A new hydrozoan, Geomackiea zephyrolata gen. nov., sp. nov. (Anthomedusae: Pandeidae), from inland marine waters of British Columbia and Washington State

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The hydromedusa *Geomackiea zephyrolata* gen. nov., sp. nov. is described and illustrated. It has been placed in the subfamily Protiarinae of the family Pandeidae on the basis of its stomach and gonad morphology and the four large perradial tentacles with conical basal bulbs. A new genus has been erected because the medusa is supplied with four broad interradial bulbs, each rimmed by up to eight closely packed solid tentaculae. A total of 29 specimens with bell heights of 0.9–3.5 mm have been collected in the plankton of Saanich Inlet, British Columbia, and Friday Harbor, Washington, between 1978 and 1981. Juvenile as well as adult specimens are described and the cnidome, gametes, seasonal and vertical distributions, and taxonomic affinities within the family Pandeidae are discussed.

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On trouvera ici la description illustrée de l'hydroméduse *Geomackiea zephyrolata* gen. nov., sp. nov. La morphologie de l'estomac et des gonades et la présence des quatre grands tentacules radiaux à bulbes basaux coniques placent cette méduse dans la sous-famille des Protiarinae, dans la famille des Pandeidae. Un nouveau genre est proposé parce que la méduse possède quatre bulbes interradiaux larges, chacun bordé de tentacules compacts et serrés les uns sur les autres (jusqu'à huit). Vingt-neuf spécimens de ce nouveau taxon, dont la hauteur de l'ombrelle varie de 0,9 à 3,5 mm, ont été récoltés dans le plancton de Saanich Inlet, Colombie-Britannique, et de Friday Harbor, Washington, de 1978 à 1981. Les jeunes et les adultes sont décrits ici; le cnidome, les gamètes, la répartition saisonnière et la répartition verticale de même que les affinités taxonomiques au sein de la famille des Pandeidae font l'objet d'une discussion.

[Traduit par le journal]

Introduction

During a 2-year investigation of the medusa, siphonophore, and ctenophore fauna of Saanich Inlet, British Columbia, Canada, 28 specimens of a new anthomedusa were collected, and an additional specimen was later taken nearby in the waters of Friday Harbor, Washington, U.S.A. The species is placed in the family Pandeidae because of its quadrate mouth lacking oral tentacles, its four adradial gonads attached to both the stomach and the radial canals, along which they extend nearly half the distance to the bell margin in large specimens, and its four large perradial tentacles with typically pandeid conical basal bulbs. It is placed in the subfamily Protiarinae because it has not more than four tentacles. A new genus, Geomackiea, is established on the basis of its four distinctive interradial marginal bulbs, each of which is rimmed by up to eight closely packed tentaculae. This type of marginal bulb structure has not been described for any other hydromedusa. The new species, Geomackiea zephyrolata, described here is the type species of the new genus.

Materials and methods

The Saanich Inlet specimens were collected in 1978 and 1979 during a 2-year series of approximately bimonthly stratified replicate plankton tows (Mills 1982) at University of Victoria Station "E" (48°37.5′ N, 123°30′ W). (One specimen was collected in a plankton tow accompanying the above series near Brentwood Bay in Saanich Inlet at 48°35′ N, 123°30′ W.) Vertical plankton tows using a 0.75 m diameter, 333- μ m mesh closing net were taken over the following intervals: 0–25, 25–50, 50–75, 75–130, and 130–180 m. Saanich Inlet is approximately 200 m deep at the sampling location.

The Friday Harbor specimen was collected from the Friday Harbor Laboratories floating docks (48°32.7′ N, 123°0.7′ W) at night, using an underwater 100-W light bulb that provided dark-field illumination.

This was the only *Geomackiea zephyrolata* gen. nov., sp. nov. specimen seen during 7 years of extensive day- and night-time inspection of jellyfishes in Friday Harbor from 1977 to 1984 (Miller 1979; Mills 1981; C. E. Mills, unpublished data). The specimen was collected in a glass bowl and was maintained in the laboratory for several days before its preservation.

Nematocysts were examined in four specimens by using differential interference contrast optics and were identified according to the scheme of Mariscal (1974). At least 20 unfired nematocysts of each type were measured at 1000× magnification; the numbers are presented here as size ranges, and were obtained from specimens measuring 1.3-3.0 mm in bell height.

Results

Geomackiea gen. nov.

DIAGNOSIS: Pandeidae with four perradial tentacles having tapering conical bases and with four broad, interradial bulbs, each rimmed by a cluster of short tentaculae.

TYPE SPECIES: Geomackiea zephyrolata sp. nov.

ETYMOLOGY: The genus is named in honor of Professor George O. Mackie of the University of Victoria, British Columbia. Professor Mackie has made numerous insightful contributions to our understanding of the biology of jellyfishes and a wide variety of other marine organisms.

Geomackiea zephyrolata sp. nov.

Undescribed anthomedusa, Mills 1982, pp. 58, 326, 336
HOLOTYPE: U.S. National Museum of Natural History
(Smithsonian Institution) USNM No. 72381. Collected by the
author in Saanich Inlet on June 14, 1978, at approximately
1530 in a vertical plankton tow which sampled between 130
and 75 m deep. This specimen was immediately preserved in

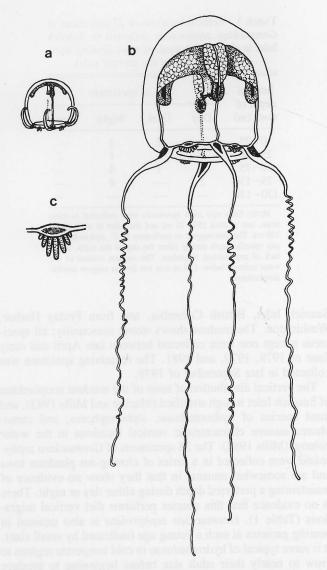


FIG. 1. Geomackiea zephyrolata. (a) Preserved juvenile specimen of undetermined sex, collected April 27, 1978, in Saanich Inlet, British Columbia, measuring 1.3 mm in bell height and bell diameter. (b) Living male specimen collected May 18, 1981, at Friday Harbor, Washington, measuring 3.5 mm in bell height and 3.0 mm in bell diameter. (c) Enlarged view of an interradial marginal bulb with tentaculae extended (they are normally held curved up against the bulb).

5% formalin and has preserved dimensions of 2.0 mm in both bell height and bell diameter.

PARATYPES: Five paratypes, USNM Nos. 72382–72386, were collected on April 27, 1978, May 18, 1978, May 19, 1978, May 5, 1979, and May 14, 1979. Two additional paratype specimens have been deposited at the British Columbia Provincial Museum, BCPM Nos. 984-354-1 and 984-355-1. They were collected May 14, 1979 and May 5, 1979, respectively. Further specimens are on deposit at the British Columbia Provincial Museum, BCPM Nos. 984-356-1 to 984-358-1 (three specimens), and the Friday Harbor Laboratories Synoptic Collection (four specimens).

Description of adult specimens (Fig. 1b)

Medusa with a rounded, bell-shaped umbrella, slightly higher than wide; the largest specimen collected was 3.5 mm high and 3.0 mm in diameter in life. Jelly of medium thickness,

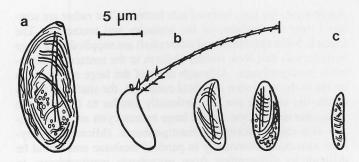


FIG. 2. Nematocysts of *Geomackiea zephyrolata*. (a) Microbasic mastigophore (?) or eurytele (?), seen only in the unfired condition; occurring on both the perradial and interradial marginal bulbs, on the surface of the manubrium, and on the exumbrella. (b) Microbasic mastigophores, fired and unfired; occurring on the perradial tentacles and on the interradial tentaculae. (c) An undetermined elongate type of nematocyst, seen only in the unfired condition; occurring on or near the interradial bulbs and tentaculae, but their exact position could not be determined.

without apical projection. Without a peduncle; stomach small, extending about one-third of the depth of the subumbrella; mouth quadrate, with four simple lips that are not armed with nematocysts (see below, Nematocysts). With four narrow radial canals. With four interradial gonads attached to and ringing the stomach wall and attached to the radial canals, along which they extend nearly half the distance to the bell margin, forming a pendant cruciform structure with lobed ends. With four large hollow perradial tentacles having scattered nematocysts and with tapering, conical basal bulbs. At each of the four interradii is a broad, flat bulb rimmed by five to eight closely packed, solid, short tentaculae which are covered with scattered nematocysts (Fig. 1c). These tentaculae are graduated in size, with the longest occupying the center position, and decreasingly shorter tentaculae adjacent to them. The tentaculae are generally held curved up and outward against the bulb. Both the perradial and interradial marginal bulbs are pigmented a dark gray-brown color. The velum is narrow. The medusa is without statocysts and without ocelli.

Description of juvenile specimens (Fig. 1a)

The smallest specimens collected were approximately 1 mm high and 1 mm wide and have a nearly spherical bell with thin jelly. The stomach is short, with a simple quadrate mouth hanging down about one-fourth the depth of the subumbrellar space. Even in the smallest specimens, the gonadal tissue is prominent, with the perradial arms extending about one-quarter of the distance along the radial canals. Mature sperm or primary oocytes were seen in the gonads of specimens as small as 1.3 mm in bell height (see below, *Gametes*). The four perradial tentacles with conical marginal bulbs are present, as are the four interradial bulbs, these having two to four tentaculae each. The velum is narrow. The medusa is without statocysts and without ocelli.

Nematocysts

Nematocysts (shown in Fig. 2) were examined in four preserved specimens which had bell heights of 1.3, 1.5, 1.5, and 3.0 mm. The nematocyst sizes and locations are similar in all four specimens. The large perradial tentacles and the small interradial tentaculae are supplied with microbasic mastigophores which measure $8.0-9.2 \times 3.6-4.0 \mu m$ (all dimensions given are those of unfired capsules). These tentacular

nematocysts are not clustered into batteries, but rather are scattered over the surfaces of the tentacles and tentaculae. The tentacle bulbs (perradial and interradial) are supplied with large nematocysts that look similar in form to the tentacular microbasic mastigophores. Although none of the large nematocysts on the bulbs were seen in a fired condition, the shaft and thread inside the capsule are proportionally similar to those of the tentacular nematocyst, so the large nematocysts are provisionally also called microbasic mastigophores. (Microbasic euryteles also occur commonly in pandeid medusae and would be difficult to differentiate from microbasic mastigophores in the unfired condition.) The large nematocysts measure 14.4- $17.6 \times 6.4 - 8.0 \mu m$. A third type of nematocyst is associated with the interradial bulbs and tentaculae. These elongate nematocysts occur in a loose cluster of about 50, although their precise position could not be determined from the squash preparations. These nematocysts measure $5.6-7.2 \times 1.6-1.7 \mu m$; they are given no descriptive name at present, since none were seen in a fired condition. Microbasic mastigophores similar to those on the tentacles and tentaculae, but measuring 8.0- $9.2 \times 4.0 - 4.4 \,\mu\text{m}$, are also sprinkled over the surface of the exumbrella, being more abundant near the bell margin than on the upper portions.

Most hydromedusae have a dense aggregation of nematocysts at the edge of the mouth. In contrast, the lips of the mouth of *Geomackiea zephyrolata* are not provided with nematocysts, but consist of an 80 μ m wide band of fusiform cells. These cells have a finely granular internal structure and are presumed to be adhesive—secretory cells, based on their morphology and location. Similar glandular cells have been described in detail by Bouillon (1966) in the oral regions of a variety of hydrozoan polyps and medusae. Above the lips of *G. zephyrolata*, the surface of the manubrium is provided with sparsely scattered microbasic mastigophores that measure $6.4-7.2 \times 3.2 \ \mu$ m and look similar to the tentacular nematocysts. A few of these nematocysts were also observed on the gonad surface above the manubrium.

Gametes

The gonads were examined microscopically on the four specimens whose nematocysts were measured. Three of the specimens were males. These animals, having bell heights of 1.5, 1.5, and 3.0 mm, all had large numbers of morphologically mature spermatozoa in the lobed terminal portions of the gonads (the cruciform central portion of the gonad appears to be largely composed of vacuolated rather than proper spermatogenic tissue). Many of these spermatozoa became free from the surrounding tissue in the squash preparations. The sperm heads are typically hydrozoan, acorn-shaped structures, measuring 3.2 µm in height and 2.4 µm in diameter, with two spherical mitochondria in the basal portion. The fourth microscopically examined specimen was a female with a bell height of 1.3 mm. This animal had primary oocytes in the gonads.

Hydroid

Unknown.

ETYMOLOGY: The specific name *zephyrolata* means "borne by the west wind," and is derived from *Zephyros*, the ancient Greek personification of the west wind and *latus*, past participle of the Latin verb *fero*, to bear.

Discussion

Geomackiea zephyrolata has been collected only from

TABLE 1. Vertical locations of 27 specimens of Geomackiea zephyrolata collected in Saanich Inlet in closing-net plankton tows (towing intervals are shown on the vertical axis)

Interval depth of tows (m)	No. of specimens			
	Day	Dusk	Night	Dawn
0-25	2	1	2	_
25-50	4	1	1	2
50-75	3	1	4	
75-130	2		4	_
130-180		_		_

Note: Only two adult specimens were collected in these tows, one at dusk (50-75 m) and the other at night (75-130 m). The data suggest no preference by *G. zephyrolata* for any specific depth during either the day or the night, and a lack of any vertical migration. The oxygen content of the water column below 130 m was too low to support aerobic zooplankton.

Saanich Inlet, British Columbia, and from Friday Harbor, Washington. The medusa shows strong seasonality; all specimens except one were collected between late April and early June of 1978, 1979, and 1981. The remaining specimen was collected in late September of 1979.

The vertical distribution of most of the resident zooplankton of Saanich Inlet is high stratified (Mackie and Mills 1983), and most species of hydromedusae, siphonophores, and ctenophores assume characteristic vertical locations in the water column (Mills 1982). The 28 specimens of *Geomackiea zephyrolata* were collected in a series of closing-net plankton tows and are somewhat unusual in that they show no evidence of maintaining a preferred depth during either day or night. There is no evidence that this species performs diel vertical migrations (Table 1). *Geomackiea zephyrolata* is also unusual in bearing gametes at such a young age (indicated by small size). It is more typical of hydromedusae in cold temperate regions to grow to nearly their adult size before beginning to produce mature gonadal tissue.

The family Pandeidae is a conglomeration of hydromedusae whose interrelationships are problematical. Russell (1953) proposed the division of the Pandeidae into four subfamilies, the Amphineminae, Protiarinae, Pandeinae, and Calycopsinae, based on the morphology and numbers of tentacles in adult medusae. Of Russell's four subfamilies, the last, the Calycopsidae, has been raised to family status (see Kramp, 1961). Arai and Brinckmann-Voss (1980) further removed the genus *Halimedusa* from the Pandeidae to its own family, the Halimedusidae, and divided the remaining pandeid medusae again into four subfamilies. Their subfamilies Stomotocinae, Amphineminae, Protiarinae, and Pandeinae are based on the presence or absence of a peduncle and, as in the scheme of Russell (1953), on the numbers of tentacles.

Geomackiea zephyrolata belongs to the subfamily Protiarinae, which is defined by Arai and Brinckmann-Voss (1980) as including those pandeid medusae without a peduncle and having four perradial marginal tentacles. As the subfamily Protiarinae was not represented in either the British fauna (Russell 1953) or the British Columbia fauna (Arai and Brinckmann-Voss 1980), affinities within this group have not been discussed by previous authors. A review of the literature yields eight genera of Pandeidae that qualify for the subfamily Protiarinae as defined by Arai and Brinckmann-Voss (1980)

MILLS

(the last three genera listed possess secondary marginal cirri or tentaculae in addition to the four perradial tentacles): Cnidotiara, Paratiara, Protiara, Urashimea, Zancleopsis, Halitiara, Halitiarella, and Geomackiea (Kramp 1959, 1961, 1968; Bouillon 1980; the present paper). With the exception of Urashimea, these genera further have in common a simple mouth and smooth (not folded) gonads. Urashimea, in contrast, has a folded mouth, folded gonads, and an unusual complement of nematocysts that may ultimately place it in its own family (S. Kubota, personal communication). Kramp (1959) suggests that the genus Protiara is the most primitive of the Pandeidae. I would further suggest that all members of the Protiarinae be considered relatively primitive within the family Pandeidae.

Medusae in the remaining three subfamilies of the Pandeidae may generally be characterized as having large, highly folded mouths, and gonads with prominent folds or reticulae on their surface. The small, simple mouth and smooth gonads that are typical of members of the Protiarinae are, however, also present in the pandeid genera *Merga* (whose medusae have 4, 8, or more tentacles). *Pandeopsis* (with 8–16 tentacles), and *Niobia* (which has 12 tentacles). Whereas, on the basis of tentacle number, all three of these genera fall into the subfamily Pandeinae as it has been defined by Arai and Brinckmann-Voss (1980), their mouth and gonad structures suggest that these species may be anatomically intermediate between the two subfamilies Protiarinae and Pandeinae. It seems most prudent at this time, however, to leave these species within the subfamily Pandeinae until further comparative work is done.

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