A COMPARISON OF *PSEUDOBAICALASELLUS* AND *CAECIDOTEA*, WITH A DESCRIPTION OF *CAECIDOTEA BOWMANI*, N. SP. (CRUSTACEA: ISOPODA: ASELLIDAE)

Julian J. Lewis

Abstract.—The Appalachian genus Pseudobaicalasellus is analyzed and found to be a synonym of Caecidotea. A new subterranean species, C. bowmani, is described with a redescription of C. holsingeri, along with notes on C. vandeli. An analysis of the affinities of the asellid cannulus group shows certain Caecidotea spp. from Arkansas and southern Mexico to be morphologically similar to the Appalachian species.

Bresson (1955) described 3 new species of asellids collected in the Appalachian Valley and Ridge Province of Virginia and West Virginia: Asellus vandeli, A. simonini and A. henroti. Bresson placed these species in the subgenus Baicalasellus primarily because of the unusual morphology of the male second pleopod, which resembled species inhabiting Lake Baikal, in the Soviet Union, more than North American species.

Steeves (1965) named the *cannulus* group to receive additional species morphologically similar to those described by Bresson (1955) and eventually placed 8 species in it (Steeves, 1969). A diagnosis of the *cannulus* group was not published and the assignment of species is open to further interpretation. In this paper the *cannulus* group is considered to consist of 10 species: *Caecidotea bowmani*, *C. cannulus*, *C. circulus*, *C. henroti*, *C. holsingeri*, *C. incurva*, *C. nortoni*, *C. scyphus*, *C. simonini* and *C. vandeli*.

Henry and Magniez (1970) pointed out the morphological, zoogeographical and ecological differences between the Lake Baikal and Appalachian asellids and erected the genus *Pseudobaicalasellus* to accept Bresson's (1955) 3 species.

Holsinger and Steeves (1971) assigned the ill defined *cannulus* group to *Pseudobaicalasellus*, but chose to retain the genus *Asellus* until taxonomic problems concerning the group could be resolved. Fleming (1973) followed Holsinger and Steeves (1971) and synonymized *Pseudobaicalasellus* and *Conasellus* (=*Caecidotea*) with *Asellus*. Bowman (1975) rejected Fleming's (1973) synonymy of *Conasellus* with *Asellus* but did not comment on the status of *Pseudobaicalasellus*.

Table 1 lists characters considered by Henry and Magniez (1970) in the diagnosis of *Pseudobaicalasellus*, plus others of taxonomic value. Data for

Table 1.—Comparison of diagnostic characters of Pseudobaicalasellus and Caecidotea.

Character	Pseudobaicalasellus	Caecidotea
Maxilla 1:		
—inner lobe apical setae	5	5
-outer lobe apical setae	11–13	10-13
Maxilliped oostegite	membranous, setose	membranous, setose
Pereopod 1 sexual dimorphism	absent	present or absent
Pereopod 4 specialization	male more robust	male more robust
	than female	than female
Male pleopod 1:		
—retinaculae	2–7	0-7
—distal margin	rounded or	rounded, flattened
	subtriangular	or subtriangular
Mandibles:		
palp segment 3	plumose setae	plumose setae
—incisors/lacinia mobilis	4-cuspate	4-cuspate
Male pleopod 2:		
Endopod:		
—basal apophysis	present or absent	present or absent
—basal spur	slightly produced	slightly produced
—labial spur	absent	absent
torsion	present	present or absent
-tip processes	single or multiple	single or multiple
Exopod:		
-posterior catch lobe	slightly produced	slightly produced
Female pleopod 2	subtriangular	subtriangular
Pleopod 3 suture	transverse	transverse
Pleopod 4	exopod larger than endopod	exopod larger than endopod
Uropods:		
—endopod vs. exopod	endopod longer or	endopod longer or
F F	about equal	about equal
sexual dimorphism	slight	present or absent
—length	short or elongate	short or elongate

this table came from Bowman (1967, 1974, 1975), Bresson (1955), Lewis and Bowman (1977), Mackin and Hubricht (1940), Steeves (1963a, 1963b, 1965, 1966), Steeves and Holsinger (1968), and Williams (1970). It is apparent that there is considerable overlap in the morphology of *Caecidotea* and *Pseudobaicalasellus*. Similarities of the male pereopod 1, pleopod 1 and pleopod 2 of species assigned to *Pseudobaicalasellus* suggest a monophyletic group deserving a separate genus, but as additional species have been described the morphological differences between the 2 genera have disappeared. Considering this, I believe that Holsinger and Steeves (1971) were justified in their conservative approach to *Pseudobaicalasellus*. I place *Pseudobaicalasellus* as a synonym of *Caecidotea*, and follow Bowman (1975) in considering *Caecidotea* and *Asellus* to be distinct genera.

Caecidotea bowmani, new species Figs. 1-3, 4h

Material examined.—VIRGINIA, Rockbridge Co., drain tile next to trail in park at Natural Bridge, collected by Julian J. Lewis and Teresa M. Everitt, 20 May 1977, 6 males and 12 females. The holotype 8.8 mm male (USNM 172995) and 17 paratypes (USNM 172811–172813, 172996) are deposited in the National Museum of Natural History, Smithsonian Instution.

Description.—Eyeless, unpigmented. Longest male 12.0 mm, longest female 8.5 mm; body slender, linear, about $6.4 \times$ as long as wide; coxae visible in dorsal view. Margins of head, body and telson moderately setose. Head about $1.8 \times$ as wide as long; anterior margin concave, without rostrum; postmandibular lobes rather prominent, broadly produced. Telson about $1.5 \times$ as long as wide, sides subparallel, caudomedial lobe moderately well defined.

Antenna 1 reaching middle of last segment of antenna 2 peduncle; flagellum variable, of about 8–11 segments, last 5 (8.5 mm female) to 7 (11.0 mm male) segments each bearing esthete, each esthete appearing 3-segmented. Antenna 2 reaching pereonite 6; last segment of peduncle about $1.5 \times$ length of preceding segment; flagellum variable, 46 (11.0 mm male) to 58 (8.5 mm female) segments.

Mandibles with 4-cuspate incisors and lacinia mobilis; spine row with 11 plumose spines in left mandible, 16 in right mandible; palp bearing plumose setae on distal segments. Maxilla 1, apex of outer lobe with 13 robust spines and 2 subterminal setae; inner lobe with 5 robust, plumose setae. Maxilliped with 5–6 retinaculae; oostegite well developed in female, with numerous marginal setae.

Male percopod 1 propus about $2.2 \times$ as long as wide, lacking processes; palm straight proximally, bearing 3 robust spines, slightly concave distally; dactyl flexor margin bearing about 5–6 spines. Female percopod 1 similar to male, sexual dimorphism lacking. Percopod 4 more robust in male than female, sexual dimorphism pronounced, flexor margin of dactyl bearing 2 spines.

Male pleopod 1 longer than pleopod 2; protopod about $0.75 \times$ as wide as long, with 3 retinaculae on right, 4 on left. Exopod subtriangular, about $0.4 \times$ as wide as long, lateral margin broadly convex, with many moderately long setae. Male pleopod 2 exopod, proximal segment with 3-4 lateral, 0-1 mesial plumose setae, distal segment laterally convex, mesially concave,

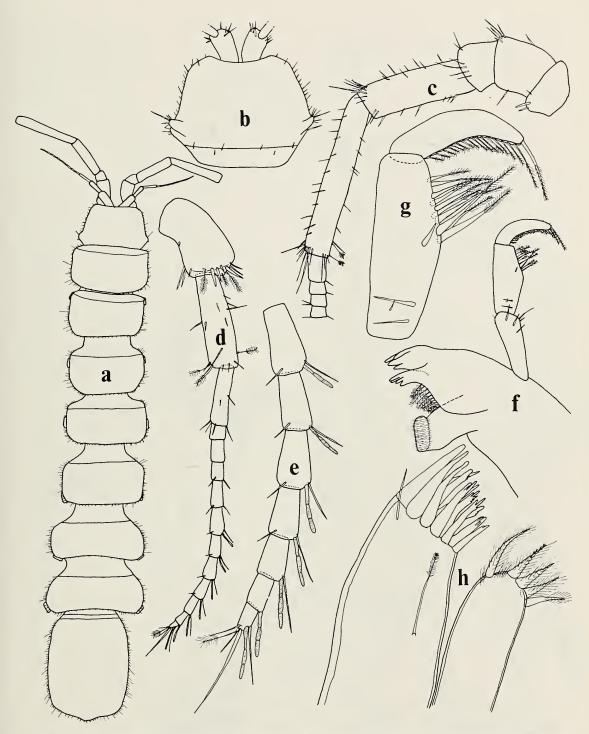


Fig. 1. Caecidotea bowmani, δ : **a**, Habitus, dorsal; **b**, Head, dorsal; **c**, Antenna 2 peduncle; **d**, Antenna 1; **e**, Antenna 1, distal segments; **f**, Left mandible; **g**, Same, distal segments of palp; **h**, Maxilla 1.

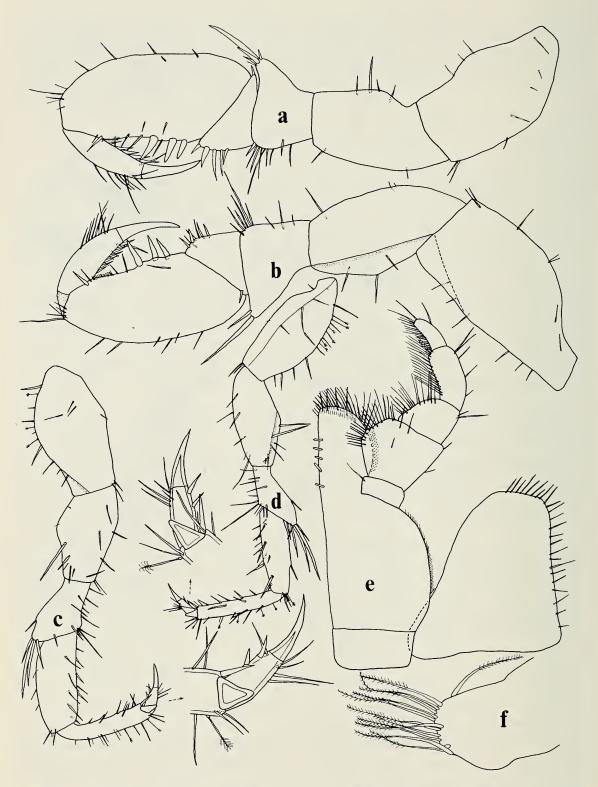


Fig. 2. *Caecidotea bowmani*: **a**, Pereopod 1, δ ; **b**, Pereopod 1, φ ; **c**, Pereopod 4, δ ; **d**, Pereopod 4, φ ; **e**, Maxilliped, δ ; **f**, Oostegite of φ maxilliped.

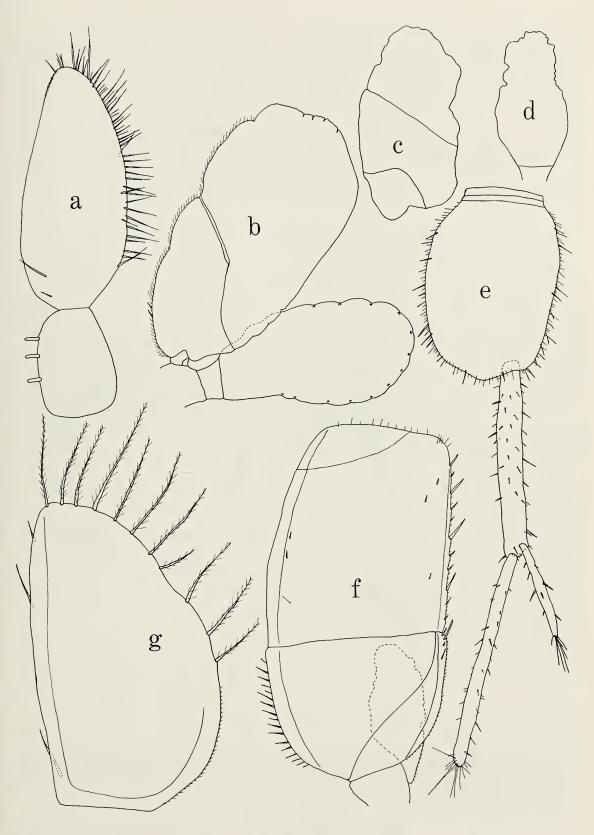


Fig. 3. Caecidotea bowmani: a-f, δ : a, Pleopod 1; b, Pleopod 4; c, d, Pleopod 5, exopod and endopod; e, Pleotelson and uropod; f, Pleopod 3. g, Pleopod 2, \Im .

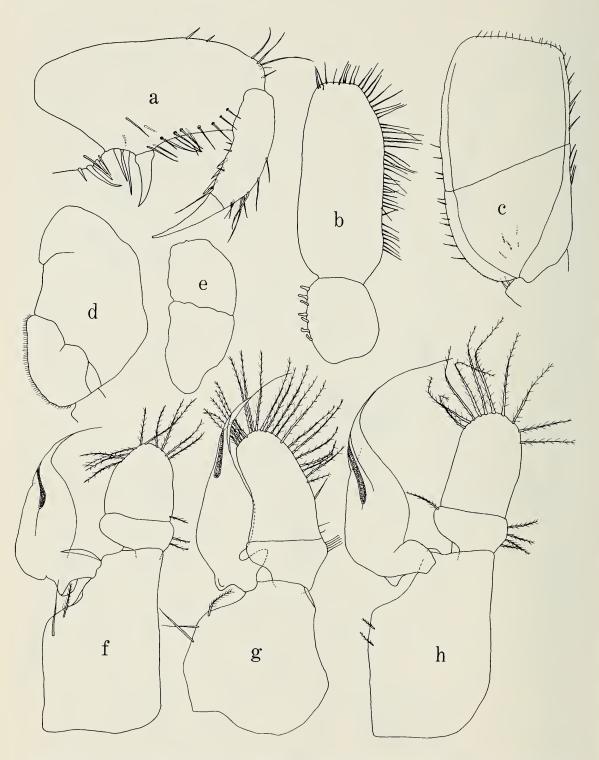


Fig. 4. *Caecidotea holsingeri*, δ : **a**, Pereopod 1; **b**, Pleopod 1; **c**, Pleopod 3; **d**, Pleopod 4, exopod; **e**, Pleopod 5, exopod; **g**, Pleopod 2. *Caecidotea vandeli*: **f**, Pleopod 2, δ . *Caecidotea bowmani*: **h**, Pleopod 2, δ .

apically broadly rounded, bearing 10–13 long, plumose setae; endopod with broadly rounded basal apophysis, tip of endopod a single process tapering to a thread extending in an arc for about $0.4 \times$ the entire endopod; entire endopod appears twisted. Female pleopod 2 triangular, lateral margin with slgith concavity, bearing about 11 plumose setae. Male pleopod 3 exopod about $2 \times$ as long as wide; distal segment about 1.5 times as long as proximal segment; marginal setae not plumose. Pleopod 4 fleshy, bearing numerous setules and single false suture; pleopod 5 fleshy, lacking setules.

Male uropod slender and elongate, endopod about 1.2, exopod about $0.5 \times$ as long as protopod.

Etymology.—It is a pleasure to name this new species after Dr. Thomas E. Bowman, Curator of Crustacea, National Museum of Natural History.

Habitat.—Caecidotea bowmani is known only from the type-locality, a small drain tile next to a tourist trail leading through a privately owned park called Natural Bridge of Virginia. The drain is obscured by soil which has slumped from the hillside in which it is placed. In this area the Cambrian aged Conococheague Formation (primarily limestone and dolomite) is exposed, but the tile appears to lie above this bedrock in a mixture of soil and hillside rubble. Water from the drain runs a few meters into Cedar Creek and eventually enters the James River.

Caecidotea bowmani was collected from the undersides of leaves in the company of an undescribed species of the subterranean amphipod genus *Stygobromus*.

Relationships.—The male pleopod 2 endopods of C. bowmani, C. vandeli, C. simonini, C. holsingeri, C. cannulus and C. chiapas all terminate in an elongate cannula. The endopods of C. bowmani and C. vandeli are nearly identical, but these 2 species can be separated by the following characteristics: (1) the average body length of C. bowmani is about twice that of C. vandeli; (2) the male pleopod 1 is subtriangular in C. bowmani, suboval in C. vandeli; (3) the male pleopod 2 exopod distal segment is longer and more linear in C. bowmani; (4) the male pleopod 3 of C. bowmani lacks distal plumose setae present in C. vandeli; and (5) the uropods of C. bowmani are longer than the pleotelson, while those of C. vandeli are less than $0.5 \times$ the length of the pleotelson.

The cannulas of *C. bowmani*, *C. holsingeri* and *C. cannulus* taper to a fine thread, but the endopods are otherwise dissimilar. *Caecidotea holsingeri* possesses a pronounced basal apophysis not exhibited by other members of the *cannulus* group. The body of the endopod is widened near the midlength in *C. cannulus*, in contrast to the slender endopods of *C. bowmani* and *C. holsingeri*. In *C. simonini* and *C. chiapas* the cannula is elongate but does not terminate in a threadlike structure.

The male first pleopod has a suboval or subtriangular distal segment bearing distal and lateral setae in all 10 members of the *cannulus* group. The pereopod 1 propus palmar margin lacks processes in these 10 species, along with C. adenta, C. richardsonae, C. tomalensis, C. occidentalis and some other Caecidotea. Sexual dimorphism is poorly described in most asellids, but is lacking in the pereopod 1 of C. bowmani, C. holsingeri and C. packardi. The sexual dimorphism of pereopod 4 in C. bowmani is common within the genus.

Caecidotea holsingeri (Steeves) Fig. 4a–e, g

Asellus holsingeri Steeves, 1963a:462–465, figs. 1–5; 1965:84; 1966:395, 397, fig. 7; 1969:56–58, 61.—Steeves and Holsinger, 1968:81.—Culver, 1971: 173, 175–177, 179–181, 183–184, tables 1, 4, fig. 2.—Holsinger and Steeves, 1971:193–195, fig. 6.—Fleming, 1972:253; 1973:286–291, 295–296, fig. 1. tables 1–6.—Culver, Holsinger and Baroody, 1974:691, table 1.—Rutherford and Handley, 1976:43, 45, table 1.—Culver, 1976:946, 948, 951, 954, table 1. Holsinger, Baroody and Culver, 1976:24–26, 59.

Asellus sensu lato holsingeri Steeves.—Holsinger, 1978:8.

Conasellus holsingeri (Steeves).-Henry and Magniez, 1970:356.

Material examined.—WEST VIRGINIA: Greenbriar Co., Organ Cave (type-locality), 27 Aug. 1978, 5 males, 1 female. Bransford Cave, 26 Aug. 1978, 2 males, 6 females (3 ovigerous, 3.2, 3.4, 3.5 mm). Monroe Co., Rock Camp Cave, 25 Aug. 1978, 1 male. Pocahontas Co., Linwood Cave, 29 Aug. 1978, 4 males, 19 females (15 ovigerous, 5.5–7.9 mm). Martha's Cave, 1 Sept. 1978, 4 males, 5 females (1 ovigerous, 3.5 mm). Randolph Co., Alpena #1 Cave, 29 Aug. 1978, 1 male, 9 females. All of these specimens were collected by D. Culver and T. Ehlinger.

Description of topotypic material.—Eyeless, unpigmented. Largest individual 9.8 mm; body slender, linear, about $5.2 \times$ as long as wide, coxae visible in dorsal view. Margins of head, pereonites and telson moderately setose. Head about $1.8 \times$ as wide as long; anterior margin concave, post-mandibular lobes moderately produced. Telson about $1.3 \times$ as long as wide, sides subparallel, caudomedial lobe somewhat produced, broadly rounded.

Antenna 1 barely reaching last segment of antenna 2 peduncle, flagellum of 5–7 segments, bearing 2–5 esthetes, varying with size of specimen. Antenna 2 reaching to about pereonite 6, last segment of peduncle about $1.3 \times$ length preceding segment, flagellum of about 36 segments (9.8 mm male).

Mandibles with 4 cuspate incisors and lacinia mobilis, (except 9.8 mm male with 5 cuspate left incisor) setae rows with 13 plumose setae in left mandible, 12 plumose setae in right mandible. Maxilla 1, apex of outer lobe with 13 spines and 1 subterminal seta, inner lobe with 5 apical plumose setae. Maxilliped with 4–6 retinaculae.

Pereopod 1, sexual dimorphism absent, propus about $2.1 \times$ as long as

wide, palm very slightly concave, processes absent, 1 large spine proximally. Dactyl flexor margin with about 3 stout spines. Pereopod 4 of male moderately setose and spinose, dactyl with 1 small mesial spine. Female pereopod 4 missing in Organ Cave specimen, in 7.8 mm ovigerous female from Linwood Cave, pereopod 4 much less robust than male, spine on dactyl absent.

Pleopod 1 larger than pleopod 2, protopod about 0.5 length exopod, with 7–8 retinaculae; exopod about $0.4 \times$ as wide as long, non-plumose setae along lateral and apical margins. Pleopod 2, protopod with 2 mesial non-plumose setae, exopod, proximal segment with 5 non-plumose setae; distal segment, mesial margin concave, about 20 long plumose setae on distal and lateral margins, 3 shorter, non-plumose setae proximal laterally. Endopod, basal apophysis distinct; tip terminating in single process tapering to a fine, elongate thread, some torsion apparent.

Pleopods 3, 4, and 5 as figured. Uropod (9.8 mm male) 3.2 mm long, protopod and endopod spatulate, endopod about 1.4, exopod about $0.8 \times$ as long as protopod.

Distribution.—Caecidotea holsingeri is known from the extreme western portion of Maryland through eastern West Virginia (Steeves, 1969) and a Bath Co., Virginia locality (Holsinger and Steeves, 1971). Fleming (1972) and Holsinger, Baroody and Culver (1976) listed a total of 27 cave localities within this range.

Variation.—Caecidotea holsingeri was known by a single specimen when described (Steeves, 1963a) and additional specimens have revealed some variation. Steeve's 8-mm specimen was apparently immature, since the uropod figured was not as elongate or spatulate as a larger 9.8 mm male. Holsinger, Baroody and Culver (1976) report a length of 12 mm for this species.

The distinct basal apophysis was fastened around the proximal segment of the exopod in several specimens (Fig. 4g). In this way the convex lateral surface of the endopod is even with the concave mesial surface of the exopod, forming a continuous surface. This presumably aids in sperm transfer in some manner.

The endopod tip was shown by Steeves (1963a) with a small apical flange, but this feature was not present in the majority of specimens examined. The male pereopod 1 bears a spine on the palmar margin which varies from small and seta-like to large, robust and distally curved. At least one specimen had a large spine on one gnathopod and a small seta on the other.

> Caecidotea vandeli (Bresson) Fig. 4f

Asellus vandeli Bresson, 1955:69–75, figs. 49–61.—Vandel, 1965:277.—Henry and Magniez, 1968:2.—Steeves, 1969:53, 56–58.—Cole and Minckley,

1972:322.—Fleming, 1972:253; 1973:286, 289–291, 295–296, fig. 1, tables 4–6.

Pseudobaicalasellus vandeli (Bresson).-Henry and Magniez, 1970:357.

Material examined.—VIRGINIA: Montgomery Co., Slusser's Chapel Cave, 21 April 1968, collected by J. Holsinger, R. Whittemore (USNM 327628), 3 males (5.9–6.7 mm), 6 females (6.8–7.6 mm).

Distribution.—The type-locality of C. vandeli is Erhardt's Cave, Montgomery Co., Virginia (Bresson, 1955). Steeves (1969) visited there without success in collecting additional specimens, but listed a second locality in the same county, Slusser's Chapel Cave. Douglas (1964) and Holsinger (1975) gave locations and descriptions of these caves. Fleming (1972) reported an additional cave locality in Montgomery Co., plus individual collections from Bath, Botetourt and Giles counties.

Comments.—Steeves (1969) believed that the cannula had been broken in the male used by Bresson (1955) since specimens from Slusser's Chapel Cave had a cannula much longer than originally figured. I have redrawn this structure as it appears undamaged (Fig. 4f).

Affinities of the cannulus group.—In 7 additional species the male pleopod 2 possesses the single elongate, tapering terminal process and torsion of the endopod characteristic of the cannulus group: C. chiapas Bowman (1975); C. pasquinii Argano (1972); C. montana (Mackin and Hubricht, 1938); C. oculata Mackin and Hubricht (1940); and C. zullini, C. vomeroi and C. mitchelli Argano (1977). Of these 7 species, C. montana and C. oculata are epigean species occurring in the Ouchita Province, although C. oculata is associated with groundwater (springs) in some collections (Mackin and Hubricht, 1940). C. chiapas, C. pasquinii, C. zullini, C. vomeroi and C. mitchelli, all members of the chiapas group (Argano, 1977), are phreatobites or troglobites occurring in Mexico. Three other species, C. laticaudata, C. foxi and C. dimorpha possess rather elongate cannulas, but in these species the cannula is associated with auxiliary processes (lateral, mesial or caudal) and exhibits no evidence of torsion.

Members of the *cannulus* group also lack processes on the gnathopod palm and possess setae along both the convex distal and lateral margins of the male pleopod 1 exopod. Of the seven species listed above in which the male pleopod 2 is of the type found in *cannulus* group species, all have processes along the gnathopod palm. The lateral margin of the pleopod 1 exopod is convex only in *C. montana* and *C. vomeroi*, concave in *C. chiapas*, *C. pasquinii*, *C. oculata*, *C. mitchelli* and *C. zullini*. All of these 7 species differ further from the *cannulus* group species in having elongate setae, usually plumose, along the distal margin only, with short spines or setae along the lateral margin.

Williams (1970) and Steeves (1966) placed emphasis on the morphology

of the male pleopod 2 endopod tip in evaluating phylogenetic relationships, although Williams included other morphological aspects.

If monophyletic groups could be determined by endopod tip morphology alone, the 17 species assemblage consisting of the *cannulus* group (10 species), *chiapas* group (5 species), *C. oculata*, and *C. montana* might be considered phylogenetically related due to the similarity of the endopod tips of these species. However, a phylogenetic group based on, e.g., the morphology of the gnathopod, would yield very different results than one based on endopod morphology. When the interrelationships of these morphological characters are better understood, it may be possible to designate subgenera within the genus *Caecidotea*.

Acknowledgments

I thank my wife, Teresa M. Lewis, for assistance in collecting C. bowmani, and Dr. David Culver for supplying material of C. holsingeri. Dr. Stuart Neff carefully reviewed the MS and Dr. John R. Holsinger both reviewed the MS and identified the Stygobromus.

My special thanks go to Dr. Thomas E. Bowman for repeatedly reading the MS, checking the drawings, making specimens available from the U.S. National Museum collections, and allowing me the use of his facilities at the museum.

Literature Cited

- Argano, R. 1972. An asellid of the subterranean waters of Veracruz, Mexico (Crustacea, Isopoda).—Quaderni Acc. Naz. Lincei 171:35-42.
- -----. 1977. Asellota del Messico meridionale e Guatemala (Crustacea, Isopoda).—Quaderni Acc. Naz. Lincei 171:101–124.
- Bowman, T. E. 1967. Asellus kenki, a new isopod crustacean from springs in the eastern United States.—Proc. Biol. Soc. Wash. 80:131-140.
 - -----. 1974. The California freshwater isopod, *Asellus tomalensis*, rediscovered and compared with *Asellus occidentalis*.—Hydrobiologia 44(4):431-441.
- ———. 1975. Three new troglobitic asellids from western North America (Crustacea:Isopoda:Asellidae).—Int. J. Speleol. 7:339–356.
- Bresson, J. 1955. Aselles de sources et de grottes d'Eurasie et d'Amérique du Nord.—Arch. Zool. Exp. Gén. 92(2):45-77.
- Cole, G. A., and W. L. Minckley. 1972. Stenasellid isopod crustaceans in the western hemisphere—a new genus and species from Mexico—with a review of other North American freshwater isopod genera.—Proc. Biol. Soc. Wash. 84(39):313–326.
- Culver, D. C. 1971. Analysis of simple cave communities III. Control of abundance.—Amer. Midl. Nat. 85(1):173-187.
 - —. 1976. The evolution of aquatic cave communities.—Amer. Nat. 110(976):945-957.
 - —, J. R. Holsinger, and R. Baroody. 1974. Toward a predictive cave biogeography: the Greenbrier Valley as a case study.—Evol. 27(4):689–695.

Douglas, H. H. 1964. Caves of Virginia.-Virginia Cave Survey, 761 pp. Falls Church, Va.

- Fleming, L. E. 1972. The evolution of the eastern North American isopods of the genus Asellus (Crustacea:Asellidae), Part I.—Int. J. Speleol. 4:221–256.
- ——. 1973. The evolution of the eastern North American isopods of the genus Asellus (Crustacea:Asellidae) Part II.—Int. J. Speleol. 5:283–310.
- Henry, J-P., and G. Magniez. 1968. Sur la systématique et al biogéographie des asellides.— C.R. Acad. Sci. Paris 267:87-89.
- ———, and ———. 1970. Contribution a la systématique des asellides (Crustacea:Isopoda).— Ann. de Spéleól. 25(2):335–367.
- Holsinger, J. R. 1975. Descriptions of Virginia Caves.—Bull. Va. Div. Mineral Res. 85:1–450.
 ——. 1978. Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae), Part II: Species of the eastern United States.—Smith. Cont. Zool. 266:1–144.
- -----, R. A. Baroody, and D. C. Culver. 1976. The invertebrate cave fauna of West Virginia.--W. Va. Speleol. Surv. Bull. 7:1-82.
- ——, and H. R. Steeves. 1971. A new species of subterranean isopod crustacean (Asellidae) from the central Appalachians, with remarks on the distribution of other isopods of the region.—Proc. Biol. Soc. Wash. 84(23):189–200.
- Lewis, J. J., and T. E. Bowman. 1977. Caecidotea carolinensis, n. sp., the first subterranean water slater from North Carolina (Crustacea:Isopoda:Asellidae).—Proc. Biol. Soc. Wash. 90(4):968–974.
- Mackin, J. G., and L. Hubricht. 1938. Records and distribution of species of isopods in central and southern United States, with descriptions of four new species of *Mancasellus* and *Asellus* (Asellota, Asellidae).—Amer. Midl. Nat. 19:628–637.
- ——, and ——. 1940. Descriptions of seven new species of *Caecidotea* (Isopoda, Asellidae) from central United States.—Trans. Amer. Micr. Soc. 59(3):383–397.
- Miller, M. A. 1933. A new blind isopod, *Asellus californicus*, and a revision of the subterranean asellids.—Univ. Cal. Publ. Zool. 39(4):97-110.
- Rutherford, J. M. and R. H. Handley. 1976. The Greenbrier Caverns.—Nat. Speleolog. Soc. Bull. 38(3):41-52.
- Steeves, H. R. III. 1963a. Two new troglobitic asellids from West Virginia.—Amer. Midl. Nat. 70(2):462–465.
 - —. 1963b. The troglobitic asellids of the United States: The stygius group.—Amer. Midl. Nat. 69(2):470–481.
- ———. 1965. Two new species of troglobitic asellids from the United States.—Amer. Midl. Nat. 73(1):81-84.
- -----. 1966. Evolutionary aspects of the troglobitic asellids of the United States: The *hobbsi*, *stygius* and *cannulus* groups.—Amer. Midl. Nat. 75(2):392–403.
- ———. 1969. The origin and affinities of the troglobitic asellids of the southern Appalachians.—In P. C. Holt, (ed), The Distributional History of the Biota of the Southern Appalachians, part I: Invertebrates, p. 51–65. Research Div. Mono. I, Va. Polytech. Inst., Blacksburg.
 - -, and J. R. Holsinger. 1968. Biology of three new species of troglobitic asellids from Tennessee.—Amer. Midl. Nat. 80(1):75-83.
- Vandel, A. 1965. Biospeleology. xxiv + 254 pp. New York, Pergamon Press.
- Williams, W. D. 1970. A revision of North American epigean species of Asellus (Crustacea: Isopoda)—Smith. Cont. Zool., 49:1–80.

Department of Biology, and Water Resources Laboratory, University of Louisville, Louisville, Kentucky 40208.