

## *APOLETHON HIPPOPERUS* (COPEPODA: HARPACTICOIDA): A NEW SPECIES FROM SOUTHEASTERN ALASKA

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### ABSTRACT

A new harpacticoid copepod species of *Apolethon* (Laophontidae) from the intertidal zone of a subarctic bay in southeastern Alaska is described and illustrated. *Apolethon hippoperus* n. sp. is distinguished from its three congeners (*A. fumator*, *A. trigonus*, *A. bilobatus*) by paired pleural glands on the third urosomite. Adult *Apolethon hippoperus* bear conspicuous ovoid mucin structures located laterally on the double genital somite, originating from the pleural glands. Based on the description of *A. hippoperus* generic affinities become problematic. An examination of the apomorphies (P1 morphology, type of sexual dimorphism of male P3, P2-P4 with 2-segmented endopods; setation on A2 exopod, maxillular arthrites and basis, setation of mandibular palp) defining the Laophontoidea sensu Huys 1990 suggests that *Apolethon* is a laophontoidean but not a laophontid. Currently, we cannot place *Apolethon* with certainty in any known family of the Laophontoidea and recommend that *Apolethon* is placed as genus incertae sedis in Laophontoidea. This is the first taxonomic report of the genus *Apolethon* from the western hemisphere.

### INTRODUCTION

A new species of harpacticoid copepod was discovered during an investigation of a meiobenthic intertidal community in southeastern Alaska. *Apolethon hippoperus* n. sp. was collected from a muddy beach in Auke Bay, Alaska, which has been the site of long-term meiofaunal studies (Sturdevant, 1987; McGregor, 1991; McCall, 1992; Schizas and Shirley, 1996).

The harpacticoid copepod fauna of southeastern Alaska is not well known (Fleeger and Shirley, 1990; Schizas and Shirley, 1996), but a number of new copepods have been described in Auke Bay (Gee, 1988; Gee and Fleeger, 1990; Schizas and Shirley, 1994a). In an unpublished Master's thesis, Cordell (1986) reported a species of the genus *Apolethon* Wells 1967 from Spuhn Island, Auke Bay, as *Apolethon* cf. *bilobatus*. They probably represented *A. hippoperus* (J. Cordell, personal communication), but these material are no longer available. With the present addition, the genus *Apolethon* now includes four species: *A. fumator* Wells 1967, *A. trigonus* Shen and Tai 1973, *A. bilobatus* Shen and Tai 1973 and *A. hippoperus* n. sp.

### MATERIAL AND METHODS

All specimens examined were collected from a single location in Auke Bay (58°22'N, 134°40'W), approximately 19 km north of Juneau, Alaska. The type locality is an intertidal beach, approximately 60 m wide, and was sampled from March, 1992 to April, 1993 (Schizas and Shirley 1996). The biota and hydrography of Auke Bay has been reviewed by Coyle and Shirley (1990). The low relief beach is characterized by a barnacle-*Fucus* zone in the high intertidal, which changes to a *Mytilus trossulus* zone in the mid intertidal. The mudflat begins just above mean low tide level. There are patches of the sea grass *Zostera marina* throughout the mudflat. Four replicate cores were collected at randomly selected sites along a transect paralleling the 0 m tidal level. Cores were extracted twice a month from March, 1992 to April, 1993. Only the upper 2 cm of the sediment within the hand-held, piston corer (50 cc syringe) were processed since >90% of the

harpacticoids occur in the upper 10 mm of muddy substrates (Shirley et al., 1990; Fleeger et al., 1995). Sediments were washed through 0.500 mm and 0.063 mm sieves to separate macrofauna from meiofauna. Meiofauna were stained with rose bengal to facilitate sorting and were preserved in 10% buffered formalin. Observations of living *A. hippoperus* were made from additional samples collected from the type locality. Methodological details were provided by Schizas and Shirley (1994b).

Copepods were dissected in lactic acid and water. The dissected copepod parts were mounted on microscope slides in Hoyer's media and cover slips sealed with clear fingernail polish. Figures were drawn using a camera lucida attached to an American Optical Microstar (One-Ten) microscope. Additional observations on dissected specimens were made with an Olympus BX51 Nomarski DIC microscope. Descriptive terminology is adopted from Huys and Boxshall (1991) and Huys et al. (1996). The caudal setae naming and enumeration system proposed by Huys (1988) was followed. Abbreviations in the text and figures are: A1, antennule; A2, antenna; ae, aesthetasc; exo, exopod; end, endopod; P1-P6 first to sixth thoracopod; exopod(endopod)-1(2,3) to indicate the proximal (middle, distal) segment of a ramus. Length of specimens was measured from tip of rostrum to posterior edge of caudal rami. Width of specimens was measured across the posterior border of the cephalosome.

### SYSTEMATICS

#### Genus *Apolethon* Wells, 1967 *Apolethon hippoperus* n. sp.

Material Examined.—Holotype: female dissected on 4 slides USNM No. (1071934). Allotype: 1 male dissected USNM No. (1071935). Paratypes: 1 dissected female USNM No. (1071936), and 1 whole male with two additional male urosomes mounted on 1 slide USNM No. (1071937), and 20 females and 10 males preserved whole in 95% ethanol USNM No. (1071938).

Type Locality.—Auke Bay, Alaska (58°22'N, 134°40'W) from a mudflat, tidal depth 0 m. All specimens were collected by the senior author during March 1993-March 1994.

Description of Female.—Body translucent; single red pigmented eye present near anterior edge of cephalothorax. Females ranged from 0.640 to 0.813 mm in length (mean  $\pm$  standard deviation =  $0.709 \pm 0.044$ ,  $n = 25$ ) and 0.189 to 0.247 mm in width (mean  $\pm$  standard deviation =  $0.210 \pm 0.013$ ,  $n = 25$ ); body length of holotype 0.767 mm. Oviparous females with a single egg sac. Body robust and tapering posteriorly (Figs. 1A, 1B); no abrupt change in body width and slight body flexure at junction of prosome and urosome. Cephalothorax including rostrum about the length of the four succeeding somites combined (Fig. 1A). Cephalothorax with fine surface striations, body somites covered with minute denticles, dorsally and laterally; posterior edges of all somites except anal somite with minutely serrate hyaline frill (Figs. 1A, 1B). Sensillae present around posterior margins of cephalothorax and four succeeding somites. Free thoracic somites with well-developed epimeral plates. Genital double somite original division marked dorsally and laterally by a cuticular ridge, (Figs. 2B, 4D) and fused ventrally. Paired pleural gland present laterally in posterior half of genital double somite (Figs. 2B, 3A). Pleural gland surface densely covered with denticles, more pronounced than those of surrounding areas. A mucin structure originates from the pleural glands and extends maximally from the second to the fourth urosomite. Genital field (Figs 2B, and 4D); vestigial P6 with a pinnate seta. Genital double-somite and urosomites 4-5 with spinules around ventral posterior margins (Fig. 2B). Anal somite (Fig. 2B) slightly divided medially; anal operculum furnished with row of short stout spinules and fine setules (Fig. 1B). Caudal rami about twice as long as wide (Fig. 2C). Setae I and II slender, naked, inserted on outer margin; seta III slender, naked, positioned lateroventrally on outer margin; terminal seta V, longest, pinnate in distal three quarters, fused at base with pinnate seta IV; seta VI slender, dorsal seta VII bi-articulate, inserting on raised pedestal.

Rostrum (Fig. 4A). Distinct, triangular, with two sensilla and a pore near anterior end of dorsal surface.

Antennule (Fig. 4B). Five-segmented. Segment I with two spinule row and seta at ventral distal corner. Segment II longer than wide, with eight setae: 5 setae in distal half along anterior margin and 3 medially pointing posteriorly. Segment III with 7 setae and aesthetasc: 5 setae medially along anterior margin, and 2 long, slender setae arising from distal, ventral pedestal. Segment IV with 1 long slender seta along anterior margin. Segment V with aesthetasc and 9 setae: 3 elements along anterior margin (2 robust spines and 1 simple seta), 5 setae medially near distal posterior corner and an acrothek consisting of 1 seta and an aesthetasc. Armature formula as follows: 1-(1), 2-(8), 3-(7+ae), 4-(1), 5-(8+acrothek).

Antenna (Fig. 4C). Coxa with row of spinules on anterior margin. Allobasis with 2 spinule rows without armature. Exopod 1-segmented with four setae: 1 lateral pinnate, 2 apical pinnate and 1 outer minute seta. Endopod with rows of spinules near proximal and distal anterior corner and fine spinules on distal posterior corner; lateral armature arising in distal half, comprising 2 spines and 1 naked seta; apical armature consisting of 2 spines and 3 geniculate setae and a very fine seta.

Mandible (Fig. 3B). Gnathobase well-developed; cutting edge with 4 short bi- or tridentate teeth (Fig. 3C), 1 pinnate seta and 1 slender spinule on distal margin. Palp 1-segmented, exopod and endopod fused to basis. The armature is: 2 lateral (basal) setae, 3 (1 bare and 2 pinnate) distal (endopodal) setae and 1 outer (exopodal) pinnate seta.

Maxillule (Fig. 3D). Precoxal arthrite with 6 recurved spines and a short pinnate seta on distal margin; anterior surface without setae. Coxa without epipodite; coxal endite with 2 setae; basal endite with 3 setae distally. Exopod and endopod incorporated into basis and represented by tiny pedestals bearing 2 and 3 setae respectively.

Maxilla (Fig. 3E). Syncoxa with spinule row on outer margin, transverse spinule row and row of very fine pinules on inner margin; with two well developed endites each with 3 setae, 3rd (proximal) vestigial endite, represented by 1 seta. Allobasis with strong terminal spine and 2 accessory setae. Endopod 1-segmented with 2 terminal setae.

Maxilliped (Fig. 3F). Subchelate. Syncoxa with 2 spinule rows, and seta on distal margin. Basis ovoid, with row of strong spinules along palmar margin. Endopod 1-segmented, claw longer than basis, with 1 tiny accessory seta.

P1 (Fig. 5A). Intercoxal plate well developed without ornamentation. Precoxa with spinule row on distal margin. Coxa with spinule row near inner distal corner; bilobed outer margin with 2 spinule rows. Basis elongate, with row of spinules around insertion of bipinnate inner spine, along inner margin, on posterior surface and around insertion of outer bipinnate spine. Exopod 3-segmented, all segments with row of spinules along outer (outer) and inner (fine) margin; proximal and middle segments with minutely spinulose outer spine (proximal segment with additional spinule row as figured); distal segment with two terminal pinnate setae and two minutely spinulose outer spines. Endopod 2-segmented; proximal segment elongate, reaching beyond exopod, with spinules on inner and outer margins; with sparsely plumose inner seta in distal third; distal segment with 1 terminal pinnate seta and 1 claw.

P2-P4 (Figs. 5B, 6A, B). Intercoxal plates well developed without ornamentation (only figured for P3). Precoxae with row of spinules on distal margin. Coxae with two lobes on outer margin; both furnished with spinules distally. Bases with spinules near insertion of endopod; outer setae slender. Exopods 3-segmented, each with row of stout spinules along outer and distal margins; outer spines minutely spinulose. Endopods 2-segmented, shorter than exopods, distal segment 3 to 4 times longer than proximal segment.

Setal formula as follows:

	Exopod	Endopod
P2	0.1.022	0.010
P3	0.1.022	0.021
P4	0.1.022	0.011

P5 (Fig. 7A). Baseoendopod and exopod separate. Exopod small, with 3 pinnate setae, apical most seta longest; row of spinule pattern as figured. Baseoendopod with outer setophore bearing naked seta; spinule pattern as figured. Endopodal lobe, relatively well developed, with 5 pinnate setae.

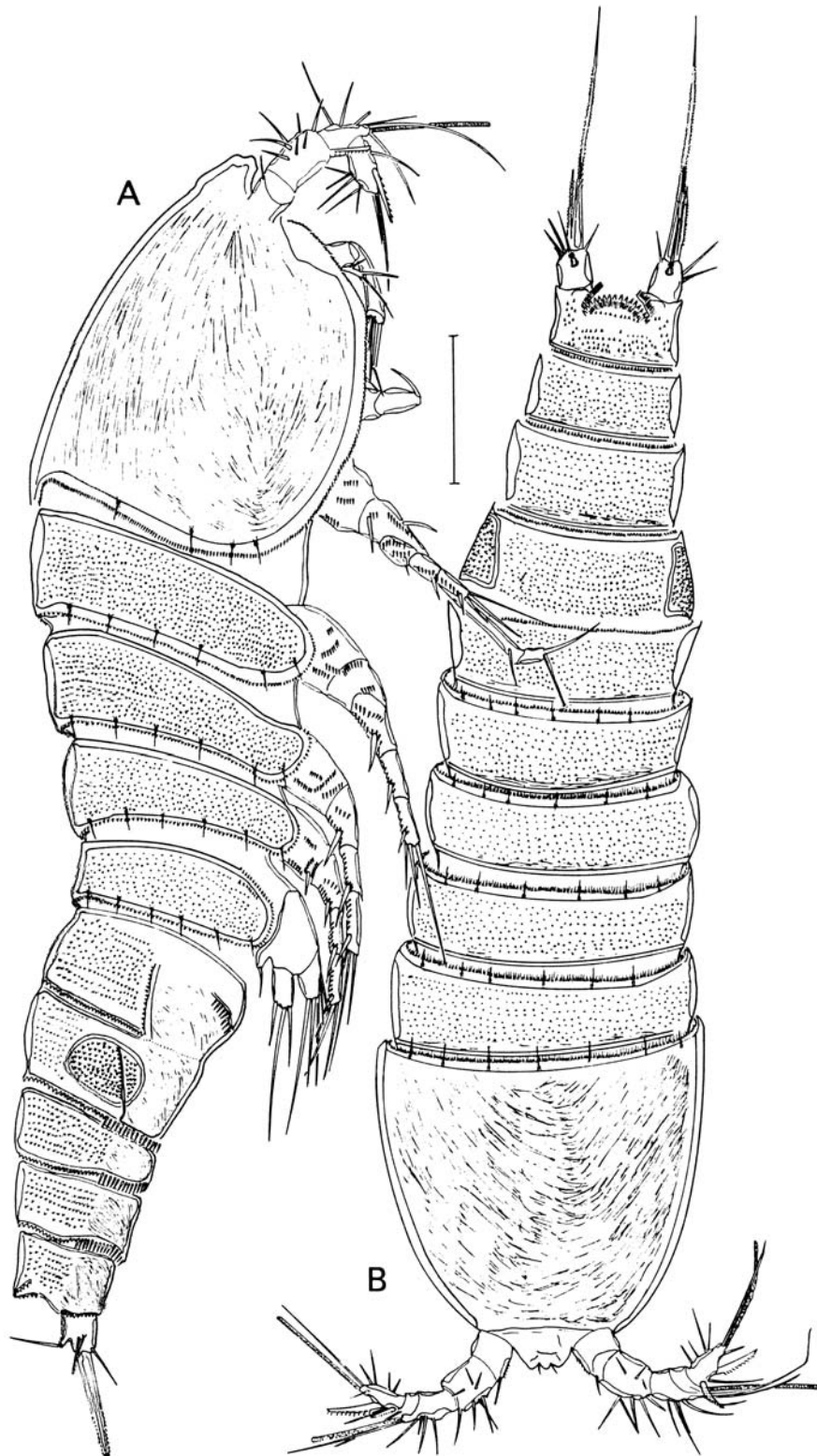


Fig. 1. *Apolethon hippoperus* n. sp. Female. A, habitus, lateral; B, habitus, dorsal. Scale = 0.1 mm.

Description of Male.—As in female, except in the following characteristics.

Body. (Figs. 8A, 8B). Smaller than female; width varied from 0.147 to 0.173 mm (mean  $\pm$  standard deviation =

$0.154 \pm 0.006$  mm,  $n = 25$ ), length varied from 0.474 to 0.589 mm (mean  $\pm$  standard deviation =  $0.525 \pm 0.032$  mm,  $n = 25$ ); body length of paratype 0.535 mm. Urosomites 2 and 3 not fused. Caudal seta V much longer than in female.

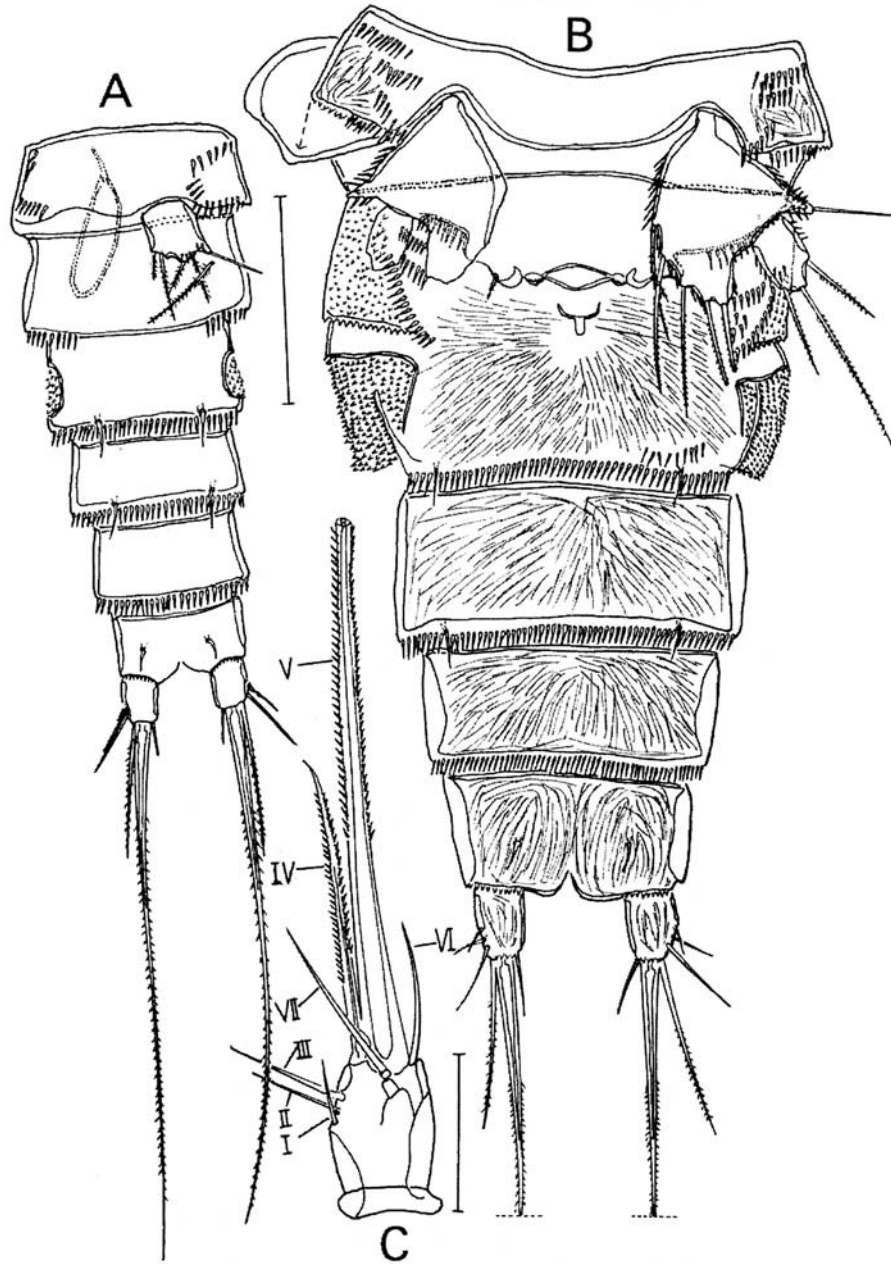


Fig. 2. *Apoletion hippoperus* n. sp. Male. A, urosome ventral. Female. B, urosome ventral (urosome has been dorsoventrally compressed due to mounting); C, dorsal right caudal ramus. A, B scale = 0.1 mm; C, scale = 0.03 mm.

Pleural gland and conspicuous mucin structure present laterally on second urosomite. Hyaline frills present on all somites except anal somite. As in female, all ventral posterior margins of urosomites 3-5 ornamented with spinules (Fig. 2A).

Antennule (Figs. 9A-D) 6-segmented, subchirocer with 1 segment distal to geniculation. Segment I, with 3 rows of spinules and 1 seta in distal corner. Segment II longer than wide, with 9 setae (3 posteriorly directed and 6 setae on anterior margin). Segment III almost square with 9 setae (Fig. 9B). Segment IV swollen, with 2 bare setae, one of them fused with aesthetasc arising from pedestal (Fig. 9C), plus 10 elements: 2 pinnate, 8 naked setae and 2 modified elements,

both as viewed in Fig 9C. A denticulated structure (proximal most crenulate, distal most spinous and striated) present on the same segment (indicated by arrow, Fig. 9C). Segment V hook-shaped, with 8 setae + aesthetasc, all bare (Fig. 9D).

P1, P2, P4. As in female.

P3 (Fig. 7B). Intercoxal plate, coxa, basis and exopod as in female. Endopod 3-segmented; middle segment with distal apophysis; distal segment, twice as long as wide, with long terminal pinnate seta.

P5 (Fig. 7D). Baseoendopod and exopod fused to form single plate; outer basal seta arising from short setophore; baseoendopodal lobe with 2 pinnate setae, outermost longest; exopodal lobe with 3 pinnate setae.

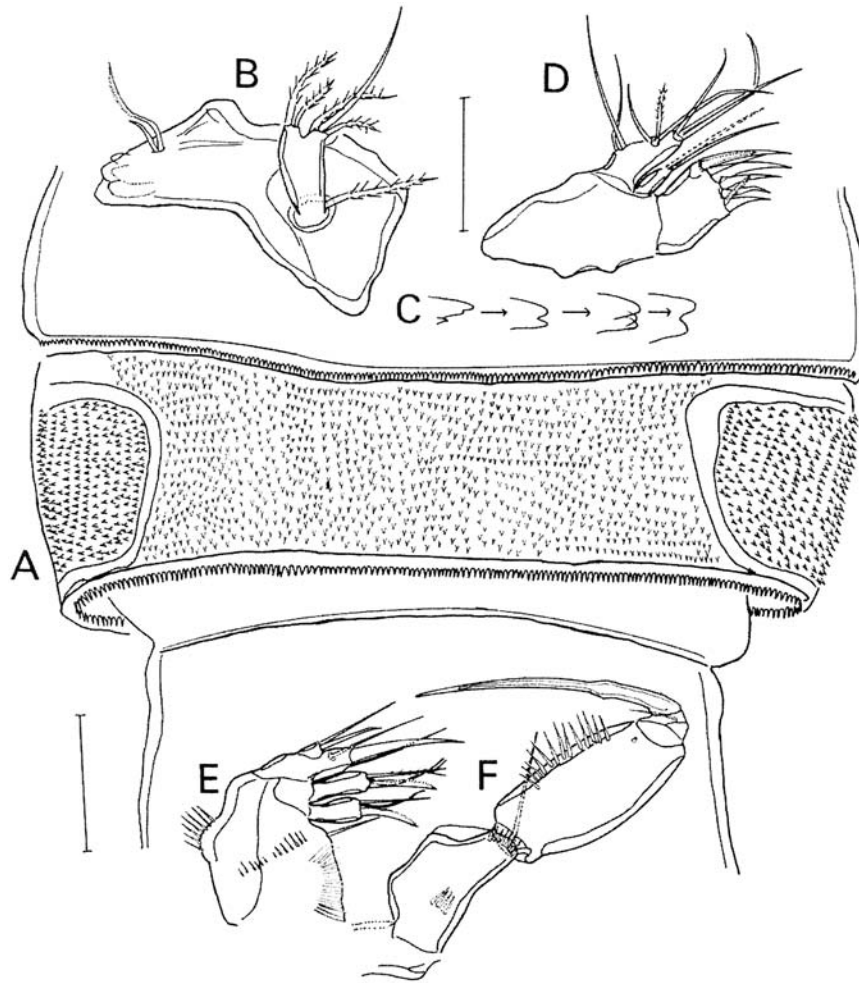


Fig. 3. *Apolethon hippoperus* n. sp. Female. A, urosomite 3 with lateral pleural glands, dorsal; B, mandible; C, mandible, successive teeth of cutting edge of gnathobase (from interior to exterior); D, maxillule; E, maxilla; F, maxilliped. Scale = 0.03 mm.

P6. Vestigial. No setae are present. Ventral side of somite slightly asymmetrical (not shown).

Spermatophore. Males have one spermatophore with short neck (Figs. 2A, 8B). Length = 60  $\mu$ m.

Variability. In one of the dissected females, asymmetry was noted between the left and the right ramus of the fourth swimming leg (Fig. 7C). All three segments of the exopod lacked outer spines, the shape of the segments was different from the common morphology; endopod with two segments, wider than in most specimens, articulation between proximal and distal segment slightly visible. The low incidence of P4 asymmetry suggests that the specimen was aberrant. Another dissected female specimen was observed with six and five pinnate setae on the right and left P5 baseoendopod (ventrally), respectively (not shown).

Remarks.—In marked contrast to females, all adult males strongly flexed when preserved.

Etymology.—The specific name *hipperus* is the Greek name for saddlebag. “Saddlebags” was the nickname originally applied to this copepod by Dr. J. McCall, referring to its conspicuous mucin structures.

Autecology.—The life history and ecology of *A. hippoperus* have been discussed in Schizas and Shirley (1994b). In summary, *A. hippoperus* was the fifth most abundant harpacticoid species at the type locality. *Apolethon hippoperus* was present in relatively high densities ( $7.6 \pm 4.5$  to  $124.3 \pm 12.5$  per 10  $\text{cm}^2$ ; mean  $\pm$  one standard error) at the 0 m tidal level from March to July, 1992. The sex ratio of *A. hippoperus* varied directly with population density, varying from 1:12.7 to 1:1.6 (male:female) during the study period. Copepodites attained maximum densities during March of 1992 and 1993 ( $27.7 \pm 2.2$  per 10  $\text{cm}^2$  and  $45.8 \pm 6.8$  per 10  $\text{cm}^2$ ).

Behavioral Remarks.—In the Laophontoidea, the female site of precopulatory clasping by the male is primitively by the caudal setae, but in Laophontidae it is on the fourth leg, an apomorphic and diagnostic character for this family. In all copulatory pairs of *Apolethon hippoperus* males grasps the female in dorsal aspect (male ventral body surface atop female dorsal surface). Male *Apolethon hippoperus* clasp female copepodites IV and V and adults with the fourth segment of the antennule. The presumptive point of attachment is a denticulate structure (Fig. 9C) on segment IV, which

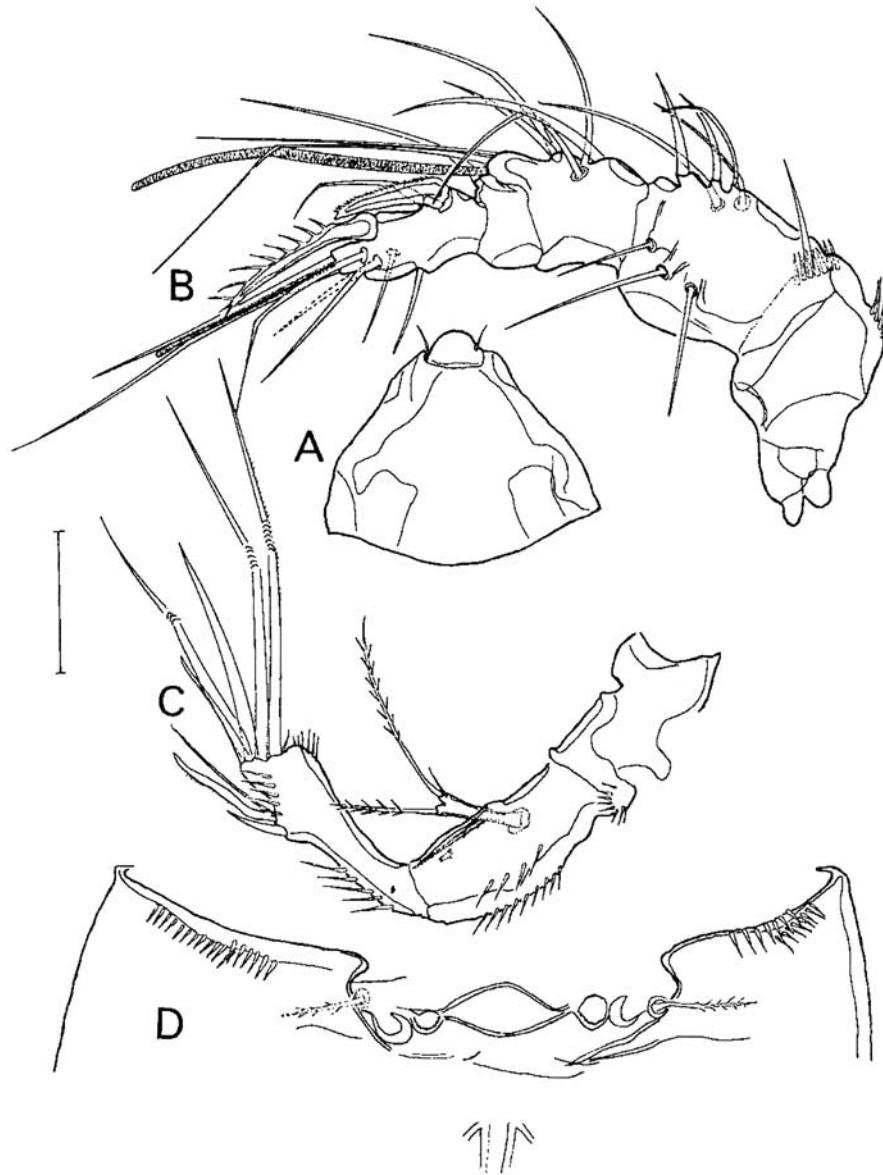


Fig. 4. *Apoethon hippoperus* n. sp. Female. A, rostrum dorsal; B, antennule ventral; C, antenna; D, genital field. Scale = 0.03 mm.

remains attached to females when preserved claspings pairs are separated.

#### DISCUSSION

The taxonomic history of the superfamily Laophontoidea is complex. The Langian scheme (Lang 1944, 1948) of the Laophontidae comprised 19 genera (in the 3 subfamilies Laophontinae, Normanellinae and Donsiellinae), which were grouped together with Cletodidae and Ancorabolidae in the superfamily Cletodidimorpha. Por (1986) suggested the name Laophontoidea to accommodate the Laophontidae and Ancorabolidae. Por's concept of Laophontoidea has been refuted (Huys 1990b) and redefined by subsequent work from several workers. Hicks (1988) moved the subfamily Donsiellinae (ex Laophontidae) to Thalestridae. Huys and Willems (1989) showed that the subfamily Normanellinae Lang, 1944 is a polyphyletic assemblage of

genera, most of which are unrelated to the Laophontidae. Huys and Willems (1989) removed *Laophontopsis* Sars (syn. *Cleta* Claus) to a new family, the Laophontopsidae, and under the nominal family Normanellidae defined two sub-families, the Normanellinae (to include the genus *Normanella* Brady) and the Cletopsyllinae (to accommodate the genus *Cletopsyllus* Willey and possibly incertae sedis *Pseudocletopsyllus* Vervoort). Huys (1990a) showed that the genus *Pholoneta* was not a laophontid but a specialized member of the Diosaccidae. Huys (1990b) established the family Cristacoxidae to accommodate the genera *Cristacoxa* Huys, *Noodtorthopsyllus* Lang (ex Canthocamptidae) and *Cubanocleta* Petkovski (ex Laophontidae). In Huys (1990c), the family Adenopleurellidae was established to accommodate *Miroslavia* Apostolov, *Proceropes* Huys, and the laophontid *Sarcocletodes* Wilson. The superfamily Laophontoidea was redefined by Huys (1990b) to include the

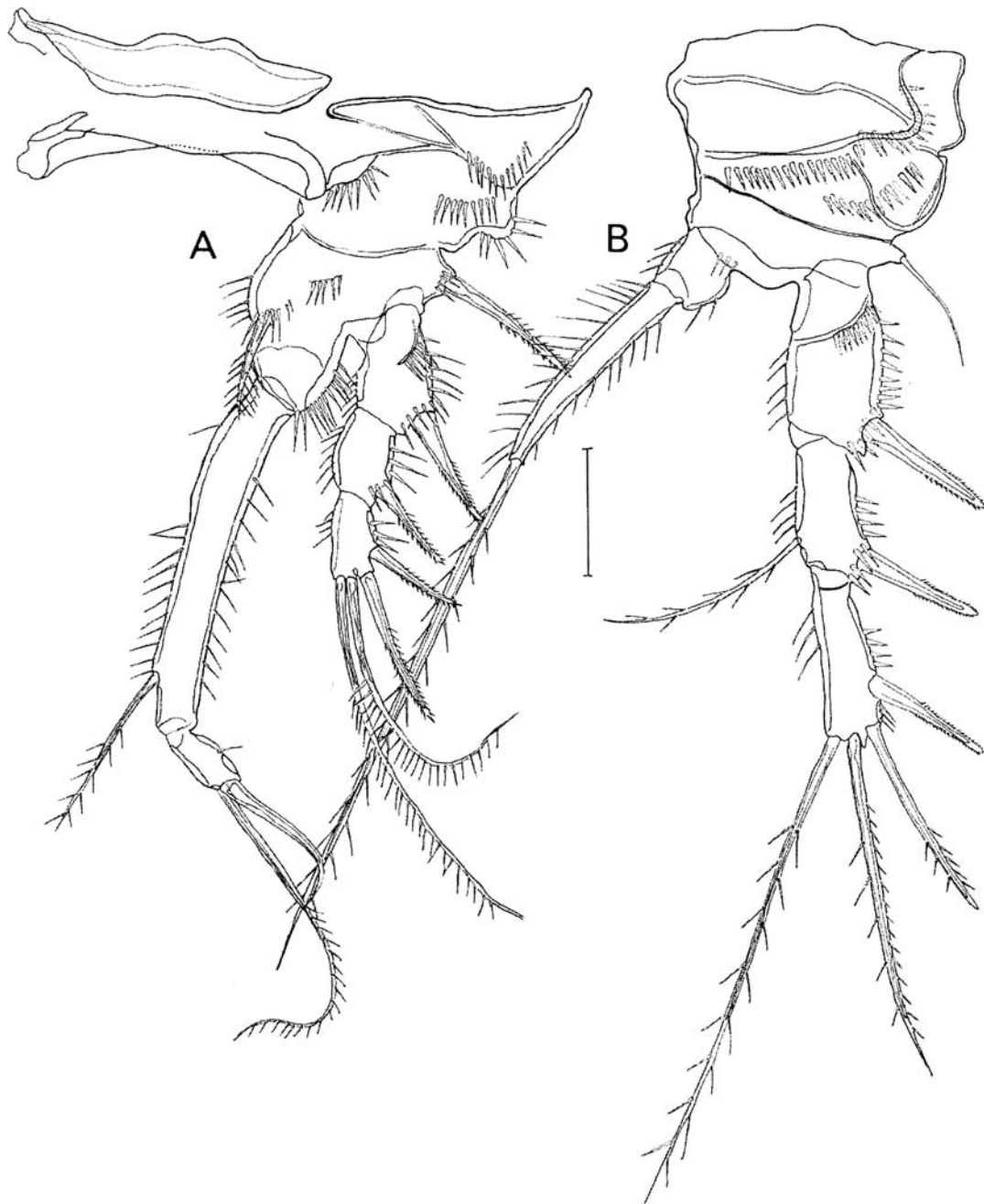


Fig. 5. *Apolethon hippoperus* n. sp. Female. A, P1 anterior; B, P2 anterior. Scale = 0.03 mm.

families Laophontidae, Laophontopsidae, Orthropsyllidae, Cristacoxidae and Adenopleurellidae on the basis of eight apomorphies. Lee and Huys (1999) erected new laophontid genera (*Bathylaophonte*, *Psammoplatypus*, and *Heteronychocamptus*) and redefined *Paronychocamptus* and *Onychocamptus*. In a phylogenetic study of Laophontidae, Huys and Lee (2000) recognized 2 sub-families within Laophontidae: the Laophontinae, and the Esolinae.

Wells (1967) created and placed the genus *Apolethon* in the Langian family Laophontidae, based primarily on the structure of the P1 endopod, but could not assign it with certainty to either of the then recognized Laophontinae or

the Normanellinae. Wells (1967) stated 4 characters that render the position of *Apolethon* within Laophontidae problematic: 1) fused P5 in females, 2) reduced setation in swimming legs, 3) the 3-segmented endopod of P3 in males, and 4) modified P4 endopod in males. With the presence of other problematic genera in the family Laophontidae sensu Lang (1948) such as *Pholoneta* Vervoort, 1964, Wells (1967) suggested that Lang's subfamilial division was not valid and that the Laophontidae should be regarded as a heterogeneous mixture of genera with certain shared characters which differentiate them from other harpacticoid families. Since then, the Normanellinae has been elevated

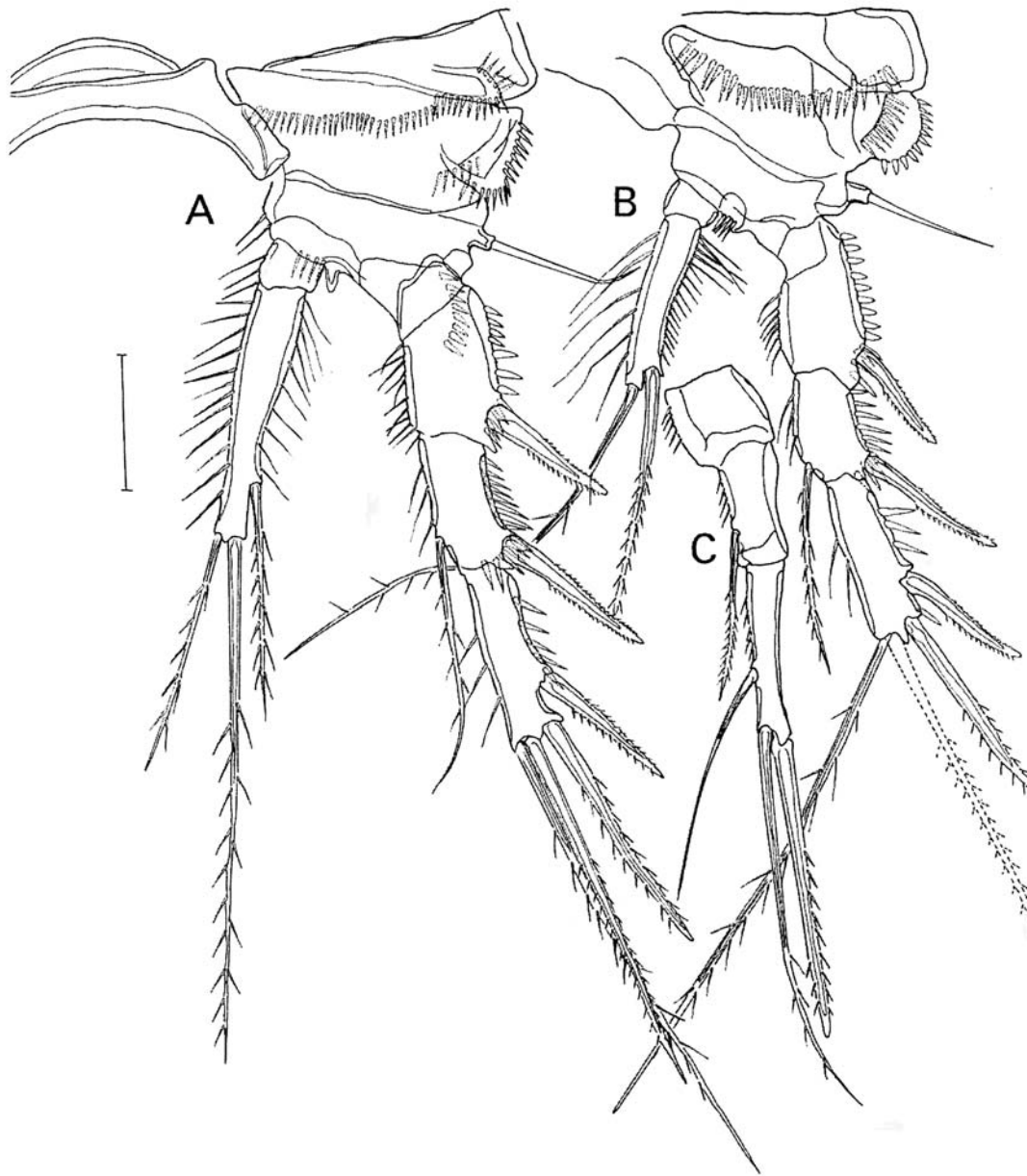


Fig. 6. *Apolethon hippoperus* n. sp. Female. A, P3 anterior; B, P4 anterior; C, exopod of aberrant P4 of second female, anterior. Scale = 0.03 mm.

to family status and removed from the Laophontoidea, and *Apolethon* has remained in what is now known as Laophontidae (1 of the 5 families comprising the Laophontoidea, sensu Huys 1990b). *Apolethon* currently comprises of 4 species: *A. fumator*, *A. trigonus*, *A. bilobatus* and the currently described *A. hippoperus*. The new species is placed in *Apolethon* based on the shape of habitus, the 5-segmented antennule in females, shape and setation of P1 endopod, overall reduced setation in swimming legs, and 3-segmented P3 endopod in males.

An examination of the eight laophonoidean apomorphies recognized by Huys (1990b) in relation to the present description of *Apolethon hippoperus* leaves the placement of *Apolethon* in a tenuous position. Apomorphies as listed by Huys (1990b) in parentheses.

1. (Ap. 1) The Laophontoidea typically possess a thorn-like process on segment-II of the antennule. Huys (1990b) considered this character an apomorphy for the superfamily. The thorn-like process is secondarily lost in Laophontopsidae and reduced in some Cristacoxidae. The process is not also present in members of the subfamily Esolinae nor in some Laophontinae genera such as *Onychocamptus*, *Coullia*, *Loureirophonte*, *Heterolaophonte*, and *Namakosiramia*. The secondary loss of the antennular process is regarded as a derived character within the superfamily (Huys 1990b, Huys and Lee 2000). Therefore, the absence of this process from *Apolethon hippoperus* does not preclude it from inclusion in the superfamily Laophontoidea.
2. (Ap. 2) In Laophontoidea, the antenna possesses an allobasis, which bears one seta on the abexopodal



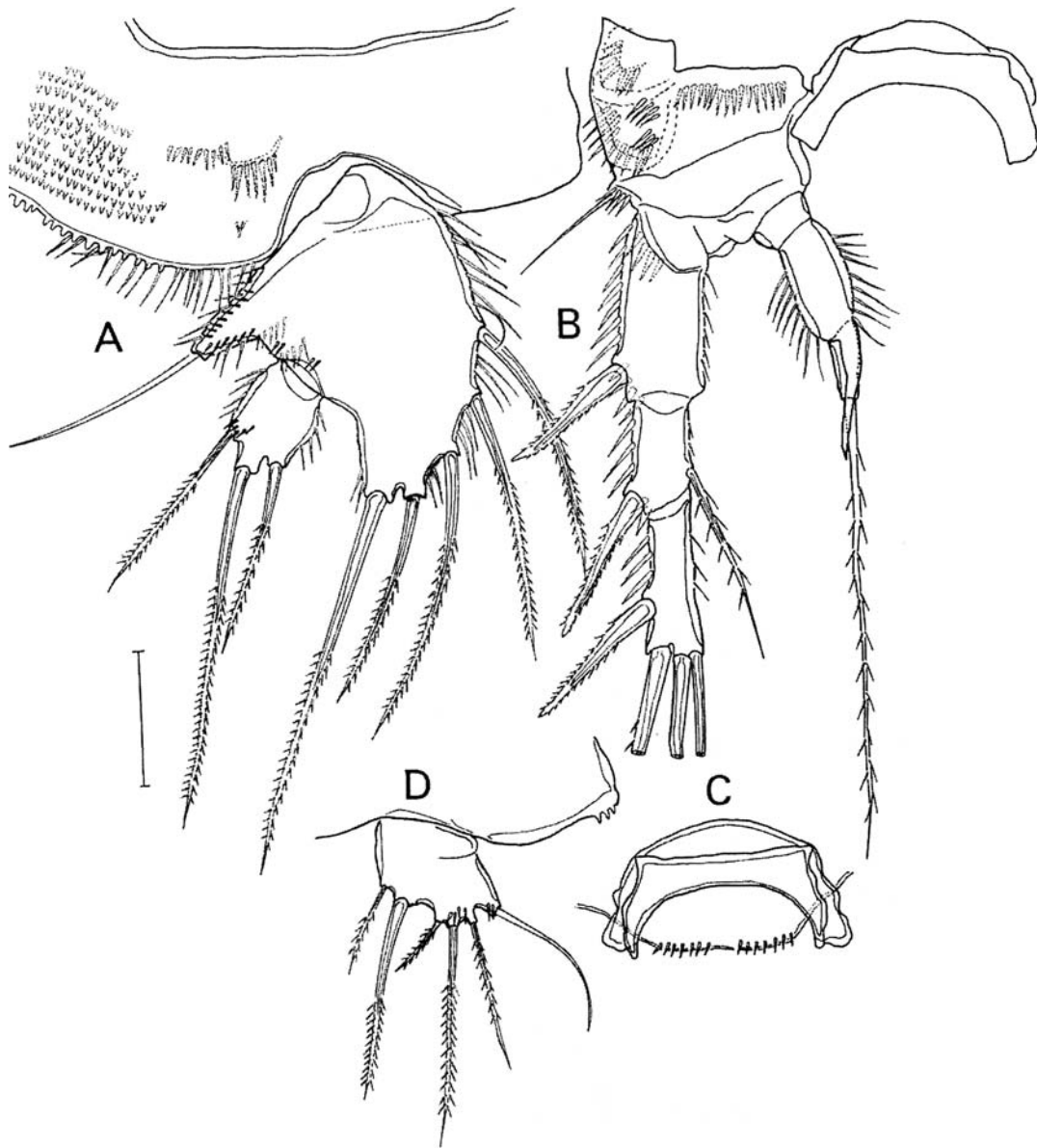


Fig. 7. *Apolethon hippoperus* n. sp. Female. A, P5. Male. B, P3; C, intercoxal sclerite of P3 of another male; D, P5. Scale = 0.03 mm.

margin. The seta has been secondarily lost in the Cristacoxidae and the genera *Novolaophonte* Cotarelli, Saporito & Puccetti and *Afrolophonte* Chappuis of Laophontidae (Huys 1990b), similar to the condition found in *Apolethon*.

3. (Ap. 3) In Laophontoidea, there are 4 setae on the antennary exopod, similar to the setal armature found in *Apolethon*.
4. (Ap. 4) In Laophontoidea, the exopod-2 of P1 does not have an inner seta and exopod-3 is ornamented with 4 elements. The P1 setation is similar to the one found in *Apolethon*.
5. (Ap. 5) In Laophontoidea, the P1 endopod is typically 2-segmented. The elongated proximal segment primitively bears one seta, which is the ancestral laophontoidean state (Huys 1990b). The seta has been lost in all Laophontoidea except the Laophontopsidae, a genus of Cristacoxidae (*Noodtorthopsyllus*), and the *Archilaophonte* and *Archesola hamondi*, *Archesola typhlops* (Huys and Lee 2000), which still possess a lateral seta. *Apolethon* also carries a large lateral seta on this segment, therefore retaining the plesiomorphic state.
6. (Ap. 6) In Laophontoidea, the P2-P4 endopods are 2-segmented and exopod-1 does not have an inner seta, similar to the condition found in *Apolethon*.
7. (Ap. 7) In Laophontoidea, sexual dimorphism is exhibited on the male P3 endopod. The typical (plesiomorphic) condition is a 3-segmented endopod (female 2-segmented), the middle segment bears an apophysis, which is homologous with the outer spine of the female; and the distal segment bears setal elements which are homologous to those of the female distal segment. The distal segment in the male is derived from the separation of the distal half of endopod 2 in the female. In *Apolethon*,

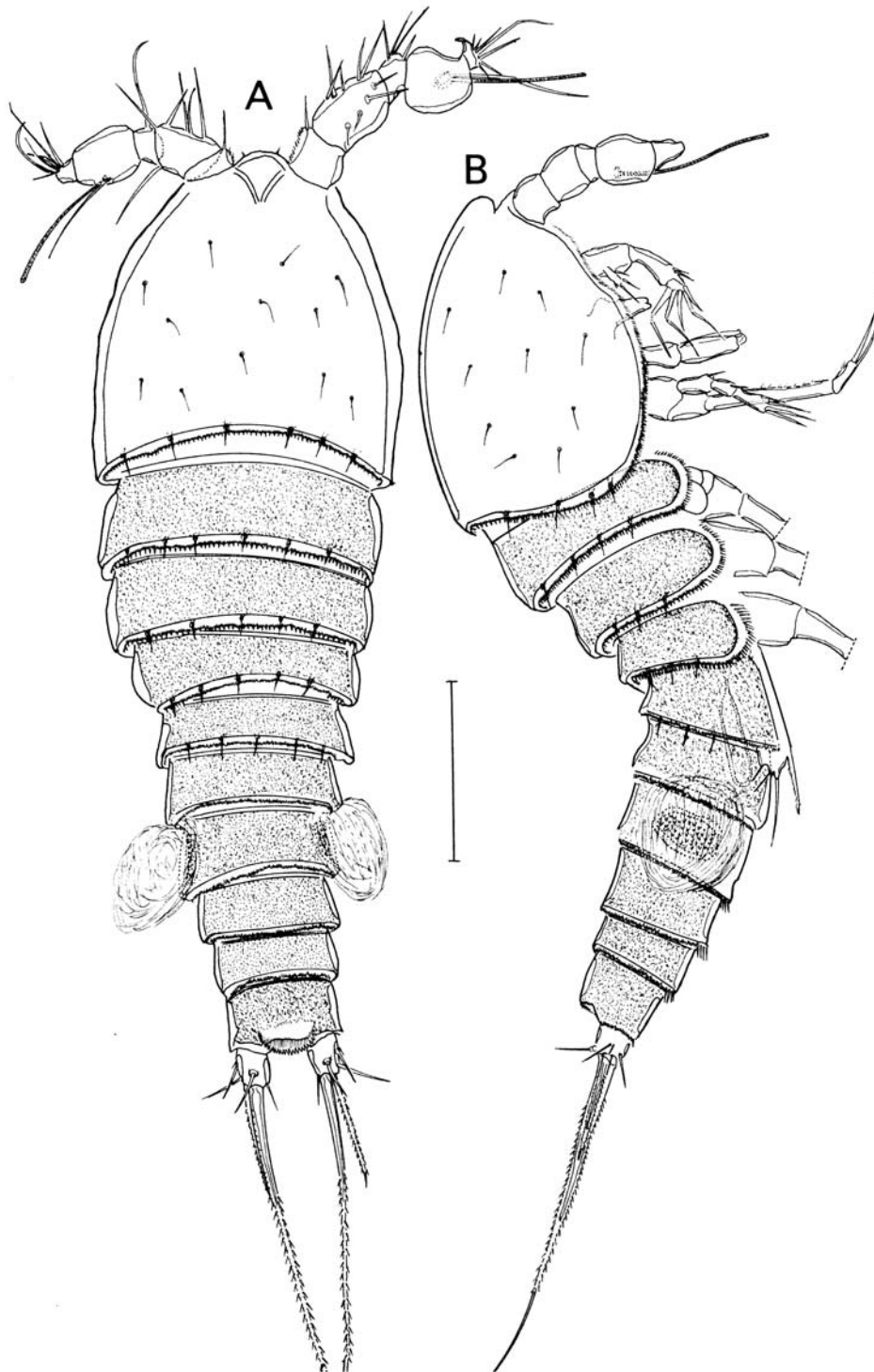


Fig. 8. *Apolethon hippoperus* n. sp. Male. A, habitus, dorsal; B, habitus, lateral. Scale = 0.1 mm.

although the male P3 endopod is 3-segmented, the second segment bears an apophysis, which has originated from the outer margin (unpub. obs). During the 5th copepodite stage the outer element of P3 endopod-2 has been transformed to a strong spine in males and a pinnate seta in females. During the final molt the outer spine extends to become the P3 apophysis. In *Cubanocleta*, the apoph-

ysis is derived from the outer spine but in *Cristacoxa* and *Noodtorthopsyllus* the apophysis is derived from the inner seta.

8. (Ap. 8) In all Laophontoidea, the vestigial P6 in the female genital apparatus bears three elements, and the male P6 consists of two asymmetrical plates, one fused to the somite and one articulating with the somite, each

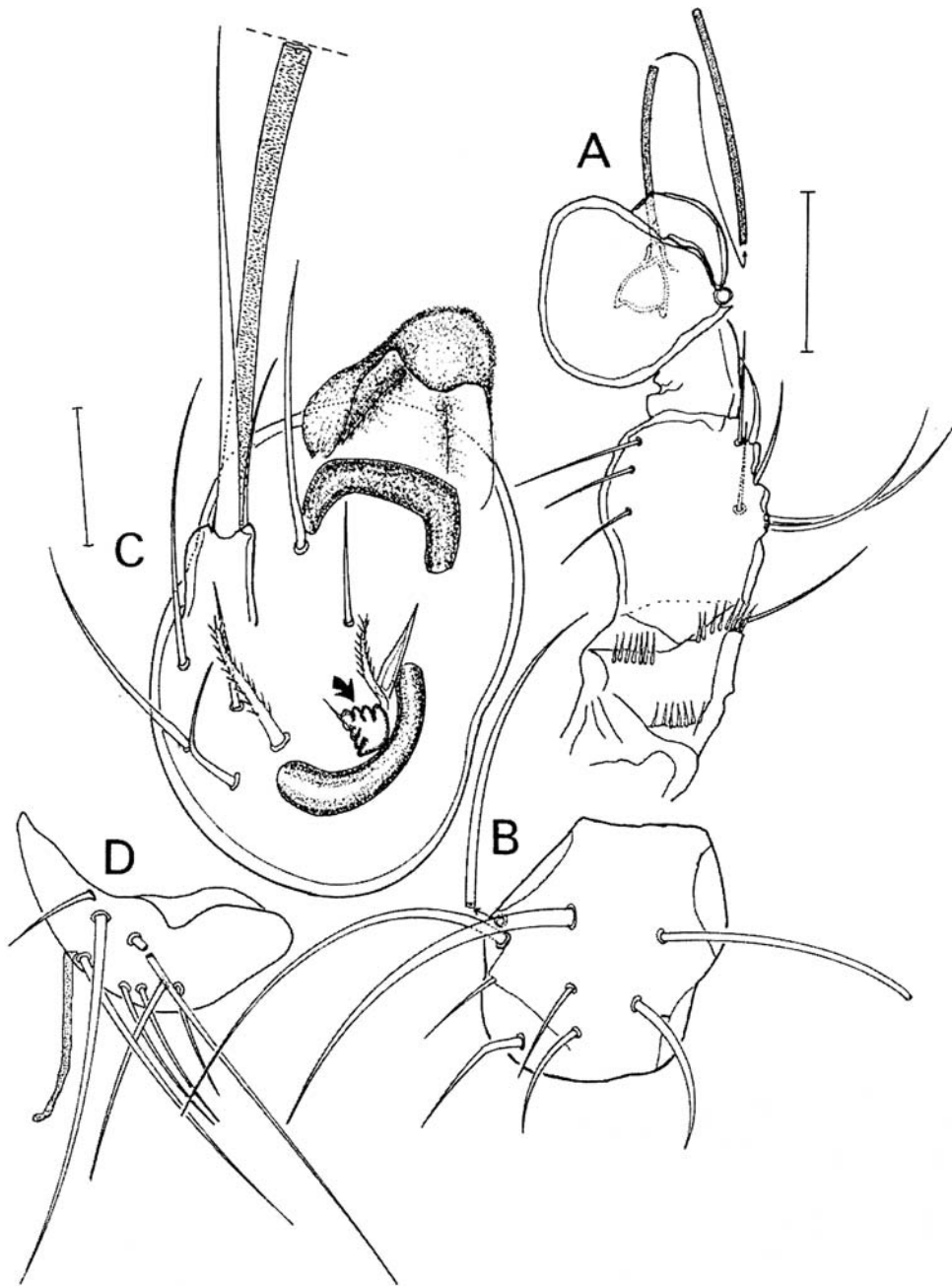


Fig. 9. *Apolethon hippoperus* n. sp. Male. A, antennule dorsal (armature omitted from segments 3-5); B, antennular segment III; C, antennular segment IV view (arrow) indicate modified crenulate and striated elements; D, antennular segment V. A, scale = 0.03 mm; B, C and D, scale = 0.01 mm.

plate of which bears two setae. Observations on multiple *Apolethon* males did not result in the identification of P6, except a slightly asymmetric sclerite. It is possible that the condition in *Apolethon* resembles that of *Archilaophonte* where male P6 is reduced to a small seta (Willen 1995) or even more the condition in Ancorabolidae where P6 is extremely reduced, present by an asymmetric small sclerite (Huys 1990b).

The genus *Apolethon* cannot be placed in any of the 5 existing families of Laophontoidea because of the following differences.

Laophontidae.—*Apolethon* exhibits a non-laophontid mate guarding behavior where the male attaches on the dorsal surface of the female cephalosome. In laophontids, the male grabs with the antennules the fourth legs of the female. The proximal endopod-1 of P1 bears a seta in *Apolethon*. Out of all laophontids, *Archilaophonte* (Willen, 1995), and *Archesola hamondi* and *Archesola typhlops* still possess a lateral seta on P1 endopod-1. The 2 setae of P1 endopod-2 are reduced to a setule and a large claw in laophontids whereas in *Apolethon* the 2 elements are modified to large pinnate seta and a claw.

Laophontopsidae.—4-segmented female antennule (5-segmented in *Apolethon*); cylindrical shape of P5 endopod and exopod in Laophontopsidae (non-cylindrical shape in *Apolethon*).

Orthropsyllidae.—*Apolethon* cannot be placed in Orthropsyllidae because of the following differences: 4-segmented female antennule (5-segmented in *Apolethon*); presence of brush setae on P1 (non-brush setae on *Apolethon* P1).

Cristacoxidae.—4-segmented female antennule (5-segmented in *Apolethon*); mandible with 2-segmented palp (1-segmented in *Apolethon*); 8 setae/spines on P5 of both sexes (unequal number of setae/spines in both sexes in *Apolethon*).

Adenopleurellidae.—4-segmented female antennule (5-segmented in *Apolethon*); cephalothorax, prosome (except P4-bearing somite) and urosome with globular glands usually laterally (even though gland homology has not been established, in *Apolethon* pleural glands are present on the third urosomite of both sexes).

In conclusion, we cannot place *Apolethon* in any families of Laophontoidea as they are currently defined and may belong to a new family, within Laophontoidea. However, we do not feel in a position to take this step at the moment and, therefore, propose that the genus is placed as incertae sedis in Laophontoidea until a new revision of the superfamily clarifies the problematic relationships of the recognized families. *Apolethon* exhibits further derived states (loss of outer spinous process on antennular segment 2; loss of a seta on the abexopodal margin of A2 allobasis) or retention of primitive laophontoidean states in some cases (A2 exopod with 4 setae, P1 exopod without inner seta on exopod-2 with 4 elements on exopod-3, P1 endopod 2-segmented with elongated endopod-1 and 2 elements on endopod-2, P2-P4 exopod-1 with 2-segmented endopods and exopod-1 without inner seta, sexual dimorphism of P3 and P6 bisetose with one member fused to somite) and which in combination with additional characters (maxillular arthrite without surface setae; P1 basal seta slightly displaced to anterior surface; type of sexual dimorphism of P3, type of P5) point towards an affinity with the laophontidean families.

Affinities with other ex-Laophontoidean families such as the Normanellidae are superficial. Although *Apolethon* has an A2 (except for absence of abexopodal seta) and a P1 endopod-1 (2 distal and 1 small lateral element), similarly to the Normanellidae, it cannot be placed in this family. The Normanellidae has a distinctly biramous mandibular palp, a distinct maxillular exopod, a maxillar endopod with 3-4 setae, a maxillipedal syncoxa with 2-3 setae, an inner seta on P1 exopod 2 and five elements on P1 exopod-3, a higher number of setae/spines on P2-P4, and a male P6 with symmetrical plates bearing 1-3 setae and somewhat different sexual dimorphism of male P3.

The new species *Apolethon hippoperus* possesses several morphological characters of taxonomic interest. First, are the paired pleural glands on the third urosomite of both sexes. Paired pleural glands have been reported from several members of the superfamily Laophontoidea: Huys (1990c) erected the family Adenopleurellidae on the basis of this character. Mielke (1981) depicted analogous glands on *Esola longicauda galapagoensis*, present on the inner margin of the caudal rami.

Second, *A. hippoperus* possesses paired mucin structures (“saddlebags”) in both sexes which seem to originate from the pleural glands. These structures were not observed on the holotype and the male paratypes of *A. fumator*. If these two characters are also absent from *A. trigonus* and *A. bilobatus*, then *A. hippoperus* may belong to a different but closely related genus. The presence of this mucus is not an artifact of preservation since it was obvious in most of the live specimens examined. No copepodites possessed these mucin structures. Mucus secretion by harpacticoids has been reported for cyst building (Coull and Grant, 1981) and for sediment binding and tube building (Chandler and Fleeger, 1984; Williams-Howze and Fleeger, 1987; Williams-Howze et al., 1987). We have been able to maintain *A. hippoperus* in the laboratory for extended periods but have not seen tubes or sediment binding in our preliminary observations. Tubes of harpacticoids can be extremely delicate and difficult to observe (Dahms and Bresciani, 1993; Nehring, 1993); and it would not be surprising if *A. hippoperus* constructed tubes. The species’ deeper distribution within sediments would make the tubes difficult to observe.

Third, the precopulatory posture of *Apolethon hippoperus* is not laophontid-like. In the Laophontoidea the female site of precopulatory clasping by the male is primitively by the caudal setae, but in Laophontidae it is on the fourth leg, an apomorphic and diagnostic character for this family. Detailed observations on the mating behavior of the laophontid *Robustunguis unguulatus* Fiers, 1992, have revealed that during leg development, the P4 exopod is transformed temporarily, presumably to aid in the clasping process during precopula (Fiers 1998). Male *Apolethon hippoperus* clasp copepodites IV and V and adults from the posterior margin of the cephalothorax, uncharacteristic of the Laophontidae, but is found in other families such as Tachidiidae. Similar precopulatory guarding behavior has been observed in the ancorabolid *Lobopleura ambiducti* Conroy-Dalton 2004 (Conroy-Dalton 2004), where the male grasps the female in dorsal aspect, by placing the antennules under the female P2. In Auke Bay, Alaska, the copulatory activity of *A. hippoperus* seems to be highly seasonal and may be linked to elevated water temperatures or increased photoperiod. The majority of *A. hippoperus* clasping pairs were collected between March and early April 1992 (57 pairs), comprising >75% of the total number of copepod pairs collected; no *A. hippoperus* clasping pairs were collected from May through mid-July, 1992.

Comparison of *Apolethon hippoperus* with its congeners yielded additional diagnostic characters. The setation and shape of the swimming legs is highly conserved in all reported females of the genus. However, the males of *A. fumator* and *A. hippoperus*, (the only species with reported males) have different setation on the P3 endopod. The distal segment of P3 endopod in *A. fumator* bears two setae vs. one seta for *A. hippoperus*. Sexual dimorphism on the P4 endopod, which Wells (1967) observed in *A. fumator*, was not obvious in *A. hippoperus*. Although the male of *A. fumator* is the same size as the female (Wells, 1967), the male of *A. hippoperus* is significantly smaller than the female ( $P < 0.001$ , paired  $t$ -test,  $n = 25$  for each sex). The males of the Chinese species remain to be found to extend

this observation. *Apolethon hippoperus* may be more closely related to *A. bilobatus* based on the similarity of the articulated P5 of females. Both *A. fumator* and *A. trigonus* bear non-articulated P5.

The females of the genus *Apolethon* have separated rami in P5 with an unusual setal formula, the exopod bears reduced number of setae (3) but the baseoendopodal lobe with 5 setae. The P5 condition in most Laophontoidea (Laophontidae, Laophontopsidae, Orthopsyllidae) is 6 exopodal and 5 baseoendopodal setae, except in Adenopleurellidae where there are 4 setae on the exopod and 3 setae on the baseoendopodal lobe. In Cristacoxidae, P5 of males and females is similar, the rami are fused and setation is also reduced (8 setae). The typical male P5 condition shared by Laophontidae, Laophontopsidae, Orthopsyllidae is 5 exopodal and 2 baseoendopodal setae. The males of *Apolethon* have fused rami bearing 5 setae (3 exopodal and 2 baseoendopodal setae). Even though the P5 setal formula of *Apolethon* is reduced, the general shape of P5 represents the typical laophontoidean condition.

The setal condition of the mandibular palp in *Apolethon* is the most primitive exhibited i.e., 1 exopodal, 3 endopodal [Wells (1967) probably overlooked the third seta in *A. fumator*] and 2 basal setae. The presence of 2 basal setae is only retained in some Esolinae, but in the latter the exopod is sometimes demarcated.

The maxillular morphology of *Apolethon* resembles that found in *Archilaophonte maxima* Willen 1995 (Willen 1995) except that the exopod is a distinct segment and an additional seta inserted at or near the base of the exopod in the latter. Generally, the proximal basal endite is lost; Laophontopsidae and the Cristacoxidae are the only laophontoidean families with both the proximal and distal endite (Huys 1990b). The distal armature represents the distal endite which comprises 3 elements in total (2 setae + modified element [geniculate seta/claw] as shown in *Archilaophonte*). In *Apolethon*, there are 3 elements (2 setae and what appears to be a claw).

We consider that the condition of male antennule has not been fully resolved in *Apolethon*. The female *Apolethon* has a 5-segmented A1 and a 6-segmented A1 in males would be the typical condition. Special attention was paid to the possibility that segment 4 may have been overlooked since it is usually a small, U-shaped arthrite but no definitive conclusion could be made. However, as noted by Huys (1990b) in the non-laophontid families antennular segment 4 is fully incorporated in the ae-bearing segment and *Apolethon* is most likely not a laophontid taxon. The typical male A1 condition in Adenopleurellidae and Orthopsyllidae is 7-segmented, geniculation between segments 4 and 5; in Laophontopsidae and Cristacoxidae is 5-segmented, geniculation between segments 4 and 5; in Laophontidae A1 segmentation (5 to 8-segmented) and geniculation point varies because of different fusing patterns.

Only the caudal setae IV and V were described by Wells (1967) for *A. fumator*. At least two more caudal setae were observed from the paratypes; however, unequivocal conclusions on the caudal setal formula could not be made because of the poor preservation of the type material. All caudal setae, except seta I, seem to be absent on the cope-

pods from China; however, we have not examined the type specimens, and the figures of Shen and Tai (1973) do not have sufficient detail. The caudal seta V of female *A. trigonus* is two to three times longer than caudal seta V of *A. hippoperus*. Most likely, the discrepancy of caudal setation or shape in the genus *Apolethon* is attributed to the non-detailed drawings in the original descriptions; therefore we do not recommend their use as diagnostic characters. *Apolethon hippoperus* and *A. fumator* have somites with a hyaline frill edge; this character is either absent or has not been reported for the other two members of the genus. The structure is not easily visible.

The following remarks can be made concerning zoogeography. In Auke Bay, Alaska, *A. hippoperus* is restricted to a narrow zone within the deep subtidal (Schizas and Shirley, 1994b). The majority of specimens were recovered from the -1 m intertidal stations (Schizas and Shirley 1994b). Individuals of *Apolethon hippoperus* have been consistently recovered from the type locality over a decade (1992-2003), suggesting the presence of a temporally stable population (unpub. data). Copepods of the genus *Apolethon* have been sampled from strikingly different habitats and locations around the world. *Apolethon fumator* was collected from detritus and sand of the Island of Inhaca, Indian Ocean (Wells, 1967). *Apolethon trigonus* and *A. bilobatus* were discovered in the Pearl River and Pacific River respectively, Guangdong Province, China (Shen and Tai, 1973). *Apolethon hippoperus* was found in a muddy habitat where salinity varied from 22-37‰ and sea surface temperature varied from 2.3-12.1°C. The occurrence of the genus in rivers and intertidal areas suggests a euryhaline and eurythermic distribution of *Apolethon*. The presence of *A. hippoperus* in Auke Bay, Alaska, and its possibly close relationship with *A. bilobatus* certainly do not support Shen and Tai's hypothesis (1973) favoring a distant relationship between the harpacticoid copepod fauna of China and the Americas. Rather, the presence of *A. hippoperus* in Alaskan mudflats is congruent with Wells' observation (1986) that most marine harpacticoid genera have a worldwide distribution.

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