

ACANTHOMOLA PUBESCENS, A NEW GENUS AND SPECIES OF HEPTAGENIIDAE (EPHEMEROPTERA) FROM WESTERN CANADA

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Abstract

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Acanthomola pubescens, a new genus and species of Heptageniidae (Ephemeroptera), is described from larvae collected in Saskatchewan and Alberta. *Acanthomola* superficially resembles *Bleptus*, *Epeorus*, and *Raptoheptagenia*, but differs from these genera, and all other heptageniids, in the structure of the mandibles and maxillae. The molar area of the mandible is greatly reduced and bears only a few stout spines. The crown of the maxillary galea-lacinia is rounded and lacks setae near the apex. The apical segment of the maxillary palpus is long, slender, and bare. Generic and specific descriptions of the larva of *A. pubescens*, gen. nov., sp. nov., are given, along with biological notes. *Acanthomola* appears to be a very primitive heptageniid, related to *Bleptus*, *Epeorus*, and *Ironodes*. It is probably most closely related to *Spinadis*.

Résumé

Acanthomola pubescens, un genre nouveau et une espèce nouvelle de Heptageniidae (Ephemeroptera), est décrit à partir de larves recoltées en Saskatchewan et en Alberta. *Acanthomola* ressemble superficiellement à *Bleptus*, *Epeorus* et *Raptoheptagenia*, mais il diffère de ces genres, et de tous autres heptageniids, par la structure des mandibules et maxillaires. La portion molaire de la mandibule est réduite beaucoup et ne porte que quelques épines fortes. La couronne de la galea-lacinia de la maxillaire est arrondie et sans soies au sommet. Le segment apical de la palpe maxillaire est long, mince et nu. Les descriptions générique et spécifique de la larve d'*Acanthomola pubescens*, gen. nov., sp. nov., sont données, suivies par des remarques biologiques. *Acanthomola* semble être un heptageniid très primitif, qui est apparenté à *Bleptus*, *Epeorus* et *Ironodes*. Il est probablement plus étroitement apparenté à *Spinadis*.

Introduction

During the past several years, larvae of an undescribed heptageniid species (Fig. 1) have been collected from the South Saskatchewan River in Saskatchewan and from the Athabasca River in Alberta. These larvae superficially resemble those of *Epeorus* and the oriental genus *Bleptus* in general body shape and in the absence of a median caudal filament. However, they differ from *Epeorus* in the very small gill lamellae on the first abdominal segment and from both *Epeorus* and *Bleptus* in the single basal denticle on the tarsal claw, ventral insertions of the first two abdominal gills; lateral expansion of the labrum, and shapes of the mandibles and maxillae (which are unlike those of any described heptageniid). The molar area of the mandible is only 0.3–0.5 times as large as that of other Heptageniinae, but is larger than that of predaceous genera (*Raptoheptagenia*, *Pseudiron*, and *Spinadis*). The armature of the molar area is reduced to a few stout spines. The crown of the maxillary galea-lacinia is rounded and bare. The apical segment of the maxillary palpus is long, very slender, and bare.

The undescribed larvae resemble *Raptoheptagenia* larvae in general body shape, dorsal setation, and the shapes and insertions of the first abdominal gills, but differ in the large lamellae on gills 2–7, lateral (instead of ventral) insertions of gills 3–7, and absence of a median caudal filament. They key to *Spinadis* in the Edmunds *et al.* (1976) key to North American mayflies (although the dorsal tubercles are very small). If the ventral insertions of abdominal gills 1 and 2 are ignored, they key to *Epeorus*.

Because of the distinctive mouthparts and unique combination of other characters, we propose a new genus, *Acanthomola*, for these larvae. Adults of *Acanthomola* are unknown.

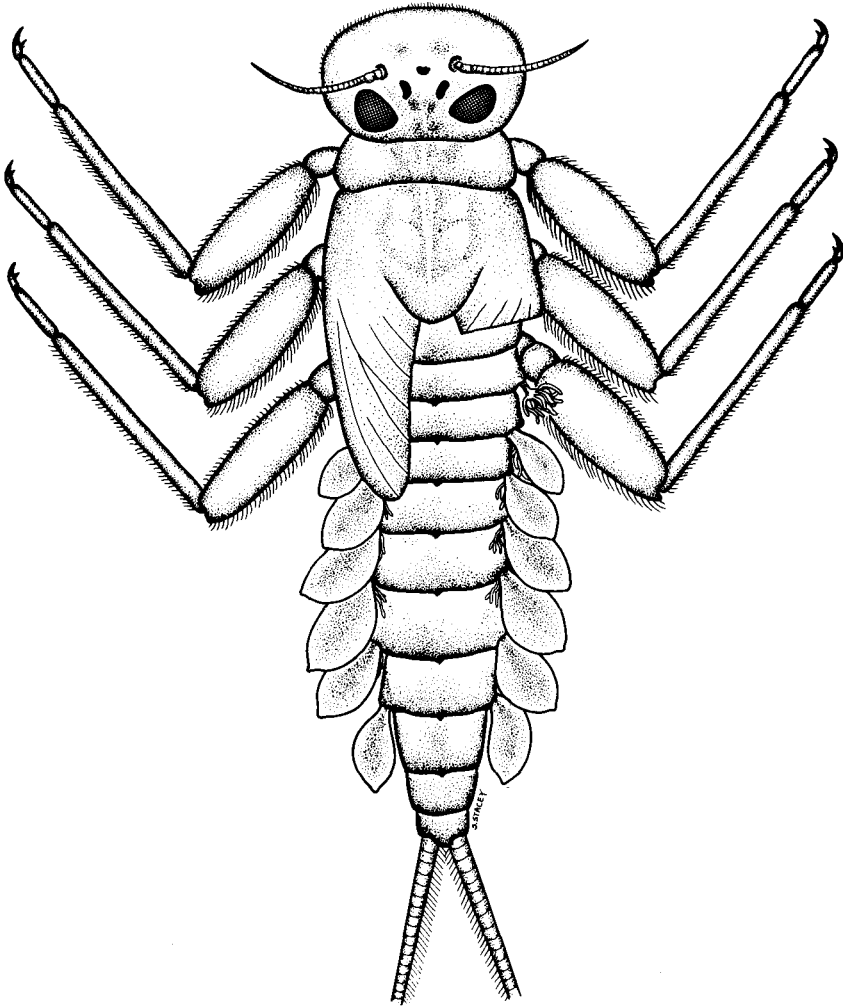


FIG. 1. *Acanthomola pubescens* larva: dorsal, wing pads on right side removed to expose abdominal gills.

***Acanthomola*, gen. nov.**

Nearly mature larva (Fig. 1). Lengths: body, 9 mm; caudal filaments (broken), approximately 8–8.5 mm.

Head. Head capsule 1.3–1.6 times as wide as long, approximately trapezoidal in shape and widest just anterior to antennal bases; anterior and lateral margins convex, posterior margin straight to slightly concave; anterior margin with a fringe of very short, fine setae. Compound eyes not extending to postero-lateral margins of head capsule in either sex. Dorsal surface of head capsule between compound eyes from just anterior to antennal bases to posterior margin with dense, fine setae; rest of dorsal surface with very short, fine setae. Labrum (Fig. 2a) 0.5–0.7 times as wide as head capsule, anterior margin with a dense fringe of setae. Left and right mandibles (Fig. 2b) similar; incisors (Fig. 2c) well developed; outer incisor blunt apically, with four or five long spines on the inner surface, and a row of short denticles on the outer surface; inner incisor bifid or trifid with a row of stout setae; molar area (Fig. 2d) reduced to a small raised area with a sharp apical and

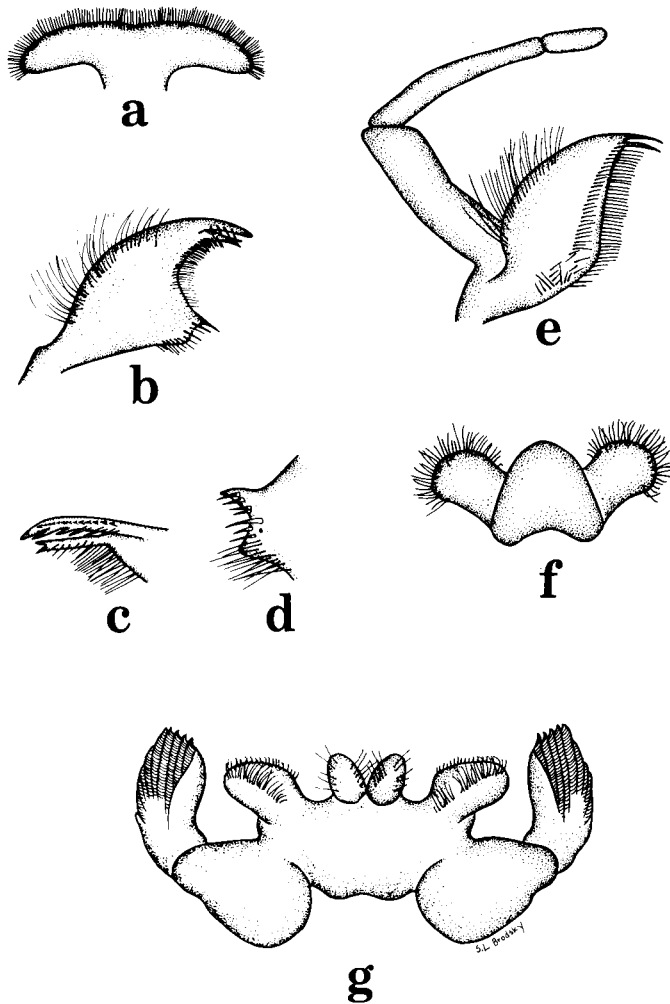
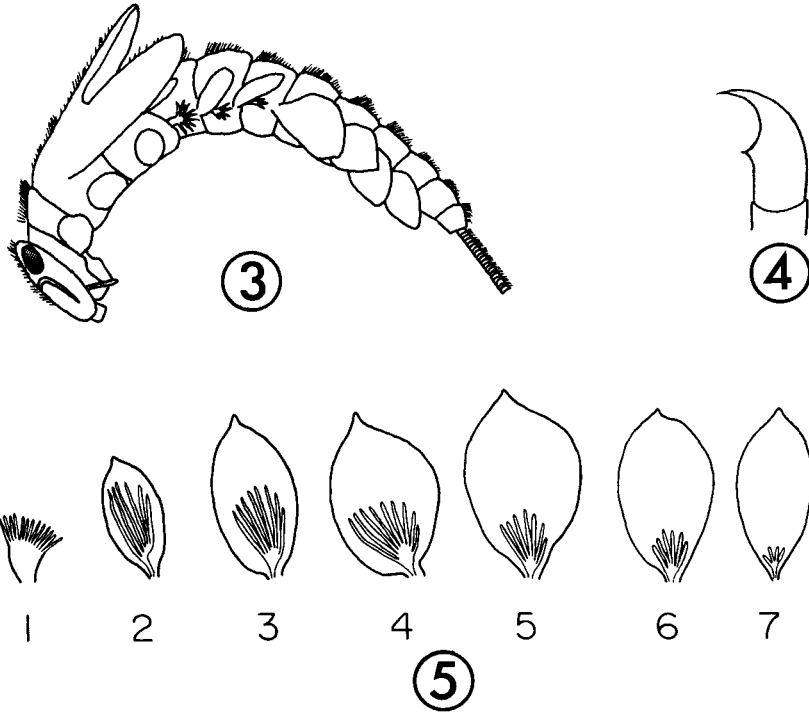


FIG. 2. Mouthparts of *Acanthomola pubescens* larva, ventral: (a) labrum, (b) right mandible, (c and d) details of incisor and molar area of left mandible, (e) right maxilla, (f) hypopharynx, (g) labium.

a blunt basal spine, several smaller spine-like setae between these spines, and a number of longer, hair-like setae near the basal spine; a row of long setae extending from the base of the inner incisor to the base of the molar area; outer surface of mandible with a fringe of long hair-like setae. Galea-lacinia of maxilla (Fig. 2e) with two or three elongate apical spines, a dense row of long inner setae, a row of shorter lateral setae, and a fringe of long hair-like setae on the outer margin; crown of galea-lacinia bare; maxillary palpus long and slender, 2-segmented, second segment 1.5–2 times as long as basal segment, with a distinct subapical constriction separating an apparently moveable but unarticulated apical subsegment; palpus bare. Hypopharynx (Fig. 2f) with ligula conical and superlinguae slightly expanded. Labium (Fig. 2g) with glossae twice as long as wide; paraglossae broader, only slightly longer than wide; labial palpi large, basal segment quadrate, apical segment twice as long as wide and twice as long as paraglossae, apex of apical segment



FIGS. 3-5. 3, *Acanthomola pubescens* larva: lateral, showing dorsal setation; 4, tarsal claw of *Acanthomola pubescens* larva; 5, gills of *Acanthomola pubescens* larva from abdominal segments 1-7, ventral.

with several dense rows of apically curved setae; glossae with sparse setae, paraglossae with two dense apical fringes of stout setae.

Thorax. Pronotum widest at or near middle; posterior margin broadly and shallowly emarginate. Pro-, meso-, and meta-notum covered with dense, fine setae (Fig. 3); setae longest mid-dorsally, becoming shorter laterally and absent on lateral margins; wing pads covered with shorter, fine setae. Legs of typical heptageniid shape; femur quite broad, approximately 0.3 times as wide as long, with a short, blunt, apical, thumb-like projection; tibia 1.3 times as long as femur, tarsus 0.3 times as long as femur; tarsal claw (Fig. 4) with a slender, basal denticle but no subapical denticles; posterior margins of coxa, femur, and tibia, and anterior margin of femur with dense fringes of long setae; anterior margins of femur, tibia, and tarsus with a row of small peg-like setae.

Abdomen. Posterior margins of tergites 1-9 with a small median tubercle; lateral margins of tergites 1-7 expanded laterally, especially in the posterior half; a short, sharp posterolateral spine on tergites 3-7; abdominal tergites densely covered with fine setae (Fig. 3), which are longest mid-dorsally, shorter laterally, and absent on lateral margins. Gill (Fig. 5) on segment 1 inserted ventro-laterally, lamella greatly reduced and shorter than fibrilliform tuft; gill on segment 2 inserted ventrally, lamella larger and broader, longer than fibrilliform tuft; gill on segment 3 inserted ventrolaterally, lamella larger than but similarly shaped as that on segment 2; gills on segments 4-6 inserted laterally, lamellae broader than that on segment 3; gill on segment 7 inserted laterally, lamella somewhat narrower than those on segments 4-6; fibrilliform tufts becoming progressively smaller anteriorly to posteriorly, from 0.6-0.8 times as long as lamella on segment 2, to 0.2-0.3 times as long as lamella on segment 7; gill lamellae each with a small, blunt point on the outer

margin; no visible tracheae on gill lamellae except a faint branch near the anterior margin. Two caudal filaments, with setae along their inner margins and outer margins bare; terminal filament absent.

Etymology. *Acantho*, Gr., spiny; *mola*, L., a mill; referring to the spiny molar area of the mandible.

Type-species. *Acanthomola pubescens*, sp. nov.

Acanthomola pubescens, sp. nov.

Mature larva. Lengths: body, 9 mm; caudal filaments (broken), approximately 8–8.5 mm. General color dirty white to very pale greyish brown with darker brown markings.

Head. Head capsule mostly white to pale greyish brown, with a brown median area between the compound eyes extending from the lateral ocelli to the posterior margin, and a diffuse brown spot anterior to each antennal base. Antenna entirely white to pale greyish brown. Mouthparts white to pale greyish brown except for setae on the maxilla, labium, and labial palp, which are golden brown.

Thorax. Pronotum mostly white to pale greyish brown with a wide brown median stripe, a narrow brown submedian streak, and a brown posterior margin (Fig. 1). Mesonotum white to pale greyish brown with a brown median stripe, a brown lateral spot anterior to each wing pad base, and a brown area in the posterior 1/3–1/2 between the wing pad bases; mesothoracic wing pads white to pale greyish brown with brown veins and brown mesal and lateral margins. Metanotum white to pale greyish brown with a brown posteromesal spot. Venter of thorax entirely white to pale greyish brown. Legs white to pale greyish brown; femur tinged with brown in posterior 1/4–1/2, posterior edge dark brown; tibia and tarsus entirely white to pale greyish brown; tarsal claw tipped with dark brown; setae on posterior margin of femur golden brown; other setae white to pale greyish brown to faintly tinged with brown.

Abdomen. Tergites 1–9 brown mesally fading to white or pale greyish brown laterally, each with a white or pale brown submedian spot; tergites 1–4 with submedian spots approximately round, restricted to the anterior half of the tergite, and extending to or nearly to the anterior margin; tergites 5–9 with submedian spots narrower, elongate, and centered on or near the middle of each tergite; submedian streaks on tergites 8 and 9 sometimes faint; tergite 10 mostly white to pale greyish brown with a brown median stripe and a brown posterior margin. Venter of abdomen entirely white to pale greyish brown. Gill lamellae and fibrilliform tufts translucent and colorless to white or very pale brown. Caudal filaments pale brown with darker brown articulations basally, fading to uniformly white or pale smokey apically.

Holotype. Nearly mature male larva, in alcohol. Saskatchewan: South Saskatchewan River at Lemsford Ferry (south of Kindersley), 12 July 1970, D.M. Lehmkuhl, Vial No. 70-7-12 (CNC, Ottawa).

Paratypes. Three immature larvae in alcohol and 1 immature larva on slide, same collection data as holotype; 1 nearly mature larva, body in alcohol, head and mouthparts on slide, Alberta: Athabasca River 200 km downstream from Athabasca, 22 June 1981, Alberta Environment; 1 immature larva in alcohol, same locality, 18 June 1981, Alberta Environment; 2 immature larvae in alcohol, Alberta: Athabasca River 120 km downstream from Athabasca, 18 June 1981, Alberta Environment; 3 immature larvae in alcohol and 1 immature larva on slide, same locality, 22 June 1981, Alberta Environment. The paratypes are in the collections of the authors. We also have approximately 50 earlier instar larvae from the above locations.

Etymology. Latin, named for the dense hair setae on the dorsum of the body and legs.

Systematic Remarks

Acanthomola appears to be a very primitive heptageniid. The larvae possess several character states that are plesiomorphic for the family Heptageniidae, according to Jensen (1972), including the following: the oval, dorsally convex head capsule; sparse setae on the anterior margin of the head capsule; slender, subequal incisors; submedian row of setae and absence of apical pectinate spines on the galea-lacinia; rounded glossae; conical ligula and slightly expanded superlinguae of the hypopharynx; thickened lamellae and well-developed fibrilliform tufts of the abdominal gills; and setaceous caudal filaments. The very small gill lamellae on abdominal segment 1, shared by *Acanthomola*, *Cinygma*, and *Bleptus*, may also be plesiomorphic.

Acanthomola appears to belong to Jensen's (1972) Phyletic Line I, which includes *Epeorus*, *Ironodes*, and *Bleptus* and is a sister group to the rest of the Heptageniinae. *Acanthomola* possesses two character states that are plesiomorphic for Phyletic Line I but apomorphic for the family Heptageniidae: a reduced number of setae on the crown of the galea-lacinia, and absence of a median caudal filament. An apical thumb-like projection on the femur (present in *Acanthomola*, *Bleptus*, and *Epeorus*), dorsal abdominal spines or tubercles (single, median tubercles in *Acanthomola* and *Bleptus*, and paired, submedian spines in *Ironodes* and some *Epeorus*), and faint to indistinct tracheae on the abdominal gills (present in *Acanthomola*, *Epeorus*, *Ironodes*, and *Bleptus*) may also be plesiomorphic for this lineage.

Although *Acanthomola* belongs to the same phyletic line as *Bleptus*, *Epeorus*, and *Ironodes*, it does not appear to be closely related to any of the other genera in this line. It is most similar to *Bleptus*, but this similarity appears to be due to symplesiomorphy. All characteristics shared by *Bleptus* and *Acanthomola* are plesiomorphic for Phyletic Line I or for the entire family.

Acanthomola shares several apomorphic characteristics with the three predaceous heptageniid genera (*Pseudiron*, *Raptoheptagenia*, and *Spinadis*), including the following: molar area of the mandible reduced in size, and bearing only a few spines; apex of the galea-lacinia without hair setae; maxillary palpus with a long slender apical segment, but lacking setae, or possessing only sparse setae; tarsal claw with a single basal denticle (except in *Pseudiron*, which has no denticles on its claws); abdominal gills 1 and 2 inserted ventrally (except in *Pseudiron*); gill lamellae with pointed apices. The size and shape of the molar area and shape of the galea-lacinia of *Acanthomola* appear to be intermediate between those of "typical" heptageniines and those of the predaceous genera.

The resemblance is greatest with *Spinadis*, and also includes the apical thumb-like projection on the femur, shapes of the abdominal gills, dorsal abdominal tubercles, and absence of a median caudal filament. Because of the large number of apomorphic characters shared by *Acanthomola* and *Spinadis*, we tentatively propose that they are sibling genera (Fig. 6, Table 1).

The relationship between *Pseudiron* and *Acanthomola* is not entirely clear. *Pseudiron* shares several apomorphic characteristics with *Acanthomola* and *Spinadis*, including the size and armature of the molar area of the mandible, width of the labrum, shape of the galea-lacinia, lack of setation on the maxillary palpus, absence of subapical denticles on the tarsal claws (although *Pseudiron* also lacks a basal denticle), and pointed apices of the gill lamellae. Based on these and other similarities in mouthpart and gill morphology, McCafferty and Provonsha (1986) suggested that *Pseudiron* and *Spinadis* are sister genera. However, *Pseudiron* is more primitive than *Acanthomola*, *Spinadis*, or any other genus in Phyletic Line I in its possession of a median caudal filament and absence of dorsal abdominal tubercles. Thus, *Pseudiron* may be either a sibling of *Spinadis*, or *Acanthomola* and *Spinadis*, which has regained a median filament and lost its abdominal tubercles, or an

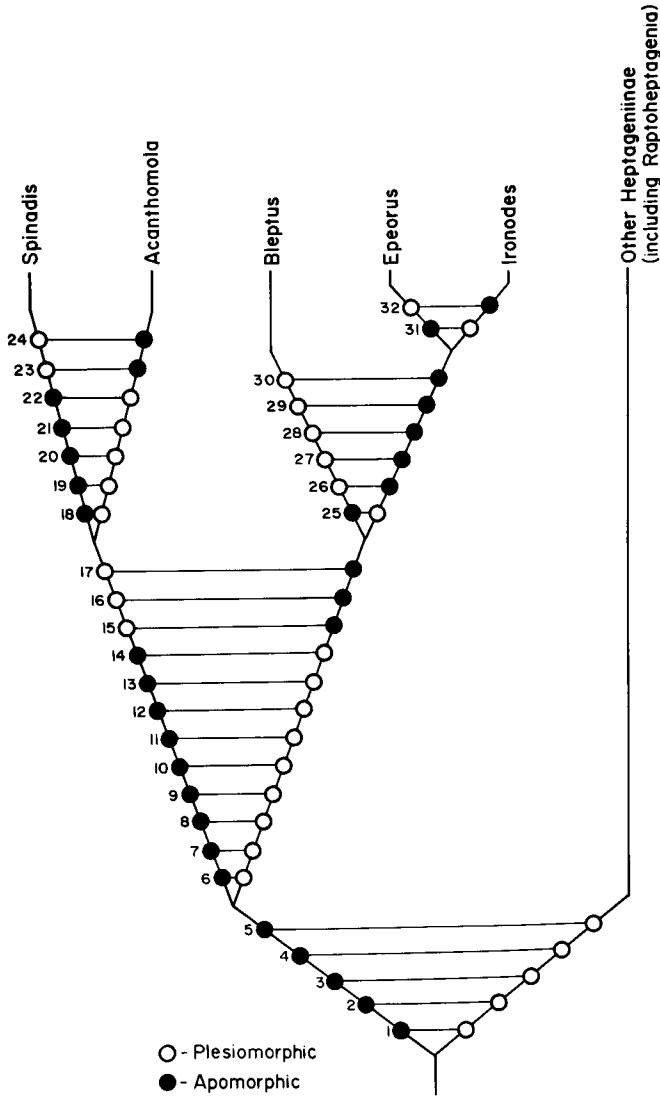


FIG. 6. Proposed phylogenetic relationships of *Acanthomola* to other Heptageniidae. Illustrated relationships among genera other than *Acanthomola* and *Spinadis* are taken from Jensen (1972). Characters used to define relationships are described in Table 1.

unrelated genus that has convergently evolved several apomorphic characteristics (including several details of the mouthparts that may be subject to convergence in predaceous genera).

Acanthomola is probably not very closely related to *Raptoheptagenia*. The internal larval structure (Jensen 1972; as *Anepeorus*) and adult male genitalia (Whiting and Lehmkuhl 1987) of *Raptoheptagenia* indicate that it belongs to Jensen's Phyletic Line II, and is most closely related to *Heptagenia*. Similarities between *Acanthomola* and *Raptoheptagenia* are probably the result of convergent evolution which may have occurred because of similar predaceous habits. Although the gut contents of *Acanthomola* larvae

Table 1. Characters used to define proposed relationships among *Acanthomola* and related genera. Character numbers correspond to those in Figure 6

No.	Character*	Plesiomorphic state†	Apomorphic state†
1.	Setae on crown of galea-lacinia	Numerous	Sparse
2.	Apical projection on femur	Absent	Present
3.	Tracheae on abdominal gills	Distinct	Faint
4.	Dorsal abdominal spines	Absent	Present
5.	Median caudal filament	Present	Absent
6.	Labrum	Narrow	Wide
7.	Armature on molar area	Ridges	Spines
8.	Size of molar area	Large	Intermediate
9.	Outer angle of galea-lacinia	Rounded	Moderately angular
10.	Apical segment of maxillary palpus	Short and triangular	Long and narrow
11.	Setation on maxillary palpus	Dense	Sparse
12.	Denticles on tarsal claw	3-5 subapical	1 basal
13.	Insertion of gills 1 and 2	Lateral	Ventral
14.	Outer edge of gill lamellae 3-5	Rounded	Pointed
15.	Lateral setae on mandible	Dense	Sparse
16.	Level of incisors (relative to molar area)	Raised	Moderately raised
17.	Setae on caudal filaments	Dense	Sparse
18.	Size of molar area	Intermediate	Small
19.	Outer angle of galea-lacinia	Mod. angular	Very angular
20.	Width of paraglossae:glossae	Twice as wide	Subequal
21.	Lateral margin of head capsule	Convex	Straight
22.	Width of femur	Wide	Narrow
23.	Setation on maxillary palpus	Sparse	None
24.	Armature on labial palpus	Setae	Recurved spines
25.	Separation between glossae	Triangular	Subrectangular
26.	Lateral setae on mandibles	Sparse	Absent
27.	Level of incisors	Mod. raised	Slightly raised
28.	Length of inner:outer incisor	Subequal	Shorter
29.	Size of lamella on gill 1	Small	Large
30.	Armature on caudal filaments	Setae	Spines and setae
31.	Setae on crown of galea-lacinia	Present	Absent
32.	Armature on caudal filaments	Spines and setae	Spines

*Characters used by Jensen (1972).

†Plesiomorphy and apomorphy of character states defined by Jensen (1972).

examined do not contain animal material, the shapes of the mandibles and maxillae suggest that *Acanthomola* or one of its recent ancestors are predaceous.

Proposed phylogenetic relationships of *Acanthomola* to other heptageniids are described in Figure 6. The characters used to define these relationships are described in Table 1. The relative plesiomorphy or apomorphy of each character state is either taken from Jensen (1972), or based on comparison with *Cinygma*, which, according to Jensen (1972), is the most primitive extant genus in the Heptageniidae. Further study, including comparisons of adults and internal larval structure, is required to verify the proposed relationships shown in Figure 6 and clarify the phylogenetic position of *Pseudiron*.

Because of its many primitive characteristics, its resemblance to genera in Jensen's Phyletic Line I, and the speculative nature of its relationship to predaceous genera, we tentatively assign *Acanthomola* to the subfamily Heptageniinae.

We have not seen specimens of *Bleptus* or *Spinadis*. Comparisons of these genera with *Acanthomola* are based on descriptions in Jensen (1972) (*Bleptus*), and in Edmunds and Jensen (1974), Flowers and Hilsenhoff (1975), and McCafferty and Provonsha (1986) (*Spinadis*).

The larva of *Anepeorus* is unknown. The predaceous larva previously associated with *Anepeorus* has been shown to belong to *Raptoheptagenia* (= *Heptagenia*, in part) *cruentata* (Walsh) (Whiting and Lehmkuhl 1987). *Acanthomola pubescens* may be the immature stage of *Anepeorus*. Both are known from the South Saskatchewan River in Saskatchewan, and are extremely rare. However, it is premature to make such an association without rearing. Unfortunately, it is doubtful that *A. pubescens* will ever be reared because of the extreme rarity of its larvae and environmental threats to its habitat.

We can find no differences between the South Saskatchewan River and Athabasca River specimens. The two populations apparently belong to the same species.

Biology

The biology of *Acanthomola* is poorly known. All specimens have been collected from large rivers, and the Saskatchewan specimens were collected from an area of fast current and high silt load. The habitats from which the Athabasca River specimens were collected are not known.

Acanthomola is very rare in the South Saskatchewan River. It has been collected at only one site, on only two occasions, in spite of intensive collecting in the area for 15 years. *Acanthomola* may be slightly more common in the Athabasca River.

The guts of two dissected larvae (including one nearly mature specimen) contained detritus and a few diatom cells, but no recognizable animal fragments.

Acanthomola appears to have a summer life cycle. The occurrence of only early-instar larvae in collections from mid- to late-May suggests that most of the year is passed in the egg stage, with eggs hatching in late spring. Adult emergence may occur in late June and early July.

Acknowledgments

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