

SYSTEMATICS OF PELAGIC AEOLID NUDIBRANCHS OF THE FAMILY GLAUCIDAE (MOLLUSCA, GASTROPODA)

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ABSTRACT

Specimens of pelagic aeolid nudibranchs of the family Glaucidae, collected from several localities in the Pacific Ocean, were anatomically examined and described. The comparative study of their external morphology and anatomy revealed that the genera *Glaucus* and *Glaucilla* share a number of synapomorphies. Maintenance of two sister monotypic genera is irrelevant and does not provide additional information. Thus, *Glaucus* is regarded as the single valid genus within the family, with two valid species *Glaucus atlanticus* Forster, 1777 and *Glaucus marginatus* Forster, 1777. *Glaucus marginatus* is reported from the northeastern Pacific for the first time and an aberrant specimen of *G. atlanticus*, with smooth radular teeth, is described. The presence of a penial spine and a penial gland together and the abnormal cleioproct condition in *Glaucus* suggests that this taxon could be closely related to *Cuthona* (Family Tergipedidae) rather than to *Facelina* and other related groups, as several authors have proposed. However, there is no compelling evidence one way or the other.

Pelagic aeolid nudibranchs are divided into two groups. The Fionidae Gray, 1857 includes the single species *Fiona pinnata* Eschscholtz, 1831, which is unable to swim and lives on floating objects. The true pelagic forms, which have the ability to swim on their own, are classified in the subfamily Glaucinae Gray, 1827, and are the subject of this paper. Members of Glaucinae are found in all oceans, spend their lives floating upside-down, and feed on colonial floating cnidarians (Miller, 1974). To maintain buoyancy they use their long cerata and a gas bubble in their stomach that is gulped periodically (Miller, 1974). Ross and Quetin (1990) have described the reproductive behavior of this group.

Despite the wide geographic range of true pelagic aeolid nudibranchs, the systematics of this group is poorly understood. There are two genera currently recognized as valid in the subfamily Glaucinae: *Glaucus* Foster, 1777 and *Glaucilla* Bergh, 1860, with one species each, *Glaucus atlanticus* Forster, 1777 and *Glaucilla marginata* Bergh, 1860. Most authors dealing with this group considered that *G. marginata* deserves generic rank distinct from *Glaucus* (Macnae, 1954; Bergh, 1860; Thompson and Bennett, 1970), whereas Keen (1971) considered *Glaucilla* as a synonym of *Glaucus*. No compelling evidence has been provided one way or another, and the systematic status of *G. marginata* is an open question.

Miller (1974) included both *Glaucus* and *Glaucilla* in the subfamily Glaucinae, with the subfamilies Babakininae Roller, 1973, Facelininae Bergh, 1889, Favorininae Bergh, 1889, Pteraeolidiinae Risbec, 1953, Crateninae Bergh, 1889, and Herviellinae Burn, 1967, in the family Glaucidae Gray, 1827.

The present paper deals with the systematic position of members of the Glaucidae and discusses their relationships with other groups of aeolid nudibranchs based on anatomical examination. The material examined was deposited at the Natural History Museum of Los Angeles County (LACM).

SYSTEMATICS

Genus *Glaucus* Forster, 1777

Glaucus Forster, 1777: 49. Type species: *Glaucus atlanticus* Forster, 1777, by monotypy.

Glaucilla Bergh, 1860: 325. Type species: *Glaucilla marginata* Bergh, 1860, by monotypy.

Diagnosis.—Body long and slender, widest just behind the head. Head short with very small, simple tentacles, widely separated, rhinophores positioned low on the side of the head. Cerata arranged in several arch-like groups, some of them penduculate. Cerata long, conical. Anus cleioproctic, renal pore abanal, interhepatic. Jaws bilobed with a denticulate masticatory border. Radular teeth with a prominent conical cusp flanked by sharp denticles. Reproductive system diaulic, with a large penis sheath. Penis armed or not with a hook. Seminal receptacle absent. Oral tube highly chitinized.

Remarks.—The genus *Glaucilla* has been considered to deserve a generic rank distinct from *Glaucus* on the basis of several anatomical differences, including the absence of a penial spine, the different arrangement of the cerata in multiseriata groups, the short posterior end of the body and the position of the nephroproct between the second and third groups of cerata (Macnae, 1954; Thompson and Bennett, 1970; Miller, 1974). On the contrary, Keen (1971) synonymized *Glaucus* and *Glaucilla*, but did not provide an explanation for such a change.

Even though there are several consistent morphological differences between the type species of *Glaucus* and *Glaucilla*, all of them are autoapomorphies of one of these two species. Morphological evidence indicates that *Glaucus* and *Glaucilla* are sister taxa. Maintenance of two monotypic sister genera is irrelevant and does not provide additional information. Unless the Glaucinae is, in the future, found to be much more diverse than is currently recognized, the maintenance of a single genus is sufficient to express the diversification that has taken place in this group.

Glaucus atlanticus Forster, 1777

(Figs. 1A, 2–3)

Glaucus atlanticus Forster, 1777: 49. For a full list of synonyms see Thompson and McFarlane (1967).

Material Examined.—Galápagos, Ecuador (1°18'N, 91°45'W), 12 May 1984, four specimens 9–14 mm preserved length, collected in a neuston plankton tow by R. J. Lavenberg (LACM 111410). Darwin Island, Galápagos, Ecuador, 13 May 1948, one specimen 9 mm preserved length, collected in a neuston plankton tow (LACM 111447). La Audencia, near Mazatlán, Mexico, 25 January 1976, 12 specimens 8–12 mm preserved length, collected in an intertidal pool by F. and R. Poorman (LACM 140852). R/V SCOFIELD, station 67S4-8, ca. 1300 km SW of Los Angeles, California, U.S. (29°50'N, 133°11'W), 2 June 1967, two specimens 11–16 mm preserved length (dissected), leg. W. L. Craig and J. J. Geibel (LACM 152967).

External Morphology.—Body slender and elongate (Fig. 1A), with up to three groups of cerata on each side. Head short and not distinctly separated from the body. Oral ten-

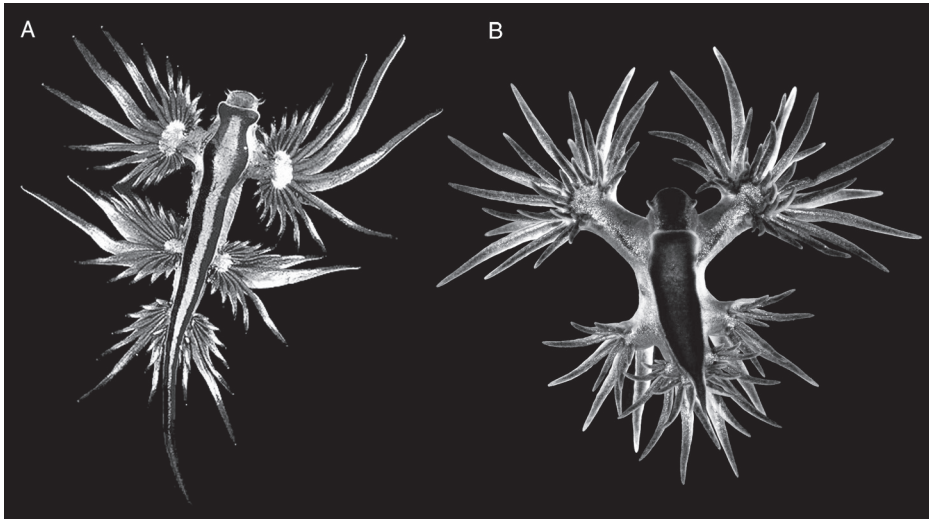


Figure 1. Ventral view of the living animals from the tropical Indo-Pacific, photos by W. Rudman. A) *Glaucus atlanticus* Forster, 1777. B) *Glaucus marginatus* (Bergh, 1860).

tacles and rhinophores short and smooth (Fig. 2C). The first group of cerata is pedunculate, with a short stalk. The other two groups are sessile. All of them are perpendicular to the body mid-line. The cerata are inserted in each group in a single series, the most dorsal cerata in each group being the largest. The cerata decrease in size ventrally on each side. The cerata are conical, narrower near the tip, and easily autotomizable. The foot is broad and well developed. Its anterior corners are rounded. The posterior end of the body is very long and slender, and the foot extends to its tip. The anus lies between, and level with the top of the second and third groups of cerata. The renal pore is situated at the same level but a little distance in front of the second group of cerata.

The general body color is silver, with the rhinophores, oral tentacles, and the lower edge of the cerata electric blue. The dorsum varies from dark blue to brown. The foot is silver in the central portion, flanked by bands of light blue that join together at the head and near the tip of the foot.

Internal Anatomy.—The reproductive system is dialucic (Fig. 2A). The ampulla is long convoluted. It branches into the female glands and the prostate. The prostate is also long and convoluted; it narrows into the deferent duct that expands again into the large and muscular penial sheath. Connected to the penial sheath of the deferent duct is a short penial gland. The penis is long and armed with a single, strong, curved and hollow hook, about 250 μm long (Fig. 3C). The vagina is situated next to the penial sheath and is wide and muscular. The vagina connects to a curved bursa copulatrix that has a rounded caecum at its proximal end (Fig. 2B). Radular formulae of examined specimens are: $11 \times 0.1.0$ (LACM 152962), $11 \times 0.1.0$ (LACM 011447), $16 \times 0.1.0$, and $20 \times 0.1.0$ (LACM 111410). The rachidian teeth have a strong central cusp and a concave base. Most specimens examined have 3–7 denticles on each side of the cusp, but one of the specimens (LACM 111410) lacks denticles (Fig. 3B). Each jaw is about 2 mm long (Fig. 3A), with a masticatory border composed of several denticles.

Remarks.—*Glaucus atlanticus* is a well-known circumtropical species. The main distinctive character of this species is the curved spine in the penis that it is used to secure copulation between the individuals (Thompson and Bennett, 1970; Miller, 1974, Ross

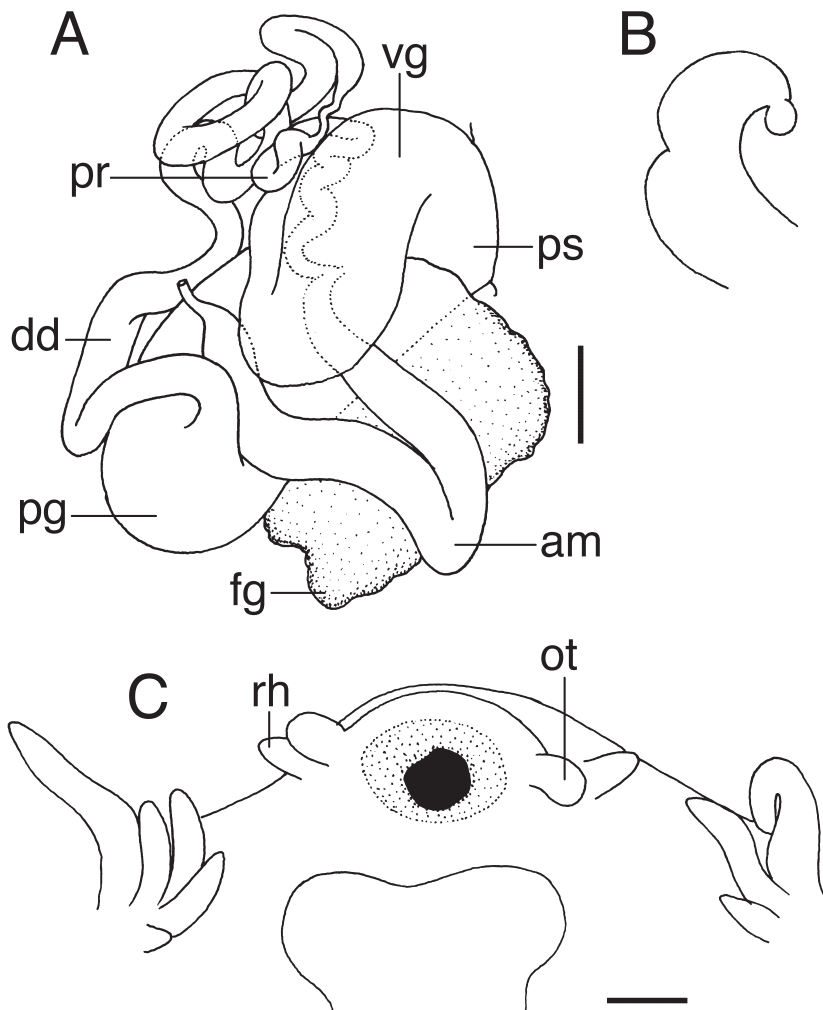


Figure 2. *Glaucus atlanticus* Forster, 1777. A) Reproductive system, scale bar = 1 mm. B) Detail of the bursa copulatrix, scale bar = 1 mm. C) Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: am, ampulla; dd, deferent duct; fg, female gland; ot, oral tentacle; pg, penial gland; pr, prostate; ps, penial sheath; rh, rhinophore; vg, vagina.

and Quetin, 1990), and the arrangement of the cerata, in 3–4 sessile or slightly pendunculated groups. Several names have been introduced for this species since its original description by Forster (1777), but they have been synonymized by Thompson and McFarlane (1967).

The radular teeth of *G. atlanticus* have been described as having a series of denticles on each side of the central cusp (Thompson and Bennett, 1970; Miller, 1974), but in the present study a specimen with smooth teeth, lacking denticles, was observed. Since this individual showed no morphological or anatomical differences with other specimens with denticulated teeth and was collected from the same localities, we assume that differences are due to intraspecific variability (see Bertsch, 1976).

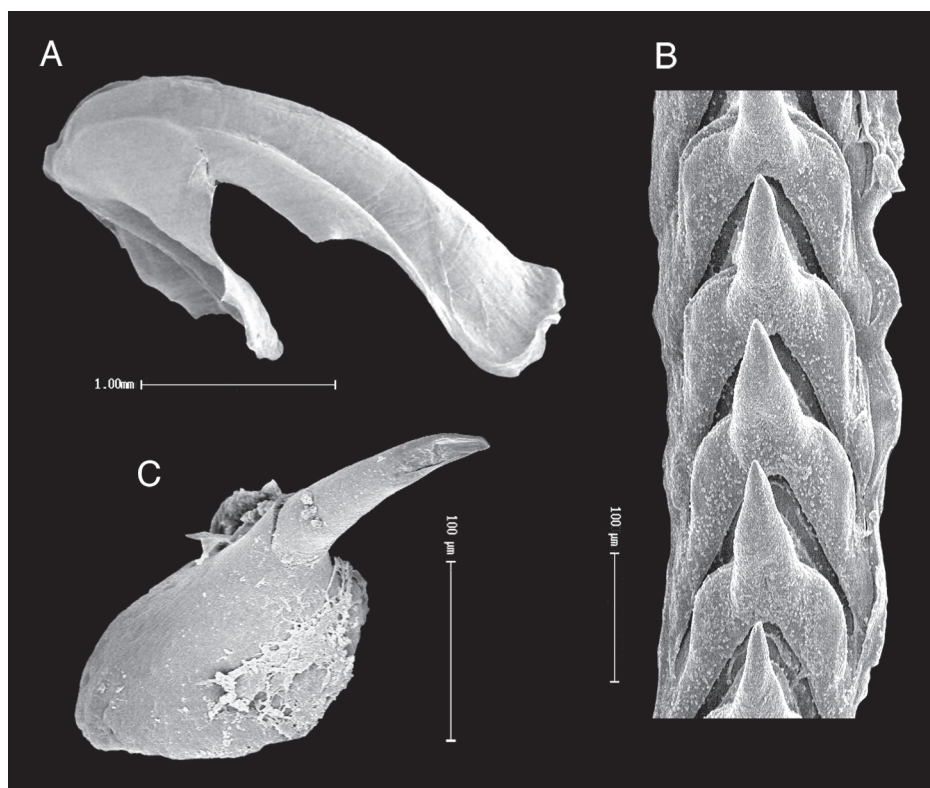


Figure 3. *Glaucus atlanticus* Forster, 1777, scanning electric micrographs of A) jaw, B) radular teeth of an aberrant specimen, and C) penial spine.

Glaucus marginatus (Bergh, 1860)

(Figs. 1B, 4–5)

Glaucilla marginata Bergh, 1860: 325, pl. 8, fig. 9.

Glaucilla briareus Bergh, 1860: 325–326.

Material Examined.—Isla San Benedicto, Revillagigedo Islands, Mexico, 18 January 2000, five specimens 5–8 mm preserved length (two of them dissected), leg. J. L. Arreola (LACM 153064). Darwin Island, Galápagos, Ecuador, 13 May 1948, one specimen 9 mm preserved length, collected in a neuston plankton tow (LACM 153063).

External Morphology.—Body elongate (Fig. 1B), with up to four groups of cerata on each side. Head short and not distinctly separated from the body. Oral tentacles and rhinophores short and smooth (Fig. 4B). The first two groups of cerata are pedunculate, with a long stalk. The last two groups are sessile. The first group forms an angle with the mid-line of the body, pointing towards the head. The other three are perpendicular to the body mid-line. The third and fourth groups are partially fused. The cerata are inserted in multiple series presenting an irregular arrangement of cerata. The cerata are conical, narrower near the tip. The foot is broad and well developed. Its anterior corners are rounded. The posterior end of the body is very short. The anus is situated between,

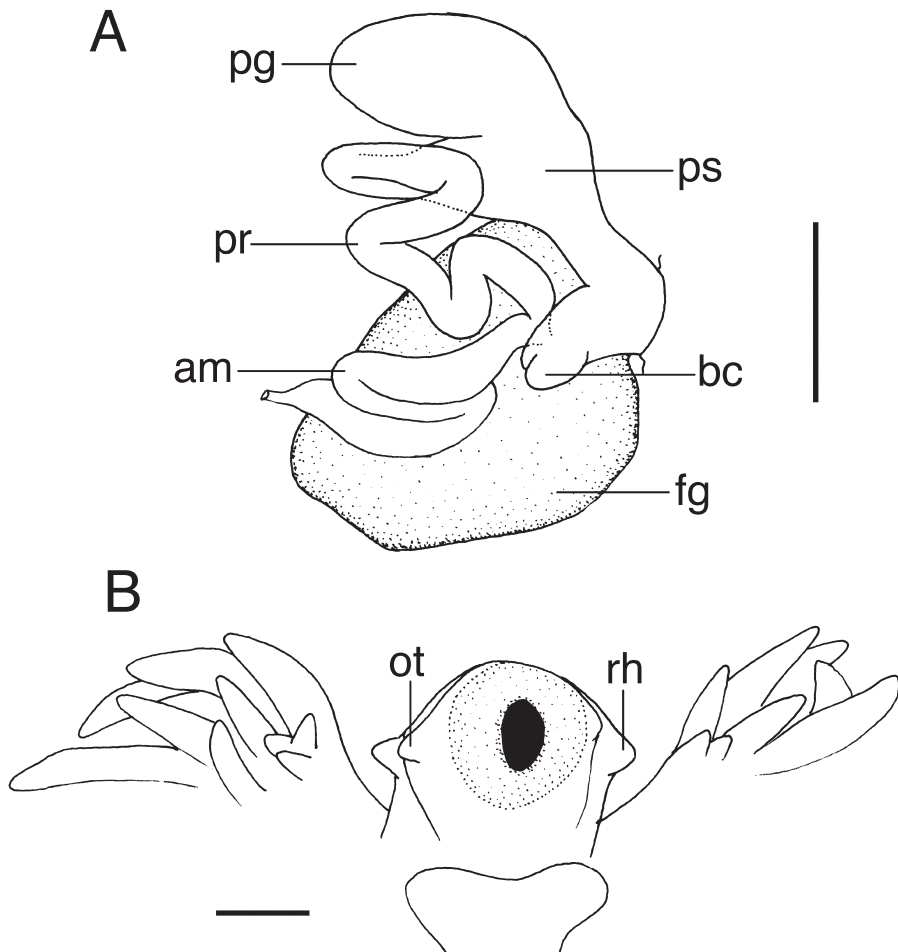


Figure 4. *Glaucus marginatus* (Bergh, 1860). A) Reproductive system, scale bar = 1 mm. B) Ventral view of the mouth area, scale bar = 1 mm. Abbreviations: am, ampulla; bc, bursa copulatrix; fg, female gland; ot, oral tentacle; pg, penial gland; pr, prostate; ps, penial sheath; rh, rhinophore.

and level with the top of the second and third groups of cerata. The renal pore is situated at the same level but a short distance in front of the second group of cerata.

The general body color is silver blue. The ventral surface is brownish, paling towards the edges of the foot and on the cerata. The bases of the groups of cerata have small iridescent blue-green spots. The cerata are dark blue with small light blue spots. The foot is dark bluish.

Internal Anatomy.—The reproductive system is diallic (Fig. 4A). The ampulla is long and convoluted. It branches into the short oviduct and the prostate. The prostate is also long and convoluted and expands into the muscular penial sheath. Connected to the penial sheath there is a large penial gland. The penis is long and devoid of hooks. The vagina is situated next to the penial sheath and is wide and muscular. The vagina connects to a small bursa copulatrix. Radular formula $22 \times 0.1.0$ (LACM 153064). The rachidian teeth have a strong central cusp and a concave base. Each tooth has 4–5 denticles on each

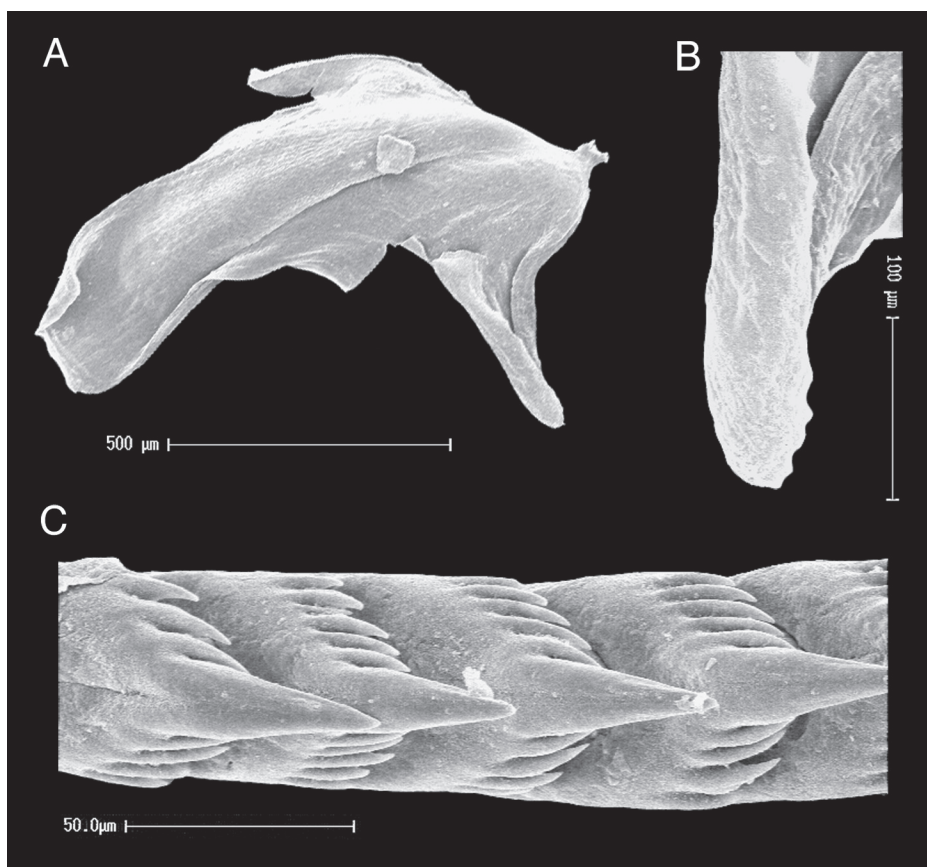


Figure 5. *Glaucus marginatus* (Bergh, 1860), scanning electric micrographs of A) jaw, B) masticatory border, and C) radular teeth.

side of the central cusp (Fig. 5C). The jaws are about 1 mm long (Fig. 5A), with masticatory border composed of several denticles (Fig. 5B).

Remarks.—Bergh (1860) described *Glaucilla marginata* from the North Pacific and *G. briareus* from the South Pacific. According to Thompson and Bennett (1970) there are no consistent differences that justify separation of two taxa, and therefore they synonymized both names. In addition, Thompson and Bennett (1970) selected the name *G. marginata* for this species, under the principle of first reviser (ICZN, 1999: Article 24.2.1). The northeastern Pacific specimens here examined are identical to those studied by Thompson and Bennett (1970) from Australia and there is no doubt that *G. briareus* and *G. marginata* are synonyms.

Glaucus marginatus is known on the basis of a few specimens collected from Hawaii, Juan Fernández Islands (Bergh, 1868), and Australia (Thompson and Bennett, 1970; Ross and Quetin, 1990). The present paper constitutes the first record of this species from the northeastern Pacific.

Glaucus marginatus is clearly distinguishable from *G. atlanticus* in several regards. The body of *G. marginatus* is shorter, with the cerata arranged in uneven lines, one over the other, whereas they are arranged in a single series in *G. atlanticus*. The penis of *G. marginatus* is shorter than that of *G. atlanticus* and lacks a copulatory spine. Other differences between these two taxa have been discussed above.

DISCUSSION

Macnae (1954) considered that *Glaucus* and *Glaucilla* are closely related to the families Facelinidae and Aeolididae but provided no compelling reasons. He also pointed out the presence of a penial gland in both Glaucidae and Tergipedidae (as Cuthonidae), but argued that this structure is not in any way homologous with the penis gland characteristic of the Tergipedidae (as Cuthonidae). Miller (1974) proposed a classification for the Aeolidacea in which the Glaucinae are included with the subfamilies Babakininae Roller, 1973, Facelininae Bergh, 1889, Favorininae Bergh, 1889, Pteraeolidiinae Risbec, 1953, Crateninae Bergh, 1889, and Herviellinae Burn, 1967, in the family Glaucidae Gray, 1827. This scheme was based on Miller's (1974) opinion that *Glaucus* is a facelinid modified to the pelagic life. Synapomorphies that support the Glaucidae in the meaning of Miller (1974) are a cleioproct anus and presence of cerata arranged in arched clusters. However, the cleioproct position of the anus in *Glaucus* is abnormal. The anus in a cleioproct position is usually among the cerata (between the rows or within an arch), not above the rows as in *Glaucus*. Thus, the cleioproct condition in *Glaucus* appears not to be homologous with that of other members of Glaucidae.

The presence of a combination of a penial gland and a penial spine in both *Glaucus* and in the Tergipedidae (see Gosliner and Griffiths, 1981) seems to indicate that these two groups are more closely related to each other than to other aeolid nudibranchs. However, penial spines are also present in some facelinids such as *Phidiana* Gray, 1850 and *Anetarca* Gosliner, 1991, and *Dondice* Marcus, 1958 has a penial gland. Penial spines in aeolid nudibranchs appear to vary considerably in function and shape, and it is possible that this structure evolved several times independently.

With the available anatomical evidence it is not possible to determine the systematic position of *Glaucus* and a phylogenetic analysis of the Aeolidacea is necessary before a modification of the current classification.

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