



HETEROLAOPHONTE NATATOR N. SP. (COPEPODA, HARPACTICOIDA)
FROM HAIDA GWAI, BRITISH COLUMBIA — AND POSSIBLE
RELATIVES IN THE U.K. AND ICELAND

BY

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ABSTRACT

A new species of the genus *Heterolaophonte* Lang, 1948 is described. *Heterolaophonte natator* n. sp. was first collected from eelgrass in Louscoone Inlet, Moresby Island, Haida Gwaii. The leg armature is provided for the new species and others that are either similar or reported from British Columbia coastal waters. Although both the female and male have distinct paddling leg armatures, the male fourth leg with its unique minute endopodite and third leg with a plug on the endopodite are characteristics shared with the male of a European laophontid copepod, *H. littoralis* (T. Scott & A. Scott, 1893). Both unique and shared characteristics are provided in the description as well as a discussion of similar copepods, particularly the association with a European species, as well as three others with similar characteristics, all of whom live in formerly glaciated areas.

Key words. — Copepoda, Harpacticoida, *Heterolaophonte*, sub-Arctic, minute male P4 endopodite

RÉSUMÉ

Une nouvelle espèce du genre *Heterolaophonte* Lang, 1948 est décrite. *Heterolaophonte natator* n. sp. avait été tout d'abord collectée dans les zostères à Louscoone Inlet, Île Moresby, Haida Gwaii. L'armature des pattes est fournie pour cette nouvelle espèce et pour d'autres qui sont, soit similaires, soit citées des eaux côtières de Colombie britannique. Bien que la femelle comme le mâle aient des armatures des pattes natatoires distinctes, la quatrième patte du mâle avec son endopodite minuscule unique et sa troisième patte avec une protubérance sur l'endopodite sont des caractéristiques partagées avec le mâle d'un copépode Laophontidae européen, *H. littoralis* (T. Scott & A. Scott, 1893). Les caractéristiques uniques et partagées sont données dans la description ainsi qu'une discussion sur des copépodes similaires, en particulier la ressemblance avec une espèce européenne, ainsi que trois autres ayant des caractéristiques similaires, tous vivant dans les régions ayant autrefois subi une glaciation.

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Mots clés. — Copepoda, Harpacticoida, *Heterolaophonte*, subarctique, endopodite P4 mâle minuscule

INTRODUCTION

Members of the harpacticoid genus *Heterolaophonte* Lang, 1948, form a component of harpacticoid communities on the west coast of North America (Cordell, 2007). They are somewhat unique, a result of their swimming habit. Although many Laophontidae are considered to be near benthic (Bang et al., 2011), members of the genus are slender and better designed for swimming rather than for firmly attaching to a substrate (e.g., eelgrass or algae), respectively, for crawling on and/or in a soft, e.g., muddy, substrate. Frequently associated with algae and eelgrass (Walters & Bell, 1986), their tendency to swim also exposes the adult as well as the preadult stages to uptake and dispersal in tidal waves and longshore currents. This also exposes them to uptake in ballast water with subsequent release in different areas, as an invasive, during ballast water exchange (e.g., Tellez, 2019).

Several *Heterolaophonte* species have been reported from British Columbia, mostly in studies of benthic communities (e.g., Kask et al., 1986) or environmental impacts (e.g., Cordell, 2018). Material for the present study came from collections of eelgrass (*Zostera marina* Linnaeus, 1753) from selected sites in the Strait of Georgia, the west coast of Vancouver Island and Haida Gwai (fig. 1), in a study under the direction of Dr. Mary O'Connor (University of British Columbia). In examining the ethanol preserved material, *H. natator* was first found in samples from Louscoone Inlet, a 12 km long inlet at the southern end of Moresby Island in Haida Gwai.

Haida Gwai, formerly known as the Queen Charlotte Islands, are — from sociological, biological, geological, oceanographic, and environmental standpoints — a unique set of islands (Scudder & Gessler, 1989). A good deal of geochemical and biological work has been done on the islands; marine work includes oceanography, fish, introduced species (Sloan & Bartier, 2004), and marine mammals (Heise et al., 2004). Very little work has been done on harpacticoid copepods.

In examining the unique characteristics of the species there was an opportunity to relate the new species to several previously described species and offer possible relationships and a geographic origin for the new species. Of the unique characteristics found in both the male and female, several of those, especially in the male, are structural characteristics also found in species from European waters (e.g., *H. littoralis* (T. Scott & A. Scott, 1893)). A discussion of these characteristics is presented at the end of this paper, along with the possible association of the new species with European counterparts.

MATERIALS AND METHODS

All copepods came from eelgrass (*Zostera marina*) samples collected at 16 locations between Haida Gwaii and the Strait of Georgia Southern Gulf Islands (fig. 1). Each sample consisted of all the eelgrass in a quadrat of $0.25 \times 0.25 \text{ m}^2$, manually removed and detached at the rhizome, and isolated in a $300 \mu\text{m}$ mesh bag or plastic Ziploc[®] bag to prevent escape of small invertebrates. Preservation of eelgrass samples was with 95% ETOH. Organisms and particulates sedimenting from the preserved samples were placed in 50 mm centrifuge tubes and preserved in 95% ethanol. Copepods were isolated from the tube collections using an AmScope dissecting microscope, stained with Chlorazol Black E, in lactic acid, then placed in benzyl alcohol. Specimens were dissected in benzyl alcohol; dissected parts were mounted on slides in Acrytol mounting medium. All figures were obtained using an AmScope Laboratory compound microscope with an 18 mb camera. Amlite was used as an imaging and development environment to obtain picture series; Zerene Stacker was used to produce a focus stack from each series. Adobe Photoshop CS6 was used to adjust or combine stacks. Pictures of entire animals, from individual or combined stacks, were used directly or converted to gray. Procreate I-pad software was used to trace outline figures of appendages and body parts. Using Procreate, background details on the slide picture could be partially retained to provide details deemed beneficial for scientific or artistic purposes.

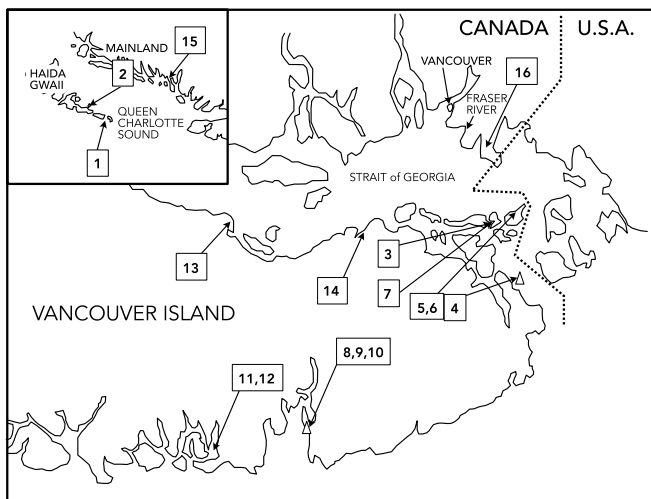


Fig. 1. Map showing the location of the sampling area off British Columbia where the material for this study was collected. Legends: 1–16, the 16 sampling localities visited; HG, Haida Gwaii = formerly Queen Charlotte Islands.

Abbreviations used in descriptions (P1–P6) are from Huys et al. (1996) and used for legs 1–4 on the prosome and legs 5–6 on the urosome. Selection of specimens for the study was not random; female specimens, ovigerous females if available, were chosen to provide the adult figures needed. Adult male specimens were only used to obtain the fully adult dimensions and appendages.

Abbreviation used for reference to the collection: CMNC, Musée Canadien de la Nature/Canadian Museum of Nature, 240 McLeod Street, Ottawa, ON, Canada K2P 2R1.

SYSTEMATICS

Family LAOPHONTIDAE T. Scott, 1905

Genus *Heterolaophonte* Lang, 1948

***Heterolaophonte natator* new species (figs. 2-12)**

Material examined. — Types: Holotype (CMNC 2021-0099) 1 female in 70% ethanol; collected from type-locality [see below] in June 2018. Allotype (CMNC 2021-100) 1 male in 70% ethanol.

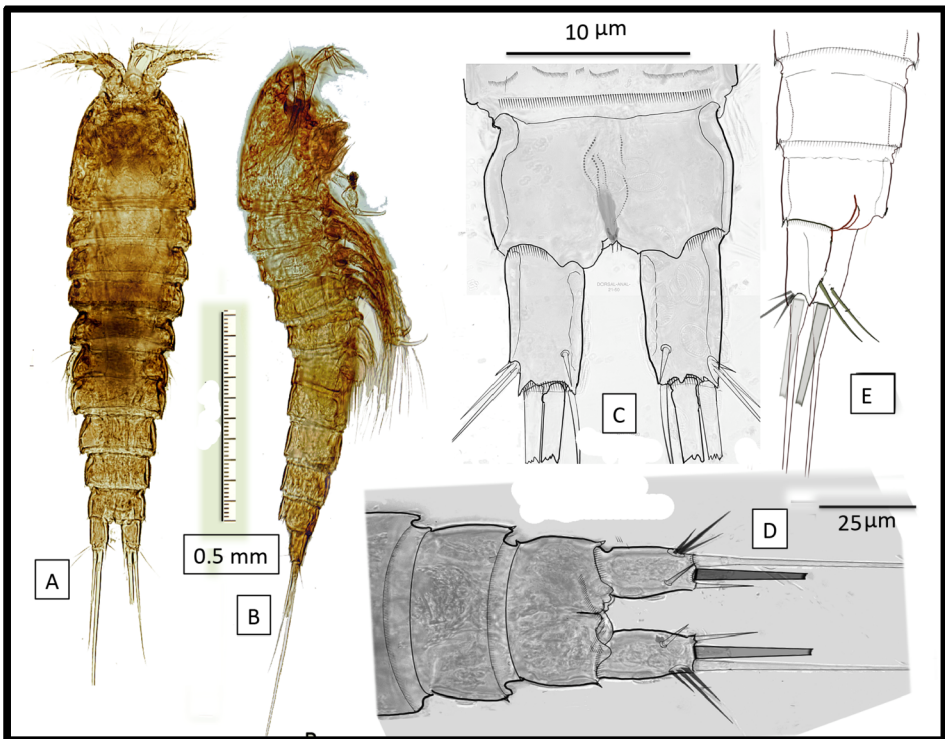


Fig. 2. *Heterolaophonte natator* n. sp. female: A, dorsal view; B, lateral view; C, ventral view — anal segment and caudal rami; D, dorsal view — posterior urosome and caudal rami; E, lateral view — posterior urosome and caudal rami.

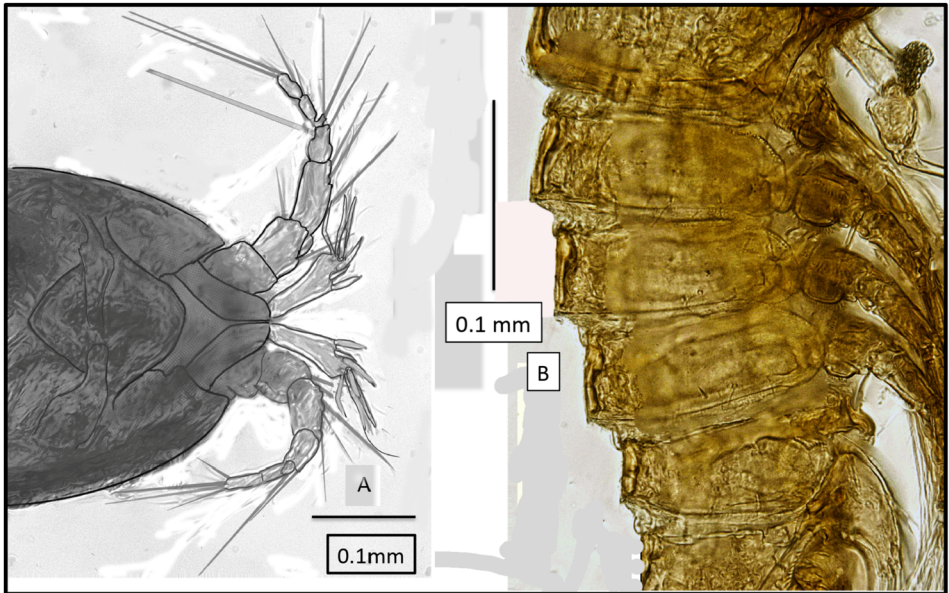


Fig. 3. *Heterolaophonte natator* n. sp. female: A, rostrum, dorsal view; B, metasome, lateral view.

Paratypes (CMNC 2021-0101): 5 females and 2 males (2 tubes) in 70% ethanol; slides: 1 male and 1 female dissected and mounted in Acrytol.

Other material. — Twenty-nine other females from the same locality — examined and measured; mounted after dissection but not part of type material. These specimens were used in a study of the distribution of two species in British Columbia coastal waters. One other, also non-type, male was used in that same way.

Type locality. — Tidal eelgrass (*Zostera marina*) meadow near head of Louscoone Inlet, Moresby Island, Haida Gwaii (52.23°N 131.39°W); all specimens were initially preserved in 95% ethanol.

Description of female (figs. 2-8). — Adult female (fig. 2A, B), total body length average 115 μm ($n = 36$; range = 104–129 μm) measured from anterior margin of rostrum to posterior margin of caudal rami. Body slender from dorsal view, widening from rostrum to widest location, posterior edge of cephalosome (fig. 2A) then tapering irregularly to posterior margin of anal somite (fig. 2A); similar taper observed in lateral view (fig. 2B).

Length of cephalothorax, with its overlaps, slightly greater than metasome length. Cuticle forming envelope, lobate in dorsal view, covering anterior part of prosome (fig. 2A); thickenings support antennules and antennae (fig. 3A). Bar-like cuticular thickenings present on posterior margin of cephalosome. Rostrum small but distinct, lobe-shaped, projecting from cephalothorax, with pair of sensory setules (fig. 3A).

Metasomite surfaces roughened, with lateral areas thickened to appear plate-like (fig. 3B). Plates with scattered, minute sensilla; intersomite connections without

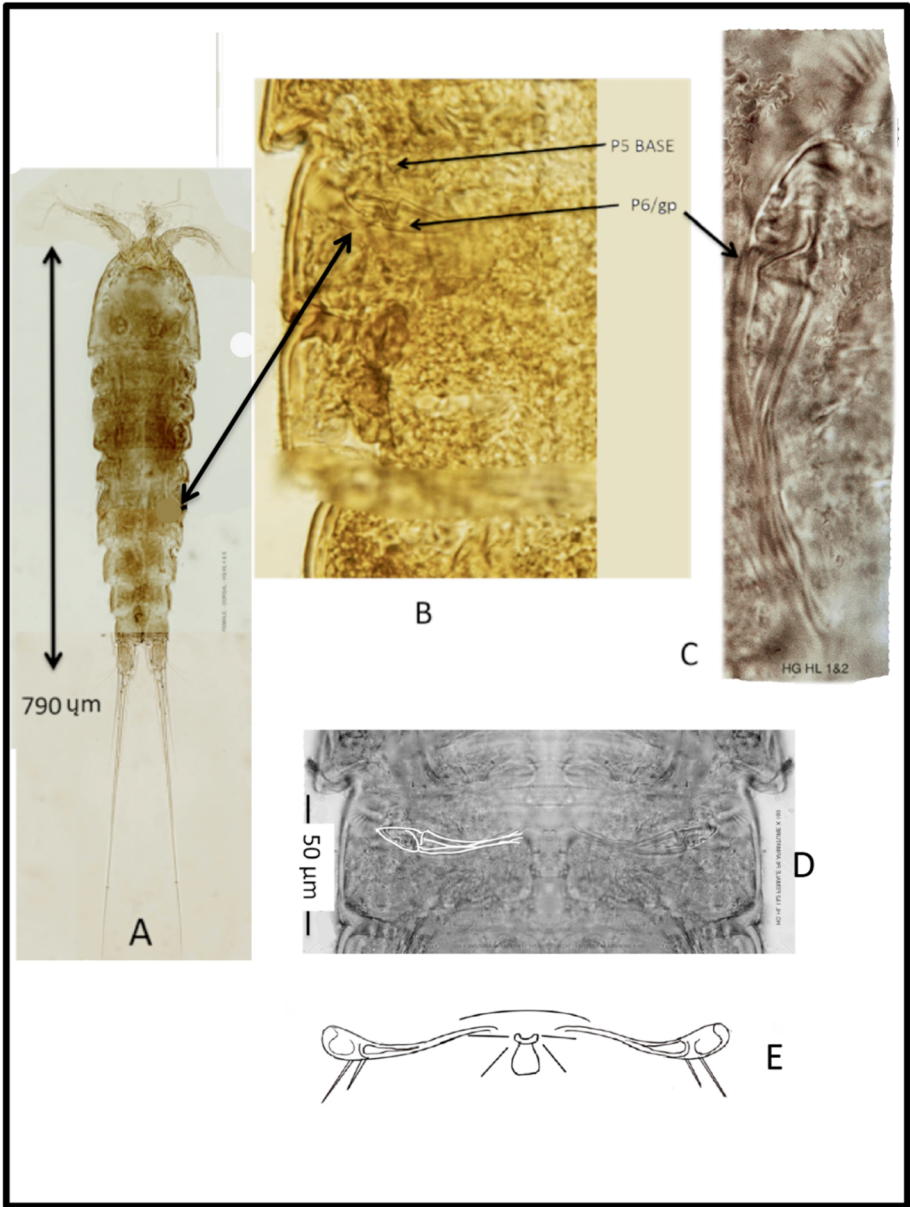


Fig. 4. *Heterolaophonte natator* n. sp. female: A, location of ventral cuticular structures (pair of genital slits) on ventral face of genital double somite; B, this same structure in situ, i.e., ventral aspect of the slit on the right side, with arrows indicating the situation of the basis of the P5 as well as the genital slit with the P6 and the location of the genital pore (gp); C, enlargement of the same slit and genital structures on the right side, also in ventral view, but rotated over 90°; D, ventral view of part of the P5-P6 genital double somite showing genital structures, with the complex on the right side shown in outline. E, *Heterolaophonte mendax* (Klie, 1939), as redrawn from Klie (1941, fig. 37) showing the genital slits with genital pores and associated structures (reduced P5 and P6).

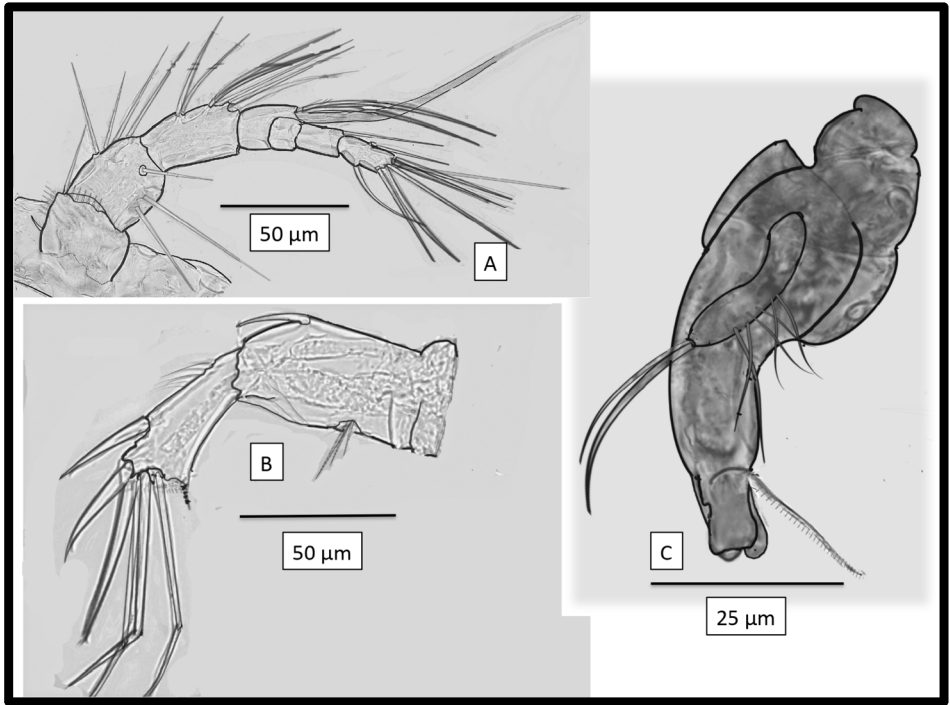


Fig. 5. *Heterolaophonte natator* n. sp. female: A, antennule; B, antenna; C, mandible with gnathobase.

obvious frills. Urosome (fig. 2A, B) of five free somites: including P5-bearing somite, genital double-somite, two free urosomites, and anal somite bearing caudal rami. Female genital double somite showing symmetrical cuticular structure on ventral surface (fig. 4A–D) consisting of two large, transversal genital slits, each lodging much shortened P6 and genital pore. Urosome cuticular surface irregular, with very small denticulations occurring in rows, primarily on posterior dorsal and lateral surfaces of each somite; hyaline areas connecting successive somites narrow. Anal somite with small anal operculum (fig. 2C) flanked by one sensillum on each side and row of denticulations on outer edge of socket of each caudal ramus.

Caudal rami (fig. 2C–E) sub-rectangular in shape, longer than wide (length/width ratio = 1.67–1.70). Each ramus bearing 7 setae: 2 outer dorsal, biarticulate at base (plus spinule at base), 1 very short ventral, 1 longer from near distal inner surface, 1 short terminal and 2 much longer terminal setae; inner one more than 1.5 times length of outer.

Antennule (fig. 4A) 7-segmented; first segment shortest, with spinule rows, third segment longest; fourth segment with long aesthetasc, seventh segment with

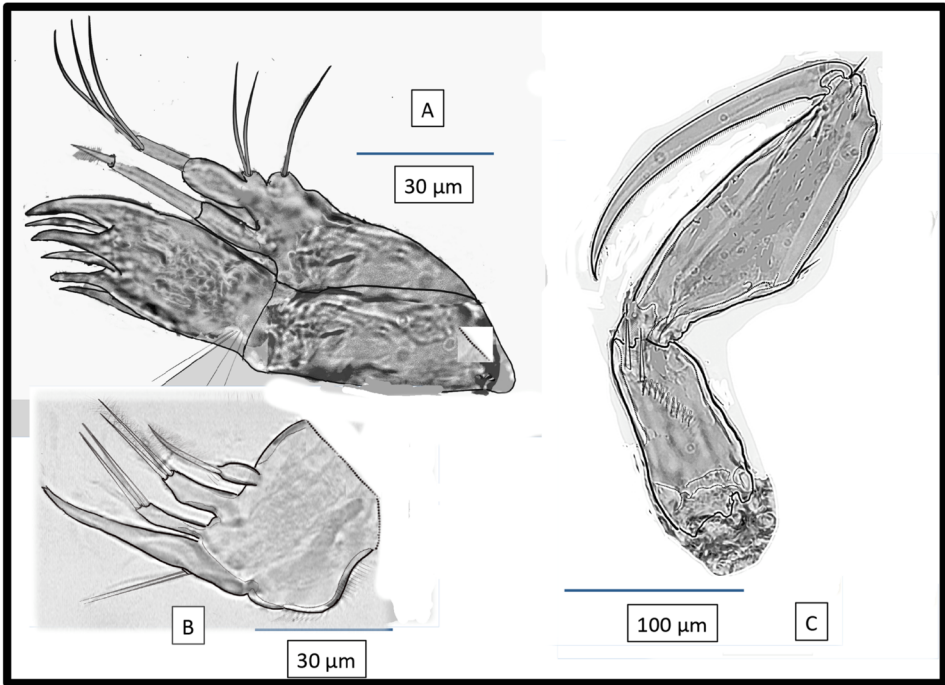


Fig. 6. *Heterolaophonte natator* n. sp. female: A, maxillule; B, maxilla; C, maxilliped (claw serrations present but very small).

acrothek formed by aesthetasc attached to base of pair of terminal setae. Armature formula: 1-[1 + spinules], 2-[7], 3-[7], 4-[2 + (1 + aesthetasc)], 5-[1], 6-[2], 7-[7 + acrothek].

Antenna (fig. 5B) 3-segmented (coxa, allobasis and distinct endopodite). Coxa small and bare, length less than one-third that of allobasis. Allobasis columnar, with one naked abexopodal seta on anterior edge. Exopod (diagnostic) abbreviated, occupying a slight indentation on outer margin of allobasis and bearing 3 setules. Endopodite slender, shorter than allobasis; medial inner margin and distal inner margin each with row of coarse setae, distal row overlapping base of strong spine and situated adjacent to short, spine-like projection. Apical surface of antennae each with one elongate seta, three geniculate setae, and one saber-shaped spine near anterior edge.

Mandible (fig. 5C) with lobate coxa tipped by gnathobase with its three chisel-shaped teeth and slender, long and easily broken pinnate seta on outer margin. [This seta is most likely used for food ingestion (e.g., Lewis et al., 1998).] Mandibular palp one-segmented, elongate, with several small, naked setules and 2 naked terminal setae.

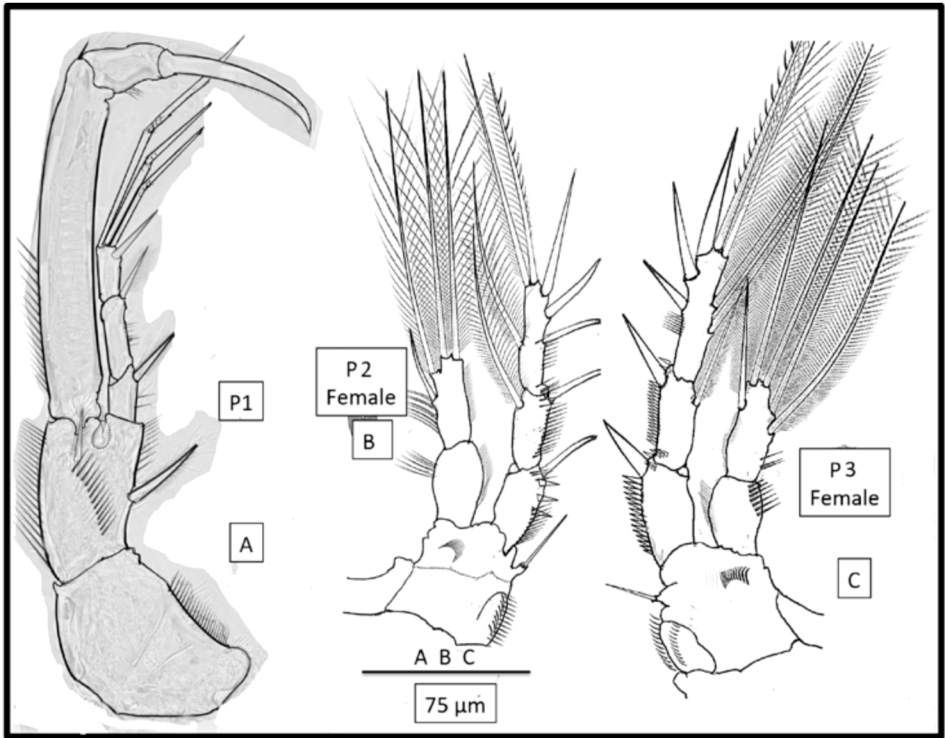


Fig. 7. *Heterolaophonte natator* n. sp. female: A, P1; B, P2; C, P3.

Maxillule (fig. 6A). Praecoxal arthrite with 6 claws on distal surface, one seta on distal surface, and single seta on anterior side (last not visible in fig. 6A). Posterior surface of arthrite palm with 4 hair-like setules. Coxa with hair-like setules on anterior margin; with tube-shaped endite with 1 naked seta and 1 seta with finely toothed margin. Basis with tube-shaped endite bearing 2 naked setae and probe-shaped rod with bushy termination. Knob-like exopodite with single naked setule; knob-like endopodite with 2 naked setae.

Maxilla (fig. 6B) with syncoxa with 3 endites; proximal endite slender, containing seta with bushy termination. Middle endite with slender, naked seta and larger, feathered seta. Distal endite with 2 naked setae. Allobasis with strong, distally feathered claw bearing tiny, knob-shaped endopodite with 2 naked setae.

Maxilliped (fig. 6C) syncoxa with two spines and row of spinules and hairs near outer surface. Basis with single spinule on medial outer surface. Endopodite segment with strong claw with minute serrations and single setule from outer distal surface (base of claw).

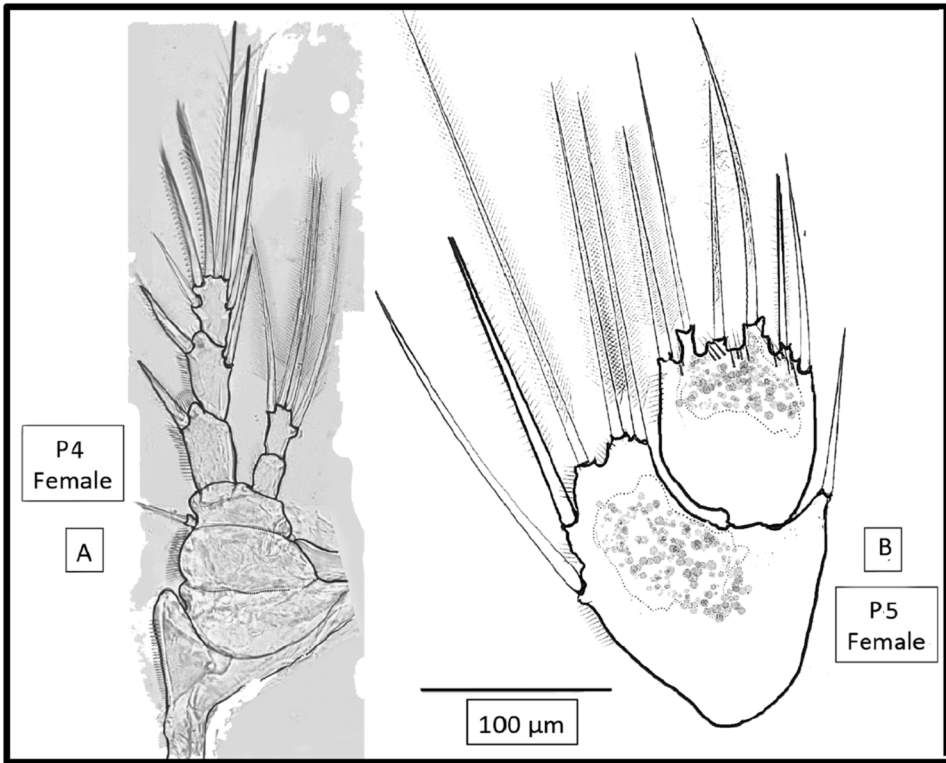


Fig. 8. *Heterolaophonte natator* n. sp. female: A, P4; B, P5.

Thoracic legs 1–4 (figs. 7A, 8B) all with 3-segmented exopodites and 2-segmented endopodites. Intercoxal sclerites variable although generally flat and wide; coxae and bases with rows of spinules.

Thoracic leg 1 (P1; fig. 7A), protopodite with broad coxa, tapering to slightly narrower basis; both segments armed with rows of spinules on lateral margins. Basis also with row of spinules on anterior and posterior surfaces as well as one plumose setule on anterior surface and plumose seta on outer surface. Outer margin of each of all three exopodite segments armed with setules. Segments 1 and 2 each having a plumose spine; segment 3 with a single naked spine, a geniculate seta on distal inner surface and 2 geniculate setae on distal surface. Endopodite segment 1 approximately twice the length of exopodite and bearing row of spinules on proximal half of inner surface and one tiny setule on inner distal margin. Armature of short second segment including row of hair-like setules on outer surface and a large terminal, claw-like spine with a tiny seta at the base; spine with fine, comb-like projections on curved, claw-like outer surface.

Thoracic leg 2 (P2; fig. 7B; table I) (greatest length of figured specimen, excluding armature, 0.99 mm). Coxa and basis together forming 25% of greatest

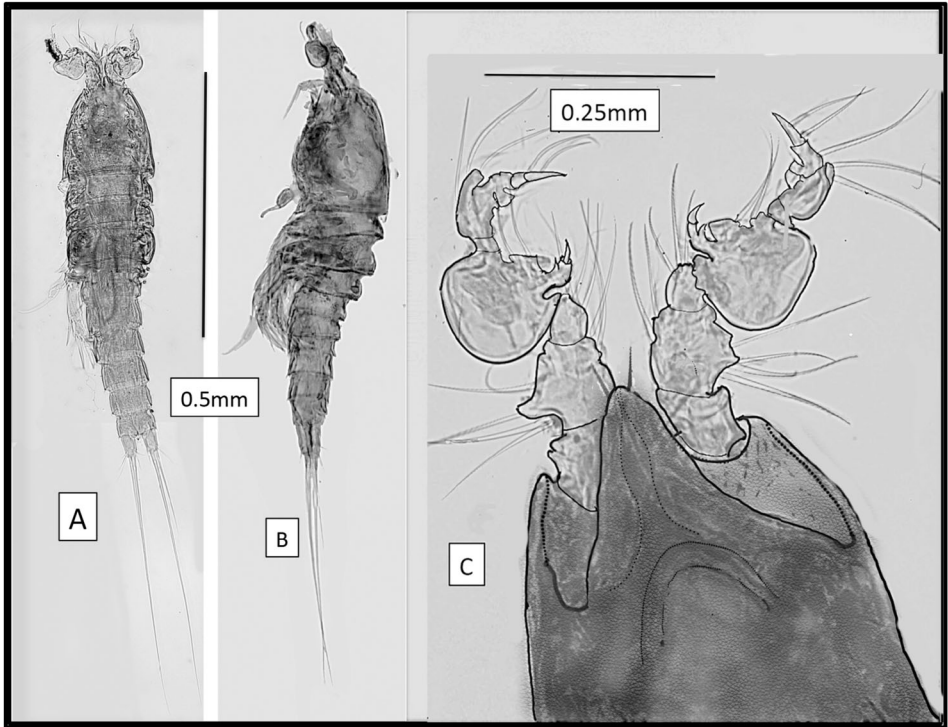


Fig. 9. *Heterolaophonte natator* n. sp. male: A, dorsal view; B, lateral view; C, rostrum and antennules, dorsal.

length of this leg, exopodite 75%; length of 2-segmented endopodite 62% of that of exopodite. Exopodite narrowing distally, endopodite with width remaining fairly constant. (Rows of spinules on outer surface of each exopodite segment, along with the spinule-laden, moon-shaped lobe on outer surface of coxa and the long, naked seta on the basis, being all features of this leg as well as of the third and fourth thoracic legs.)

Thoracic leg 3 (P3; fig. 7C; table I) (greatest length of figured specimen, excluding armature, 1.07 mm). Coxa and basis together forming 28% of greatest length of this leg, exopodite 75%; length of shorter 2-segmented endopodite 49% of that of exopodite. Both rami narrow and tapering only slightly from base to tip. (The unique armatures of the exopodite third segment (2.2.3) and endopodite second segment (1.2.1) are diagnostic features of the female of this species.)

Thoracic leg 4 (P4; fig. 8A; table I) (the smallest of all thoracic legs in the female and the largest in the male). In female, greatest length, excluding armature, 0.49 mm. Coxa and basis together forming 41% of greatest length of this leg, exopodite 59%; endopodite very small, length only 24% of that of exopodite. Both

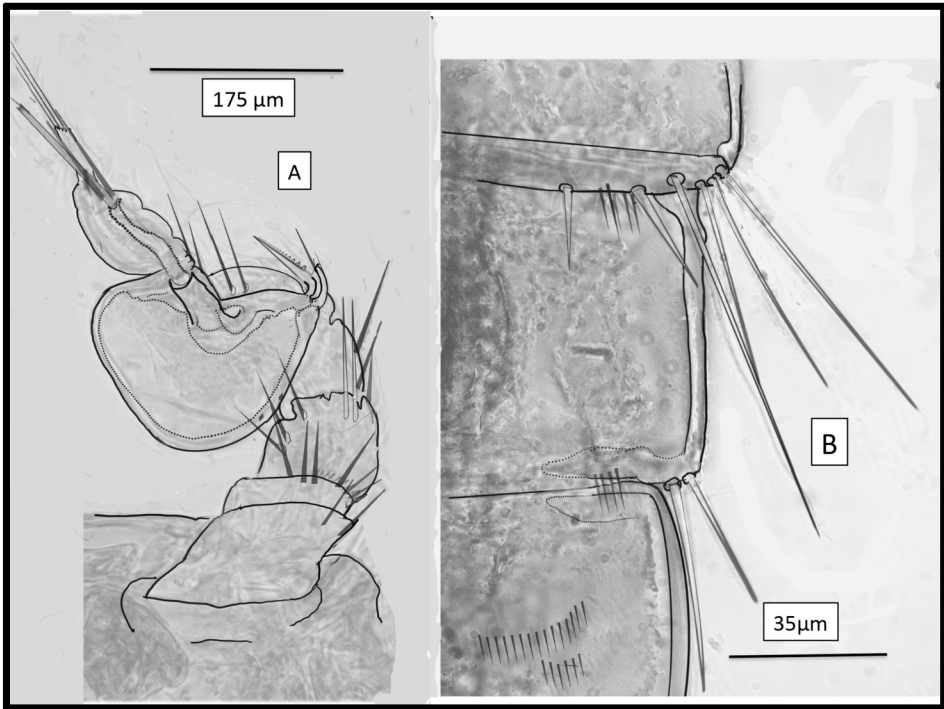


Fig. 10. *Heterolaophonte natator* n. sp. male: A, antenna; B, male P5 and P6 armature.

rami narrow, segment width changing only slightly with length. (Although small, the leg secondary armature (e.g., rows of spines) similar to that of both P2 and P3.)

Fifth leg (P5; fig. 8B). Proximal inner region of baseoendopodite extending laterally to outer margin of exopodite, bearing one naked seta. Inner, lobate surface of baseoendopodite projecting distally to below middle of exopodite, bearing two naked setae on inner surface and three pinnate setae on outer surface. Cup-shaped exopodite bearing 4 pinnate setae in addition to one lightly plumose seta and one naked seta. Surfaces of both endopodite and exopodite covered with very fine spinules.

Description of male (figs. 9–12). — Adult males (fig. 9A, B) smaller and more slender than females. Body length 0.95 mm ($n = 5$; range: 0.85–1.04 mm) measured from anterior margin of rostrum to posterior margin of caudal rami. Body slender, greatest width (26 µm) measured at posterior end of cephalosome. Urosome narrow, 60% of width of P4-bearing somite, narrowest at anal somite. Cuticle ornamentation similar to that of female. Sexual dimorphism present in antennule, swimming legs (P2–P4), P5, P6 and genital body segmentation.

Prosome (fig. 9A) 4-segmented, comprising cephalothorax (including P1 somite) and 3 free pedigerous somites. Rostrum present, in cuticular point of dorsal

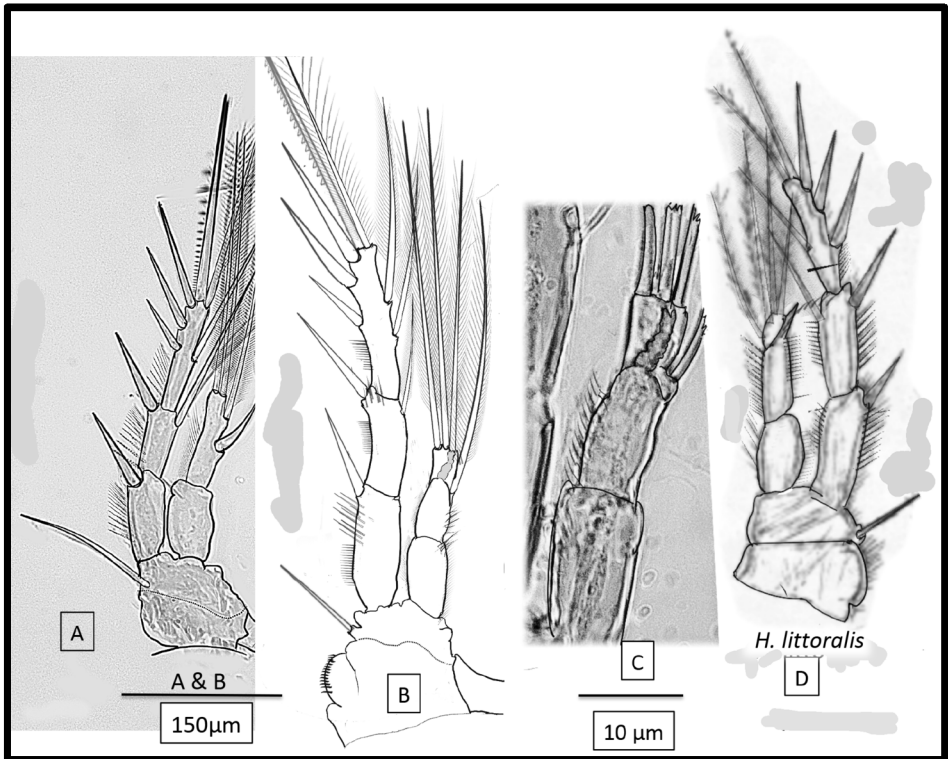


Fig. 11. *Heterolaophonte natator* n. sp. male: A, P2; B, P3; C, P3 endopod enlarged to show second segment with stump; D, P3 of male *H. littoralis* (T. Scott & A. Scott, 1893) with similar modification of endopodite second segment.

head cap; with pair of sensilla (fig. 9C). Urosome (fig. 9A) consisting of P5-bearing somite, genital somite, and 4 free somites, all with densely spaced spinules on posterior margins. Armature of P5 and P6 (fig. 10B) simplified in comparison to female, consisting of 4 large spines, 4 smaller spines and several small clusters of spinules.

Antennule 8-segmented (figs. 9C, 10A), with subchirocer (segment 5) separated from segment 6 by geniculation. Segments 6 (swollen), 7 (slightly swollen), and segment 8 (arrow-shaped) forming attachment structure that, with toothed seta on segment 5, form a crab-like claw. Armature formula: 1-[1], 2-[6 + denticulations], 3-[6], 4-[2], 5-[5 + 1 pinnate], 6-[1 + 2 aesthetascs + 1 special], 7-[0], 8-[2].

Male P1 (see female P1), P2 and P3 similar to those of female (fig. 11A, B), with 3-segmented exopodites and 2-segmented endopodites; intercoxal sclerites relatively flat and wide; coxae and bases both with spinules. In contrast, male inner spine on P2 stronger, coxa and basis shorter than in female.

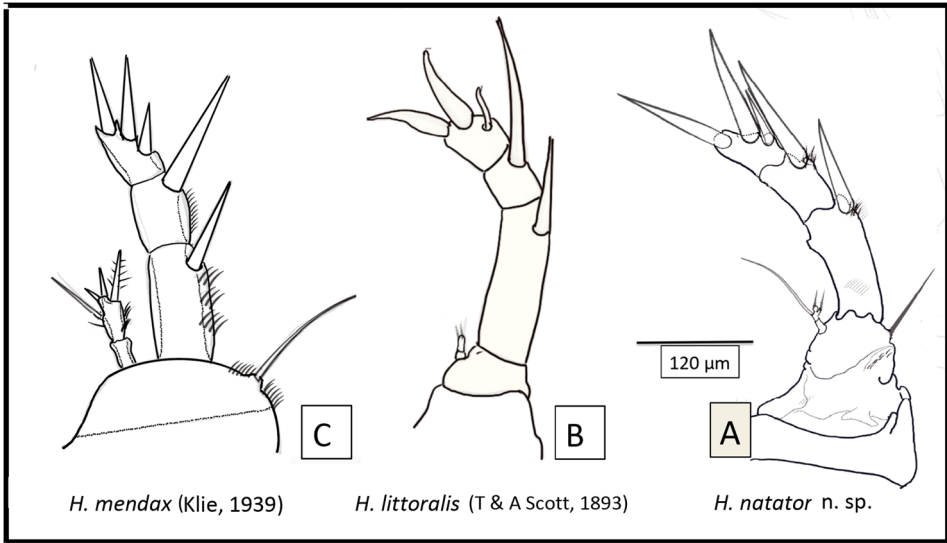


Fig. 12. *Heterolaophonte natator* n. sp. male: A, P4. B-C, Same appendage of two congeners, shown for comparison (see text): B, P4 of *Heterolaophonte littoralis* (T. Scott & A. Scott, 1893); C, P4 of *Heterolaophonte mendax* (Klie, 1939). Adapted from Klie (1941).

TABLE I

P2–P4 armature of female *Heterolaophonte natator* n. sp. as well as similar and local species of *Heterolaophonte*

Species (female)	Data source	P2 Exo	P2 Endo	P3 Exo	P3 Endo	P4 Exo	P4 Endo
<i>H. natator</i> n. sp.	Present study	0;1;1.2.3	0;2.2.0	0;1;2.2.3	0;2.2.1	0;1;1.2.3	0;1.2.1
<i>H. longisetigera</i> (Klie, 1950)	Boer (1971)	0;1;1.2.3	0;2.2.0	0;1;2.2.2	0;1.2.2	0;1;1.2.3	0;1.2.2
<i>H. variabilis</i> Lang, 1965	Lang (1965)	0;1;1.2.3	0;2.2.0	0;1;1.2.3	0;3.2.1	0;1;0.2.2	0;1.2.1
<i>H. stroemii</i> (Baird, 1837)	Sars (1911)	0;1;1.2.3	0;2.2.0	0;1;1.2.3	0;3.2.1	0;1;1.2.3	0;1.2.1
<i>H. discophora</i> (Willey, 1929)	Lang (1965)	0;1;1.2.3	0;2.2.0	0;1;1.2.3	0;3.2.1	0;1; variable	0;1.2.1
<i>H. littoralis</i> (T. & A. Scott, 1893)	Sars (1911)	0;1;1.2.3	0;2.2.0	0;1;1.2.3	0;2.2.1**	0;0.2.3	0;1.2.1
<i>H. hamondi</i> Hicks, 1975	Hicks (1975)	0;1;0.2.3	0;0.2.0	0;1;0.2.3	0;2.2.1	0;1;0.2.3	0;1.2.1
* <i>H. mendax</i> (Klie, 1939) (male)	Klie (1941); Wells (2007)	0;1;0.2.3	0;1.3.0 (0;1.2.1)	0;0;0.2.3	0;1.3.1	0;0;0.2.1	0;1.2.1

*Klie (1939) only provides figures of the male P2–P4.

Male thoracic leg 3; combined lengths of coxa, basis and rami approximating 75% of similar lengths in female. Outer setule of female endopodite replaced by stub in male endopodite (fig. 11A, C). (An analogue of the structure is found in the male P3 of *Heterolaophonte littoralis*, a species that shares many similarities with *H. natator* (fig. 10D).)

Male thoracic leg 4 (P4; fig. 12A) basis and exopodite longer and much larger than in female; endopodite minute, much smaller than female endopodite. Although endopodite seemingly 2-segmented, the division appears incomplete. Distal end of endopodite with one well-developed setule and two very short, hair-like processes. (Wells (1970: 463) notes that the small endopodite is also found in both *H. littoralis* and *H. longisetigera* Klie, 1950 “. . . sometimes with a trace of the ancestral 2-segmented condition — with only 1 well-developed seta.” See fig. 12B for a representation of male P4 of *H. littoralis*.)

Etymology. — The name *natator* (masculine), used in apposition to *Heterolaophonte* (feminine), is Latin for swimmer. It was chosen because the shapes of the body and thoracic legs indicate the potential for swimming. As well, there are no apparent adaptations for long time period attachment to eelgrass or algae although the species could burrow into soft mud. The antennae, mouthparts, and first thoracic legs appear capable of selecting and picking diatoms and other food from a food source. The relatively simple maxillipeds are presumed to serve for short term holding, for protection, to obtain food, or reproduction.

DISCUSSION

Table I provides the armature of legs P2–P4 for similar and locally reported species of the genus *Heterolaophonte*. The species are arranged on the armature similarity of the P3 exopodite and secondarily on the armature of the P3 endopodite. The P3 exopodite armature in *H. natator*, with 2 setae on the inner surface of the third segment and 3 spines on the outer surface, separates the species from *H. littoralis*, as well as from a number of other species reported from British Columbia marine waters (cf. Kask et al., 1986; Webb & Parsons, 1992; Bravender et al., 1993; Cordell, 2000, 2018). One tends to draw conclusions from single armature element differences between species, differences in one ramus that are often offset by the armature of the other ramus. Similarities rather than conclusions often indicate useful trends when attempting to suggest species groups or biogeographically similar origins. Considering a two-element difference — for the P3, the exopodite of *H. natator* with 2 setae on the inner margin of P3 exopodite 3 is only found in *H. longisetigera* (cf. Klie, 1950), while the 2 setae on the inner surface of the P3 endopodite is a feature only found in *H. littoralis* and *H. hamondi*

Hicks, 1975. Of the species in table I, the female P4 exopodite armature is identical in *H. natator* and *H. stroemii stroemii* (Baird, 1837). The trends in both rami of the P3 and P4 suggest similarity between 6 of the 8 species in table I. All 6 are northern, European or Icelandic species, and all are from regions previously exposed to glaciation. This suggests that previously existing species may have followed the advance and retreat of the ice during one or more periods of glaciation, and that this may have caused isolation and subsequent speciation.

The P4 of male *H. littoralis* and *H. natator* (fig. 12) are similar but not identical; the males of these species also have similar but not identical P2–P4 armature. Since *H. littoralis* is from northern Europe and *H. natator* from northern North America, were there links across the North Atlantic during ice-free or low ice conditions in the Arctic, something found in the distribution of the echinoderm *Strongylocentrotus droebachiensis* (O. F. Müller, 1776) (Echinozoa) (cf. Addison & Hart, 2005)? The links may include species in which the male P4 exopodite armature is similar, but the endopodite is of near normal size. *H. mendax* (Klie, 1939) [also erroneously cited as *H. mendax* (Klie, 1941)], for example (fig. 12C), is a species from Iceland that fits the trans-Arctic distribution pattern and, except for the larger endopodite, is comparable with *H. natator* and *H. littoralis*. *H. hamondi* has a P4 similar to that of *H. mendax*, so could be included if the size of the endopodite is relaxed. Interestingly, the P3 endopodite stub or claw is also present on the males of *H. mendax*, *H. littoralis* and *H. hamondi*.

The particular structure of the genital slit complex in female *H. natator* (e.g., fig. 4A–D herein) is comparable to but not identical with the genital structure reported for *H. mendax* (cf. Klie, 1939; fig. 4D herein; see also fig. 37 in Klie, 1941). Although this is another similarity between the North Atlantic species discussed previously, a similar structure has been reported from at least one other species in another genus (*Laophonte depressa* T. Scott, 1894 (compare fig. 33 in Klie, 1941)).

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