differs from the present species primarily in having very large, isolated, smooth, rounded tubercles which are pink. *Phyllidiella rudmani* n.sp. also has rounded, white capped tubercles but its background colouration is bright pink and it has two longitudinal black stripes. *Phyllidiella rudmani* n.sp. possesses a greater number of lamellae on each rhinophoral clavus (23-26 for specimens greater than 27 mm) and has large, slender, curved penial spines.

Etymology. The specific epithet refers to the granular grey patches on the dorsum.

Phyllidiella lizae n.sp.

Fig.29C, Pl.7B

Type. Holotype here designated (36 mm live length) AM C159493, Plate 7B; the remaining specimens are designated paratypes.

Material examined. *Western Pacific Ocean* – 43 mm specimen (AM C159546), Suva Reef, Fiji 1 July 1987, RCW; 33 mm specimen (AM C159546), Suva, Fiji, 1 July 1987, RCW; 2 specimens (AM Photo), Wallis & Futuna, New Caledonia, 14 m depth, 1 Aug. 1989; 16 mm specimen, Orontes Reef, Cobourg Peninsula, 14 m depth, 9 Aug. 1986, RCW.

Eastern Australia – 1 specimen (AM C168773), Smith Rock, north-east of Cape Moreton, Qld, 14 m depth, 12 Aug. 1981, RCW.

Great Barrier Reef – holotype specimen (36 mm, AM C159493), Heron Island Reef, 9-10 m depth, 26 Nov. 1987,

DJB; 19 mm specimen, Heron Island, 11 m depth, 1 Sept. 1983, RCW; 36 mm specimen (MV), 1987; 1 specimen (MV), Heron Island, 14 July 1975, N. Coleman; 34 mm specimen, Lady Musgrave Island, 21 m depth, 1 Apr. 1986, Ms C. Buchanan; 31 mm specimen (AM C159492), Norman Reef, Cairns, 10 m depth, 15 Nov. 1986, DJB; 70 mm specimen (AM C145081), Swain Reefs, 21-230, 3 m depth, 15 Jan. 1985, I. Loch.

Papua New Guinea – 1 specimen, Milne Bay, 1 Feb. 1983, R. Vanderloos; 33 mm specimen (AM C162786), Horseshoe Reef, 18-24 m depth, 21 June 1988, DJB; 32 mm specimen (AM C162785), patch off Lion Island, 14 m depth, 17 June 1988, DJB & SKB; 42 mm specimen (WAM 321-87), Madang, 15-25 m depth, 2 July 1987, F. Wells; 22 mm specimen (AM C162784), Madang Lagoon, 15-25 m depth, 1 Feb. 1988, RCW.

External morphology (Pl.7B). Live specimens ranged in length from 16-70 mm and mean size was 32 mm. *Phyllidiella lizae* is an elongate ovate species which possesses a pale pink background, pale pink tubercles and irregular, narrow black lines on the dorsum. The notal tubercles are simple, rounded, and usually isolated (rarely coalesced), and are the same pale pink colour as the background of the dorsum. Narrow black lines of variable length occur irregularly on the dorsum; usually they cross over each other forming an "X" (up to 4 may occur) on the median area (Pl.7B). There is a narrow, smooth, pale pink to white edge to the mantle. The rhinophoral openings have low, pink rims. The rhinophores are black apically, pink centrally, and white basally. These colours blend into each other rather than being discrete bands. Specimens greater than 35 mm in length (alive) possess 23 to 28 lamellae on the rhinophoral clavus. Ventrally, the hyponotum and gills are pale grey. The digitate oral tentacles are pale pink to white and arise from a square base. The foot sole is pale pink to white.

Anatomy. Typical for the genus *Phyllidiella*. The foregut is pale pink to white in colour. The digestive gland mass is reddish pink in live animals (paler in the preserved state). The intestine is pale and semi-translucent. The reproductive system is characterised by a long, convoluted, cream prostatic vas deferens and a short penis (about 1.5 mm). The ampulla is yellow-brown; the bursa copulatrix is opaque, glossy and black. The receptaculum seminis is translucent cream and similar in size to the bursa copulatrix. The nidamental glands are cream in colour. The penial spines (15-20 μm in vertical height) have a very broad, deeply pitted base. The recurved stem has an irregular surface and tapers to a rounded apex (Fig.29C).

Distribution. *Phyllidiella lizae* is presently known from the tropical western Pacific Ocean.

Remarks. In the field, *P. lizae* is recognisable by its pale pink notum with simple, rounded, pale pink tubercles, narrow black lines crossing the dorsum, and black, white and pink rhinophores. Other distinguishing

characters are the pale, pinkish white oral tentacles and foot sole.

The present species appears to have a greater number of lamellae (23-28) to the rhinophoral clavus than *P. pustulosa* (22-26), although their ranges overlap. However, the two species differ considerably in the colouration of the rhinophores, and in their dorsal and ventral background colouration. The large penial spines of *P. pustulosa* are different to those of the present species as are features of the foregut, digestive gland mass and intestine. *Phyllidiella granulatus* has a granular pink-grey dorsum with tall compound white tubercles, fewer lamellae to the rhinophoral clavus, and bright orange digestive gland mass. *Phyllidiella rudmani* n.sp. also has a pink background colour to the dorsum, has tall, steep tubercles (low in *P. lizae*) and two, straight, longitudinal black stripes (irregular, criss-crossing black lines in *P. lizae*), and smooth, slender, sinuous penial spines.

Etymology. This species is named for a friend, my sister, Liz Hannaway.

Phyllidiella rudmani n.sp.

Fig.29D, Pl.7C-D

Type. Holotype here designated (29 mm live length) AM C159477; the remaining specimens are designated paratypes.

Material examined. *Western Pacific Ocean* – 45 mm specimen, Uepi Island, Solomon Islands, 15 m depth, 24 May 1987, P. Chapman-Smith; 25 mm specimen (AM C142266), Solomon Islands, 26 Feb. 1984, I. Knight; 29 mm specimen (AM C168777), Suva Reef, Fiji, 1 July 1987, RCW; 18 mm specimen (AM C168777), Suva Reef, Fiji, 1 July 1987, RCW; 1 specimen, Kaohsiung, Taiwan, 14 m depth, Ms Shuw-ing Lou.

Eastern Australia – Great Barrier Reef – 22 mm specimen (AM C132511), Creech Reef, 9 m depth, 18 Dec. 1981, I. Loch; 1 specimen (AM C168780), "Hole in the wall", Heron Island, 10-12 m depth, 1 Sept. 1983, RCW; 1 specimen (AM C95071), Yamacutta Reef, 6 m depth, 23 July 1974, I. Loch; 1 specimen (AM C95687), Centipede Reef, 23 Aug. 1974, I. Loch; 24 mm specimen (MV F54951), Pennys' Bay, Orpheus Island, 1 June 1968, N. Coleman; 21 mm specimen (AM C159475), John Brewer Reef, Townsville, 12 m depth, 14 May 1986, DJB; 25 mm specimen (AM C99303), Slashers Reefs, Townsville, 10-12 m depth, 31 Mar. 1975, I. Loch.

Papua New Guinea – holotype specimen (29 mm, AM C126010), Bootless Inlet, 20-30 m depth, 1 Aug. 1980, J. Wyche; 17 & 23 mm specimens (AM C168775), patch off Lion Island, 12 m depth, 17 June 1988, DJB & SKB; 22 mm specimen (AM C159538), patch off Lion Island, 8 m depth, 17 June 1988, DJB & SKB; 28 & 36 mm specimens (AM C159537), patch off Lion Island, 12 m depth, 17 June 1988, DJB & SKB; 32 & 39 mm specimens (AM C159536), patch off Lion Island, 16 m depth, 18 June 1988, DJB & SKB; 2 specimens (26, 26 mm, AM C159535(1) & (2)), patch off Lion Island, 18 m depth, 20 June 1988, DJB & SKB; 28 mm

specimen (AM C159534), patch off Lion Island, 18 m depth, 24 June 1988, DJB & SKB; 21 mm specimen, Horseshoe Reef, 10 m depth, 21 Apr. 1984, Carlson-Hoff; 3 specimens (32, 33, 17 mm, AM C168776), Horseshoe Reef, 18-24 m depth, 21 June 1988, DJB & SKB; 40 mm specimen, Horseshoe Reef, 5 m depth, 21 Apr. 1984, Carlson-Hoff; 32 mm specimen, Horseshoe Reef, 18-24 m depth, 21 June 1988, DJB; 28 mm specimen (AM C137020), Milne Bay, 5 m depth, 1 Dec. 1981, N. Coleman.

Indian Ocean – Thailand – 59 & 56 mm specimens, Phi Phi Island, 4-10 m depth, 25 Nov. 1989, DJB; 23 & 28 mm specimens (AM C159528), Phi Phi Island, 4-10 m depth, 25 Nov. 1989, DJB; 17 mm specimen, Phi Phi Island, 7-15 m depth, 25 Nov. 1989, DJB; 33 mm specimen (AM C159529), Phi Phi Island, 5 m depth, 26 Nov. 1989, DJB; 36 mm specimen (AM C159530), Phi Phi Island, 16 m depth, 27 Nov. 1989, DJB; 3 specimens (53, 17, 34 mm, AM C168779), Phi Phi Island, 8-10 m depth, 28 Nov. 1989, DJB; 45 mm specimen (AM C159531), Phi Phi Island, 16 m depth, 28 Nov. 1989, DJB; 3 specimens (22, 21, 14 mm), Phi Phi Island, 16 m depth, 1 Dec. 1989, DJB; 40 mm specimen (AM C159532), Phi Phi Island, 18 m depth, 2 Dec. 1989, DJB; 26 mm specimen (AM C159533), Phi Phi Island, 12 m depth, 4 Dec. 1989, DJB.

External morphology (Pl.7C-D). Live specimens ranged in length from 14-59 mm and mean size was 29 mm. *Phyllidiella rudmani* is an elongate species with a pale pink background and two longitudinal black stripes. The notal tubercles are the same pink colour as the background of the dorsum. In shape, individual tubercles are tall and rounded in juveniles (i.e., specimens greater than 27 mm), but in larger specimens the tubercles may become compound by way of additional outgrowths. The tubercles themselves are arranged, more or less, in longitudinal rows but are never joined together into ridges. Some larger specimens possess two additional black stripes marginally. Additional black lines, if present, are less distinct and usually interrupted. The edge of the mantle is the same pale pink colour as the dorsum. The rhinophores are curved and pointed; their apical half is black and the basal half is pale pink. Each rhinophoral clavus possesses 20-24 lamellae (specimens greater than 27 mm). Ventrally, the hyponotum is pale grey and the gill leaflets are darker grey towards their base. The white oral tentacles are long and conical and they have short lateral grooves. The foot is white and it has a thin, slightly undulating edge.

Anatomy. Typical for the genus *Phyllidiella*. The foregut is very pale (white) and lacks markings. Individual oral glands are elongate and club shaped in this species (cf. flattened, leaf shaped). The digestive gland mass is orange in live specimens but fades to pale cream in preserved material. The reproductive system is also very pallid except for the bursa copulatrix which is brown. The penis is short, but quite broad. The small (about 10-15 µm in vertical height) penial spines are slender, smooth, and gently curve in a sinuous shape (Fig.29D).

Distribution. *Phyllidiella rudmani* is known from

the tropical western Pacific Ocean and eastern Indian Ocean.

Remarks. *Phyllidiella rudmani* is characterised by its pale pink notum with two black stripes, and the black and pink banded rhinophores. Ventrally, the foot and oral tentacles are white. The digestive gland mass is orange (pale cream in the preserved state), but the rest of the viscera are pale. The short broad penis possesses slender, smooth, sinuous spines. *Phyllidiella pustulosa*, *P. zeylanica*, *P. nigra*, *P. annulata*, and *P. rosans* all possess a black background colouration and are therefore easily separated from the present species. Other differences are the bicoloured rhinophores and basically white ventral surfaces of *P. rudmani*. *Phyllidiella lizae* resembles the present species as it also possesses pink background colouration and black to white, colour graded rhinophores. However, substantial differences are apparent: the irregular, broken, intersecting black lines (2 straight longitudinal black stripes in *P. rudmani*); a different number of rhinophoral lamellae; pink digestive gland mass (orange in *P. rudmani*); and ventrally, pale grey to pink colouration (white in *P. rudmani*) and digitate oral tentacles (conical in *P. rudmani*). The penial spines of *P. lizae* are large, with a very broad pitted base and irregular surface, whereas those of the present species are smaller, slender, smooth and sinuous in shape.

Etymology. This species is named in honour of Dr W.B. Rudman.

Phyllidiopsis Bergh, 1875

Phyllidiopsis cardinalis Bergh

Figs 10A-C, 14, 15, Pl.7E-F

Phyllidiopsis cardinalis Bergh, 1875: 670-673, pl.16, figs 11-15.—Eliot, 1904: 284.—Dawydoff, 1952: 111.—Pruvot-Fol, 1957a: 118-120, fig.35.—Burn, 1975: 516.—Gosliner & Behrens, 1988: 308-309, 312-313, figs 1b, 3.

Phyllidia tuberculata Risbec, 1928: 59-60, fig.3, pl.1, fig.2.—Risbec, 1953: 12-13 (n.syn.).

?*Phyllidia* sp. 3.—Tan *et al.*, 1987: 76, fig.9.

Comments on synonymy. Examination of the type specimen of *Phyllidia tuberculata* Risbec by the author has confirmed that it is *Phyllidiopsis cardinalis* (see Pruvot-Fol, 1957a; Gosliner & Behrens, 1988). The specimen illustrated by Tan *et al.* (1987: fig.9 as *Phyllidia* sp.) is probably *P. cardinalis*.

Types. *Phyllidiopsis cardinalis* Bergh. Holotype lost (dissected by Bergh; 50 mm preserved length), figured by Bergh, 1875: pl.16, figs 11-15.

Phyllidia tuberculata Risbec. Syntype (probable holotype; 33 mm preserved length) MNHN, figured by Risbec, 1928: fig.3, pl.1, fig.2.

Material examined. *Western Pacific Ocean* — 33 mm specimen (MNHN), New Caledonia, ?Risbec, 1928; 1 specimen, Suva Reef, Fiji, 27 Feb. 1986, G. Brodie; 1 specimen, Suva Reef, Fiji, 10 Dec. 1985, G. Brodie; 13 mm specimen (AM C162746), Suva Reef, Fiji, 13 July 1987, RCW; 19.5 mm specimen, Bile Bay, Guam, 2 m depth, 12 June 1973, Carlson-Hoff; 20 mm specimen (AM C162742), Bile Bay, Guam, 1-3 m depth, 7 Mar. 1987, Carlson-Hoff; 25 mm specimen, Oronte Point, Guam, 29 m depth, 18 Apr. 1984, Carlson-Hoff; 40 mm specimen, Lady Musgrave Island, south GBR, 21 m depth, 1 Aug. 1989, C. Buchanan; 43 mm specimen, Cooks Arch, Norfolk Island, 21 m depth, 1 Oct. 1991, K. Whysall.

Papua New Guinea — Madang — 23 mm specimen, Anemone Reef, 11 m depth, 10 Jan. 1988, RCW; 1 specimen, Cement Mixer Reef, 3-9 m depth, 11 Jan. 1988, RCW; 25 mm specimen (AM C162747), Planet Rock, 12-20 m depth, 19 Jan. 1988, T. Gosliner; 2 specimens (19, 14 mm & food sponge, AM C162747), Planet Rock, 12-20 m depth, 19 Jan. 1988, RCW & T. Gosliner; 64 mm specimen (AM C162748), Madang Lighthouse, 7-8 m depth, 22 Jan. 1988, RCW; 9 mm specimen (AM C162745), Kranket Island, 3-20 m depth, 24 Jan. 1988, T. Gosliner; 1 specimen, Rasch Passage, 4-15 m depth, 25 Jan. 1988, RCW; 14 & 25 mm specimens (AM C162743), Planet Rock, 7-15 m depth, 28 Jan. 1988, RCW; 1 specimen, Barracuda Point, 7-14 m depth, 29 Jan. 1988, RCW; 25 mm specimen (AM C162744), Wreck-‘USS Boston’, 15-35 m depth, 31 Jan. 1988, RCW; 1 specimen, Barracuda Point, 9 m depth, 8 Feb. 1988, RCW; 1 specimen, Christmas Bay, 6 m depth, 10 Feb. 1988, RCW; 1 specimen, The Quarry, 9-12 m depth, 14 Feb. 1988, RCW; 1 specimen, Barracuda Point, 5-8 m depth, 18 Feb. 1988, RCW; 7 mm specimen, The Quarry, 9 m depth, 19 Feb. 1988, RCW.

Indian Ocean — 1 specimen (MV), Warroora, north WA, 3 m depth, 8 July 1972, N. Coleman; 39 mm specimen (MV F54946), Warroora, WA, 3 m depth, 2 July 1972, N. Coleman.

Réunion — 3 specimens (50, 50, 25 mm), 1-20 m depth, 1987, M. Jay; 8 mm specimen, 18? m depth, 1 Dec. 1989, M. Jay; 5 specimens (44, 46, 62, 38, 35 mm, AM C168924), 5-20 m depth, 1989, M. Jay.

External morphology (Pl.7E-F). Live specimens ranged in length from 7-64 mm and mean size was 24 mm. *Phyllidiopsis cardinalis* is elongate-ovate in shape. The dorsum possesses a complex array of various colours and shades. The general background colouration is dark mustard yellow to red-orange or red-brown. Shades of dark olive to purple may be present on some specimens. The isolated tubercles are large and multicomponent with numerous, small, rounded tubercles. There are two medial rows of very large globose tubercles. The large tubercles usually have a pattern of reddish orange veins. Smaller, paler yellow, compound tubercles occur between the coloured veins on the large tubercles (Pl.7E-F). Shades of purple, grey, pink or yellow occur around the tubercle bases. The rim of the anal opening may be edged in dark grey-black. The mantle margin is yellow to olive-yellow with dark grey-black spots. A few smaller, darker, rounded tubercles occur around the mantle margin. The rhinophores are slightly club-shaped and deep yellow in colour with the outer edge of the lamellae dark olive. The dark olive colouration becomes more predominant at the apex of each rhinophore. Each rhinophoral clavus

possesses 18-20 broad lamellae (specimens 25-64 mm in length). Ventrally, the hyponotum is yellow and the gill leaflets are darker yellow. The side of the foot is yellow with irregularly spaced dark grey to black spots. The foot sole is uniformly yellow. The fused, yellow oral tentacles have a very broad base imparting an overall triangular appearance, and possess long ventrolateral grooves.

Anatomy. *Phyllidiopsis cardinalis* is the type species for the genus *Phyllidiopsis* and its anatomy has been previously described in detail (see Review of Genera; Figs 10A-C, 14, 15). Distinctive features of the present species include the elongate-ovate muscular oesophageal segment (up to 5 mm in large specimens) and the dark olive-grey digestive gland mass. The reproductive system is mostly pale in colour, however both the spherical bursa copulatrix and oval ampulla are large and darkly pigmented. The nidamental gland mass is elongate. Penial spines could not be isolated for SEM examination. Under the light microscope they appeared to be very short (less than 5 µm) with an extremely broad base and strongly recurved.

Distribution. *Phyllidiopsis cardinalis* occurs throughout the tropical Indo-west Pacific. It is often found on the underside of encrusted coral boulders (Gosliner & Behrens, 1988; Brunckhorst, 1991).

Remarks. *Phyllidiopsis cardinalis* has a complex, multicoloured dorsum that is characteristic of the species. The median tubercles are very large and globose. Small, pale yellow, rounded tubercles arise on the large basal tubercle (i.e., multicomponent). A network of reddish-orange veins runs between the pale yellow tubercles. The ventral yellow colouration is also characteristic. The side of the yellow foot has dark spots and the fused oral tentacles have a very broad base and deep, long grooves.

The unique and complex colouration render *P. cardinalis* totally different from any other known phyllidiid species. In external appearance, it is unlike any of its congeners which possess either pink, white or blue colouration and which lack yellow colouration ventrally. *Phyllidia ocellata* Cuvier has gold-yellow colouration but none of the other colours of the present species. It also possesses quite different anatomy, especially of the foregut.

The pattern and behaviour of this species are consistent with its cryptic nature (Brunckhorst, 1991).

Phyllidiopsis dautzenbergi (Vayssière)

Pl.7G

Phyllidia dautzenbergi Vayssière, 1911: 1165 (nomen nudum).
Phyllidia dautzenbergi Vayssière, 1912: 85-87, pl.1, figs 14-15.-O'Donoghue, 1929: 732.-Pruvot-Fol, 1956: 69.-Heller & Thompson, 1983: 341, fig.8h-i.-Yonow, 1984b: 36,

pl.37, fig.6.-Yonow, 1986: 1405-1406, figs 10d-e.-Yonow, 1988: 143, pl.2.

Phyllidia monacha Yonow, 1986: 1407-1408, figs 3, 11a.-Yonow, 1988: 145-146, fig.2a (n.syn.).

Comments on synonymy. Vayssière (1911: 1165) introduced the name "*Phyllidia dautzenbergi*" in a species list but a description was not published until later (Vayssière, 1912). The name *Phyllidia monacha* of Yonow (1986) is a synonym. Yonow had no information on the colour of the live specimen. It closely matches specimens of *Phyllidiopsis dautzenbergi* illustrated by Heller & Thompson (1983) and Yonow (1984b). My examination of the holotype confirmed its synonymy.

Types. *Phyllidia dautzenbergi* Vayssière. Holotype (16 mm preserved length) MNHN, figured by Vayssière, 1912: pl.1, figs 14, 15.

Phyllidia monacha Yonow. Holotype (14 mm preserved length) BMNH 1985.205; figured by Yonow, 1986: figs 3, 11a.

Material examined. *Indian Ocean - Red Sea* - 16 mm specimen (MNHN), Djibouti, 1904, Gravier; 14 mm specimen (BMNH 1985.205), "Creek", 8 m depth, 15 Dec. 1983, N. Yonow; 6 mm specimen (BMNH Acc.2337), 1983, N. Yonow; 19 mm specimen (BMNH Acc.2337), Jezirat, 10-15 m depth, 23 June 1983, N. Yonow; 6 mm specimen (BMNH Acc.2337), Tower Reef, 15 m depth, 16 Mar. 1984, N. Yonow; 19 mm specimen (BMNH), 1983, G. Bermert.

External morphology (Pl.7G). Live specimens ranged in length from 6-19 mm. *Phyllidiopsis dautzenbergi* is ovate to elongate in shape and black and white in colour. The background colour is white and long notal spicules can be seen in transparency. There are two, median, longitudinal, black lines from which broad, black rays extend to the mantle margins. Typically, there is a single, longitudinal, central area of white, but this may be divided into two or three white areas in some specimens. Numerous, large semicircles of white divided by the black rays occur around the margins. The central white region usually possesses a low, irregular tuberculate ridge, which may be broken. Isolated, rounded tubercles are scattered over the notum, but are usually confined to white areas. The rhinophores are white and pointed. Each rhinophoral clavus possesses 8-12 lamellae (14-19 mm specimens). The ventral colouration is entirely white. The hyponotum possesses some pale cross-hatching. The fused oral tentacles are square and have tiny, indistinct lateral grooves.

Anatomy. Typical for the genus *Phyllidiopsis*. *Phyllidiopsis dautzenbergi* possesses a very elongate muscular oesophageal segment. The foregut, digestive gland mass and intestine are entirely white in colour. The reproductive system is uniformly pale cream to white. Penial spines were not isolated.

Distribution. *Phyllidiopsis dautzenbergi* is presently known only from the Red Sea (Yonow, 1986, 1988; present work). The holotype was collected by Gravier at Djibouti.

Remarks. *Phyllidiopsis dautzenbergi* is the only member of its genus with large, white semicircles around the margin and a median, longitudinal white area (which may be interrupted). Notal tubercles are small and rounded. Notal spicules are long. Other characteristic features include the white pointed rhinophores, white ventral colouration and pale (white) viscera.

Three other *Phyllidiopsis* species have black and white colouration. *Phyllidiopsis striata* Bergh differs in having three, low, white dorsal ridges, a white mantle rim, lemon yellow rhinophores, and an elongate-ovate muscular oesophageal segment. *Phyllidiopsis phiphiensis* n.sp. has two, low, white ridges, black spots on the white margin, white rhinophores, black spots on the side of the foot, and a spherical-oval muscular oesophageal segment. *Phyllidiopsis loricata* (Bergh) has a white notum with many small tubercles and dark brown to black spots, an oval, muscular oesophageal segment and orange-brown nidamental glands. Other differences are emphasised in the following descriptions of these species.

Phyllidiopsis gemmata Pruvot-Fol

Pl.7H

Phyllidiopsis gemmata Pruvot-Fol, 1957a: 121-122, figs 50-53, pl.1, figs 5-6.

Phyllidia cf. *gemmata*.—Lin, 1983: 152, pl.1, fig.10.

Comments on synonymy. The specimen illustrated by Lin (1983) as "*Phyllidia* cf. *gemmata*" appears to belong to the present species. It matches Pruvot-Fol's (1957a) type specimens which I have examined.

Type. Lectotype here selected (syntype, 45 mm preserved length, dissected) BMNH 1887.6.7.11; figured by Pruvot-Fol, 1957a: figs 50-53, pl.1, figs 5-6; paralectotypes (28 mm and 25 mm preserved lengths, both dissected) BMNH 1887.6.7.8-9.

Material examined. 3 specimens (28, 25, 45 mm, BMNH 1887.6.7.8-9, 11), Java, ?1880; 36 mm specimen (AM C162780), Phi Phi Island, southern Thailand, 16 m depth, 27 Nov. 1989, DJB; 38 & 30 mm specimens (AM C162781), Phi Phi Island, southern Thailand, 16 m depth, 1 Dec. 1989, DJB; 37 & 35 mm specimens (AM C162782), Phi Phi Island, southern Thailand, 18 m depth, 2 Dec. 1989, DJB; 40 mm specimen, Réunion Island, Indian Ocean, 1-20 m depth, 1987, M. Jay; 20 mm specimen, Réunion Island, Indian Ocean, 5-20 m depth, 1989, M. Jay.

External morphology (Pl.7H). Live specimens

ranged in length from 25-45 mm. *Phyllidiopsis gemmata* is an elongate species possessing greyish pink to greyish blue background colouration and narrow, black lines. Low, compound, conical tubercles are numerous over the notum but do not occur on the black lines. There are three, narrow, tuberculate, median longitudinal ridges and a broad, lateral, tuberculate region extends around the mantle margin. Four narrow, black lines occur on either side of, and between the ridges. The outer most black lines extend to the mantle edge anteriorly and posteriorly (Pl.7H). The anal opening is situated far posteriorly on a pink tubercle. There is no contrasting colour to the mantle edge. The rhinophores are primarily black but grade to pale pink-grey at their bases. Each rhinophoral clavus possesses 19-22 lamellae (specimens greater than 34 mm). The outer edge of the hyponotum is pale grey becoming dark grey towards the gills. The gills are grey. The foot sole is uniformly grey except the edge which is pale grey. The side of the foot is dark grey. The fused oral tentacles are pale grey with dark grey down the margins.

Anatomy. Typical for the genus *Phyllidiopsis*. Distinctive internal features of *P. gemmata* include the pale pink foregut, the elongate-oval muscular oesophageal segment, and the apparently large stomach which partially protrudes dorsally from the digestive gland mass. The digestive gland mass is yellow. The ovotestis and nidamental glands are white. The receptaculum seminis is small and white, whereas the bursa copulatrix is very large and brown. Penial spines were not isolated.

Distribution. This species is currently known from three localities in the Indian Ocean: Réunion Island, southern Thailand, and Java (type locality).

Remarks. *Phyllidiopsis gemmata* can be distinguished in the field by its greyish pink to greyish blue tuberculate dorsum, three tuberculate ridges, four narrow black lines, fused oral tentacles with dark grey margins, dark grey colouration around the gills, and dark grey foot sole with a pale edge.

Phyllidiopsis annae n.sp. and *P. striata* also possess three median longitudinal ridges on the dorsum. *Phyllidiopsis striata* is a smaller species with white and black colouration (white ventrally), and lemon yellow rhinophores. The dorsal ridges of *P. annae* n.sp. are bright blue and granular in appearance with minute, isolated tubercles (very tuberculate and grey in *P. gemmata*). *Phyllidiopsis annae* n.sp. has black rhinophores and uniform grey colouration ventrally (except for the small oral tentacles which are dark grey to black). Furthermore, *P. annae* n.sp. is a smaller species and internally it possesses a spheroid-ovoid muscular oesophageal segment (elongate-ovate in *P. gemmata*), and it has darker pigmentation to the reproductive organs.

Phyllidiopsis krempfi Pruvot-Fol

Fig.29E, Pl.8A

Phyllidiopsis krempfi Pruvot-Fol, 1957a: 120-121, figs 41-49, pl.1, fig. 7-8.

Type. Holotype (60 mm preserved length) MNHN; figured by Pruvot-Fol, 1957a: figs 41-49, pl.1 figs 7-8.

Material examined. 60 mm specimen (MNHN), Nha-Trang, Thailand, Pruvot-Fol, 1957; 33 mm specimen (AM C162776), Phi Phi Island, southern Thailand, 4-10 m depth, 25 Nov. 1989, DJB; 43 mm specimen (AM C162775), Phi Phi Island, southern Thailand, 8-10 m depth, 28 Nov. 1989, DJB; 52 & 48 mm specimens (AM C162774), Phi Phi Island, southern Thailand, 16 m depth, 28 Nov. 1989, DJB; 62 & 55 mm specimens (AM C162777), Phi Phi Island, southern Thailand, 16 m depth, 1 Dec. 1989, DJB; 65 mm specimen, Seribu Island, Java, 1984, J. Randall.

External morphology (Pl.8A). Live specimens ranged in length from 33-65 mm. *Phyllidiopsis krempfi* is elongate-ovate in shape. The general dorsal colouration is pink with irregular, black longitudinal lines that may meander between the tubercles. Long spicules are visible through the translucent pink notum. The notal tubercles are large, and their base, which is broad and tapering, is the same shade of pink as the background of the dorsum. The median, multicomound tubercles are paler pink on their apices. There are two primary longitudinal black lines which extend around the rhinophores and join in front of the rhinophores. Other irregularly directed black lines, which may be very short, occur around, and between some tubercles (Pl.8A). Some specimens have short black rays which extend to the mantle edge. The edge of the mantle has the same pink colouration as the background of the dorsum. The rhinophores are pink on their anterior face and around the base, and black on their pointed apices and posterior face. Each rhinophoral clavus possesses 26-28 lamellae (specimens greater than 40 mm). Ventrally, the hyponotum and foot are uniformly pale pink. The gills are pale grey. The fused oral tentacles are pale pink with small, pointed, grey tips and long, ventrolateral grooves.

Anatomy. Typical for the genus *Phyllidiopsis*. The muscular oesophageal segment is very elongate and it ends posteriorly in a larger swollen section which appears to be the anterior part of the stomach. A distinct stomach region is present and is primarily contained within the digestive gland mass. The digestive gland mass, intestine and rectum/anal papilla are pale pink in colour. Most of the reproductive system is pale pink, except for the translucent white seminal receptacle and the bursa copulatrix which is brown to black. The large, conical penial spines (22-25 μ m in vertical height) are relatively straight (*cf.* recurved), but appear slightly twisted at their distal end (Fig.29E).

Distribution. This species is presently known only from the Andaman Sea (eastern Indian Ocean) and Java.

Remarks. The material studied in the present work was recently collected by the author from the vicinity of the type locality in southern Thailand. *Phyllidiopsis krempfi* is a large species that is characterised by predominantly pink colouration, and broad based, multicomound tubercles with paler apices. Apart from two primary longitudinal black lines, other black lines of variable size occur irregularly across the dorsum. The ventral surfaces are predominantly pale pink; the gills pale grey. The oral tentacles are also pale pink and have grey pointed tips. Distinctive internal features are the very elongate muscular oesophageal segment, large stomach and pale pink digestive glands and hindgut. The large penial spines have a characteristic twisted appearance.

Phyllidiopsis krempfi is unlike any described species. Besides being more elongate, *P. gemmata* has grey ventral colouration, pink-grey to blue-grey tuberculate ridges and black rhinophores. *Phyllidiopsis shireenae* is pale pink to white and differs in having a large median crest and salmon-pink rhinophores. Of the new species recognised here, *Phyllidiopsis pipeki* n.sp. has bright pink colouration and, consistently has two straight black lateral lines (but no others as in the present species), rounded white tubercles (multicomound pink ones in *P. krempfi*) and fewer rhinophoral lamellae (22-25 for specimens greater than 36 mm) than *P. krempfi* (26-28 for specimens greater than 40 mm). *Phyllidiopsis burni* n.sp. is even more elongate than the present species and is pointed at each end. It differs from *P. krempfi* in having a black background with tall multicomound, dark pink tubercles and a smooth pink edge to the mantle. *Phyllidiopsis burni* n.sp. has fewer lamellae (17-20 for specimens greater than 31 mm) on the rhinophoral clavus than *P. krempfi*. It possesses large, rounded oral tentacles, and its foot sole is grey with a pink margin (uniformly pale pink in *P. krempfi*). *Phyllidiopsis fissuratus* n.sp. is also pink and black, but is extremely tuberculate, having very tall, compound and coalesced tubercles with many deep black valleys running between. In addition, *P. fissuratus* n.sp. has a translucent raised rim around the rhinophoral pockets and a smooth, tall, conical, translucent pink anal papilla. Anatomical differences will be discussed in the following descriptions of the new species.

Phyllidiopsis shireenae Brunckhorst

Fig.29F-G, Pl.8B

Phyllidia sp.—Brunckhorst, 1989a: 7 (colour illustration).

Phyllidiopsis shireenae Brunckhorst, 1990b: 577-576, figs 1-4.

Type. Holotype (90 mm live length) AM C140057; figured by Brunckhorst, 1990b: fig.1a; 13 paratypes in AM and one

paratype in MV.

Material examined. *Western Pacific Ocean* – 1 specimen, Kaosung, South Taiwan, 14 m depth, 23 Mar. 1985, Ms Shuwing Lou; 78 & 65 mm specimens (AM C142261), Bonege River, Solomon Islands, 1983, I. Knight; 46 mm specimen (AM C142259), Bonege River mouth, Solomon Islands, 1983, I. Knight; 69 & 58 mm specimens (AM C142258), Bonege River, Solomon Islands, 23 m depth, 12 Nov. 1983, I. Knight; 65 mm specimen (AM C144565), Osprey Reef, Coral Sea, 1 Dec. 1984, D. Young; 1 specimen (AM C144565), Osprey Reef, Coral Sea, 13 m depth, 14 Dec. 1984, I. Loch.

Eastern Australia – Great Barrier Reef – 90 mm specimen (AM C140057), Pelorous Island, 1 Oct. 1983, R. King; 29 mm specimen (AM C132519), Sand Bank No.5 Reef, I. Loch; 1 specimen, Lady Musgrave Island, 12-14 m depth, 1 Sept. 1979, R. Reichelt; 2 specimens (AM C137525), Raine Island, 30 m depth, 11 Dec. 1982, I. Loch; 1 specimen (AM C137277), Raine Island, 1 Dec. 1982, I. Loch; 1 specimen, Lady Musgrave Island, 12 m depth, 1 Sept. 1979, R. Reichelt; 70 mm specimen, Lady Musgrave Island, 21 m depth, 1 Aug. 1989, C. Buchanan.

Papua New Guinea – 1 specimen, Milne Bay, 1 Aug. 1982, R. Vanderloos; 1 specimen, Milne Bay, "eastern island", 12-15 m depth, 1 Aug. 1982, R. Vanderloos; 48 mm specimen (AM C159470), patch off Lion Island, 20 m depth, 18 June 1988, DJB & SKB; 106 & 50 mm specimens (AM C159470), patch off Lion Island, 18 m depth, 18 June 1988, DJB & SKB; 71 mm specimen (MV), Horseshoe Reef, 20 m depth, 1 Aug. 1980, N. Coleman; 23 mm specimen (MV), Horseshoe Reef, 10 m depth, 1 Aug. 1980, N. Coleman; 1 specimen (AM C136946), China Reef, 10 m depth, 20 Apr. 1982, N. Coleman; 23 mm specimen (MV F54959), Horseshoe Reef, 8 m depth, 1 Aug. 1980, N. Coleman; 1 specimen (AM C136919), China Reef, 15 m depth, 20 Apr. 1982, N. Coleman; 1 specimen (AM C126011), Bootless Inlet, 20-30 m depth, 1 Aug. 1980, J. Wyche; 1 specimen (AM C126017), Bootless Inlet, 20-30 m depth, 1 Aug. 1980, J. Wyche; 3 specimens (73, 81, 71 mm, AM C159469), 'The Pinnacle', Madang, 18 m depth, 7 Feb. 1988, G. Williamson; 1 specimen, Bombes Reef, Madang, 10-18 m depth, 11 Jan. 1988, RCW; 48 mm specimen, Kranket Wall, Madang, 10-25 m depth, 4 Feb. 1988, RCW; 1 specimen, Christmas Bay, Madang, 6-30 m depth, 10 Feb. 1988, RCW.

External morphology (Pl.8B). Live specimens ranged in length from 23-106 mm and mean size was 61 mm. *Phyllidiopsis shireenae* is elongate in shape and possesses a relatively soft, but firm body. The dorsum is generally a very pale shade of pink (ranging to white in a few specimens). In lateral view, the body's visceral hump appears tall, forming a raised, longitudinal crest, which is triangular in cross section. This distinctive shape is not caused solely by the viscera, but is the result of a thickening of the mid-dorsal body wall which contains a mass of longitudinally orientated spicules (sectioned material). Encircling the perimeter of the visceral hump is a black band. In most specimens, four black lines diverge from the black band and run to the mantle edge (Pl.8B). One black line occurs anteriorly and one at the posterior extremity. Two lines arise laterally, one on either side of the dorsal crest. Minor variations of this pattern include a diverging black line which does not run right to the mantle edge, a black line running across the dorsal crest, or a few, small,

irregularly shaped, black patches on the dorsal crest. A number of small, rounded tubercles occur on the mantle skirt. Larger tubercles with angular edges are sparsely scattered over the dorsal crest. The rhinophores are pale salmon pink and each clavus possesses 17-20 lamellae (specimens greater than 40 mm). The anus opens at the posterior end of the crest. Ventrally, the hyponotum, foot and oral tentacles are white. The fused oral tentacles have a broad base and are short with broad, rounded tips. The gills are dark grey. There is a black band behind the gills where the notum meets the side of the foot.

Anatomy. Typical for the genus *Phyllidiopsis*. The translucent oral tube of *P. shireenae* is soft and folded like a concertina. The tubular pharynx and the pharyngeal retractor muscles are particularly long. The muscular oesophageal segment is oval in shape and thick walled with circular muscle (sectioned material). There is no distinct stomach within the digestive gland mass. The foregut is white in colour.

The reproductive system is mostly cream in colour except for the yellow-brown bursa copulatrix, the shiny semi-transparent receptaculum seminis and brown ampulla. The prostatic vas deferens is very convoluted and ensheathed with connective tissue. Individual penial spines (16-17 μm in vertical height) have a broad base, curve smoothly for a short distance and have a rounded apex (Fig.29F-G). The surface of the penial spines is smooth and devoid of pitting or other markings.

Distribution. *Phyllidiopsis shireenae* is presently known from the western tropical Pacific Ocean (Great Barrier Reef to Papua New Guinea, the Solomon Islands and Taiwan).

Remarks. *Phyllidiopsis shireenae* is distinctive, on account of its mid-dorsal crest (i.e., the body is not dorsoventrally flattened as in other phyllidiids), very pale pink colouration with a few black lines, and salmon pink rhinophores. Characteristic internal features include the delicate, concertina-like, oral tube, long tubular pharynx and pharyngeal retractor muscles, oval muscular oesophageal segment, absence of a stomach, the convoluted prostatic vas deferens, and the smooth "fin shaped" penial spines.

No other phyllidiid possesses a large dorsal crest and salmon pink rhinophores. *Phyllidiopsis gemmata* is grey-pink to grey-blue with three tuberculate ridges, black rhinophores and an elongate, muscular oesophageal segment. *Phyllidiopsis krempfi* has multicomponent pink tubercles, black and pink rhinophores, possesses 26-28 lamellae on each rhinophoral clavus (17-20 in *P. shireenae*), and a very elongate muscular oesophageal segment. The new species described here (*Phyllidiopsis pipeki*, *P. burni* and *P. fissuratus*) differ from *P. shireenae* in having large compound tubercles, black and pink rhinophores and pink to grey ventral colouration (white in *P. shireenae*).

Phyllidiopsis sinaiensis (Yonow)

Phyllidia sinaiensis Yonow, 1988: 147-148, fig.3a,b.

Type. Holotype (21 mm preserved length) BMNH 1986.231; figured by Yonow, 1988: fig.3a,b.

Material examined. One specimen, the holotype (BMNH 1986.231), northern Red Sea, 10-15m depth, 1 May 1980, B. Picton, was examined and partially dissected by a single, circular dorsal incision.

External morphology. The specimen was collected in 1980 and by the time of its description (Yonow, 1988) and my examination (1990), most traces of the living colour had disappeared.

The holotype is elongate with a black background and whitish tubercles. The notal tubercles have a very broad base, are low and conical with rounded apices. I could not discern any orange pigmentation (nor any contrasting colour) on the apices of the tubercles as suggested by Yonow (1988: 148). A single, sinuous ridge composed of low, coalesced tubercles extends down the midline. Three isolated tubercles are aligned on either side of the central ridge (Yonow, 1988: fig.3a). Patches of white occur around the margins covering smaller, isolated tubercles. There is no contrasting edge to the mantle. The rhinophores are white on their anterior face, black on their posterior face, and have rounded apices. The rhinophoral pockets occur in a white area. The number of lamellae on the rhinophoral clavus could not be counted because the rhinophores were retracted and damaged. The anal opening is situated far posteriorly, but not on a tubercle or papilla.

Ventrally, the hyponotum is white with a few, broad, black, transverse bands. The gills are dark grey. The foot sole is uniformly coloured, translucent and yellowish in the preserved state because of the yellow viscera. The pale, fused oral tentacles have a very broad base and taper to rounded black tips.

Anatomy. The present species possesses the characteristics of the genus *Phyllidiopsis*. The oesophagus is silvery in colour and its muscular segment is very elongate (approximately 4-5 mm). The rest of the viscera are yellow except for the bursa copulatrix which is black. Penial spines were not examined.

Distribution. The unique holotype was collected from the "Amphora site", Gulf of Aqaba in the Red Sea.

Remarks. Unfortunately, the living colour and pattern of this species is not known for certain. It is probably black and pink (as observed for other *Phyllidiopsis* species with bicoloured rhinophores; present work). Yonow (1988) described this species as having white tubercles on a black background, bicoloured rhinophores and lacking markings on the foot sole, but did not dissect the specimen. The anatomy of

the holotype (present study) clearly places it in the genus *Phyllidiopsis*.

Distinguishing features of *P. sinaiensis* are: the sinuous, central ridge; the low, broad based tubercles which are not compound; rhinophores which are pale coloured apically and black basally; and the anus not occurring on a tubercle. Internal features include the predominantly yellow viscera and elongate muscular oesophageal segment. To my knowledge, no other *Phyllidiopsis* species possesses a single, sinuous, central ridge and isolated tubercles which are low and not compound. For example, *Phyllidiopsis krempfi*, *P. pipeki* n.sp., *P. burni* n.sp., and *P. fissuratus* n.sp. are pink and black and possess pink and black rhinophores, but all four species have numerous, large, compound or multicomponent tubercles. *Phyllidiopsis shireenae* has a very tall, central crest (not a tuberculate ridge) and salmon coloured rhinophores.

Phyllidiopsis loricata (Bergh)

Pl.8C

Phyllidia loricata Bergh, 1873: 72-75, pl.10, figs 7,9, 19-21, pl.11, figs 1,2.—Lim & Chou, 1970: 134, pl.15, fig.a.—Burn, 1975: 516.—Coleman, 1981: 90, pl.270.—Willan & Coleman, 1984: 53.—Karuso, 1987: 36.—Coleman, 1989: 47.

Comments on synonymy. Coleman (1981, 1989) has published colour photographs of this species. The specimen referred to this species by Bergh (1905) is possibly *Phyllidia scottjohnsoni*.

Type. Holotype could not be traced, presumed lost (one specimen was collected by Andrew Garrett and given to the Godeffroy Museum in Hamburg; possibly destroyed during World War II); figured by Bergh, 1873: pls 10, 11.

Material examined. 9 mm specimen (AM C162668), Coral Bay, Port Essington, NT, 1 May 1983, Dave Staples; 5 mm specimen (AM C162666), Orpheus Island, north Qld, 0 m depth, 25 Mar. 1982, A. Martin; 1 specimen (MV), Mandora Point, Darwin, 0-1 m depth, 22 Nov. 1972, N. Coleman; 3 specimens (18, 15, 12 mm, MV F54947), Mandora, Darwin, NT, 21 Nov. 1972, N. Coleman; 11 mm specimen (AM C162667), Kwajalein Atoll, Marshall Islands, 5 m depth, 25 Mar. 1989, S. Johnson; 12 mm specimen, Enewetok Atoll, 10 m depth, 6 Nov. 1982, L. Boucher; 7 mm specimen, Bile Bay, Guam, 2 m depth, 28 Oct. 1973, Carlson-Hoff.

External morphology (Pl.8C). Live specimens ranged in length from 5-26 mm. *Phyllidiopsis loricata* is an elongate species. It possesses white background colouration and black spots (described by Bergh, 1873 as "jet-black"). In two specimens I examined, the spots appeared to be dark brown. The mantle skirt is thin and translucent white. It possesses 10-12 large, black spots and a few much smaller dark spots occur marginally. No black spots occur in the median area of the dorsum.

The presence of many tiny, conical, rounded tubercles on the notum imparts a rough texture to the mantle. Mid-dorsally, the tubercles are usually joined to form two or three, interrupted, irregular, low ridges. The white to cream rhinophores are pointed apically. Each rhinophoral clavus possesses 16-19 fine lamellae (specimens greater than 15 mm). Ventrally, the hyponotum is translucent white with fine cross-hatched sculpturing and dark patches showing through from the dorsum. The foot and gills are white. The fused oral tentacles are squarish in shape and very large (e.g., 2 mm in an 18 mm specimen); they possess short, fine lateral grooves.

Anatomy. Typical for the genus *Phyllidiopsis*. The alimentary system is cream in colour. The tubular pharynx is very long. The muscular oesophageal segment is short and spherical-oval in shape. There is no distinct stomach region within the digestive gland mass. The reproductive organs are cream except for the nidamental gland mass which is brown-orange. Penial spines were not isolated.

Distribution. *Phyllidiopsis loricata* is known from the Great Barrier Reef, Timor Sea (northern Australia), Guam, the Marshall Islands, Enewetok Atoll and the type locality, Tahiti.

Remarks. *Phyllidiopsis loricata* (Bergh) is distinguished by the following: its white dorsum with black to dark brown spots; rough mantle surface; pointed white rhinophores with 16-19 lamellae on each clavus (specimens greater than 15 mm); white ventral colouration; and large, square shaped oral tentacles. Distinctive internal features are the long tubular pharynx, spherical-oval muscular oesophageal segment, and brown-orange nidamental glands. Bergh (1873) described this species before he had differentiated the genus *Phyllidiopsis* (Bergh, 1875).

Phyllidiopsis phiphiensis n.sp., *P. annae* n.sp. and *P. striata* possess white and black colouration but differ considerably in being striped. *Phyllidiopsis loricata* is superficially similar to *Phyllidia scottjohnsoni* which has large black spots, medially, on a pale cream-white background. It is difficult to separate these two species on external characters alone. The main external features which differentiate the two species are the lack of spots mid-dorsally and the large, fused, square oral tentacles of the present species. *Phyllidiopsis loricata* has a greater number of lamellae on the rhinophoral clavus than *Phyllidia scottjohnsoni*. The considerable differences in anatomy, particularly of the foregut region, clearly separate these two species and is grounds for their placement in separate genera.

Phyllidiopsis striata Bergh

Fig.29H, Pl.8D-E

Phyllidiopsis striata Bergh, 1888: 756. (nomen nudum)

Phyllidiopsis striata Bergh, 1889: 866-867, pl.84, figs 23-27.– Eliot, 1903b: 563.–Dawydoff, 1952: 111.–Coleman, 1989: 48.–Brunckhorst, 1990b: 582, fig.5.
Phyllidia xishaensis Lin, 1983: 153, pl.1, fig.2. (n.syn.)

Comments on synonymy. Lin's (1983) description and illustration of *Phyllidia xishaensis* match Bergh's species, *Phyllidiopsis striata*, precisely. Photographs of *P. striata* have been published recently by Coleman (1989) and Brunckhorst (1990b).

Types. *Phyllidiopsis striata* Bergh. Holotype lost (dissected by Bergh); figured by Bergh, 1889: pl.84, figs 23-27.

Phyllidia xishaensis Lin. Holotype (8.5 mm preserved length) in Institute of Oceanology, Academia Sinica, number M25453; figured by Lin, 1983: pl.1, fig.2.

Material examined. *Western Pacific Ocean* – 19 mm specimen, Magic Pass, Madang, 15-22 m depth, 14 Jan. 1988, RCW; 12 mm specimen (AM C168915), Rasch Passage, Madang, 14 m depth, 15 Jan. 1988, Greg Williamson; 14 mm specimen (AM C162749), Kranket Island, Madang, 3-20 m depth, 24 Jan. 1988, RCW; 11 mm specimen (AM C144578), Osprey Reef, Coral Sea, 15 m depth, 15 Dec. 1984, I. Loch; 19 mm specimen (AM C132252), Lizard Island, north Qld, 19 Nov. 1981, J. Gates.

Micronesia – 19 & 8 mm specimens (AM C162752), Bile Bay, Guam, 7 m depth, 1 July 1988, DJB & SKB; 18.5 mm specimen (AM C162753), Bile Bay, Guam, 6 m depth, 14 July 1988, DJB & SKB; 15 mm specimen, Bile Bay, Guam, 6 m depth, 14 July 1988, DJB & SKB; 14 mm specimen, Bile Bay, Guam, 6 m depth, 13 July 1988, DJB & SKB; 12.5 mm specimen, Bile Bay, Guam, 9 m depth, 15 Nov. 1969, Carlson-Hoff; 11 & 14 mm specimens (AM C162751), Ponape, 3-6 m depth, 22 Aug. 1985, Carlson-Hoff; 16 mm specimen (AM C162750), Enewetok Atoll, 15 m depth, 23 Aug. 1981, S. Johnson; 14 mm specimen (AM C168919), Enewetok Atoll, 12 m depth, 29 Mar. 1983, S. Johnson; 1 specimen (AM C168920), Kwajalein Atoll, Marshall Island, 15 m depth, 5 June 1983, S. Johnson.

Indian Ocean – 1 specimen (WAM 2423-8), Scott Reef, north-west WA, C. Bryce; 14 mm specimen (AM C140616), off Dampier, north WA, 4 m depth, 1 June 1982, Sauveracker; 16 mm specimen (AM C140615), Bedout Island, north WA, 5 m depth, 15 Aug. 1982, Sauveracker.

Thailand – 11 mm specimen (AM C162754), Phi Phi Island, 4-10 m depth, 25 Nov. 1989, DJB; 3 specimens (15, 12, 6 mm, AM C168916), Phi Phi Island, 4-10 m depth, 25 Nov. 1989, DJB; 4 specimens (12, 6, 12, 8 mm, AM C162755), Phi Phi Island, 16 m depth, 27 Nov. 1989, DJB; 9 & 13 mm specimens (AM C168918), Phi Phi Island, 10 m depth, 28 Nov. 1989, DJB; 12 mm specimen (AM C162756), Phi Phi Island, 16 m depth, 28 Nov. 1989, DJB; 6 mm specimen (AM C162757), Phi Phi Island, 2 m depth, 29 Nov. 1989, DJB; 9 & 10 mm specimens (AM C162758), Phi Phi Island, 16 m depth, 1 Dec. 1989, DJB; 12 mm specimen (AM C16275), Phi Phi Island, 12 m depth, 4 Dec. 1989, DJB; 3 specimens (9, 11, 12 mm, AM C168917), Phi Phi Island, 16 m depth, 5 Dec. 1989, DJB.

External morphology (Pl.8D-E). Live specimens ranged in length from 6-19 mm and mean size was 12 mm. *Phyllidiopsis striata* possesses black and white dorsal colouration. Three, low, white median-longitudinal

ridges originate from the vicinity of the anal opening and run anteriorly. The central ridge is always shorter, terminating just posterior to the rhinophores, and it may be interrupted anteriorly in some specimens (Pl.8D). The lateral ridges are longer and run through the rhinophoral pockets almost to the anterior edge of the mantle. There is a relatively broad, white mantle skirt. In a few specimens, tiny black spots occur on this white marginal band. The black areas, occurring between the ridges and the white margin, occur as four longitudinal bands. Tiny, conical white tubercles are scattered along the ridges and on the white mantle margin. The rhinophores are lemon yellow and each rhinophoral clavus possesses 11-13 lamellae (specimens 12-19 mm). Ventrally, the margin of the hyponotum is white, it grades to dark grey, and there is a band of black close to the gills. The gills are grey. The side of the foot is dark grey to black whereas the sole is grey with a pale marginal edge. The fused oral tentacles are square in shape and grey in colour.

Anatomy. Typical for the genus *Phyllidiopsis*. The tubular pharynx of this species is relatively short. The muscular oesophageal segment is elongate-ovate. The digestive gland mass is cream or (rarely) greenish. The reproductive system is cream with the exception of the bursa copulatrix which is brown-orange, the receptaculum seminis which is translucent, and the ampulla which is silver-white. The smooth penial spines (8-10 μm in vertical height) have a rounded base and initially curve gently, but are recurved sharply near the pointed apex (Fig.29H).

Distribution. *Phyllidiopsis striata* is presently known from the central and western Pacific Ocean and Indian Ocean.

Remarks. *Phyllidiopsis striata* is easily distinguished in the field by its three low, white longitudinal dorsal ridges, white mantle skirt, four black longitudinal bands and lemon-yellow rhinophores. Other characteristic features are the black areas on either side of the grey gills, the elongate-ovate muscular oesophageal segment, brown-orange bursa copulatrix, silvery ampulla, and smooth penial spines which are strongly hooked apically.

As far as is known, there are four, small species of *Phyllidiopsis* with black stripes. External features which contrast with *P. striata* are as follows. *Phyllidiopsis phippiensis* n.sp. has two white ridges and three black bands (three white ridges and four black bands in *P. striata*), black spots on the mantle margin, white rhinophores (lemon yellow in *P. striata*) and is white ventrally (grey and black in *P. striata*). *Phyllidiopsis annae* n.sp. has three blue ridges, and black rhinophores. *Phyllidiopsis sphingis* n.sp. has three irregular white ridges which are usually separated (straight ridges join at the anus in *P. striata*), iridescent blue colouration to the mantle skirt, cream rhinophores (white mantle skirt and yellow rhinophores in *P. striata*) and a cream to white foot sole (grey in *P. striata*).

Phyllidiopsis phippiensis n.sp.

Fig.30A, Pl.8F

Type. Holotype here designated (15 mm live length) AM C159509; the remaining ten specimens are designated paratypes.

Material examined. *Western Pacific Ocean – Thailand* – holotype (15 mm; AM C159509), Phi Phi Island, 16 m depth, 5 Dec. 1989, DJB; 10 mm specimen (AM C159503), Phi Phi Island, 4-10 m depth, 25 Nov. 1989, DJB; 13 & 14 mm specimens (AM C159504), Phi Phi Island, 16 m depth, 27 Nov. 1989, DJB; 29 mm specimen (AM C159505), Phi Phi Island, 9 m depth, 27 Nov. 1989, DJB; 13 mm specimen (AM C159506), Phi Phi Island, 16 m depth, 28 Nov. 1989, DJB; 10, 11 & 12 mm specimens (AM C159507), Phi Phi Island, 18 m depth, 2 Dec. 1989, DJB; 12 mm specimen (AM C159508), Phi Phi Island, 12 m depth, 2 Dec. 1989, DJB; 13 mm specimen (AM C162803), Phuket Island, 5-20 m depth, 7 July 1989, RCW.

External morphology (Pl.8F). Live specimens ranged in length from 10-29 mm and mean size was 14 mm. *Phyllidiopsis phippiensis* is white with three longitudinal black lines and black spots. There are two, low, white ridges running down the mid-dorsum. They unite at the anus. Anteriorly, each ridge continues over each of the rhinophoral pockets to the anterior margin of the mantle. Three narrow, longitudinal black lines run between the ridges and the white marginal area. Small black spots occur along the white marginal areas. Tiny notal tubercles, supported only by a single vertical spicule, are scattered over the white dorsal areas. The rhinophores are white and each clavus possesses 12-14 lamellae (specimens greater than 15 mm). Ventrally, the hyponotum is white with small black spots along its margin. The gills, foot and oral tentacles are white. There are small isolated, black spots along the side of the foot. The fused white oral tentacles are small with indistinct lateral grooves.

Anatomy. Typical for the genus *Phyllidiopsis*. The foregut, digestive gland mass and intestine are white. The muscular oesophageal segment is spherical-oval in shape. There is no distinct stomach region. The reproductive system is white with the exception of the bursa copulatrix which is cream. The penial spines (15 μm in vertical height) are conical and almost straight (Fig.30A).

Distribution. *Phyllidiopsis phippiensis* is presently known only from southern Thailand (Andaman Sea, north-eastern Indian Ocean).

Remarks. *Phyllidiopsis phippiensis* has the following distinctive external characteristics: two low, white ridges separated by three furrows lined with black; white mantle margin with black spots; white rhinophores; and white ventral colouration with black spots on the

margin of the hyponotum and on the side of the foot. The internal organs are characteristically white (bursa copulatrix cream). The muscular oesophageal segment is spherical-oval in shape. The penial spines are relatively large (15 μm) for a small species; they are conical and almost straight, being slightly recurved at the apex (Fig.30A).

There are three other, small, longitudinally striped species of *Phyllidiopsis*. Two of these, *P. annae* n.sp. and *P. sphingis* n.sp., are easily separated from the present species because they possess blue pigmentation, grey gills and black (*P. annae*) or pale yellow (*P. sphingis*) rhinophores. *Phyllidiopsis striata* Bergh is less easily separated. However, *P. striata* has three low, white ridges and four black bands (2 white ridges and 3 black bands in *P. phiphensis*), lemon yellow rhinophores, grey and black ventral colouration, and an elongate-oval muscular oesophageal segment. The penial spines of *P. striata* are small (8-10 μm) and quite strongly recurved (15 μm and relatively straight in the present species).

Etymology. The name for this species is derived from its type locality, the Phi Phi Islands (pronounced "pee pee"), 48 km to the south east of Phuket, southern Thailand.

Phyllidiopsis annae n.sp.

Pl.8G

Type. Holotype here designated (14 mm live length)

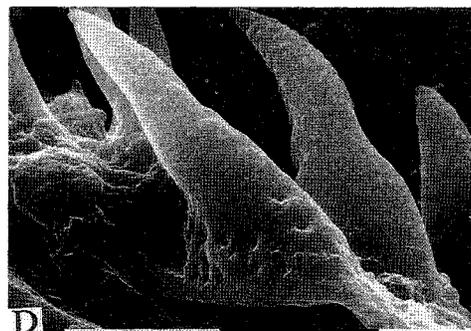
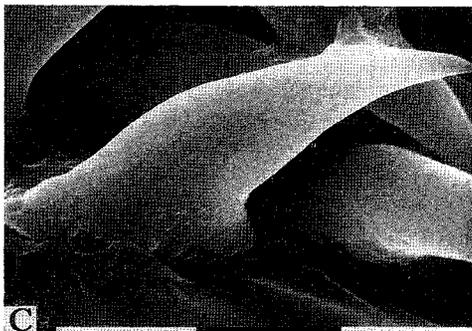
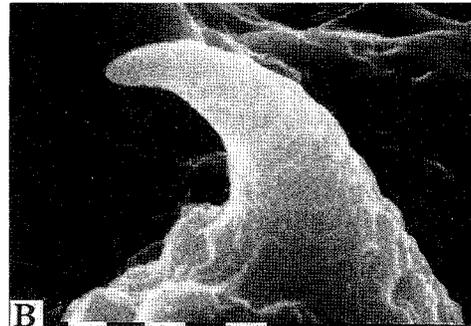
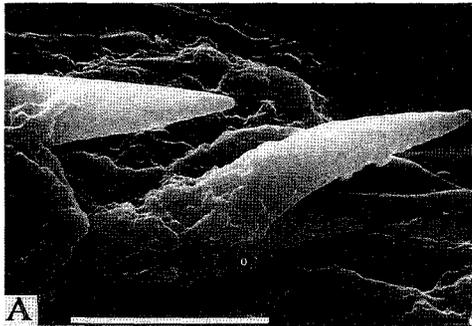


Fig.30. A, *Phyllidiopsis phiphensis* n.sp. SEM of penial spines; B, *Phyllidiopsis pipeki* n.sp. SEM of a single penial spine; C, *Phyllidiopsis burni* n.sp. SEM of penial spines; D, *Phyllidiopsis burni* n.sp. SEM of penial spines. Each scale = 10 μm .

AM C162762; the remaining specimens are designated paratypes.

Material examined. Holotype (14 mm; AM C162762), Phi Phi Island, southern Thailand, 10 m depth, 28 Nov. 1989, DJB; 13 mm specimen (AM C162761), Phi Phi Island, southern Thailand, 4-10 m depth, 25 Nov. 1989, DJB; 10 mm specimen (AM C162763), Phi Phi Island, southern Thailand, 16 m depth, 5 Dec. 1989, DJB; 1 specimen (WAM 346-87), Madang, PNG, 1 June 1987, F. Wells.

External morphology (Pl.8G). Live specimens ranged in length from 10-14 mm. *Phyllidiopsis annae* is elongate-ovate in shape and possesses blue and black stripes on the dorsum. There are three median longitudinal, low, granular, blue ridges. They extend to the vicinity of the anus. On either side of the ridges are narrow black stripes, four in total. The mantle perimeter is also blue and granulose with a few tiny black spots. The notal tubercles occur in the blue areas and are tiny and rounded. They are most numerous around the margins. The anal opening is black. The rhinophores are black with a grey base. Each rhinophoral clavus possesses 7-10 lamellae (10-14 mm specimens). Ventrally, the hyponotum is white with black spots. The gills are dark grey. The foot is uniformly grey. The fused oral tentacles are black dorsally and ventrolaterally, and grey midventrally.

Anatomy. Typical for the genus *Phyllidiopsis*. The pharyngeal bulb is elongate and almost cylindrical in shape. The muscular oesophageal segment is oval. The intestine is dark grey. The reproductive system is cream,

with the exception of the ampulla which is yellow-brown, and the bursa copulatrix which is dark grey. Penial spines were not isolated.

Distribution. *Phyllidiopsis annae* is presently known from northern Papua New Guinea (Madang) and southern Thailand.

Remarks. *Phyllidiopsis annae* is distinguished by its black rhinophores, three low, granular blue ridges, a granular blue mantle skirt, four intervening longitudinal black stripes, and predominantly grey ventral colouration including very dark oral tentacles. Internal characteristics include the elongate pharyngeal bulb, oval oesophageal segment, dark intestine, yellow-brown ampulla and dark grey bursa copulatrix.

This species is closest to *P. striata* Bergh and *P. sphingis* n.sp. *Phyllidiopsis striata* also has dorsal ridges but they are white. The mantle margin of *P. striata* is white (blue in the present species) and its rhinophores are lemon yellow (black in *P. annae*). *Phyllidiopsis annae* and *P. sphingis* n.sp. both possess blue colouration dorsally. When live specimens of both species are viewed together *P. annae* is granular blue-grey whereas *P. sphingis* n.sp. is iridescent blue (Pl.8G,H). However, more substantial differences are apparent. In *P. sphingis* n.sp., the blue pigmentation is confined to the margins where there are numerous lateral black rays (absent in *P. annae*) and medially it has irregular, low, white ridges (blue in *P. annae*) and fewer tubercles. *Phyllidiopsis sphingis* n.sp. possesses white colouration whereas *P. annae* does not. The rhinophores of *P. annae* are black and have 7-10 lamellae (specimens 10-14 mm) on each rhinophoral clavus. *Phyllidiopsis sphingis* n.sp. has pale cream oral tentacles (dark grey in *P. annae*) and a pale cream to white foot (grey in *P. annae*). Internally they differ in the morphology of the muscular oesophageal segment which is oval in the present species and elongate in *P. sphingis*.

Etymology. This species is named for my mother, Anne.

Phyllidiopsis sphingis n.sp.

Pl.8H

"Blue-black" *Phyllidia*.—Bertsch & Johnson, 1981: 77.
Phyllidia sp.—Johnson, 1989: 3.

Type. Holotype here designated (17 mm live length) AM C159495; the remaining five specimens are designated paratypes.

Material examined. Holotype (17 mm; AM C159495), Pupukea, Oahu, Hawaii, 12 m depth, 27 Aug. 1985, S. Johnson; 22 mm specimen, 'Three Tables', Hawaii, 15 m depth, 1980, S. Johnson; 23 mm specimen (AM C159494), Pupukea, Oahu, Hawaii, 12 m depth, 8 July 1985, S. Johnson;

13 mm specimen (AM C159510), The Chimney, Madang, 27 m depth, 17 Jan. 1988, RCW; 4 mm specimen, Agana Bay, Guam, 9 m depth, 29 May 1986, Carlson-Hoff; 4 mm specimen, The Pinnacle, Madang, PNG, 6-30 m depth, 25 Jan. 1988, RCW.

External morphology (Pl.8H). Live specimens ranged in length from 4-23 mm. *Phyllidiopsis sphingis* is oval and it possesses blue, black and white markings dorsally. There are three, white, low, median longitudinal ridges. They do not usually join at the anus, which opens on the central ridge. The two outer ridges pass over the rhinophoral pockets and extend to the mantle margin where they become blue. Black stripes occur between the ridges. A black band runs, in a "U", around the median area where the ridges occur (Pl.8H). Black rays extend from this band to the mantle edge. The areas between the rays around the mantle margin are vivid, iridescent blue. Small, rounded notal tubercles occur on the mantle margin. Minute, conical tubercles are present on the median ridges. The rhinophores are cream to pale yellow in colour. Each rhinophoral clavus bears 14-17 lamellae (specimens greater than 13 mm). Ventrally, the hyponotum is pale grey to white with black markings along the edge (from the black rays). The gills are dark grey. The foot is uniformly cream to white.

The fused, squarish oral tentacles are cream coloured and possess short, deep ventrolateral grooves.

Anatomy. Typical for the genus *Phyllidiopsis*. The alimentary tract is white. The muscular oesophageal segment is elongate and relatively narrow. There is no distinct stomach region. The reproductive system is cream to yellow in colour, except for the receptaculum seminis which is transparent and the penis which is silvery white. Penial spines were not isolated.

Distribution. This species is presently known from northern Papua New Guinea (Madang), Guam and Hawaii (Bertsch & Johnson, 1981; present work).

Remarks. Diagnostic external features of *Phyllidiopsis sphingis* are: the low white ridges and intervening black stripes mid dorsally; a U-shaped black band around the perimeter of the median area; black rays extending to the mantle edge; iridescent blue colouration on the broad mantle margin; cream to pale yellow rhinophores; cream colouration ventrally; dark grey gills. Distinctive internal features are the elongate muscular oesophageal segment and the absence of a distinct stomach region.

This species is superficially similar to *P. annae* and *P. striata* Bergh. However, *P. striata* has a white mantle skirt without black rays, lemon yellow rhinophores and grey ventral colouration. *Phyllidiopsis annae* has granular blue, median ridges and mantle margin (white median ridges in *P. sphingis*) but has neither white colouration, nor black rays on the margin, and possesses black rhinophores with 14-17 lamellae on their clavus (rhinophores cream with 7-10 lamellae on each rhinophoral

clavus in the present species). *Phyllidiopsis annae* has dark grey oral tentacles whereas those of the present species are pale cream. Internally, the muscular oesophageal segment of *P. annae* is oval whereas in *P. sphingis* it is elongate.

Etymology. The specific epithet is derived from the Sphinx (*Sphingis*, fem.), a mythical monster at Thebes who posed riddles for people passing by and consumed them if they could not answer.

Phyllidiopsis pipeki n.sp.

Fig.30B, Pl.9A

Phyllidia nobilis.-Lim & Chou, 1970: 134, pl.16, fig.a (non *Phyllidiella nobilis* Bergh, 1869).

Comments on synonymy. The specimen identified and illustrated as *Phyllidia nobilis* by Lim & Chou (1970) matches the present species.

Type. Holotype here designated (45 mm live length) AM C162772; the 21 remaining specimens are designated paratypes.

Material examined. *Western Pacific Ocean* – 1 specimen (AM C138167), Mactan Island Cebu, 18 m depth, 18 Apr. 1983, ?collector; 45 mm specimen, Uepi Island, Solomon Islands, 14 m depth, 24 May 1987, P. Chapman-Smith; 50 mm specimen (AM C142266), Bonege Island, Solomon Islands, 26 Feb. 1984, I. Knight; 1 specimen, Rove Caves, Solomon Islands, 1982, I. Knight; 45 & 48 mm specimens, Bonegi, Solomon Islands, 15 m depth, 1 Aug. 1987, S. Johnson; 85 mm specimen (MV F30501), Wistari Reef, south GBR, 25 m depth, 24 July 1975, N. Coleman; 53 mm specimen (MV F30714), Samaurez Reef, Coral Sea, 18 m depth, 16 Aug. 1977, N. Coleman; 36 mm specimen (AM C162771), Suva, Fiji, 1 July 1987, RCW.

Papua New Guinea – holotype 45 mm (AM C162772), Madang Lagoon, 5-21 m depth, 1 Feb. 1988, RCW; 1 specimen (AM C136946), Milne Bay, 1 Apr. 1982, N. Coleman; 1 specimen, Milne Bay, 1 Apr. 1983, R. Vanderloos; 1 specimen, Milne Bay, 1 Apr. 1983, R. Vanderloos; 57 mm specimen (MV F54958), Horseshoe Reef, 10 m depth, 1 Aug. 1980, N. Coleman; 40 mm specimen (WAM 321-87), south of Wongati, 15-25 m depth, 2 June 1987, F. Wells.

Madang – 42 mm specimen (WAM 321-87), 15-25 m depth, 2 June 1987, F. Wells; 52 mm specimen, The Pinnacle, 11 Jan. 1988, RCW; 52 mm specimen (AM C162773), The Pinnacle, 11 Jan. 1988, RCW; 46 mm specimen, Madang Lagoon, 1 Feb. 1988, RCW; 48 mm specimen (AM C162770), Madang Lagoon, 15-25 m depth, 4 Feb. 1988, RCW; 56 mm specimen, Madang Lagoon, 15-25 m depth, 4 Feb. 1988, RCW; 50 mm specimen, Madang Lagoon, 15-25 m depth, 4 Feb. 1988, RCW; 58 & 49 mm specimens (AM C162770), Madang Lagoon, 15-21 m depth, 4 Feb. 1988, RCW.

External morphology (Pl.9A). Live specimens ranged in length from 36-85 mm and mean size was 50 mm. *Phyllidiopsis pipeki* is a large and elongate

species. The dorsum is bright pink with two meandering longitudinal black lines (they may be interrupted and/or sinuous). A few specimens possess either a few black spots or one or two black rays extending to the mantle edge. The large tubercles, which can be single or compound, are sparsely but evenly scattered over the dorsum. They have a steep, pink base and rounded white apices. The mantle edge lacks any contrasting colour. The rhinophores are tall and pointed. They are black apically and there is a black stripe down the posterior two-thirds. Basally, the rhinophores are pink. Each rhinophoral clavus bears 22-25 lamellae (specimens greater than 36 mm). Ventrally, the hyponotum and gills are pale pink to grey. The foot is uniformly pink. The pink, fused oral tentacles have straight sides and slightly rounded tips.

Anatomy. Typical for the genus *Phyllidiopsis*. The foregut is white and the digestive gland mass is grey to pink. The pharyngeal retractor muscles are bulbous at their anterior attachment to the pharyngeal bulb, but taper quickly, and are very long. The muscular oesophageal segment is extremely elongate (e.g., 15 mm in a 58 mm specimen). A large stomach region is present in the digestive gland mass. In some preserved specimens, the anterior part of the stomach protruded a little, dorsally, from the digestive gland mass where the oesophagus entered. The reproductive system is cream in colour except for the nidamental glands (yellow) and the bursa copulatrix (dark brown to black). The ampulla is large and kidney shaped. The penis is elongate and the spinous section is very short. Penial spines are very small (approximately 5-6 μ m in vertical height), robust and smoothly curved (Fig.30B).

Distribution. This species is presently known from the Coral Sea north to Papua New Guinea, the Solomon Islands, and the Philippines, and as far east as Fiji.

Remarks. Diagnostic features of *P. pipeki* include the bright pink background with meandering black lines and sparsely scattered single and compound tubercles which have white apices. The rhinophores are bicoloured - pink and black. The foot and gills are pale pink to pale grey. The pink oral tentacles are square in shape. Internal characteristics are the very elongate muscular oesophageal segment and the large kidney shaped ampulla.

Phyllidiopsis pipeki resembles *P. krempfi* in the colouration of the mantle and rhinophores, but *P. krempfi* is very tuberculate with many multicomponent pink tubercles. *Phyllidiopsis krempfi* also differs in having oral tentacles with pointed tips and grey lateral margins. Each rhinophoral clavus of *P. krempfi* possess 26-28 lamellae, whereas those of the present species possess 22-25 lamellae for similar sized specimens.

Etymology. This species is named in honour of Mr George Pipek who encouraged me in research diving and trained me to instructor level in scuba.

Phyllidiopsis burni n.sp.

Fig.30C-D, Pl.9B

Type. Holotype here designated (31 mm live length) AM C159542; the 15 remaining specimens are designated paratypes.

Material examined. *Western Pacific Ocean* – 19 mm specimen, Heron Island, south GBR, 10 m depth, 1 Sept. 1983, RCW; 29 mm specimen (AM C159496), patch off Lion Island, PNG, 18 m depth, 20 June 1988, DJB & SKB.

Micronesia – 45 mm specimen, Ponape, Mwahnd Pass, 16 m depth, 24 Aug. 1985, Carlson-Hoff; 35 mm specimen (AM C159544), Enewetok Atoll, 31 May 1982, S. Johnson.

Guam – holotype specimen (31 mm, AM C159542), Bile Bay, 18 m depth, 20 Aug. 1987, Carlson-Hoff; 24 & 35 mm specimens (AM C159497), Bile Bay, 18 m depth, 29 June 1988, DJB & SKB; three specimens (45, 34, 50 mm, AM C159498), Bile Bay, 14 m depth, 29 June 1988, DJB & SKB; 45 mm specimen (AM C159499), Bile Bay, 7 m depth, 1 July 1988, DJB & SKB; 40 mm specimen (AM C159500), Bile Bay, 10 m depth, 2 July 1988, DJB & SKB; 55 mm specimen (AM C159543), Bile Bay, 5 m depth, 14 Feb. 1988, Carlson-Hoff; 38 mm specimen (AM C159502), Bile Bay, 24 Dec. 1973, Carlson-Hoff; 61 mm specimen (AM C159501), Sponge Mound, Apra Harbour, 22m depth, 5 July 1988, DJB & SKB; 40 mm specimen, Annae Island, 9 m depth, 5 July 1988, DJB & SKB.

External morphology (Pl.9B). Live specimens ranged in length from 19–61 mm and mean size was 39 mm. *Phyllidiopsis burni* is elongate-ovate in shape and its body is more acutely tapered (*cf.* rounded), anteriorly and posteriorly, than in other phyllidiids. *P. burni* possesses black background colouration and deep pink tubercles. The large tubercles arise from broad bases. Apically, they consist of many small, acute, multicomponent tubercles. The median ones are often oblong in shape. The anus opens at the summit of a large tubercle. The edge of the mantle is very thin, smooth and translucent pink. A few, fine, black rays extend to the mantle edge. The rhinophores are pointed and black (paler at their base). Each rhinophoral clavus possesses 17–20 lamellae (specimens greater than 32 mm). Ventrally, the hyponotum is pale pink along the margin and dark grey around the gills. The gills and sides of the foot are dark grey. The foot sole is grey (darker grey medially), with a pale pink edge. The fused oral tentacles are large, oval in shape, and pink. They possess very long, deep, lateral grooves which are dark grey in colour.

Anatomy. Typical for the genus *Phyllidiopsis*. The pharyngeal bulb is white; the rest of the viscera are cream to grey in colour. The muscular oesophageal segment is broad and oval. There is a second, non muscular swelling behind the muscular oesophageal segment. The oesophagus narrows before entering the digestive gland mass dorsally. There is no distinct stomach region within the digestive gland mass. The reproductive system is cream to yellow except for the

bursa copulatrix which is dark grey. The penial spines are large and robust (20–24 µm in vertical height). Individual spines have a broad, pitted base, and a broad, slightly recurved stem for most of their length before tapering to a point (Fig.30C-D).

Distribution. Most specimens of *P. burni* have been collected from Micronesia. There is one record from the northern Great Barrier Reef, and one record from Papua New Guinea.

Remarks. Characteristic external features of *Phyllidiopsis burni* include: the tapering of the body anteriorly and posteriorly; deep pink, acute, multicomponent tubercles (oblong in shape medially); smooth, translucent pink mantle edge; black rhinophores with 17–20 lamellae on the clavus (specimens greater than 32 mm); dark grey to black gills; grey foot with pink edge; and large, oval, oral tentacles with deep, long, dark grey lateral grooves. Diagnostic internal features include the broad, oval, muscular oesophageal segment and the large, robust penial spines which are slightly recurved.

The black background colouration of the dorsum, deep pink tubercles, black rhinophores (and fewer lamellae to the rhinophoral clavus) of the present species distinguish it from *P. pipeki* and *P. kremphi* (both possess a pink background and pink and black rhinophores). *Phyllidiopsis fissuratus* n.sp. is closer to the present species, but it differs in having very tall, pale pink tubercles with deep, black lined valleys. It has pink rhinophores with a black posterior stripe and 29–32 lamellae on the rhinophoral clavus. *Phyllidiopsis fissuratus* n.sp. also has translucent pink rims to the rhinophoral pockets and a very tall, smooth, translucent pink anal papilla (both absent in *P. burni*), and uniformly pink, square shaped oral tentacles (oval with dark grey lateral margins in sp. 5). *Phyllidiopsis fissuratus* n.sp. has a more elongate muscular oesophageal segment than the present species, and its penial spines appear to be small and strongly recurved.

Etymology. This species is named in honour of Mr Bob Burn.

Phyllidiopsis fissuratus n.sp.

Pl.9C-D

Phyllidia ?varicosa var. *quadrilineata*—Yonow, 1986: 1415–1417, figs 7, 8, 12e.—Yonow, 1988: 148, fig.2b (non *Phyllidia varicosa* var. *quadrilineata* Bergh, 1905).
Phyllidia nobilis—Tan *et al.*, 1987: 76, fig.6 (non *Phyllidiella nobilis* Bergh, 1869).

Comments on synonymy. The above references probably refer to the present species. This decision is based on the published illustrations because the accompanying descriptions are insufficient for

confirmation.

Type. Holotype here designated (79 mm live length; partially dissected) AM C159491, Plate 9C-D; the remaining four specimens are designated paratypes.

Material examined. Holotype specimen (79 mm, AM C159491), Flinders Reef, south-east Qld, 9 m depth, 31 Mar. 1984, RCW; 74 mm specimen (AM C159490), Wistari Reef, south GBR, 8 m depth, 6 July 1981, RCW; 1 specimen (AM C132339), Heron Island, 4 m depth, 1 Dec. 1981, G. Avern; 34 mm specimen, Suva, Fiji, 9 m depth, 1 July 1987, RCW; 32 mm specimen (MV F54967), Malabar, Lord Howe Island, 13 m depth, 27 Nov. 1979, N. Coleman.

External morphology (Pl.9C-D). The live specimens ranged in length from 32-79 mm. *Phyllidiopsis fissuratus* is elongate and evenly rounded both anteriorly and posteriorly. *Phyllidiopsis fissuratus* has a black background to the dorsum and many tall, pale pink tubercles. The black is seen only as numerous, irregular meandering lines between these large tubercles. Minute black areas occur on some tubercles or at the line of fusion between compound tubercles. The pale pink notal tubercles have a broad, smooth base and they taper smoothly along the stem. They are very tall. Apically, the tubercles broaden (like a mushroom) but have a very irregular surface consisting of tiny, rounded, compound tubercles. Overall, the dorsal impression is that of many tall outgrowths of pink tubercles with the intervening areas appearing as deep valleys or fissures lined in black. Small, rounded tubercles occur just inside the mantle margin. The mantle edge is smooth, very narrow and pink, but interrupted by numerous black rays. The anus occurs at the summit of a very tall (approximately 2-3 mm above the level of the tubercles), conical, smooth, translucent pink papilla. The rims of the rhinophoral pockets are raised (to approximately half the height of surrounding tubercles) and are pale pink. The rhinophores are tall and pink with a black stripe extending from the apex down the posterior face to the base. Each rhinophoral clavus possesses 29-32 lamellae (specimens greater than 49 mm). Ventrally, the hyponotum is pink with fine cross hatching and a few dark grey transverse rays. The gills are dark grey. The long broad foot is uniformly pink and its margin is slightly undulating (Pl.9D). The fused, squarish oral tentacles are pink.

Anatomy. Typical for the genus *Phyllidiopsis*. The muscular oesophageal segment is large and elongate-oval in shape. The digestive gland mass is pale pink. The reproductive system is white except for the nidamental glands which are pink and the bursa copulatrix which is dark brown. Penial spines were not isolated for SEM study. However under light microscope, they appeared to be relatively small (less than 10 µm) and strongly hooked.

Distribution. *Phyllidiopsis fissuratus* is currently

known from the south-western, tropical Pacific region (Fiji and the central Great Barrier Reef to Lord Howe Island; present work).

Remarks. *Phyllidiopsis fissuratus* is a very large species. Its distinctive external features are its very tall, pale pink tubercles which broaden apically with many tiny, rounded, compound tubercles, and the resultant deep valleys, lined with black. Some tubercles also have minute black markings. A notable feature on the dorsum is the extremely tall, smooth, conical, translucent pink anal papilla (Pl.9C). The rhinophores are pink with a black stripe posteriorly. The rhinophoral pockets possess raised, translucent pink rims. Ventral features include the pink colouration, dark grey gills, and undulating edge to the large foot (Pl.9D).

The black background colouration of the dorsum, the very tall pale pink tubercles, the greater number of lamellae to the rhinophoral clavus and the unique morphology of the anal papilla, separate this species from the two previously described species and *Phyllidiopsis kremphi* Pruvot-Fol. *Phyllidiopsis burni* appears to be the closest but it has dark pink tubercles (not as tall), and black rhinophores with 17-20 lamellae on their clavus (pink with a black posterior stripe and 29-32 lamellae in the present species). *Phyllidiopsis burni* has neither a large, conical anal papilla nor raised rims to the rhinophoral pockets. *Phyllidiopsis burni* has a broader muscular oesophageal segment (more elongate in *P. fissuratus*) and large, broad, slightly recurved penial spines (small and strongly hooked in *P. fissuratus*).

Etymology. The specific epithet refers to the deeply fissured dorsal appearance of this species.

Ceratophyllidia Eliot, 1903

Ceratophyllidia africana Eliot

Figs 17, 18

Ceratophyllidia africana Eliot, 1903a: 250-251.-Eliot, 1910: 437.-Gosliner, 1987: 91, pl.155.-Gosliner & Behrens, 1988: 305-308, figs 1a, 2a-c.
Ceratophyllidia grisea Eliot, 1910: 436-437, pl.25, figs 3-7.

Comments on synonymy. *Ceratophyllidia africana* was recently redescribed by Gosliner & Behrens (1988) and illustrated in colour by Gosliner (1987). These authors have shown that Eliot's (1910) *C. grisea* is indistinguishable from *C. africana*.

Types. *Ceratophyllidia africana* Eliot, 1903. Holotype presumed lost; could not be located in BMNH; dissected by Eliot.

Ceratophyllidia grisea Eliot, 1910. Holotype presumed lost; could not be located in BMNH.

Material examined. 20 mm specimen (CASIZ 063262), Passe Du Bois, Aldabra Atoll, 10 m depth, 22 Mar. 1986, T.M. Gosliner; 30 mm specimen (MNHN), Réunion Island, Indian Ocean, 5-20 m depth, 1 Dec. 1989, M. Jay.

External morphology. The available specimens measured 30 mm and 20 mm alive. After three years preservation, they still retained some colouration although some of the papillae were contracted. Live specimens of *C. africana* have a uniform creamish yellow notum from which arise the stalked papillae (see colour photograph in Gosliner, 1987: 91). The papillae are cream and their uppermost surfaces possess an aggregation of small black spots. The notum is heavily spiculate but notal tubercles are absent. The mantle margin is thin, slightly undulating and its edge is cream. The anus has a raised rim around it. The rhinophoral openings each have a raised rim. The rhinophores are cream to white and are rounded apically. Each rhinophoral clavus bears 16-20 lamellae.

The ventral surfaces, oral tentacles and gills are pale yellow. The partially fused oral tentacles are broad and cylindrical with rounded ends. The foot sole lacks contrasting markings.

Anatomy. Typical for the genus *Ceratophyllidia* Eliot (Figs 17, 18) (see also Gosliner & Behrens, 1988). Penial spines appear to be absent in this species (Gosliner & Behrens, 1988).

Distribution. *Ceratophyllidia africana* is presently known from the western Indian Ocean. There are five records to my knowledge: East Africa (Eliot, 1903a); South Africa (Gosliner, 1987); Seychelles (Eliot, 1910 as *C. grisea*; Gosliner & Behrens, 1988); and Réunion Island (present work).

Remarks. The principal distinguishing characteristics of *Ceratophyllidia africana* include its uniform creamish yellow dorsum and the numerous cream to white papillae with dense black spots apically. Neither of the two following species has yellow colouration and one has brown markings on its dorsum. Both species also lack the minute black spots found on the apices of the papillae of *C. africana*.

Ceratophyllidia sp. 1

Fig.16, Pl.9E

Material examined. 10 mm specimen (CASIZ), Madang Lagoon, PNG, 1 Feb. 1988, T.M. Gosliner; 7.5 mm specimen, Bile Bay, Guam, 5 m depth, 19 June 1975, Carlson-Hoff.

External morphology (Fig.16, Pl.9E). The two live specimens measured 10 mm and 8 mm respectively. One specimen was slightly damaged (posterior margin of mantle torn, Fig.16). Preserved specimens of this species

appear to retain most of their live colouration. Live specimens of *Ceratophyllidia* sp. 1 have a white background to the notum and 10-16 tan brown spots (variable in size) which are arranged, approximately, in two mediolateral, longitudinal lines (Fig.16, Pl.9E). The stalked papillae are white with tan brown markings on their uppermost surface. The mantle margin is broad, thin, and slightly undulating. Fine spicules could be seen through the notum. The rhinophores and anus each possess a low, raised rim around the edge of their openings. The rhinophores are cream-brown in colour. Each rhinophoral clavus possesses approximately 7-10 lamellae. The ventral surfaces, oral tentacles and gills are white in colour. The partially fused oral tentacles are broad and rounded anteriorly. The foot sole has no distinctive markings.

Anatomy. Typical for the genus *Ceratophyllidia*. Both the alimentary and reproductive systems were entirely white in the preserved state.

Distribution. *Ceratophyllidia* sp. 1 is presently known from Madang, Papua New Guinea (1 specimen) and Guam (1 specimen).

Remarks. *Ceratophyllidia* sp. 1 can be distinguished from *C. africana* by its notal colouration, tan brown markings on the dorsal surface of the papillae (black spots on papillae of *C. africana*), fewer lamellae on the rhinophoral clavus and white ventral colouration (pale yellow in *C. africana*). *Ceratophyllidia* sp. 2 is white and grey in colour, but it has no dorsal markings. *Ceratophyllidia* sp. 1 probably attains a larger size.

Ceratophyllidia sp. 2

Pl.9F

Material examined. 15 mm specimen (AM C159571; partially dissected but viscera and most dorsal papilla intact), Kwajalein Atoll, Marshall Island, 15 m depth, 4 June 1983, S. Johnson.

External morphology (Pl.9F). The single specimen measured 15 mm alive. The preserved specimen is white to pale grey. Alive, *Ceratophyllidia* sp. 2 has a white background to the notum with no contrasting markings. The notum is heavily spiculate. The stalked papillae are pale grey in colour apart from a single, large apical circle of dark grey, dorsally. The mantle margin is narrow and relatively straight. The rhinophores are pointed apically and white. Each rhinophoral clavus possesses 12-14 lamellae. The dorsal posterior anus opens on a single rounded tubercle. The ventral surfaces, oral tentacles and gills are pale grey-white in colour. The oral tentacles are conical in shape. The foot sole has no distinctive markings.

Anatomy. Typical for the genus *Ceratophyllidia*. The reproductive organs and ovotestis appeared to be mature in the specimen examined. The alimentary and reproductive systems were not examined in detail (partially dissected).

Distribution. The single specimen (collected by Scott Johnson) of *Ceratophyllidia* sp. 2 originated from the Marshall Islands in the central Pacific Ocean.

Remarks. *Ceratophyllidia* sp. 2 has a white dorsum (very pale grey ventrally), pointed white rhinophores, and pale grey papillae with a single, broad, dark grey spot on the apex of each. In contrast *Ceratophyllidia africana* is creamish yellow both dorsally and ventrally, and it has numerous small black spots on the apices of the papillae. The rhinophores of *C. africana* are pale yellow in colour and have rounded extremities. *Ceratophyllidia* sp. 1 has large brown spots on the dorsum and brown markings on the apices of the papillae. These two species are not named in the present work as further comparative material would be useful for more detailed descriptions of anatomy to be made.

Reticulidia Brunckhorst, 1990

Reticulidia halgerda Brunckhorst & Burn, 1990

Figs 10D-F, 18-21, 31A-C, Pl.9G

Phyllidia sp.—Coleman, 1989: 49 (colour illustration), as “decorated phyllidia”.

Reticulidia halgerda Brunckhorst & Burn, 1990 in Brunckhorst, 1990a: 567-576, figs 1, 2a-c, 3-7.

Type. Holotype (28mm preserved length) AM C144248; nine paratypes designated (in Brunckhorst, 1990a).

Material examined. *Western Pacific Ocean* – 1 specimen, south Taiwan, South China Sea, 5 Nov. 1984, Ms Shuw-ing Lou; 31 mm specimen (AM C144248), Ruaniu, Solomon Islands, 35 m depth, 12 Mar. 1984, I. Knight; 35 mm specimen (AM C142262), Bonege Island, Solomon Islands, 12 Jan. 1984, I. Knight; 27 & 23 mm specimens (AM C144246), Bonege River, Solomon Islands, 15 m depth, 15 June 1984, I. Knight; 38 mm specimen, The Pinnacle, Madang, 6-30 m depth, 25 Jan. 1988, RCW; 40 mm specimen (AM C136916), Wahoo Reef, PNG, 23 Dec. 1981, N. Coleman; 41 & 14 mm specimens (MV F30726), Samaurez Reef, Coral Sea, 18 m depth, 16 Aug. 1977, N. Coleman; 1 specimen (MV F30778), Marion Reef, 10 m depth, 1980, N. Coleman; 1 specimen (AM C159539), Kwajalein Atoll, Marshall Island, 65 m depth, 1983, S. Johnson; 43 mm specimen, Mana Island, Fiji, 14 m depth, 16 Jan. 1986, G. Brodie.

Eastern Australia – Great Barrier Reef – 33 mm specimen (AM C132368), Heron Island, 3 m depth, 19 Dec. 1981, G. Averm; 50 mm specimen, Wistari Reef, 15 m depth, 26 Sept. 1987, Leslie Newman; 1 specimen, Heron-Wistari Reefs, J.Marshall; 35 mm specimen, Gannet Cay, Swains Reefs, 27 Sept. 1985, W. Grieve; 1 specimen, One Tree Island, 22 m

depth, 1 July 1980, W. Wood; 50 mm specimen, Wistari Reef, 22 m depth, 1 Apr. 1986, R. Reichelt; 45 mm specimen, Lady Musgrave Island, 18 m depth, 1 June 1987, R. McGill; 45 mm specimen, Lady Musgrave Island, 18 m depth, 1 June 1987, Carol Buchanan; 52 mm specimen, Lady Musgrave Island, 18 m depth, 1 Apr. 1986, C. Buchanan; 60 mm specimen (AM C159476), Jupiter Reef, 15 m depth, 13 Apr. 1985, DJB; 62 mm specimen, North-west Island, 1 May 1988, J. Brodie; 1 specimen (MV), R. Catala; 40 mm specimen (AM C95672), Wheeler Reef, 18 m depth, 5 Sept. 1974, I. Loch.

External morphology (Pl.9G). Live specimens ranged in length from 14-65 mm and mean size was 44 mm. The smooth ridges of the dorsum are orange in colour and the crest may be finished with a fine white line. The intervening background areas are black. A narrow base to the ridges gives them a sharp appearance. There are three, longitudinal primary ridges (in a median position) and three primary ridges run transversely across the dorsum. The effect of this pattern is the general appearance of four median quadrates having a black background (Pl.9G). Various secondary ridges may occur, usually at right angles to the mantle edge. Marginally, these finer secondary (and, if present, tertiary) ridges may be white in colour and run to the edge of the mantle. Both dorsally and ventrally, the mantle margin is edged in orange. The rhinophores are orange, slightly recurved, and pointed at the apex. The rhinophoral clavus possess 24-28 fine lamellae (in specimens measuring 30-60 mm, alive). The anus opens on the apex of a ridge. Ventrally, the foot is orange, and the oral tentacles are long and tipped with orange.

Anatomy. Typical for the genus *Reticulidia* (Brunckhorst, 1990a). The pharyngeal bulb, internally, has radially arranged glandular discs (Figs 10D-F, 19, 20). The number of discs within the pharyngeal bulb varied between 39 and 48 in five specimens examined. The digestive gland mass was pale yellow in colour in the preserved state. A distinct stomach region occurs within the digestive gland (Fig.20).

In preserved specimens, the reproductive organs (Fig.21) were pale yellow-orange in colour, with the exception of the receptaculum seminis which was translucent and cream in colour, and the bursa copulatrix which was variable (translucent to cream to opaque yellow-orange). There is a long, muscular ejaculatory duct (= penis, Fig.21). The penis is eversible and armed with rows of recurved spines at its distal end. Arising from a broad base, the spines taper rapidly to a point approximately half way up their length; at this point the curvature of the spine becomes more pronounced and the distal half tapers more gradually to a fine point (Fig.31A-C). The penial spines have some pitting and tiny furrows on the base. Paired spines (i.e., two spines arising from a single base) are present (Fig.31A,B). Individual spines of a pair may be of equal or unequal length.

Distribution. *Reticulidia halgerda* is currently known from the central and western Pacific Ocean (including Fiji and the Marshall Islands), from eastern Australia to Taiwan.

Remarks. *Reticulidia halgerda* differs both internally and externally from species of *Phyllidia* and *Phyllidiopsis* which possess yellow colouration and tuberculate ridges. *Reticulidia halgerda* does not possess spiculate tubercles, but has smooth reticulate ridges on the notum whereas *Phyllidia ocellata*, *P. tula*, *P. varicosa* and *P. coelestis* have yellow capped tubercles and a different foregut (see Brunckhorst, 1990a).

Reticulidia halgerda lacks blue colouration as found in *R. fungia* n.sp. and has numerous, narrow ridges (fewer, broad ridges in *R. fungia* n.sp.). Other differences which clearly separate the two species are summarised in the following description of *Reticulidia fungia* n.sp.

***Reticulidia fungia* Brunckhorst & Gosliner, n.sp.**

Fig.31D, Pl.9H

Phyllidia sp.—Tan *et al.*, 1987: 76, fig.7 (colour illustration).

Phyllidiopsis sp.—Brunckhorst, 1989: 7 (colour illustration).

Phyllidia sp.—Coleman, 1989: 49 as “abstract phyllidia” (colour illustration).

Reticulidia sp.—Brunckhorst, 1990a: 574, fig.2d.

Type. Holotype here designated (30 mm alive) AM C159515; the remaining specimens are designated paratypes.

Material examined. *Western Pacific Ocean* — 42 mm specimen (AM C126960), Lizard Island, north Qld, 10 Feb. 1981, D. Finney; 40 mm specimen (AM C168774), Lizard Island, north Qld, 12 m depth, 28 Dec. 1989, S. Schubert; 30 mm specimen, Broadhurst Reef, central GBR, 20 m depth, 31 Jan. 1987, R. Kelly; 18 mm specimen, Wan-li-tan, southern Taiwan, 15 m depth, 8 Nov. 1984, Ms Shuw-ing Lou; 25 mm specimen, Ponape, Micronesia, 7 m depth, 18 Oct. 1987, Tony Poiner; 1 specimen (AM C144247), Rove Caves, Guadalcanal Solomon Islands, 11 May 1984, I. Knight; 1 specimen (AM C144541), Osprey Reef, Coral Sea, 1 Dec. 1984, W. Brunckhorst.

Papua New Guinea — 28 & 30 mm specimens (AM C159518), Horseshoe Reef, 14 m depth, 22 June 1988, DJB & SKB

Madang — holotype (30 mm, AM C159515), Barracuda Point, 25 m depth, 14 Feb. 1988, RCW; 1 specimen, Bombes Reef, 10-18 m depth, 11 Jan. 1988, T. Gosliner; 25 & 29 mm specimens (AM C159514), The Pinnacle, 12-24 m depth, 7 Feb. 1988, RCW; 23 mm specimen, Bombes Reef, 10 m depth, 6 Feb. 1988, RCW; 26 mm specimen, Barracuda Point, 20 m depth, 14 Feb. 1988, T. Gosliner; 23 mm specimen (AM C159516), Banana Reef, 6-30 m depth, 15 Feb. 1988, RCW; 22 mm specimen (AM C159517), Rasch Passage, 18 m depth, 19 Feb. 1988, RCW; 4 specimens (30, 26, 30, 30 mm), Madang Lagoon, 15-25 m depth, 14 Feb. 1988, RCW.

Indian Ocean — 33 mm specimen (AM C126996), off Mosque, Christmas Island, 26 m depth, 3 Dec. 1980, J. Burgess.

External morphology (Pl.9H). Twenty two specimens ranged in length from 18-42 mm and mean size was 27 mm. This species has fewer broad based, smooth, notal ridges. The ridges have a broad base and are orange

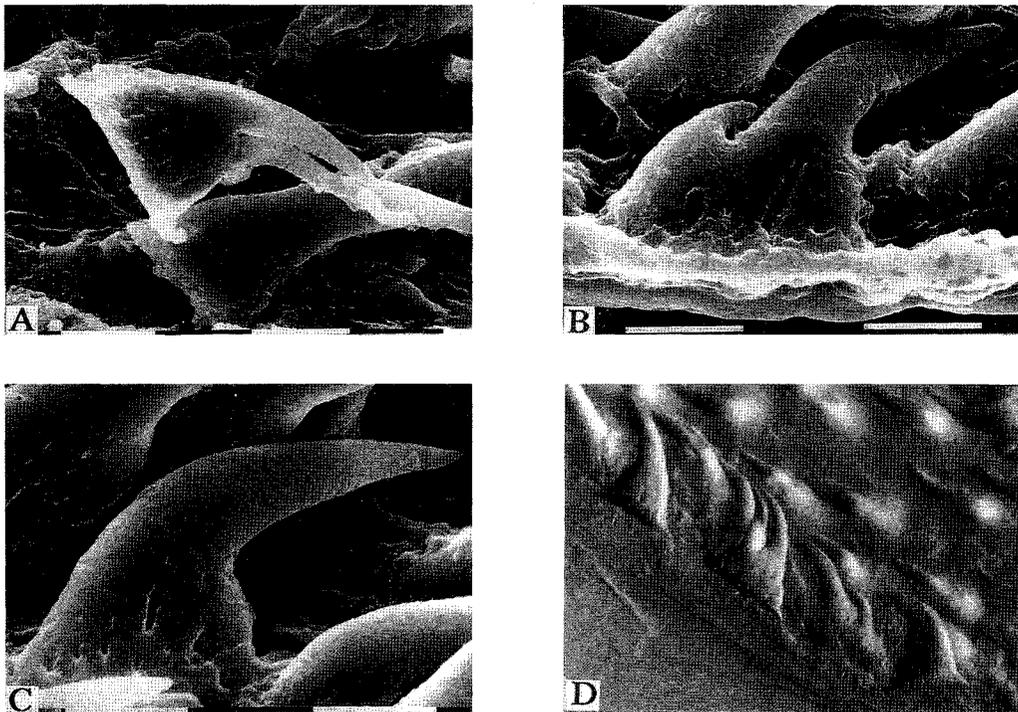


Fig.31. A, *Reticulidia halgerda*. SEM of “paired” penial spines; B, *Reticulidia halgerda*. SEM of “paired” penial spines; C, *Reticulidia halgerda*. SEM of a single penial spine; D, *Reticulidia fungia* n.sp. Phase-contrast microscope photo of penial spines x 1000. A,B,C scale = 10 μ m.

in colour, except for the top-most edge and the bases of the ridges which are bordered in white. The intervening background areas of the dorsum are black. There is a single, median longitudinal ridge from which other meandering ridges arise. These secondary ridges do not run right to the edge of the notum. Anteriorly, the central ridge bifurcates; each branch passes behind a rhinophore to the lateral margin (Pl.9H). There is a broad blue-grey band around the mantle margin.

The pointed rhinophores are orange and possess 14-18 lamellae on the clavus (in specimens measuring 28-35 mm). The anus opens on the apex of a ridge. Ventrally, the foot is pale yellow and the orange digestive gland mass can be seen through it. There is a broad black line (broken black line in a few specimens) running around the underside of the mantle (hyponotum) just above the line of the gills. The oral tentacles are cylindrical in shape (live specimens) and yellowish in colour.

Anatomy. The anatomy of this species confirms the generic features described by Brunckhorst (1990a). The number of glandular discs within the pharyngeal bulb varied between 26 and 40 in four specimens. The digestive gland mass was orange in colour in live specimens (brown in the preserved state). A distinct stomach region occurs within the digestive gland mass. The reproductive system is typical for *Reticulidia*. It is cream to yellow in colour except for the receptaculum seminis which is translucent. The long penis possesses rows of recurved spines at its distal end. The penial spines of *R. fungia* have a broad rounded base and taper evenly to a fine point (Fig.31D). Paired penial spines are present, however their frequency was not determined.

Distribution. *Reticulidia fungia* is currently known from the central to western Pacific Ocean (including Fiji and Micronesia), from eastern Australia to Taiwan. This shows that it occurs sympatrically with *R. halgerda*. *Reticulidia fungia* is also known from Christmas Island, in the eastern Indian Ocean.

Remarks. *Reticulidia fungia* is the second species of *Reticulidia* Brunckhorst and it confirms generic features previously described (Brunckhorst, 1990a). The present species apparently does not attain the size of *Reticulidia halgerda*. *Reticulidia fungia* is separable from *R. halgerda* by having: broad based ridges which are fewer in number, the bases being finely bordered in white; a broad blue-grey mantle margin (narrow and orange in *R. halgerda*); paler colouration ventrally, a black line around the side of the foot just above the gills; rhinophores with 14-18 lamellae on the clavus (24-28 in *R. halgerda*); and penial spines which taper evenly to their apex.

Etymology. This species is named for the resemblance of the dorsal ridges to the septae of the

solitary corals belonging to the family Fungiidae, genus *Fungia*.

Phylogenetic Relationships within the Family Phyllidiidae

Ultimately, the aim of systematic classifications is to reflect the natural phylogeny (genealogy) of the particular group under consideration (Darwin, 1859). Comparative and functional anatomical studies are an important basis for resolving phylogenetic relationships among opisthobranch gastropods (e.g., Ghiselin, 1966; Gosliner, 1981; Rudman, 1984; Willan, 1987). It is appropriate, therefore, to conclude the present work with a genealogical study. No phylogeny of phyllidiid genera has previously been proposed and the relationship of the family to other dorid-like nudibranchs is unresolved.

The concepts and principles of phylogenetic analysis through cladistics as espoused by Hennig (1966) and Wiley (1981) have gained considerable acceptance. However, various problems in the theoretical application of cladistic methodologies have been identified (for recent discussions see Eldridge & Cracraft, 1980; Ghiselin, 1980; Archie, 1989; Chappill, 1989; Nelson, 1989; Crowson, 1991). In particular, opisthobranchs display considerable convergent evolutionary development, possibly because adult body form and internal morphology are no longer confined by a shell (Ghiselin, 1966, 1980; Rudman, 1984; Faulkner & Ghiselin, 1983; Gosliner & Ghiselin, 1984; Willan, 1987). In consequence, parsimony based cladistic analysis of the phylogeny of opisthobranch groups must be approached with some caution because an incorrect resolution may be widely accepted (Gosliner & Ghiselin, 1984; Crowson, 1991). A further difficulty is the characterisation of an ancestor, as no single extant species will have retained all primitive states and there is no fossil record of these soft bodied groups (Gosliner, 1981).

Todd (1981, 1983) and Thompson & Brown (1984) suggested that *Phyllidia* was close to *Armina* on the basis of the position (ventrolateral) of the gills in both groups. However, the structure of the gills differs in both genera and their anatomy is very different. To my knowledge, *Armina* shares no uniquely derived characters with *Phyllidia*. *Armina* would appear to be an early (primitive) nudibranch offshoot (Thompson & Brown, 1984) whereas I agree with most current opisthobranch systematists in considering phyllidiids as advanced dorids (see also Healy & Willan, 1991). Traditionally, the Phyllidiidae have been placed with the Dendrodoridae in the Porostomata (e.g., Bergh, 1892; Thompson, 1976; Boss, 1982; Ev. Marcus, 1983) on the basis of the loss of jaws and radula. However, specialisation of dorid nudibranchs to deal with various food types (Young, 1969) may have led to parallel developments in the mode of feeding (e.g., sponge sucking) and perhaps convergence of the feeding apparatus itself. Gosliner & Ghiselin (1984) suggest that parallel, independent development of an

apomorphic condition may be identified if the plesiomorphic and apomorphic conditions are present in both the ingroup and the outgroup. I think the loss of jaws and radula in both dendrodorids and phyllidiids is most probably convergence, because details of their foregut anatomy are quite different (Young, 1969; present work). The present analysis, using a range of characters, attempts to test this hypothesis.

The aims of the present analysis are, firstly, to provide a preliminary, inferred phylogeny for phyllidiid genera and, secondly, to use this phylogeny to examine the relationship of the family with dendrodorids.

Methods

Data relating to 49 qualitative characters were compiled for each of the six phyllidiid genera (*Phyllidia*, *Fryeria*, *Phyllidiella*, *Phyllidiopsis*, *Ceratophyllidia* and *Reticulidia*), *Chromodoris* and *Dendrodoris*. A hypothetical ancestor (HANC) is used to root the phylogenetic tree because it is very difficult to ascribe an extant, ancestral species. Use of an extant dorid outgroup to root the tree was abandoned because of the artificial relationship that would be inferred with that particular group and because disparate taxa may exclude

otherwise useful characters. However, *Chromodoris* is used for outgroup comparison to decide direction of change or polarity and also to assess uniquely derived apomorphy (see Gosliner & Ghiselin, 1984). *Dendrodoris* is included in order to elucidate its relationship with phyllidiid genera, as it also lacks radula and jaws and has become a suctorial feeder on sponges (Young, 1969).

The characters reflect a wide range of morphological and anatomical features (including divergent derived conditions of the alimentary and genital organs); data on sperm ultrastructure (Healy & Willan, 1991; J. Healy, personal communication), histology, egg spirals, food/feeding and biochemistry. A brief explanation of each character and direction of change or polarity (see Table 3) is given below. Characters are mostly coded as binary attributes (three characters are coded as continuous), with “-” representing missing data or characters which logically do not apply. No relative weighting of characters was used. The IBM-DOS computer program HENNIG 86 (Farris, 1988) was used to calculate the shortest inferred phylogenetic tree. Characters were treated as ordered and Wagner optimisation was employed.

Data on *Chromodoris* and *Dendrodoris* are derived from Young (1969) and Rudman (1982, 1983, 1984, 1986), and from my dissections of *Chromodoris splendida* (Angas) and *Dendrodoris nigra* (Stimpson) (specimens collected from Moreton Bay, Queensland, 1986-1989).

Table 3. Character list and direction of change (polarity). Zero scores are given to plesiomorphic states; higher scores indicate relative apomorphic level.

No	Character	States
1	body shape	0 = oval; 1 = elongate
2	body texture	0 = soft to firm; 1 = hard, tough, stiffened by large spicules
3	integumentary spicules	0 = absent or few, minute; 1 = numerous large calcareous and chitinous spicules
4	notal tubercles	0 = absent; 1 = present, hard, stiffened by spicules
5	soft ‘mushroom’ papillae	0 = absent; 1 = present
6	smooth reticulate ridges	0 = absent; 1 = present
7	lamellate rhinophores	0 = not lamellate; 1 = lamellate
8	rhinophores retractile	0 = rhinophores non retractile; 1 = rhinophores retractile
9	short rhinophore ‘sheaths’	0 = absent; 1 = present
10	rhinotubercles	0 = absent; 1 = present
11	dorsal, circumanal gill circler or secondary ventrolateral gills	0 = dorsal anal gill circler present 1 = ventrolateral gills
12	gills retractile	0 = non retractile; 1 = retractile
13	gills branched	0 = not branched; 1 = branched
14	anal position	0 = dorsal; 1 = ventral, posterior
15	anus protrusible	0 = non protrusible; 1 = protrusible
16	black stripe on midline of foot sole	0 = absent; 1 = present
17	two oral tentacles	0 = present; 1 = absent
18	secondary fusion of oral tentacles	0 = not fused; 1 = fused
19	lateral groove on oral tentacles	0 = absent; 1 = present
20	jaws	0 = present; 1 = absent
21	radula	0 = present; 1 = absent
22	ptyaline glands	0 = present; 1 = absent
23	salivary glands	0 = present; 1 = absent
24	salivary glands attached to posterior oesophagus	0 = not attached; 1 = attached
25	site of oral glands	0 = glands external to buccal bulb/pharyngeal bulb; 1 = glands internal
26	‘cauliflower’ oral glands within pharyngeal bulb	0 = absent; 1 = present

27	mass of soft 'leaf' oral glands, externally, with ducts to pharyngeal bulb	0 = absent; 1 = present
28	orange glandular discs in pharyngeal bulb	0 = absent; 1 = present
29	minute white oral glands enveloping pharyngeal bulb	0 = absent; 1 = present
30	number of foregut retractor muscles	0 = numerous (>2) pairs; 1 = a single pair
31	site of exit of pharynx from pharyngeal bulb	0 = posterior; 1 = posteriodorsal; 2 = dorsal
32	pharyngeal bulb shape (& associated musculature)	0 = bulb small, extensive musculature; 1 = bulb large, elongate, reduction in musculature; 2 = bulb larger, broad & conical; 3 = very broad, upright & cylindrical
33	posterior bulbous segment/portion to oesophagus	0 = absent; 1 = present
34	posterior oesophageal segment very muscular	0 = absent or not muscular; 1 = very muscular
35	posterior oesophageal segment glandular	0 = absent or not glandular; 1 = glandular
36	large posterior oesophageal retractor muscle	0 = absent; 1 = present
37	intestine with right hand loop	0 = present; 1 = absent
38	intestinal path to anus	0 = intestinal path entirely dorsal; 1 = arising dorsally, but immediately passing ventrally & running to anus ventrally
39	serial dorid-like, triaulic repro. system	0 = absent; 1 = present
40	sperm nucleus length	0 = short & broad; 1 = elongate, narrow
41	spawn mass spiral	0 = not spiral; 1 = spiral
42	egg ribbon attachment	0 = attachment on edge of tall spawn ribbon; 1 = attachment on underside of rounded flat coil of spawn
43	oviduct & prostate separate at exit from ampulla	0 = no separation; 1 = separate
44	vaginal duct exits at base of bursa copulatrix i.e., bursa not stalked	0 = bursa stalked; 1 = bursa not stalked
45	penis shape	0 = elongate; 1 = short, bulbous
46	penial spines	0 = absent; 1 = present
47	defence chemicals - sesquiterpene isocyanides	0 = absent; 1 = present
48	defence chemicals - terpenoid furans	0 = absent; 1 = present
49	defence chemicals - drimane sesquiterpenoids	0 = absent; 1 = present

Characters

External morphology. Oval body shape (1) is considered the plesiomorphic state. Body texture (2) is tough, hardened by large spicules, in the apomorphic condition. Soft to firm body texture is considered plesiomorphic. The possession of many, very large spicules (3) of two types, calcareous and chitinous, is an apomorphy of phyllidiids as is the presence of hard spiculose tubercles (4) or tubercular ridges. Soft "mushroom" papillae (5) are unique to *Ceratophyllidia*. Smooth reticulate ridges (6) are an autapomorphy of *Reticulidia*. Character states, (7) and (8) (lamellate and retractile rhinophores respectively) are synapomorphs of "dorid" nudibranchs (absent in the hypothetical ancestor). Presence of short rhinophoral sheaths (9) is an autapomorphy of *Phyllidiopsis*. The possession of rhinotubercles (10) is a synapomorphy of *Phyllidia* and *Fryeria*.

The primitive dorid condition includes the possession of a dorsal, circumanal gill circling (11). The secondary, ventrolateral gills of phyllidiids are an autapomorphy.

Doridoid gills may be retractile (12) and/or branched (13), both being advanced states. A posterior, ventral anal position (14) and a protrusible anus (15) are autapomorphies of the genus *Fryeria*. A black stripe on the foot sole (16) is found in some species of *Phyllidia* (e.g., *P. varicosa*, *P. tula*, *P. elegans*) and is considered an apomorphic trait. The secondary loss of oral tentacles (17) is an autapomorphy of *Dendrodoris* (see Young, 1969). A pair of oral tentacles is (primitively) retained by phyllidiids, but are secondarily fused (18) in *Ceratophyllidia* and *Phyllidiopsis*. The lateral groove (19) on the oral tentacles is a synapomorphy of all phyllidiid genera.

Anatomy. The loss of jaws (20) and radula (21) are advanced states found in dendrodorids and phyllidiids. The absence of ptyaline glands (22) and/or salivary glands (23) is an apomorphic condition (Young, 1969). *Dendrodoris* possesses salivary glands attached to the posterior of the oesophagus (24) (Young, 1969; personal observation). Oral glands would primitively occur external to the foregut (25) (e.g., *Phyllidiopsis*, *Phyllidiella*). Oral

glands situated within the pharyngeal bulb is a synapomorphy of *Phyllidia*, *Fryeria* and *Reticulidia*. The hard, swollen "cauliflower" like oral glands (26) are a synapomorphy of *Phyllidia* and *Fryeria*. The soft mass of "leaf" like oral glands (27) represent an autapomorphy of *Phyllidiella*. Orange glandular discs (28) within the pharyngeal bulb represent an autapomorphy of

Reticulidia (Brunckhorst, 1990a). Only *Phyllidiopsis* possesses minute, white oral glands (29) which ensheath the pharyngeal bulb (Brunckhorst, 1990b).

Possession of numerous pairs of retractor muscles (30) associated with the buccal bulb represents the plesiomorphic condition in dorids (see Young, 1969). I consider that the reduction to a single, long pair of

Table 4. Data matrix. Columns represent characters as defined in Table 3.

0 = primitive, 1 = advanced state, - = data missing or inapplicable.

Character No.	HANC	<i>Chromodoris</i>	<i>Dendrodoris</i>	<i>Phyllidia</i>	<i>Fryeria</i>	<i>Phyllidiella</i>	<i>Phyllidiopsis</i>	<i>Ceratophyllidia</i>	<i>Reticulidia</i>
1	0	1	1	0	0	0	0	0	0
2	0	0	0	1	1	1	1	1	1
3	0	0	0	1	1	1	1	1	1
4	0	0	0	1	1	1	1	0	0
5	0	0	0	0	0	0	0	1	0
6	0	0	0	0	0	0	0	0	1
7	0	1	1	1	1	1	1	1	1
8	0	1	1	1	1	1	1	1	1
9	0	0	0	0	0	0	1	0	0
10	0	0	0	1	1	0	0	0	0
11	0	0	0	1	1	1	1	1	1
12	0	1	1	0	0	0	0	0	0
13	0	1	1	0	0	0	0	0	0
14	0	0	0	0	1	0	0	0	0
15	0	0	0	0	1	0	0	0	0
16	0	0	0	1	0	0	0	0	0
17	0	0	1	0	0	0	0	0	0
18	0	0	-	0	0	0	1	1	0
19	0	0	0	1	1	1	1	1	1
20	0	0	1	1	1	1	1	1	1
21	0	0	1	1	1	1	1	1	1
22	0	1	0	1	1	1	1	0	1
23	0	0	0	1	1	1	1	1	1
24	0	0	1	0	0	0	0	0	0
25	0	-	-	1	1	0	0	0	1
26	0	0	0	1	1	0	0	0	0
27	0	0	0	0	0	1	0	0	0
28	0	0	0	0	0	0	0	0	1
29	0	0	0	0	0	0	1	0	0
30	0	0	0	1	1	1	1	1	1
31	0	0	0	1	1	0	0	0	2
32	0	0	0	2	2	2	1	1	3
33	0	0	0	0	0	0	1	1	0
34	0	-	-	0	0	0	1	0	0
35	0	-	-	0	0	0	0	1	0
36	0	0	0	0	0	0	1	-	0
37	0	0	1	0	0	0	0	0	0
38	0	0	0	0	1	0	0	0	0
39	0	1	1	1	1	1	1	1	1
40	0	0	0	1	-	1	1	-	-
41	0	1	1	1	1	1	1	1	1
42	0	0	0	1	-	1	1	-	-
43	0	0	0	1	1	1	1	1	1
44	0	1	0	1	1	1	1	0	1
45	0	0	0	1	0	0	0	0	0
46	0	0	1	1	1	1	1	-	1
47	0	0	0	1	1	1	1	-	-
48	0	1	1	0	0	0	0	-	-
49	0	1	1	0	0	0	0	-	-

retractor muscles (associated with the pharyngeal bulb in phyllidiids) represents a derived condition. A tubular pharynx (anterior to buccal ganglia) leaves the buccal bulb of dorids posteriorly in the primitive state (31) (see Young, 1969; Rudman, 1984). The progressive dorsal migration of the exit of the pharynx from the pharyngeal bulb is considered advanced (31) (Brunckhorst, 1990a). Three states are apparent in changes to the shape and musculature of the pharyngeal bulb (32). The plesiomorphic buccal bulb, possessing radula and jaws, is relatively small and has a complex array of muscles. The phyllidiid lineage displays a progressive increase in size and broadening of the pharyngeal bulb (32) (analogous to a modified, posterior oral tube; see Brunckhorst, 1990a) and a reduction in external musculature. The most derived state appears to be found in *Reticulidia* which has a very broad, cylindrical pharyngeal bulb (containing upright glandular discs arranged radially), and a single pair of short retractor muscles (Brunckhorst, 1990a). Both *Ceratophyllidia* and *Phyllidiopsis* possess an expanded, bulbous segment of the oesophagus (33), however, this region is glandular (34) (autapomorphic) in *Ceratophyllidia* and very muscular (35) (autapomorphic) in *Phyllidiopsis* (Gosliner & Behrens, 1988; Brunckhorst, 1990b). A posterior oesophageal retractor muscle (36) represents an autapomorphy in *Phyllidiopsis*. An intestine looping to the right (37) is the plesiomorphic condition found in all but *Dendrodoris* (Young, 1969; personal observation). The plesiomorphic path of the intestine (38) to the anal opening is dorsal. In *Fryeria*, the intestine arises dorsally, but immediately passes ventrally to the right hand side of the digestive gland mass and runs posteriorly to the ventral anal opening.

The presence of a serial, dorid-like trialectic reproductive system (39) is advanced compared to that of the hypothetical ancestor. Phyllidiid species differ from members of other dorid families primarily in having spermatozoa (40) with a long nucleus (Healy & Willan, 1991; see Fig.33 and Discussion). A spawn mass layed in a spiral (41) is a synapomorphy for dorids. Attachment by the edge of the tall spawn ribbon (42) is considered plesiomorphic. Attachment on the underside of a flat spawn coil is secondary (a synapomorphy of phyllidiid species). Primitively, the oviduct and vas deferens remain together (i.e., a single duct) at their common exit from the ampulla (43) (e.g., *Chromodoris*, Rudman, 1984). Separation of oviduct and vas deferens at their exit from the ampulla is derived. A plesiomorphic state possessed by both *Ceratophyllidia* and *Dendrodoris* is a stalked bursa copulatrix (44) (i.e., the vaginal duct does not exit at the base of the bursa copulatrix, but further posteriorly). The bursa without a stalk (i.e., vaginal duct exits immediately at the base of the bursa), is a derived condition found in *Chromodoris* (Rudman, 1984) and five phyllidiid genera. The short, bulbous penis (45) of *Phyllidia* appears to be an autapomorphy. The penis is typically elongate and slender in other phyllidiid species. The presence of penial spines (46) is here considered a derived condition.

Biochemistry. The derivation of chemicals from the nudibranchs food sponge and probable *de novo* synthesis of defence compounds is of evolutionary significance (Faulkner & Ghiselin, 1983). Sesquiterpene isocyanides (47) are apparently found only in phyllidiids (known from most genera; Karuso, 1987). Terpenoid furans (48) and drimane sesquiterpenes (49) are synthesised by *Chromodoris* and *Dendrodoris* species from their food sponges (Karuso, 1987).

Results

A single most parsimonious tree, 59 steps in length, was found. The consistency index for this tree was 0.88 and the retention index was 0.85. The inferred phylogenetic tree or 'cladogram' is illustrated in Figure 32. This figure indicates, by number, apomorphic character states at each 'branch'. Changes in multistate characters are indicated in full.

Discussion

Only one phylogenetic tree (Fig.32) was generated by HENNIG 86 for the present character set. Although there can be only one true phylogeny, the inference of a single "most parsimonious" tree for any given data set is rare (Jamieson, 1988). My examination (Brunckhorst, 1989b, 1990a,b; present work) of the morphology and anatomy of individuals representing 49 species in six genera leads me to agree, generally, with the proposed genealogy of the phyllidiid genera (the position of *Reticulidia* is discussed below). It is apparent that the phyllidiid clade is monophyletic, but the present analysis gives no information on the ancestry of the family.

Ceratophyllidia appears to be the most primitive extant phyllidiid and the sister to the remaining five genera. It is possible, however, that the "Atlantic *Phyllidiopsis*" (see Brunckhorst, 1990b) might be the sister group to *Ceratophyllidia*. Further research is required to elucidate the taxonomic status of the Atlantic species and to assess their probable genealogical position.

Dendrodoris and *Ceratophyllidia* have lost jaws and radula (homeoplasies), but have retained ptyaline/salivary glands (plesiomorphies). These glands are lost (synapomorphy), however, in all other phyllidiid genera. This analysis indicates that *Dendrodoris* shares a more recent ancestor with *Chromodoris* than with any phyllidiid. I emphasise, however, that this analysis does not indicate that *Dendrodoris* is more closely related to *Chromodoris* than to other anthobranchs. Nevertheless, it is clear that *Dendrodoris* shares a large number of advanced characters with typical dorids (e.g., *Chromodoris*). The suctorial feeding of sponges by dendrodorids and phyllidiids is a convergence of function which led to the independent loss of the rasping

apparatus (jaws and radula). These two groups show gross similarities with respect to elongation of the foregut (e.g., as a tubular pharynx or elongate oesophagus), but differ substantially in the relative size, musculature, glands and arrangement of foregut parts. In *Dendrodoris*, the buccal bulb and its associated muscles and glands are essentially like that of a rasping dorid except for the loss of the radula and jaws and elongation of a tubular pharynx (Young, 1969; personal observation, this study). The relationship of dendrodorids and, indeed, phyllidiids to other nudibranch families remains unresolved and requires further research on representatives of all dorid families.

In phyllidiids, it is surmised that the posterior oral tube developed into the large, musculoglandular pharyngeal bulb (Brunckhorst, 1989b, 1990a,b; present work). The pharyngeal bulb enlarged whilst its external musculature was reduced to a single pair of long retractor muscles. Within the phyllidiid lineage, the pharyngeal bulb has expanded transversely, the point of departure of the pharynx has shifted dorsally, and further reduction of the retractor muscles has occurred along with secondary reduction in the length of the tubular pharynx (anterior to the buccal ganglia), and oesophagus (posterior to the buccal ganglia), in the most derived genera (*Phyllidia*, *Fryeria*, and *Reticulidia*). The cladistic analysis placed *Reticulidia* as a sister group to *Phyllidia* and *Fryeria* because the latter two possess a similar pharyngeal bulb. All three genera possess oral glands contained within the pharyngeal bulb (synapomorphy). However, the foregut anatomy and other unique derived characters of *Reticulidia* suggest that it may be the "most advanced" phyllidiid genus. Therefore it may be plausible that *Phyllidia* is the sister group to *Fryeria* and *Reticulidia*

which diverged with different modifications to the alimentary system (*Fryeria* retaining the "Phyllidia type" pharyngeal bulb).

Recently, Healy & Willan (1991) have surveyed sperm ultrastructure throughout the Nudibranchia. They found that the Phyllidiidae (species of *Phyllidiella* and *Phyllidiopsis*) differed from other dorid families in having spermatozoa with a long, slender nucleus (12-25 μm length) and an oblong acrosomal vesicle (see Fig.33A,B, *Phyllidiopsis cardinalis*). In most other Doridoidea the sperm nucleus is relatively short (rarely exceeding 4-8 μm long, with usually one helical keel), and the acrosomal vesicle is round or ovoid in shape (e.g., Fig.33H,I, *Rostanga arbutus*). With regard to the morphology of the mid-piece (paracrystalline and matrix materials enclosing one glycogen helix; compare Fig.33C-F with J) and neck region (attachment of the axoneme/coarse fibre complex to the nucleus; compare Fig.33G,K), spermatozoa of phyllidiids do not differ substantially from those of other nudibranchs, or in fact other heterobranch gastropods. The glycogen piece of phyllidiid spermatozoa is apparently very poorly developed (see Fig.33F, arrow) without an intruding axoneme.

The evolutionary implications of the chemical defence compounds of dorid nudibranchs may be a useful taxonomic tool in future research (Faulkner & Ghiselin, 1983; Karuso, 1987). These compounds may also be used by individuals for specific recognition (Scheuer, 1977, 1982; Karuso, 1987).

In conclusion, the grouping of dendrodorids and phyllidiids together as the Porostomata is untenable. The porostomatous condition appears to have been achieved independently in both groups as is indicated by

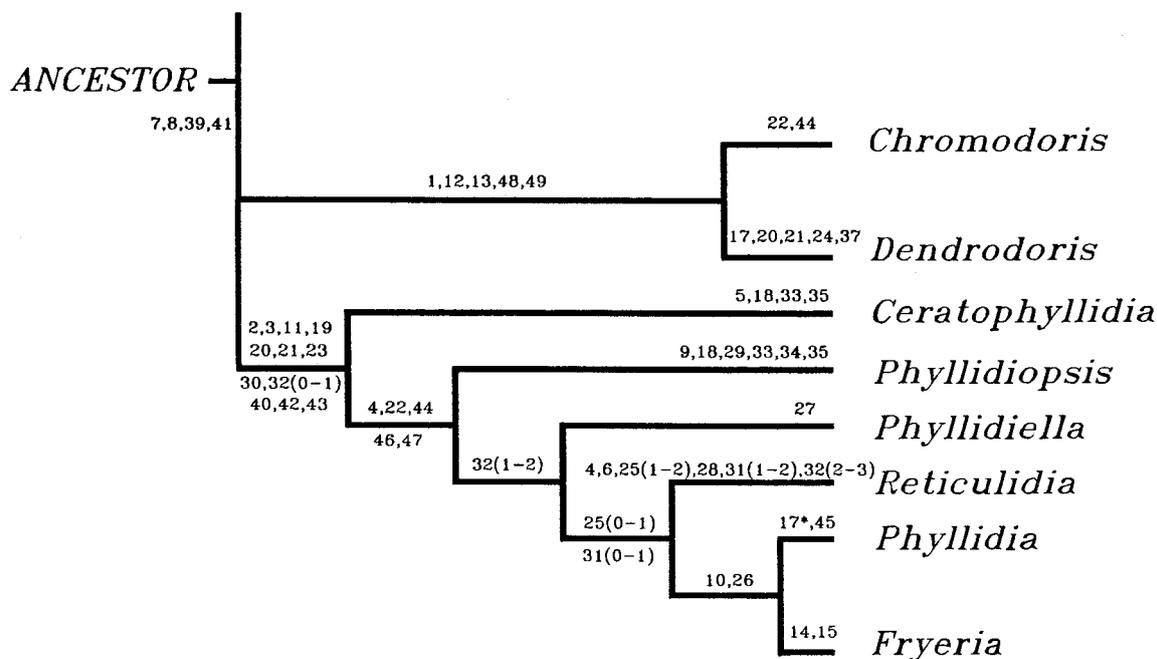


Fig.32. "Apolist cladogram" showing inferred phylogeny of phyllidiid genera. Binary characters changing from 0 (plesiomorphy) to 1 (apomorphy) are indicated only by the number of the character. Changes in multistate characters are indicated in full (the change of state in brackets). An asterisk indicates the presence of an apomorphic trait.

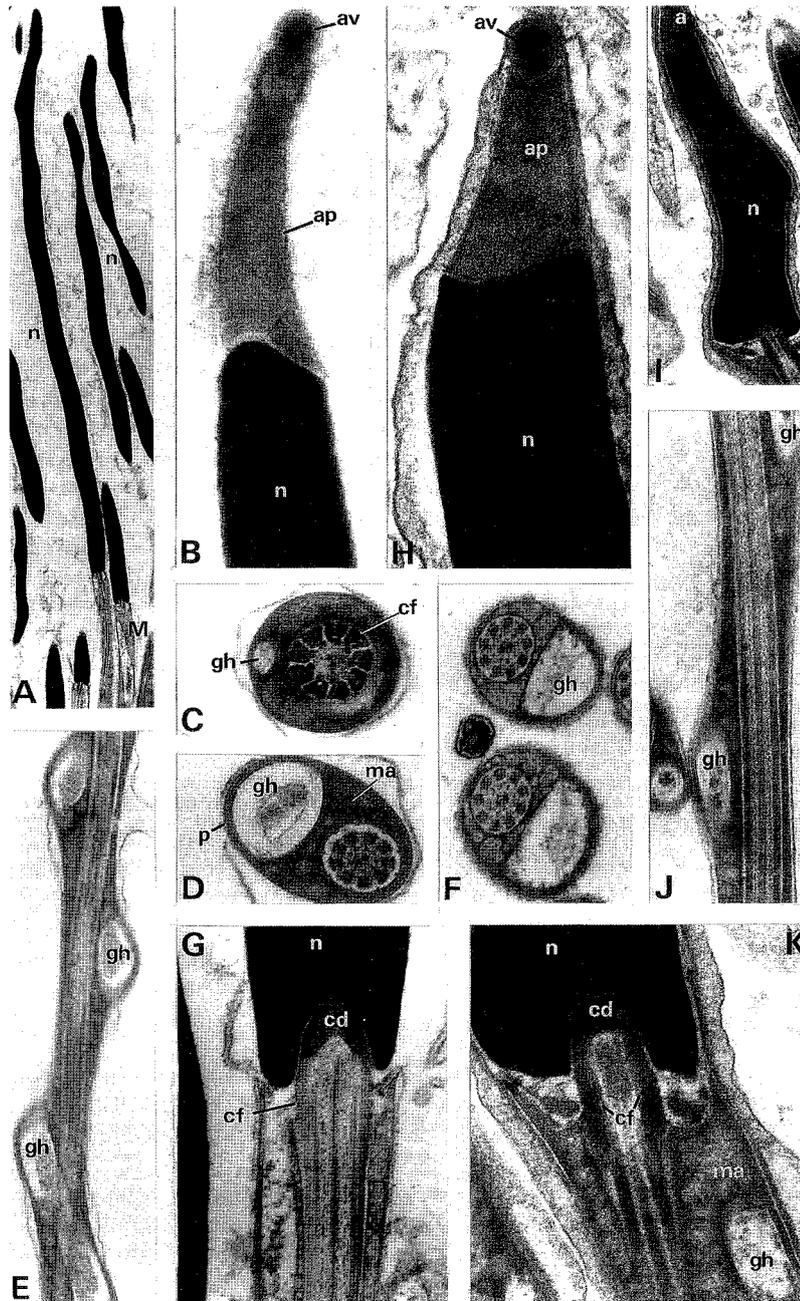


Fig.33. Sperm ultrastructure in the Phyllidiidae (A,B,F,G, *Phyllidiopsis cardinalis*; C,D, *Phyllidiella pustulosa*) in comparison with Dorididae (H-K, *Rostanga arbutus*). A, *Phyllidiopsis*. Longitudinal section through nuclear and midpiece regions. x 7800; B, *Phyllidiopsis*. Longitudinal section of acrosomal complex and nuclear apex. x 80000; C, *Phyllidiella*. Transverse section through proximal portion of midpiece showing coarse fibres of axonemal complex and glycogen helix. x 54000; D, *Phyllidiella*. Transverse section through middle of midpiece. x 64000; E, *Phyllidiella*. Longitudinal section (slightly oblique) of midpiece showing spiralling glycogen helix. x 27000; F, *Phyllidiopsis* Transverse section of middle region of midpiece and (arrow) terminal region of spermatozoon. x 60000; G, *Phyllidiopsis*. Longitudinal section of neck region (nuclear-midpiece junction), showing insertion point for axonemal complex. x 50000; H, *Rostanga*. Longitudinal section of acrosomal complex and nuclear apex of slightly immature spermatozoon. x 80000; I, *Rostanga*. Longitudinal section of acrosomal complex, nucleus and proximal portion of midpiece. x 17600; J, *Rostanga*. Longitudinal section of midpiece. x 34000; K, *Rostanga*. Longitudinal section of neck region (nucleus-midpiece junction). x 60000. Abbreviations: a, acrosomal complex; av, acrosomal pedestal; av, acrosomal vesicle; cd, centriolar derivative; cf, coarse fibres; gh, glycogen helix; M, midpiece; ma, matrix component of mitochondrial derivative; n, nucleus; p, paracrystalline component of mitochondrial derivative. Figure courtesy of Dr J.M. Healy (Zoology Dept, University of Queensland).

differences in details of their foregut anatomy. The Dendrodorididae clearly belong with other doridoids based on numerous characteristic morphological features (e.g., circumanal gill cirlet), but their phylogenetic position is yet to be clarified. Phyllidiids do not share any uniquely derived characters with arminids (see also Healy & Willan, 1991). The phylogeny of phyllidiid genera proposed from the analysis of characters used in this study appears to be a good working hypothesis. Members of the family Phyllidiidae differ considerably from other dorid families and may deserve superfamilial rank discrete from the Doridoidea. Such action is not taken in the present work for two reasons. Firstly, the higher taxonomy of dorids is presently in a state of flux, and the addition of another taxon would not help its resolution. Secondly, such a decision should, appropriately, await an analysis which includes representatives of all anthobranch families.

Biogeography and Ecology

Biogeographic and ecological information is summarised from previously published records, collection data pertaining to specimens examined in the present study, and my own field observations.

Our present knowledge of the ecology and life history of phyllidiid nudibranchs is extremely poor. The lack of ecological information reflects the rarity of such observations. For example, although a considerable amount of field work was undertaken during this study, the feeding, predation, or spawn of phyllidiids were rarely encountered. Nevertheless, it is appropriate to report here some new observations which were made in the course of this research.

Biogeographic Distribution

Phyllidia and *Fryeria* are the most widespread genera in the family, with representatives occurring throughout the tropical Indo-West Pacific Ocean and in the Mediterranean Sea. A few phyllidiids are often found in more temperate regions, their larvae having been carried by currents originating in tropical waters. However, it seems that the majority of phyllidiid species either do not survive such journeys, or are unable to find favourable conditions for metamorphosis in the cooler waters.

The distribution of the six species of *Fryeria* is interesting as each species appears to have a limited geographical range with very little or no overlap with contiguous species. *Fryeria bayi* is endemic to the Mediterranean Sea (Bouchet, 1983). *Fryeria rueppelii* is endemic to the Red Sea (Edmunds, 1972; Brunckhorst *et al.*, 1989). *Fryeria marindica* appears to be restricted to the tropical Indian Ocean. *Fryeria menindie* has only been recorded from the western Pacific. *Fryeria guamensis* has only been found in the Micronesian

region (possibly restricted to the northern-central Pacific), whilst *F. larryi* is known from a single specimen collected near Guam. The restricted range of species of *Fryeria* may reflect a combination of factors including patterns of speciation, ocean currents and availability of their specific food sponges. Factors which influence development and life history strategies of phyllidiid species probably play an important role in determining distribution. However, the developmental biology and life history of phyllidiid species is largely unknown.

The genus *Phyllidiella* is widely represented throughout the tropical Indo-West Pacific Ocean. *Phyllidiella pustulosa* is one of the most common nudibranchs encountered in reef areas. However, *P. pustulosa* appears to be less common in the Indian Ocean where it is sympatric with *P. zeylanica*. *Phyllidiella zeylanica* is relatively common in the Indian Ocean, but is not known from the Red Sea or Pacific Ocean. *Phyllidiella rudmani* is common in the region extending from the Andaman Sea (eastern Indian Ocean) and Timor Sea to Papua New Guinea and the northern Great Barrier Reef (western Pacific Ocean), but is rarely encountered outside this range.

Representatives of the genus *Phyllidiopsis* are found on tropical reefs in the Indian Ocean, Red Sea and the central and western Pacific Ocean. *P. blanca* is known from temperate waters of the Pacific coast of North America (Gosliner & Behrens, 1988). This species possesses a similar anatomy to the "Atlantic *Phyllidiopsis*" which could represent a genus distinct from *Phyllidiopsis* Bergh (Brunckhorst, 1990b). The morphological similarity of *P. blanca* to the Atlantic Ocean species, *P. berghi* Vayssière (personal observation) suggests that these two species constitute a cognate pair, with one recent species occurring on either side of central America. Perhaps the "Atlantic *Phyllidiopsis*" are representatives of the ancestral stock from which *Ceratophyllidia* and *Phyllidiopsis* diverged. Three species of *Ceratophyllidia* are known from a few localities in the tropical Indo-West Pacific Ocean (Gosliner & Behrens, 1988; this study), but further collections are required.

Members of the genus *Reticulidia* are usually found on the sides of coral drop offs (10-30 m depth), in clear, current swept waters. Two species of this genus are known to occur sympatrically in the central and western Pacific Ocean, the South China Sea and the Timor Sea to Christmas Island (Brunckhorst, 1990a; this study). There is no record of *Reticulidia* from the Indian Ocean west of Christmas Island.

The preceding remarks are general in nature because future collections will, undoubtedly, extend the known range of species and should further elucidate biogeographic patterns.

Reproduction and Development

The mating behaviour and spawn mass of *Phyllidia flava* (as *P. pulitzeri*) has been described previously

(Barletta, 1974a; Macri, 1986). Reproduction and development is known for only one species, *P. varicosa*, through the research of Soliman (1986, 1987). He described the egg coil of *P. varicosa* as 30 mm in diameter, creamish white and laid flat (i.e., not on its edge). Soliman (1986) followed the development of the larvae describing a number of embryonic stages and the newly hatched veliger. The transparent veliger possessed a laterally compressed larval shell of type B, similar to that of other dorids.

During field work on the Great Barrier Reef, Papua New Guinea and Thailand, I kept specimens of various phyllidiid species isolated in aquaria for periods of up to 16 days. However, whilst copulation was sometimes observed, no spawn was laid. I have observed, *in situ*, complete oviposition by three individuals belonging to two species. *Phyllidiella pustulosa* was observed laying spawn on coral rubble in the southern Great Barrier Reef (32 mm specimen, 9-12 m depth, "Tenements 3", Heron Island Reef, June 27, 1989) and in Papua New Guinea (36 mm specimen, 15 m depth, patch reef off Lion Island, June 18, 1988). In southern Thailand, *Phyllidiella zeylanica* was observed ovipositing on its sponge food (40 mm specimen, 8 m depth, western side of Phi Phi Don Island, 25 Nov. 1989). The spawn of *P. zeylanica* is illustrated in Plate 6G. All three spawn spirals were approximately 25-30 mm in diameter, the actual egg strand approximately 3 mm in breadth, laid flat and slightly rounded dorsally. The ova were tightly coiled and cream to white in colour as viewed underwater. A colour slide (courtesy C. Carlson, *in litt.*, 1988) of the spawn of *Phyllidia carlsonhoffi* (23 mm specimen, 8 m depth, Bile Bay, Guam, 21 June 1987)

laid in an aquarium is similar to those described above and was also creamish white in colour.

The colour of the spawn of these five species does not allow the species to be discerned. Considerable additional research into the developmental biology of phyllidiids is required and further field and laboratory observations would be useful. In addition, the role of chemical ecology in the life history of these nudibranchs is worthy of an increased research effort. Chemical cues may be important for specific identification between mating individuals and it is possible that the chemical defence compounds of adult individuals are also deposited with their spawn (see Karuso, 1987).

Food and Feeding

In situ observations of phyllidiid species actually feeding seem to be rare also. The sponge food of some phyllidiid species is reported for the first time (summarised in Table 5). This report is based on observations of a number of individuals of each species at various localities.

The functional significance of the foregut has received little attention although phyllidiids are generally considered to be suctorial sponge feeders. I have recently proposed a possible *modus operandi* for the *Reticulidia* type of foregut (Brunckhorst, 1990a). The extremely broad pharyngeal bulb of *Reticulidia*, with its radially arranged glandular discs, the large muscular pharynx which exits dorsally, the short retractor muscles, and short pharynx and oesophagus indicate that the

Table 5. Food sponges of phyllidiid nudibranchs. Sponge identification courtesy Dr J. Hooper (NTM).

Phyllidiid species	Sponge colour	Sponge identification	Specimen
<i>Phyllidia varicosa</i>	off white-pale grey	<i>Halichondria</i> sp.1 (Halichondrida: Halichondriidae)	NTM Z3575
<i>Phyllidia ocellata</i>	dark orange-red; tubular	<i>Higginsia massalis</i> Carter, 1889 (Axinellida: Desmoxyidae)	NTM Z3576
<i>Phyllidia babai</i>	yellow-orange	<i>Acanthella stipata</i> Carter, 1881 (Axinellida: Axinellidae)	NTM Z3578
<i>Phyllidiella pustulosa</i>	dark pink to reddish brown	<i>Halichondria</i> sp.2 (Halichondrida: Halichondriidae)	NTM Z3573
<i>Phyllidiella pustulosa</i>	outside deep maroon inside creamish	<i>Halichondria</i> sp.3 (Halichondrida: Halichondriidae)	NTM Z3574, NTM Z3577
<i>Phyllidiella zeylanica</i>	yellowish brown	<i>Smenospongia</i> sp. (Dictyoceratida: Thorectidae)	NTM Z3584
<i>Phyllidiella granulatus</i>	orange	<i>Phakellia cavernosa</i> Dendy, 1922 (Axinellida: Axinellidae)	NTM Z3570, AM C154744
<i>Phyllidiella rudmani</i>	orange	<i>Phakellia</i> sp. (Axinellida: Axinellidae)	NTM Z3572
<i>Phyllidiopsis striata</i>	olive green, encrusting	no specimen	-
<i>Phyllidiopsis phippiensis</i>	white, semi-transparent	<i>Gellius</i> sp. (Haplosclerida: Haliconidae)	NTM Z3585
<i>Phyllidiopsis burni</i>	orange	<i>Phakellia cavernosa</i> Dendy, 1922 (Axinellida: Axinellidae)	NTM Z3571
<i>Reticulidia halgerda</i>	orange, encrusting	<i>Aplysina</i> sp. (Verongida: Aplysinidae)	-

pharyngeal bulb is not eversible. I suggest (Brunckhorst, 1990a) that this arrangement operates as a sieve-plate or coarse filter; glandular secretions being expelled through the mouth by action of the short, muscular pharynx which would then relax producing a vacuum to take up the products of external digestion.

Each of the remaining genera possess a relatively elongate pharynx and oesophagus and long retractor muscles which suggest that the foregut is everted for feeding. Field observations of species of *Phyllidia*, *Phyllidiella* and *Phyllidiopsis* confirm that eversion of the foregut does take place. I have not observed feeding of individuals belonging to *Ceratophyllidia* or *Fryeria*.

The anatomy of *Ceratophyllidia* appears to be primitive as it has retained the salivary/ptyaline type glands, and these may secrete predigestive fluids initially when the pharynx is everted. The very long pharynx and oesophagus suggest that the pharynx could be extended beyond the mouth. The glandular segment of the oesophagus is situated far posteriorly, therefore it is unlikely that it secretes digestive fluid externally. I suggest that the main, predigestive function is performed by the glandular oesophageal segment before food products pass to the stomach within the digestive gland mass (Fig.17).

Phyllidiopsis everts the pharyngeal bulb and most of the tubular pharynx when feeding (*P. striata*, personal observation). The posterior oesophageal retractor muscle is required (in addition to the pharyngeal retractor muscles) to retract the long foregut after feeding is completed. The minute oral glands which envelope the pharyngeal bulb (Brunckhorst, 1990b; Fig.10C) secrete directly onto the sponge food when the foregut is everted inside-out. Histological examination of these glands (alcian blue-kernechtrot stain) indicate the presence of weakly acidic, sulphated mucosubstances. The posterior, muscular, oesophageal segment probably acts as a pump to assist, both in taking up the products of external digestion, and in transporting them down the long foregut to the stomach within the digestive gland mass. Some species of *Phyllidiopsis* have secondarily lost a distinct, separate stomach region.

On several occasions I have observed individuals of *Phyllidiella* feeding *in situ*, with their large pharyngeal bulb and broad, tubular pharynx everted (see Fig.12). *P. pustulosa* and *P. zeylanica* have been observed with the pharynx embedded in sponge to a depth of half to three quarters of the body length of the individual. The leaf-like oral glands possibly secrete other, unidentified, digestive fluids in addition to traces of weakly acidic, sulphated mucosubstances which were identified here.

Members of *Phyllidia* evert the pharyngeal bulb, with its internal, partly protuberant oral glands, over the top of the sponge food rather than into it (personal observation), and I liken it to the everted cardiac stomach of an asteroid. Histological sections of the pharyngeal bulb of *Phyllidia* species indicated the presence of both strongly acidic and weakly acidic, sulphated mucosubstances (alcian blue-kernechtrot stain; Pl.1A). It

is most likely that the primary function of these acidic secretions is for external digestion, probably including the breakdown of calcareous sponge spicules. I did not find calcareous spicules in the faeces of *Phyllidia* specimens. The very muscular pharyngeal bulb of *Phyllidia* and *Fryeria* species probably produces the suction necessary to take up the products of predigestion.

Summary and Conclusions

A review of the taxonomic literature identified considerable confusion in the family Phyllidiidae. Previously, generic features and the placement of species in genera have been uncertain. These problems have been referred to recently by Wägele (1985), Gosliner & Behrens (1988), Brunckhorst (1989b, 1990a,b), Brunckhorst & Willan (1989) and Brunckhorst *et al.* (1989).

I consider that quite marked differences separate the genera. The form of the alimentary system, its associated glands and muscles differ in each of the six genera (Brunckhorst, 1990b, present work). Table 6 summarises the principle features which separate the genera of Phyllidiidae (see also key to genera).

A total of 49, valid, Indo-West Pacific species are recognised and these are placed in six genera. Twenty two new species are described and named in the present work. *Phyllidia* Cuvier remains the largest genus with 15 species while *Fryeria* Gray is considered to have six species. *Phyllidiella* Bergh with nine species is reinstated. *Phyllidiopsis* Bergh, the second largest genus, contains 14 Indo-West Pacific species. An additional four species, known from the Atlantic Ocean, and one species from the Pacific coast of North America, are presently placed in *Phyllidiopsis*. However, further anatomical study may confirm their generic status as distinct from *Phyllidiopsis* Bergh of the tropical Indo-West Pacific (Brunckhorst, 1990b). *Ceratophyllidia* Eliot appears to contain three species, however very few specimens of this rare genus have been collected and further work remains to be done. I concur with Gosliner who recently rediscovered and validated *Ceratophyllidia* (Gosliner, 1987; Gosliner & Behrens, 1988). The recently described genus, *Reticulidia* Brunckhorst contains two species. Table 7 provides a summary list of valid phyllidiid species and the principle synonyms recognised in this work.

The proposed phylogeny is intuitively plausible as it reflects morphological and functional character states of each genus. *Ceratophyllidia* appears to be the sister group to the remaining genera. *Phyllidia*, *Fryeria* and *Reticulidia* are the "most derived" genera. However, the status and phylogenetic position of Atlantic species presently placed in the genus *Phyllidiopsis* requires reassessment. The general morphology of phyllidiids indicates monophyly with dorids and studies of nudibranch spermatozoa support this view (Healy &

Willan, 1991). However, the grouping of the Phyllidiidae and Dendrodoridae as "Porostomata" is rejected as homeoplaseous. Details of the anatomy, particularly the foregut and associated musculature, are quite different in both groups. In fact, *Dendrodoris* has many more synapomorphies with dorids than does *Phyllidia*. Further research into all doridoid families is required to assess their affinities.

Biogeographical data derived from specimens examined this study and previous work are previously discussed. Although further collecting is required, some

interesting patterns are evident. Of particular interest, is the apparent allopatry of the six *Fryeria* species. Ecological observations arising from field studies are also reported. The food sponges of ten species are identified and reported for the first time. There is still very little known about the reproduction and development in phyllidiid species.

In conclusion, the internal and external characters elucidated here should enable unambiguous generic placement in the future. Colouration and patterning of live animals remain important characters for the

Table 6. External and internal features of phyllidiid genera.

Character	<i>Phyllidia</i>	<i>Fryeria</i>	<i>Phyllidiella</i>	<i>Phyllidiopsis</i>	<i>Ceratophyllidia</i>	<i>Reticulidia</i>
EXTERNAL						
Oral tentacles	separate	separate	separate	fused	partially fused	separate
Rhinophore colouration	cream to yellow	cream to yellow	black	various colours; bi- or multi-coloured	white to cream	orange
Rhinotubercles	present	present	absent	absent	absent	absent
Notal ornamentation	tuberculate (may form ridges)	tuberculate	tuberculate (may form ridges)	tuberculate (may form ridges)	stalked papillae (no tubercles)	smooth ridges (no tubercles)
INTERNAL						
Pharyngeal bulb (PB)	large, ovate	small, broad	very large	very elongate	conical	large, broadly rounded
Oral glands	internal, folded; protuberant nodules	internal, folded; protuberant nodules	external; numerous, leaf shaped	external; minute, enveloping PB	external; two large salivary glands	internal glandular discs
Pharynx length	long	short	long (broad)	very long	long	short
Oesophagus length	short	moderate	moderate	very short	long	short
Oesophageal segment	absent	absent	absent	very muscular	glandular	absent
Oesophageal retractor muscle	absent	absent	absent	present	absent	absent
Buccal ganglia close to CNS	yes	yes	yes	no	no	yes
Intestinal path	dorsal	ventral	dorsal	dorsal	dorsal	dorsal
Anal position	dorsal	ventral	dorsal	dorsal	dorsal	dorsal
Anus protrusible	no	yes	no	no	no	no
Nidamental gland mass	large, spherical	small	ovate	elongate - ovate	flattened oval	small ovate
Penis	large, bulbous	short, narrow	short, narrow	elongate	short, narrow	elongate
Bursa copulatrix stalked	no	no, or very short	no	no	yes (long)	no

recognition of species. However, for taxonomic work, it is desirable to study an ontogenetic series to gain an understanding of intraspecific variation. Nevertheless, I must emphasize that a combination of morphological and anatomical characters should be used for the

description of phyllidiid species. Systematic work must include confirmation of generic and specific identity through anatomical examination. In the future, descriptions of phyllidiid species based only on external features should be deemed unacceptable.

Table 7. Summary list of valid species and main synonymy.

Phyllidia Cuvier, 1797

- Phyllidia varicosa* Lamarck, 1801
 - = *Phyllidia trilineata* Cuvier, 1804
 - = *Phyllidia borbonica* Cuvier, 1804 (n.syn.)
 - = *Phyllidia quinquelineata* Blainville, 1816 (n.syn.)
 - = *Phyllidia arabica* Ehrenbergh, 1831
 - = *Phyllidia fasciolata* Bergh, 1869 (n.syn.)
 - = *Phyllidia varicosa* var. *quadri-lineata* Bergh, 1905 (n.syn.)
 - = *Phyllidia honloni* Risbec, 1956 (n.syn.)
- Phyllidia tula* Er. Marcus & Ev. Marcus, 1970
- Phyllidia coelestis* Bergh, 1905
 - = *Phyllidia picta*, Pruvot-Fol, 1957 (n.syn.)
 - = *Phyllidia alia* Yonow, 1984
- Phyllidia elegans* Bergh, 1969
 - = *Phyllidia multifaria* Yonow, 1986 (n.syn.)
- Phyllidia flava* Aradas, 1847
 - = *Phyllidia papillosa* Aradas, 1847
 - = *Phyllidia rolandiae* Pruvot-Fol, 1951
 - = *Phyllidia aurata* Pruvot-Fol, 1962
 - = *Phyllidia pulitzeri* Pruvot-Fol, 1962
- Phyllidia ocellata* Cuvier, 1804
 - = *Phyllidiopsis carinata* Eliot, 1910
 - = *Phyllidia multituberculata* Boettger, 1918
 - = *Phyllidia tuberculata* Baba, 1930 (non Risbec)
 - = *Phyllidia japonica* Baba, 1937
 - = *Phyllidia baccata* Pruvot-Fol, 1957 (n.syn.)
 - = *Phyllidia ocellata undula* Yonow, 1986 (n.syn.)
- Phyllidia zebrina* Baba, 1976
- Phyllidia exquisita* n.sp.
- Phyllidia carlsonhoffi* n.sp.
- Phyllidia madangensis* n.sp.
- Phyllidia willani* n.sp.
- Phyllidia babai* n.sp.
- Phyllidia goslineri* n.sp.
- Phyllidia polkadotsa* n.sp.
- Phyllidia scottjohnsoni* n.sp.

Fryeria Gray, 1853

- Fryeria rueppelii* Bergh, 1869
 - = *Fryeria pustulosa* Gray, 1853 (Brunckhorst *et al.*, 1989; Opinion 1663)
 - = *Fryeria rüppelii* Bergh, 1869
 - = *Reyfriedia rüppelii* (Bergh) Yonow, 1986
- Fryeria bayi* Bouchet, 1983
- Fryeria marindica* (Yonow & Hayward, 1991)
- Fryeria guamensis* Brunckhorst, n.sp.
- Fryeria larryi* Brunckhorst, n.sp.
- Fryeria menindie* Brunckhorst, n.sp.

Phyllidiella Bergh, 1869

- Phyllidiella pustulosa* (Cuvier, 1804)
 - = *Phyllidia verrucosa* Hasselt, 1824 (n.syn.)
 - = *Phyllidia albonigra* Quoy & Gaimard, 1832 (n.syn.)
 - = *Phyllidiella nobilis* Bergh, 1869 (n.syn.)
 - = *Phyllidia spectabilis* Collingwood, 1881
 - = *Fryeria variabilis* Collingwood, 1881 (n.syn.)

- = *Phyllidia rotunda* Eliot, 1904 (n.syn.)
- = *Phyllidia varians* Pruvot-Fol, 1956 (n.syn.)
- = *Phyllidia melanocera* Yonow, 1986
- Phyllidiella annulata* (Gray, 1853)
 - = *Phyllidia meandrina* Pruvot-Fol, 1957 (n.syn.)
 - = *Phyllidia sudanensis* Heller & Thompson, 1983 (n.syn.)
- Phyllidiella nigra* (Hasselt, 1824) (non Pease)
 - = *Phyllidia serenei* Risbec, 1956 (n.syn.)
 - = *Phyllidia bataviae* Pruvot-Fol, 1957 (n.syn.)
- Phyllidiella rosans* (Bergh, 1873)
 - = *Phyllidia nigra* Pease, 1868 (non Hasselt)
 - = *Phyllidia bourgini* Risbec, 1928 (n.syn.)
 - = *Phyllidia soria* Er. Marcus & Ev. Marcus, 1970 (n.syn.)
 - = *Phyllidia mediocris* Yonow & Hayward, 1991 (n.syn.)
- Phyllidiella zeylanica* (Kelaart, 1859)
 - = *Phyllidia zeylanicus* Kelaart, 1883 (mis-spelling)
 - = *Phyllidia ceylanica* Bergh, 1869 (mis-spelling)
 - = *Phyllidia catena* Pruvot-Fol, 1956 (n.syn.)
 - = *Phyllidia seriata* Pruvot-Fol, 1956 (n.syn.)
 - = *Phyllidia empelia* Yonow, 1984 (n.syn.)
 - = *Phyllidia* sp.1 Gosliner, 1987
- Phyllidiella cooraburrana* n.sp.
- Phyllidiella granulatus* n.sp.
- Phyllidiella lizae* n.sp.
- Phyllidiella rudmani* n.sp.

Phyllidiopsis Bergh, 1875

- Phyllidiopsis cardinalis* Bergh, 1875
 - = *Phyllidia tuberculata* Risbec, 1928 (n.syn.)
- Phyllidiopsis dautzenbergi* (Vayssière, 1912)
 - = *Phyllidia monacha* Yonow, 1986 (n.syn.)
- Phyllidiopsis gemmata* Pruvot-Fol, 1957
- Phyllidiopsis krempfi* Pruvot-Fol, 1957
- Phyllidiopsis shireenae* Brunckhorst, 1990
- Phyllidiopsis sinaiensis* (Yonow, 1988)
- Phyllidiopsis loricata* (Bergh, 1873)
- Phyllidiopsis striata* Bergh, 1889
 - = *Phyllidia xishaensis* Lin, 1983 (n.syn.)
- Phyllidiopsis phippiensis* n.sp.
- Phyllidiopsis annae* n.sp.
- Phyllidiopsis sphingis* n.sp.
- Phyllidiopsis pipeki* n.sp.
- Phyllidiopsis burni* n.sp.
- Phyllidiopsis fissuratus* n.sp.

Ceratophyllidia Eliot, 1903

- Ceratophyllidia africana* Eliot, 1903
 - = *Ceratophyllidia grisea* Eliot, 1910
- Ceratophyllidia* sp.1
- Ceratophyllidia* sp.2

Reticulidia Brunckhorst, 1990

- Reticulidia halgerda* Brunckhorst & Burn, 1990 (in Brunckhorst, 1990a)
- Reticulidia fungia* Brunckhorst & Gosliner n.sp.

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PLATES

PLATE 1

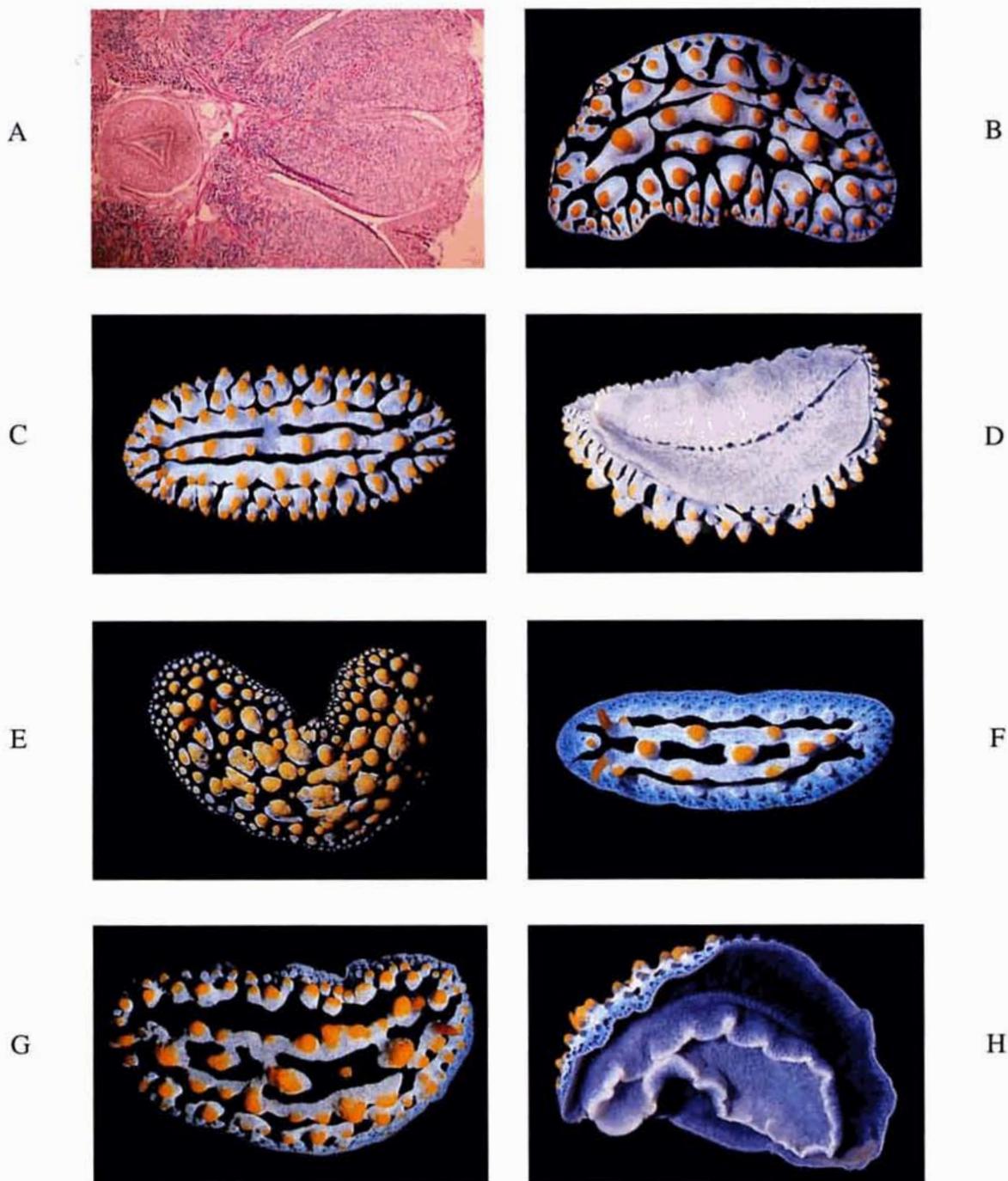


Plate 1. A, *Phyllidia varicosa*. Transverse section through pharyngeal bulb with pharynx partially everted, x 80; B, *Phyllidia varicosa*. Dorsal view of 104 mm specimen, 22 m depth, "Sponge mound", Apra Harbour, Guam, 5 July 1988; C,D, *Phyllidia varicosa*. Dorsal and ventral views respectively of 58 mm specimen, 4-10 m depth, Phi Phi Island, southern Thailand, 25 Nov. 1989; E, *Phyllidia tula*. Dorsal view of 52 mm specimen, 14 m depth, Bile Bay, Guam, 29 June 1988; F, *Phyllidia coelestis*. Dorsal view of 20 mm specimen, 18-24 m depth, Horseshoe Reef, 23 km south-east of Port Moresby, PNG, 21 June 1988; G, *Phyllidia coelestis*. Dorsal view of 39 mm specimen; 8 m depth, Loloata Island, 15 km south-east of Port Moresby, PNG, 23 June 1988; H, *Phyllidia coelestis*. Ventral view of 55 mm specimen, 1 m depth, Phi Phi Island, southern Thailand, 24 Nov. 1989.

PLATE 2

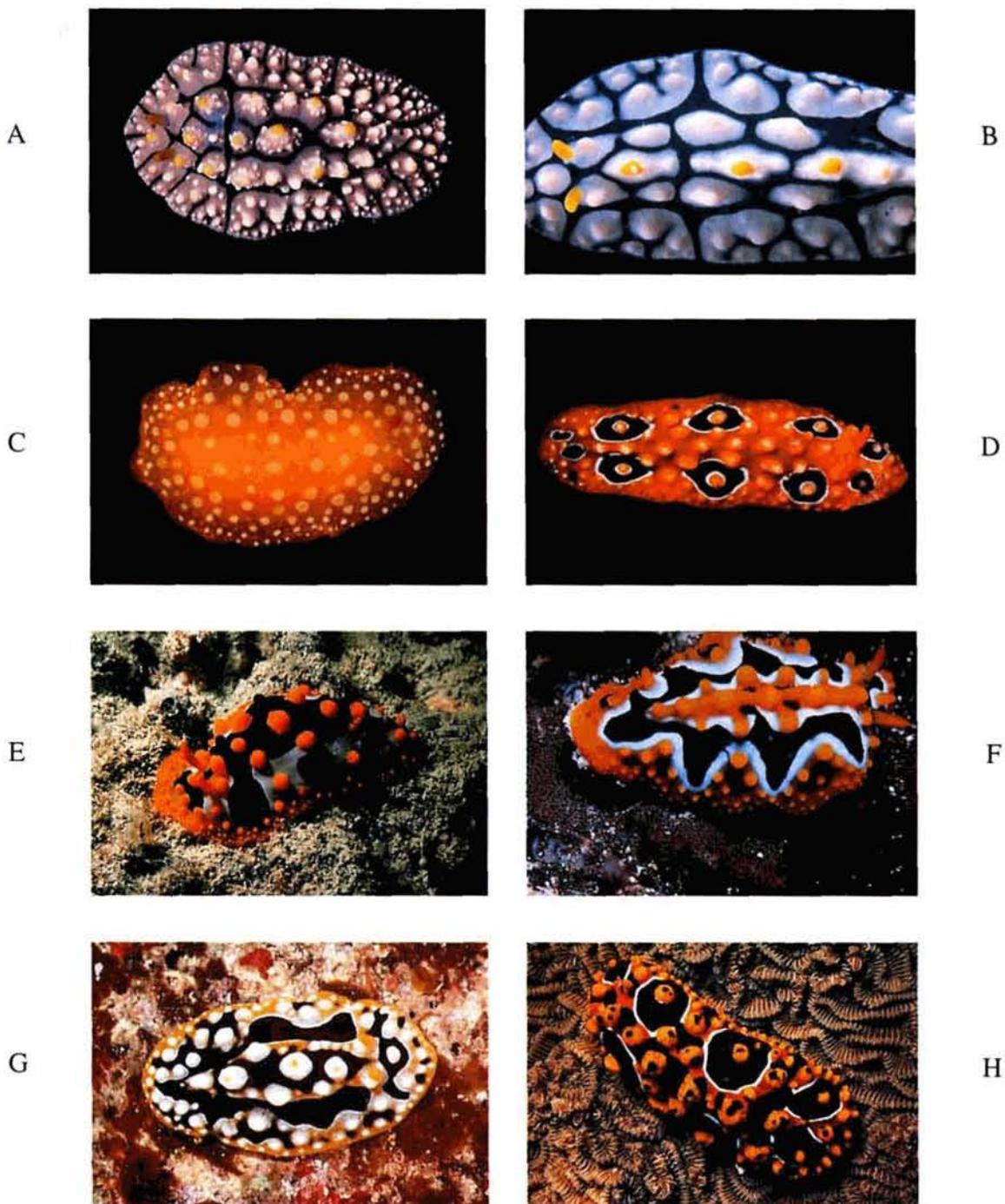


Plate 2. A, *Phyllidia elegans*. Dorsal view of 35 mm specimen, 18 m depth, Phi Phi Island, southern Thailand, 2 Dec. 1989; B, *Phyllidia elegans*. Dorsal view of *P. multifaria* Yonow, 30 mm specimen, 9 m depth, Whiskey Reef, Red Sea, 14 Jan. 1983. Photo: N. Yonow; C, *Phyllidia flava*. Dorsal view of 20 mm specimen, 6 m depth, Zaffiro Cave, Sorrentine Peninsula, Italy, May 1979. Photo: R. Cattaneo-Viatti; D, *Phyllidia ocellata*. Dorsal view of "typical" specimen, 28 mm, 22 m depth, Flat Rock, north-east of North Stradbroke Island, southern Qld, 7 Apr. 1981. Photo: R.C. Willan; E, *Phyllidia ocellata*. Dorsal view of 39 mm specimen, collected subtidally, Lucas Island, northern WA, 24 July 1988. Photo: C. Bryce; F, *Phyllidia ocellata*. Dorsal view of *P. ocellata undula* Yonow, holotype, 18 mm, 20 m depth, Tongue Island, Red Sea, 19 Apr. 1983. Photo: N. Yonow; G, *Phyllidia ocellata*. Dorsal view of 30 mm specimen, 7-8 m depth, Madang Lighthouse, PNG, 22 Jan. 1988. Photo: R.C. Willan; H, *Phyllidia ocellata*. Dorsal view of 60 mm specimen, 23 m depth, Isle of Pines, New Caledonia, Sept. 1988. Photo: P. Chapman-Smith.

PLATE 3

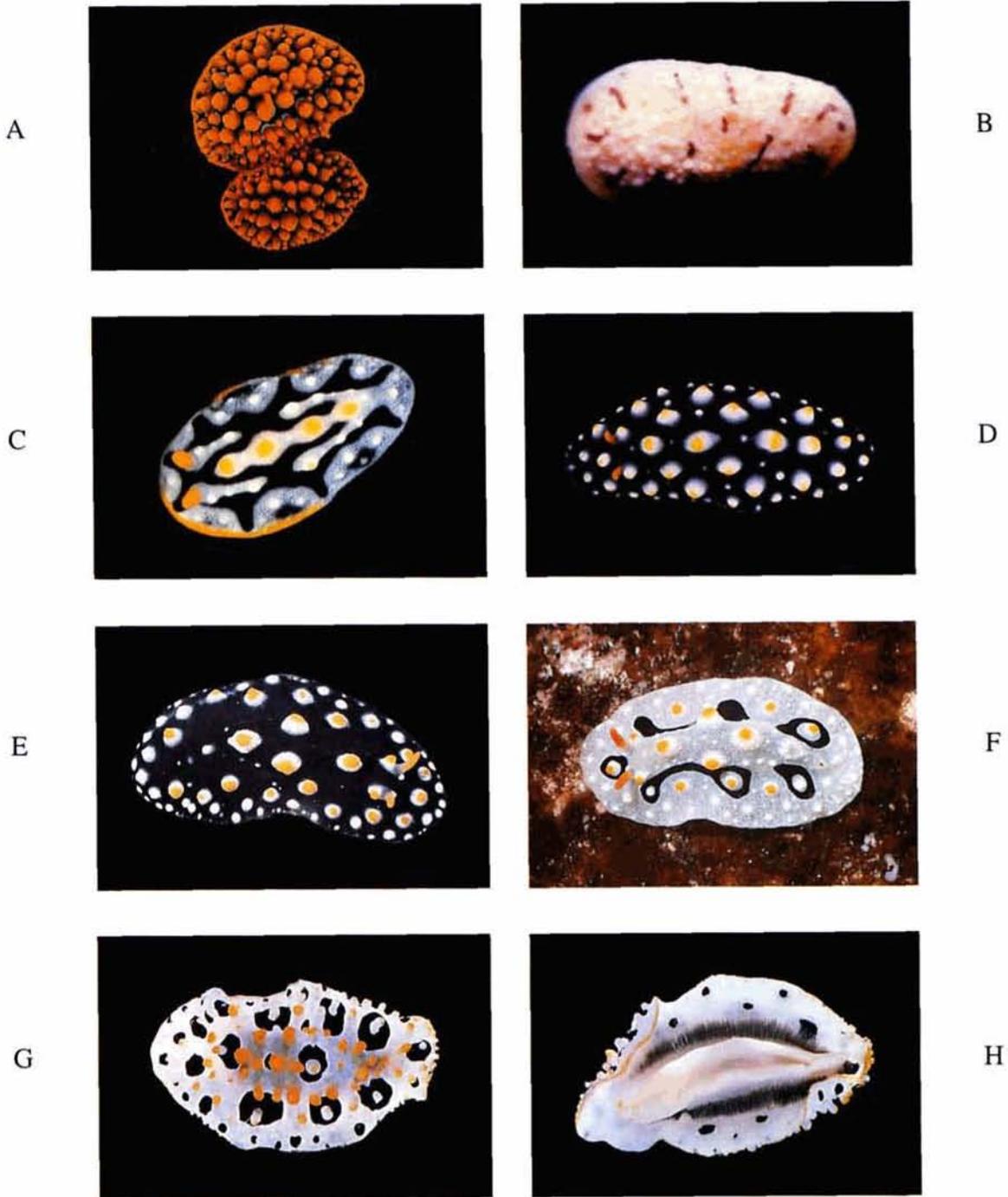


Plate 3. A, *Phyllidia ocellata*. Dorsal view of copulating pair; 36 mm (with white rings) and 33 mm (no white), 16 m depth, Phi Phi Island, southern Thailand, 5 Dec. 1989; B, *Phyllidia zebrina*. Preserved holotype, 14 mm, 60 m depth, Amadaiba, Sagami Bay, Japan. Photo: K. Baba; C, *Phyllidia exquisita* n.sp. Dorsal view of 11 mm specimen, 3 m depth, Lion Island, PNG, 18 Apr. 1984. Photo: C. Carlson & P. Hoff; D, *Phyllidia carlsonhoffi* n.sp. Dorsal view of 43 mm specimen, 14 m depth, Ponape, 21 Aug. 1985. Photo: C. Carlson & P. Hoff; E, *Phyllidia madangensis* n.sp. Dorsal view of 43 mm specimen, 18 m depth, Madang, PNG, 18 Feb. 1988. Photo: R.C. Willan; F, *Phyllidia willani* n.sp. Dorsal view of 36 mm specimen (note granular appearance), 11 m depth, Anemone Reef, Madang, PNG, 10 Jan. 1988. Photo: R.C. Willan; G,H, *Phyllidia babai* n.sp. Dorsal and ventral views respectively of 43 mm specimen, 18 m depth, North Point Reef, Lizard Island, GBR, 20 Nov. 1981. Photo: W.B. Rudman.

PLATE 4

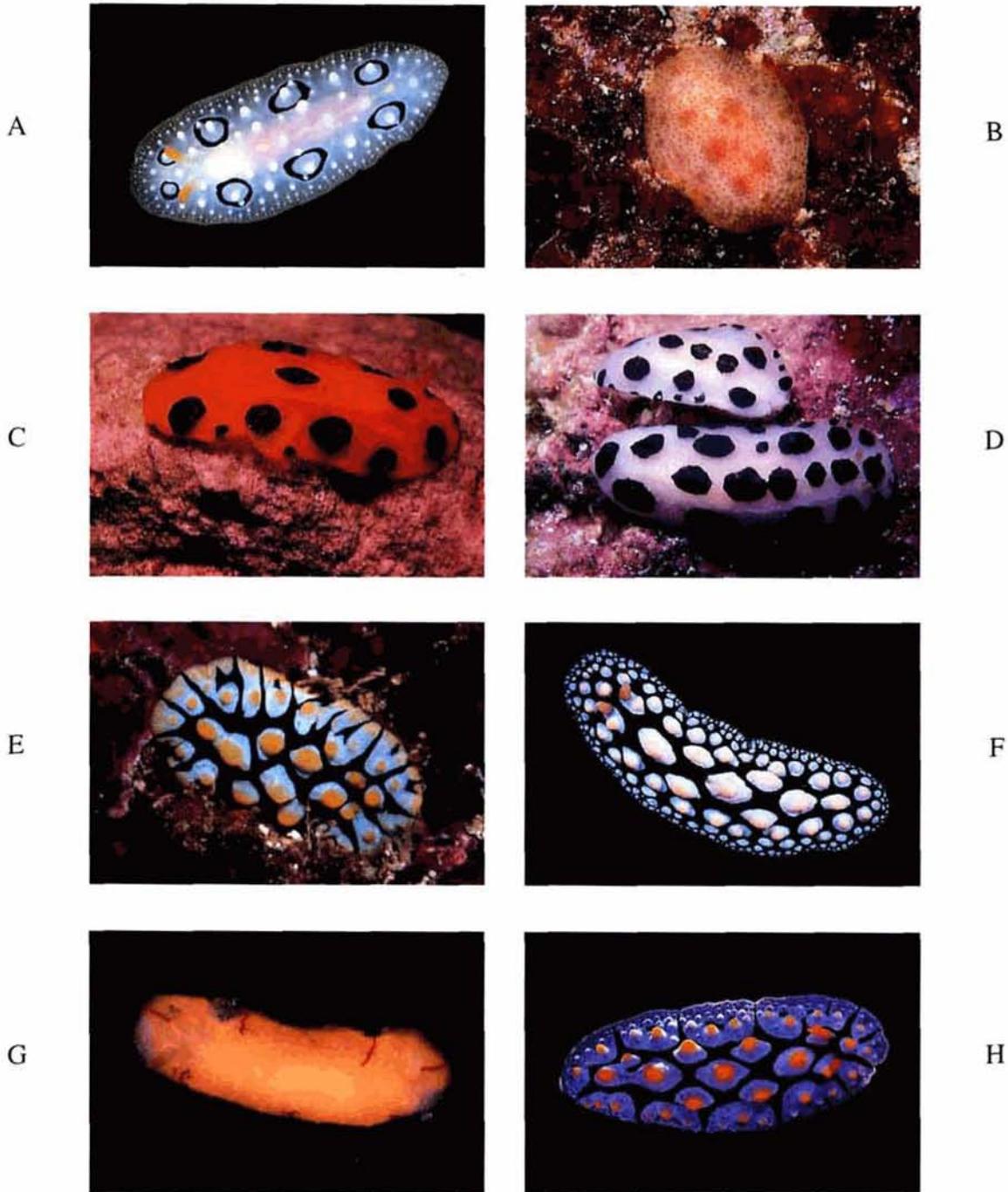


Plate 4. A, *Phyllidia babai* n.sp. Dorsal view of 27 mm specimen, 12 m depth, sunken barrier reef, south-east of Port Moresby, PNG 20 Apr. 1984. Photo: C. Carlson & P. Hoff; B, *Phyllidia goslineri* n.sp. Dorsal view of 14 mm specimen, 12-20 m depth, Planet Rock, Madang, PNG, 19 Jan. 1988. Photo: R.C. Willan; C, *Phyllidia polkadotsa* n.sp. Dorsal view of 13 mm specimen, 8 m depth, Makua, Oahu, Hawaii, 8 Feb. 1985. Photo: S. Johnson; D, *Phyllidia scottjohnsoni* n.sp. Dorsal view of 19 mm and 26 mm specimens, 8 m depth, Kure Atoll, Hawaii, Aug. 1985. Photo: S. Johnson; E, *Fryeria rueppelii*. Dorsal view of about 25 mm specimen, collected subtidally, Red Sea, 1983. Photo: N. Yonow; F, *Fryeria guamensis* n.sp. Dorsal view of 32 mm specimen, 3 m depth, Sella Bay, Guam, 29 July 1970. Photo: C. Carlson & P. Hoff; G, *Fryeria larryi* n.sp. Dorsal view of holotype (6 mm), 8 m depth, Bile Bay, Guam, 22 Sept. 1973. Photo: C. Carlson & P. Hoff; H, *Fryeria menindie* n.sp. Dorsal view of holotype (33 mm), 10 m depth, Pelorus Island, Palu Island Group, North Qld, 8 Nov. 1983. Photo: W.B. Rudman.

PLATE 5



Plate 5. A, *Fryeria menindie* n.sp. Dorsal view of 14 mm specimen, 10 m depth, patch reef off Lion Island, PNG, 17 June 1988; B, *Fryeria marindica* (Yonow & Hayward). Dorsal view of 26 mm specimen, 16 m depth, Phi Phi Island, southern Thailand, 27 Nov. 1989; C, *Fryeria marindica* (Yonow & Hayward). Dorsal view of 25 mm specimen, 9 m depth, Phi Phi Island, southern Thailand, 27 Nov. 1989; D, *Fryeria bayi*. Dorsolateral view of 8 mm specimen, 38 m depth, Punta Bianco, Corse, Mediterranean Sea, Aug. 1981. Photo: C. Huygens; E, *Phyllidiella pustulosa*. Dorsal view of 15-43 mm specimens, 15 m depth, Pelorus Island, Palu Island Group, North Qld., 8 Nov. 1983, AM C140056. Photo: W.B. Rudman; F, *Phyllidiella pustulosa*. Dorsal view of 65 and 56 mm specimens, 22 m depth, "Sponge mound", Apra Harbour, Guam, 5 July 1988; G, *Phyllidiella annulata*. Dorsal view of 31 mm specimen, 9 m depth, Asan Bay, Guam, 9 July 1988; H, *Phyllidiella annulata*. Dorsal view of 28 mm specimen, 3 m depth, Bile Bay, Guam, 28 June 1988.

PLATE 6

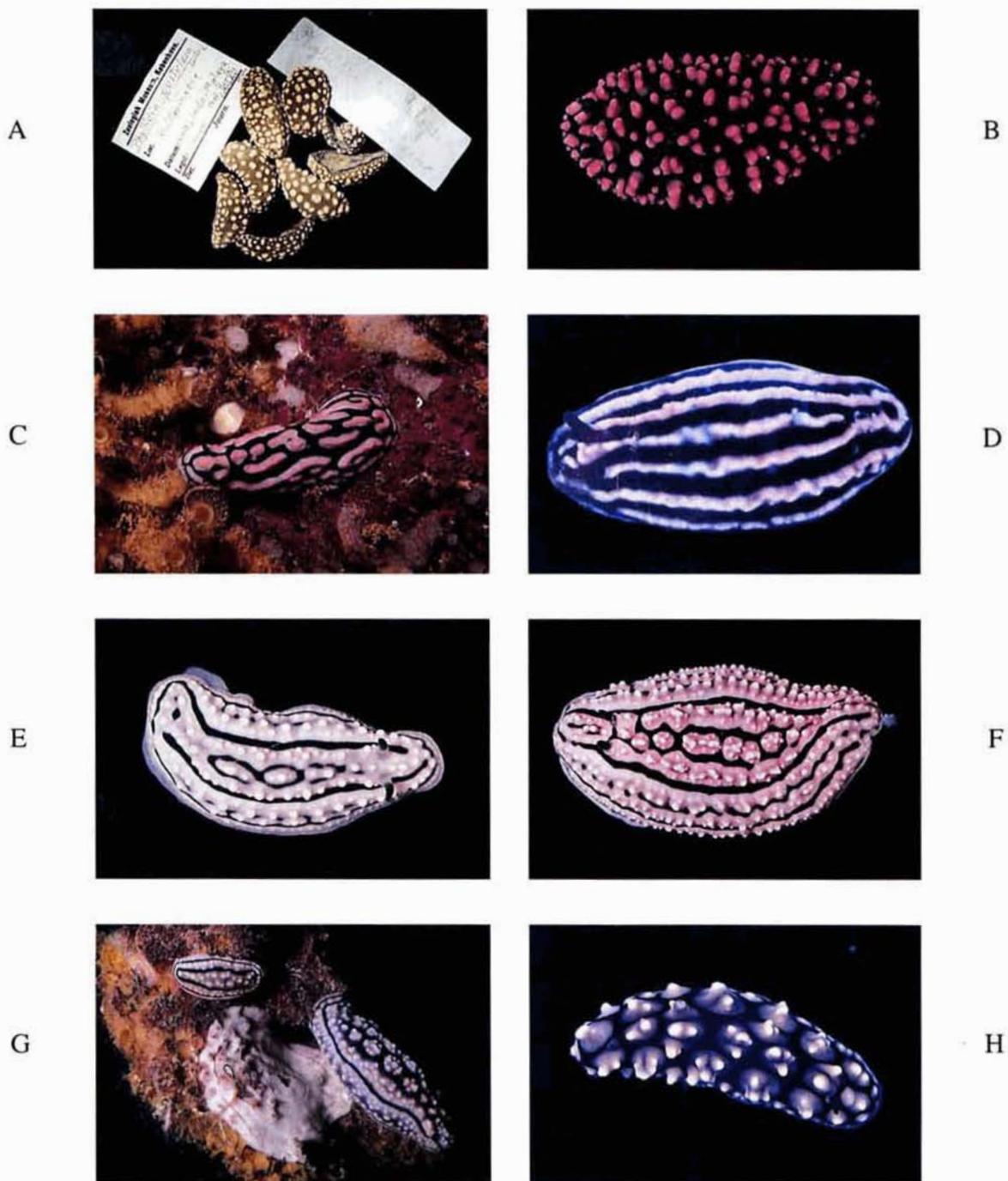


Plate 6. A, *Phyllidiella nigra*. Specimens examined by Bergh (1869) which he misidentified (as *P. pustulosa*), conserved in ZMUC; B, *Phyllidiella nigra*. Dorsal view of 40 mm specimen, intertidal reef flat, Phi Phi Island, southern Thailand, 29 Nov. 1989; C, *Phyllidiella rosans*. Dorsal view of 18 mm specimen (with smooth, broken ridges), 12 m depth, Pupukea, Oahu, Hawaii, 29 June 1983. Photo: S. Johnson; D, *Phyllidiella rosans*. Dorsal view of 35 mm specimen, 1-20 m depth, Réunion, Indian Ocean, 1989. Photo: M. Jay; E, *Phyllidiella zeylanica*. Dorsal view of 24 mm specimen, 4-10 m depth, Phi Phi Island, southern Thailand, 25 Nov. 1989; F, *Phyllidiella zeylanica*. Dorsal view of 45 mm specimen, 1 m depth, Phi Phi Island, southern Thailand, 24 Nov. 1989; G, *Phyllidiella zeylanica*. Dorsal view of 15 and 40 mm specimens with egg mass of latter, on food sponge, *Smenospongia* sp., 8 m depth, Phi Phi Island, southern Thailand, 25 Nov. 1989; H, *Phyllidiella cooraburrana* n.sp. Dorsal view of 38 mm specimen, 5 m depth, Bare Islet, Cape Ferguson, Townsville, north Qld, 8 Aug. 1986.

PLATE 7

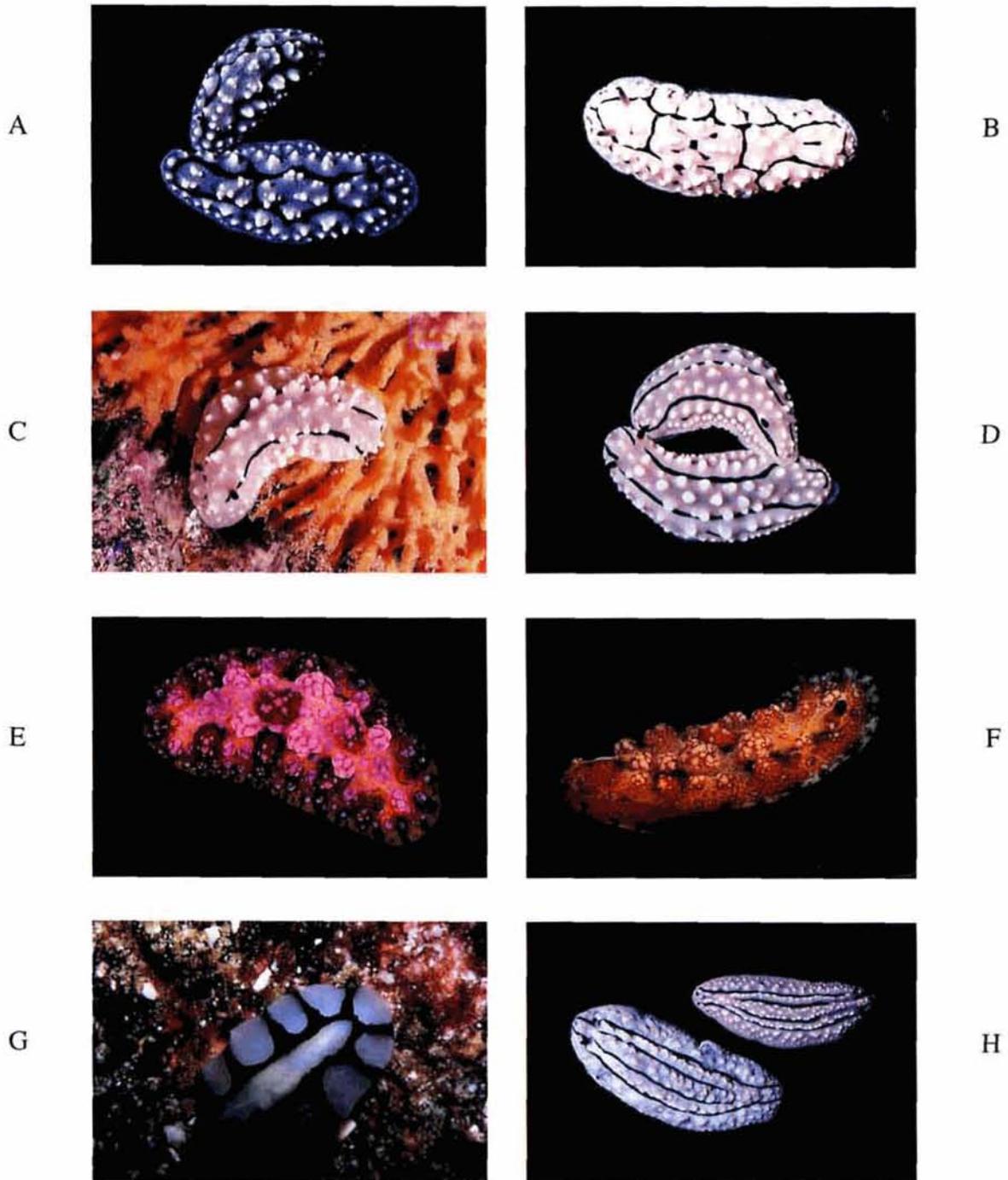


Plate 7. A, *Phyllidiella granulatus* n.sp. Dorsal view of 20 and 29 mm specimens, 18 m depth, Bile Bay, Guam, 29 June 1988; B, *Phyllidiella lizae* n.sp. Dorsal view of holotype (36 mm), 10 m depth, "Tenements 1", Heron Island Reef, GBR, 26 Nov. 1987; C, *Phyllidiella rudmani* n.sp. Dorsal view of 32 mm specimen on food sponge, *Phakellia* sp., 18-24 m depth, Horseshoe Reef, outer barrier reef, south east of Port Moresby, PNG, 21 June 1988; D, *Phyllidiella rudmani* n.sp. Dorsal view of 23 and 28 mm specimens, 4-10 m depth, Phi Phi Island, southern Thailand, 25 Nov. 1989; E, *Phyllidiopsis cardinalis*. Dorsal view of 20 mm specimen, 2 m depth, Bile Bay, Guam, 12 June 1973. Photo: C. Carlson & P. Hoff; F, *Phyllidiopsis cardinalis*. Dorsolateral view of 25 mm specimen, 29 m depth, Oronte Point, Guam, 18 Apr. 1984. Photo: C. Carlson & P. Hoff; G, *Phyllidiopsis dautzenbergi*. Dorsal view of 19 mm specimen, 10-15 m depth, Red Sea, 1983. Photo: N. Yonow; H, *Phyllidiopsis gemmata*. Dorsal view of 30 and 38 mm specimens, 16 m depth, Phi Phi Island, southern Thailand, 1 Dec. 1989.

PLATE 8

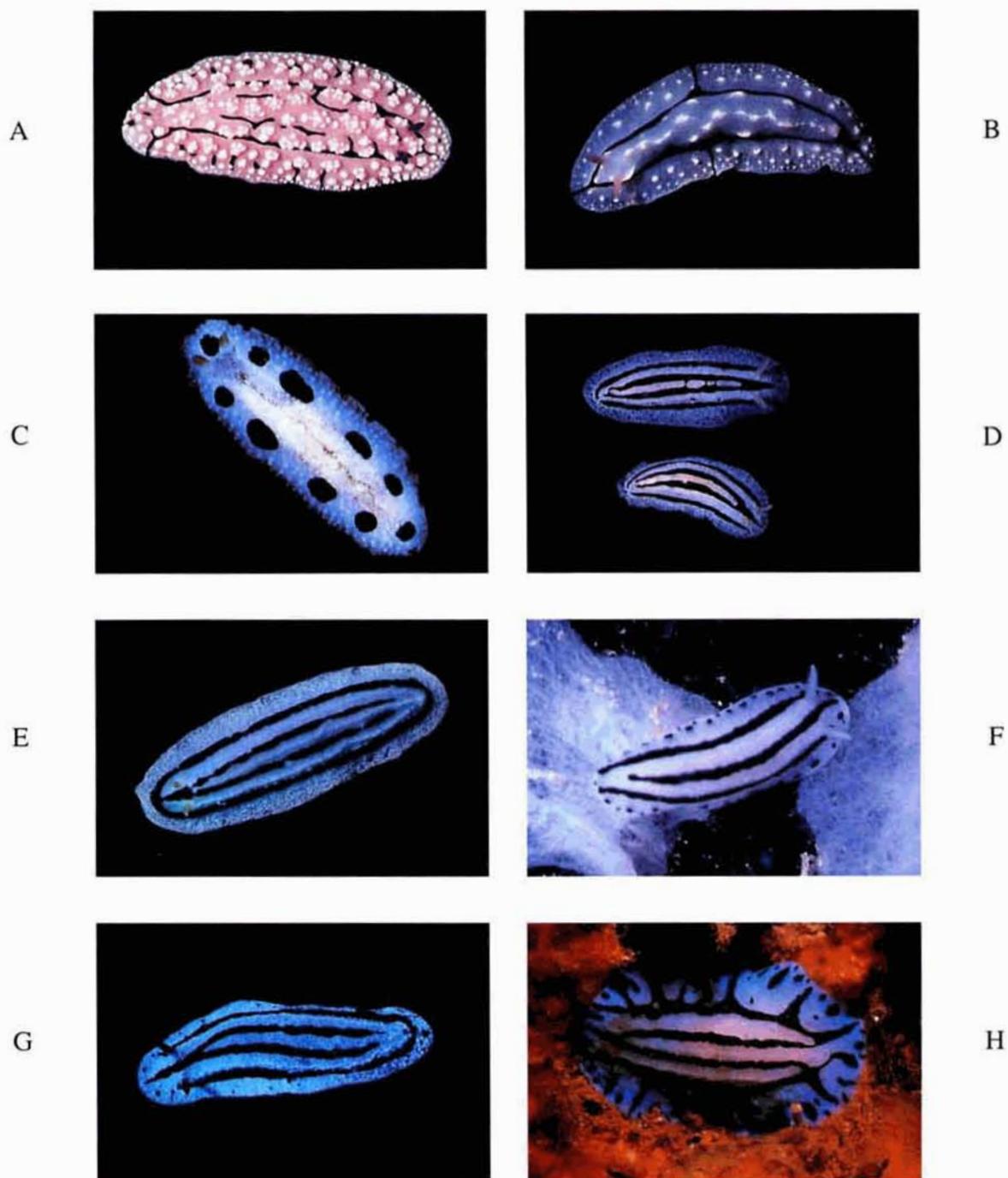


Plate 8. A, *Phyllidiopsis krempfi*. Dorsal view of 52 mm specimen, 16 m depth, Phi Phi Island, southern Thailand, 28 Nov. 1989; B, *Phyllidiopsis shireenae*. Dorsal view of 48 mm specimen, 20 m depth, patch reef off Lion Island, southern PNG, 18 June 1988; C, *Phyllidiopsis loricata*. Dorsal view of 40 mm specimen, collected intertidally, Mandora Point, Darwin, NT, 22 Nov. 1972. Photo: N. Coleman; D, *Phyllidiopsis striata*. Dorsal view of 10 and 9 mm specimens, 16 m depth, Phi Phi Island, southern Thailand, 1 Dec. 1989; E, *Phyllidiopsis striata*. Dorsal view of 19 mm specimen, 6 m depth, Bile Bay, Guam, 14 July 1988; F, *Phyllidiopsis phiphensis* n.sp. Dorsal view of 10 mm specimen on food sponge, *Gellius* sp., 4-10 m depth, Phi Phi Island, southern Thailand, 25 Nov. 1989; G, *Phyllidiopsis annae* n.sp. Dorsal view of 14 mm specimen, 8-10 m depth, Phi Phi Island, southern Thailand, 28 Nov. 1989; H, *Phyllidiopsis sphingis* n.sp. Dorsal view of 22 mm specimen, 15 m depth, "Three Tables", Hawaii, 1980. Photo: S. Johnson.

PLATE 9

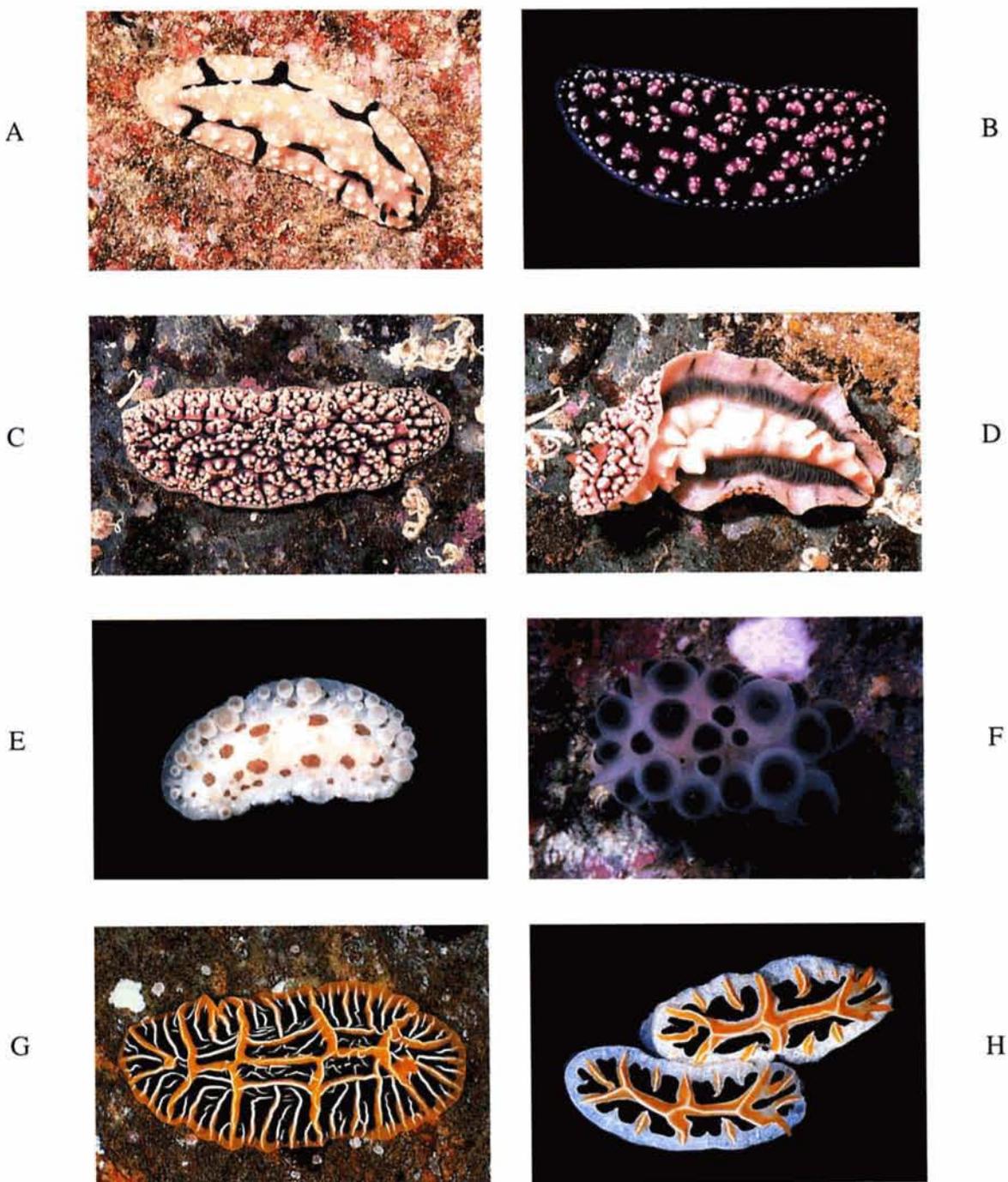


Plate 9. A, *Phyllidiopsis pipeki* n.sp. Dorsal view of 48 mm specimen, 15-25 m depth, Madang, PNG, 4 Feb. 1988. Photo: R.C. Willan; B, *Phyllidiopsis burni* n.sp. Dorsal view of 61 mm specimen, 22 m depth, "sponge mound", Apra Harbour, Guam, 5 July 1988; C,D, *Phyllidiopsis fissuratus* n.sp. Dorsal and ventral views respectively of 79 mm specimen, 9 m depth, Flinders Reef, north of Cape Moreton, southern Qld, 31 Mar. 1984. Photos: R.C. Willan; E, *Ceratophyllidia* sp. 1. Dorsal view of 10 mm specimen, collected subtidally by T.M. Gosliner, Madang, PNG, 27 Jan. 1988. Photo: R.C. Willan; F, *Ceratophyllidia* sp. 2. Dorsal view of 15 mm specimen, 15 m depth, Kwajalein Atoll, Marshall Islands, 4 June 1983. Photo: S. Johnson; G, *Reticulidia halgerda*. Dorsal view of 62 mm specimen, collected subtidally, North West Island, GBR, May 1988. Photo: J. Brodie; H, *Reticulidia fungia* n.sp. Dorsal view of 28 and 30 mm specimens, 14m depth, Horseshoe Reef, outer barrier reef, southern PNG, 22 June 1988.