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A REVISION OF THE GENUS *TYPHLOGASTRURA* IN NORTH AMERICAN CAVES WITH DESCRIPTION OF FIVE NEW SPECIES

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The peculiar troglobitic, polyphyletic nature of Typhlogastrura *and the small amount of troglomorphism found in the genus is discussed. New features of chaetotaxy are systematized and used . The Nearctic members are distinguished, keyed out and five new species—*asymmetrica, fousheensis, helleri, steinmanni *and* unica*—are described. Species are shown to occur in 5 widely separated regions ranging from Colorado to Pennsylvania.*

INTRODUCTION

Typhlogastrura is, in our view, an artificial genus consisting of all members of the *denticulata* branch of *Ceratophysella*, which have successfully invaded caves and become troglomorphic. They have a number of unusual features: A) they are the result of many widely separated invasions and most of these paraphyletic groups occur in only one cave or a few closely connected caves[1], B) there appear to be no troglophilic or edaphic species (with one possible exception[2]) and C) in the Nearctic region, there has been no evolution in any of these forms into more troglomorphic species within the cave systems they have invaded. The parallel genus from the *armata* branch of *Ceratophysella* (*Bonetogastrura*) has both cave and troglophilic species as well as one surface species *(B. variabilis*) which is the only one found in the Northern North America. Both genera are characterized by a reduction in eyes and the maintenance of a fully developed furcula. This is in contrast to the genus *Schaefferia* which includes reduced eye *Ceratophysella* that are largely edaphic and have reduced furculas, which we have shown is uniquely an edaphic phenomenon (Christiansen, 1985). Only one species of *Schaefferia* has been found in Nearctic caves (*S. hubbardi* Thibaud 1995). While this species has only been found in a cave, a number of species have been found in Palearctic caves. The majority of these are troglophiles. This study is limited to *Typhlogastrura.* We briefly discuss *T. alabamensis* and *christianseni*, redescribe *T. valentini* and describe five new species: *asymmetrica, fousheensis, helleri, steinmanni* and *unica*.

*Typhlogastrur*a was first described as a subgenus of *Hypogastrura* by Bonet (1930) and later placed by many as a subgenus of *Schaefferia,* but since Stach 1949 the majority of workers have treated it as a separate genus. Presently there are 14 described species in *Typhlogastrura*, but no Nearctic species were described until Thibaud described *alabamensis* and *christianseni* from Alabama caves in 1975 (Thibaud, 1975). Thibaud redescribed these two species in detail in his revision of the genus in 1980 (Thibaud, 1980). He described a third species, *T. valentini*, from a cave in Virginia in 1996. We herein redescribe *T. valentini*, give some supplementary details about *T. christianseni* and *alabamensis,* and describe five new species from Pennsylvania, Colorado and Missouri. Palacios-Vargas and Thibaud (1986) and Palacios-Vargas (1997) have described two species from Mexico which we include in the key and diagnostic table.

With the single exception of *Typhlogastrura valentini* from Virginia, Nearctic species of this genus have been found only in one or two closely connected caves. The striking picture of the distribution of these species bespeaks a single, separate adaptation to cave life in each species which was physiological, and only after some time allowing sufficient change to occur to make survival outside caves improbable.

The species are normally associated with guano or scat although they are also found on rotted wood. They are often found on pool surfaces, but these are almost certainly trapped there accidentally.

SPECIES CHARACTERISTICS

Thibaud's excellent works on this genus, including his large works of 1970 and 1980, distinguished species using the number of sensory setae and apical bulbs on the fourth antennal segment, the structure of the PAO (Post Antennal Organ), the number of eyes (Fig. 1), structure of the mucro and the thoracic chaetotaxy. In our study we had the good fortune of being able to study many populations of one species, *T. valentini*, to

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[1] The one exception to this is *T. korenevski* which occurs in two caves 120 km apart; however the conspecific nature of these two remains in doubt. When Babenko first saw them he thought of them as two different species but later changed his mind.

[2] Jose Palacios-Vargas reports (pers. comm.) having seen an edaphic eyeless member of the genus, but the specimens have been lost and not described in detail, and no detail of their capture or of their location is available other than they were from Chiapas.

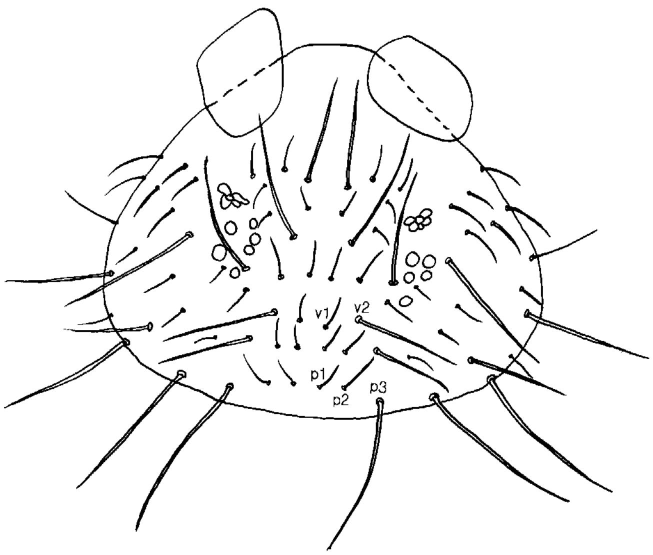


Figure 1. Generalized head with chaetotaxy.

obtain a good picture of the intraspecific variability of features. This demonstrated to us that the chaetotaxy of the second thoracic segment and abdominal segments 3–5 (Fig. 2) was extremely intraspecifically constant, but interspecifically varying, and thus furnished an excellent tool for taxonomic separation.

We found that the chaetotaxy shows a number of patterns which we defined in Table 1. In the second thoracic segment the useful character was the triangle formed by P1–P3, with A being the length of the line between setae 1 & 3 and B line from P2 perpendicular to this line, with Ratio = A/B (Fig. 2; Table 2). In abdominal segments 3–5 it is the presence or absence of setae and their relative length which are of importance as well as their positions (Fig. 2; Table 2). Except for two pairs, *fousheensis – veracruzana* and *steinmanni – asymmetrica*, all species are easily separable by their chaetotaxy alone (Table 2). We also found Yosii A measurement (number of tubercles between the P1 setae on abdominal segment 5) to be useful. A key to the Nearctic & Mesoamerican species is on the next page.

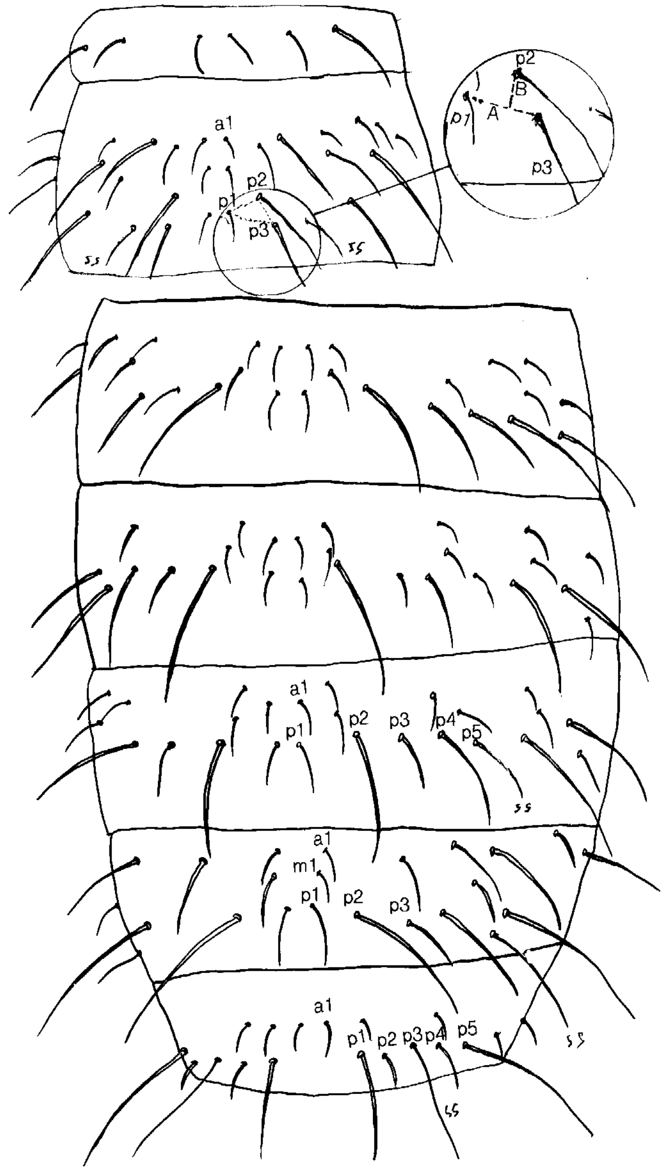


Figure 2. Generalized dorsal chaetotaxy first–second thoracic and first–fifth abdominal segments.

1) Eye 0 or 1 + 1..2
1') Eyes at least 3 + 3..3

2) Fourth antennal segment with seven blunt, thick setae
....*T. elsarzolae*
2') Fourth antennal segment with ten blunt, thick setae
....*T. veracruzana*

3) Fifth abdominal segment with a clear median swelling
(Fig. 3)..*T. unica*
3') Fifth abdominal segment without a clear median
swelling...4

4) Fifth abdominal segment with three–four setae between
the P1 setae level (Fig. 4A)...............................*T. alabamensis*
4') Fifth abdominal segment with two setae between the P1
setae level (Fig.4B)...5

5) Apical antennal bulb large and double (Fig. 5A)
....*T. steinmanni*
5') Apical antennal bulb small and single, sometimes apically
indented (Fig. 5B)..6

6) Fifth abdominal segment with setae P1–P5 all present
(Fig. 2)...7
6') Fifth abdominal segment with seta P2 and/or P4 absent
....8

7) Eyes 5–6 per side..*T. helleri*
7') Eyes 4 per side...*T. fousheensis*

8) B/A ratio on second thoracic segment less than 1.8
(Fig. 6A)..*T. asymmetrica*
8') B/A ratio on second thoracic segment greater than 3.0
(Fig. 6B)..9

9) Fifth abdominal segment with both setae P2 and P4
(Fig. 2) absent..*T. christianseni*
9') Fifth abdominal segment with seta P4 present
....*T. valentini*

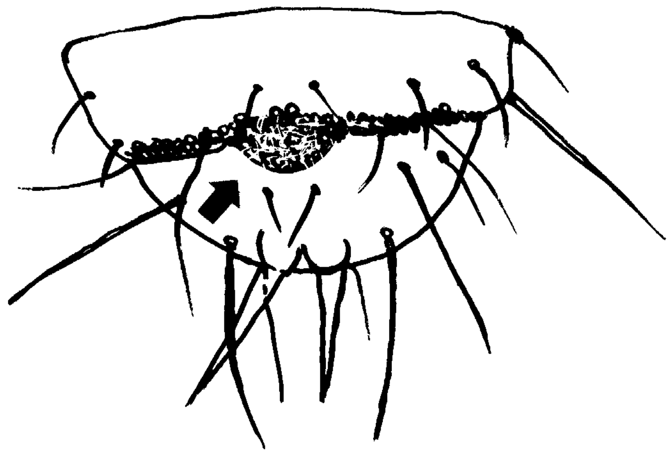


Figure 3. Fifth and sixth abdominal segments illustrating the hump in the center of the fifth segment.

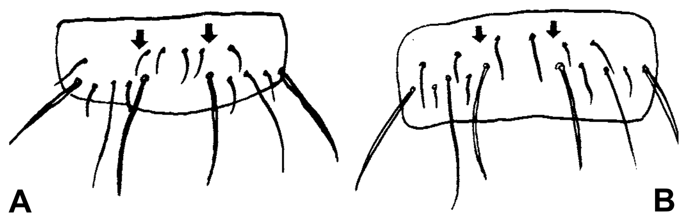


Figure 4. Fifth abdominal segment with A (left) 3-4 setae between level of P1 setae and B (right) two setae between the P1 setae.

Figure 5. Apex of antenna A (left) with two large retractile bulbs and B (right) a single small bulb.

Figure 6 (right) Second thoracic segment with B -horizontal unbroken line) / A -vertical unbroken line) ratio less that 1.8 (A) and more than 3.0 (B).

Table 1. Body Chaetotaxy Types[a]

Abdominal Segment 5	Description	Figure
Type 1	P3 long, P4 short, P2 absent, 2 A setae between level p1 setae	Fig. 14 G
Type 2	P3 long, P2 & 4 absent, 2 A setae between level p1 setae	Fig. 9 E
Type 3	P3 long, P2 & 4 short , 3-4 A setae between level p1 setae	Fig. 7 C
Type 4	P3 short, P4 absent, 2 A setae between level p1 setae (only *elsarzolae*)	
Type 5	P3 long, P2 & 4 short, 2 A setae between level p1 setae	Fig. 10 H
Abdominal Segment 4		
Type 1	P3 present , setae P1, m1, & A1' in a nearly straight line	Fig. 13 F
Type 2	P3 absent, inner setae with A1 strongly angled from M1 and P1	Fig. 7 C
Type 3	P3 absent , setae P1, m1, & A1' in a nearly straight line	Fig. 12 E
Type 4	P3 present inner setae with A1 strongly angled from M1 and P1 (only *elsarzolae*)	
Abdominal Segment 3		
Type 1	6 setae between P2 setae, either P3 or P4 missing	Fig. 9 D
Type 2	8 setae between P2 setae, P2 & P4 present	Fig. 7 C
Type 3	6 setae between P2 setae, P2 & P4 present	
Type 4	8 setae between P2 setae, P2 or P4 missing (only *elsarzolae*)	
Thoracic Segment 2		
Ratio = A/B	Length line from A) P1–P3 and B) line from p2 perpendicular to line A	

[a]Thibaud (1970) in his study of *Typhlogastrura balazuci* showed that the chaetotaxy was fully developed after the third instar.

Table 2. Species characteristics Nearctic *Typhlogastrura*

Species	Eyes/ side	Segment Type Abd.5	Segment Type Abd.4	Segment Type Abd.3	Thor.2 A/B[a]	Ant. 4 blunt thick setae	PAO lobes	Anal spine/ inner unguis	Region
steinmanni	6	2	3	1	1.2–1.8	6	(4) 5 (6)	1.3	Colorado Eagle Co.
alabamensis	4-6	3	2	2	1.4–2.4	7,8 (9)	(3) 4 (5)	1.1–2.2	Alabama Blount Jackson Co.s
asymmetrica	6 (5,7)	(2) 1	3	1	1.45–1.7	6	4 (3,5)	1.1	Colorado Custer Co.
christianseni	3-4	2	3	1	3.2–4.0	7	4	0.85–0.9	Alabama Morgan Co.
fousheensis	4	5	1	2	2.0–3.1	7	4	1.33	Arkansas Independence Co.
helleri	5-6	5	(1) 4	2	1.25–1.58	(8) 7	5	1.4	Pennsylvania Huntingdon Co.
unica	5	5	1	(3) 1	1.0–1.4	5-6	7 (5,8)	2.0	Colorado Gunnison Co.
valentini	3 (4,5)	1[b]	3	1	3.2–4.2	6-7	4 (5)	0.69–0.85	Virginia Scott, Giles, Wythe, Washington, Russell Co.
elsarzolae	0	4	4	4	1.7	7	5-6	1.1	Mexico Nuevo Leon
veracruzana	(1)-0	5	1	2	1.9–2.5	10	5-6	.8	Mexico Veracruz

( ) = rare conditions.

[a] From a triangle drawn from seta 1-3 with seta 2 as the apex. A = line drawn from seta 1 to seta 3, and B = perpendicular line drawn from this line to seta 2.

[b]A single specimen has seta P2 present, but P4 absent.

Table 3. Measurements (in mm) of individuals of new species.

Locality no. (type localities)	Total Length	Hind inner unguis	Hind unguiculus	Anal horns	Dens	Mucro	Seta P1 on Abd. 4	Seta P2 on Abd. 4	Lateral sensilla antenna 1	Ocellus B	PAO	Sensilla P3 on Abd. 5
						asymmetrica						
9676 sl.1 #2	1.9	0.082	0.04	0.106	0.07	0.028	0.052	0.142	0.018	0.018	0.028	0.05
9676 sl.1 #1	1.08	0.052	0.016	0.07	0.042	0.018	0.022	0.07	0.016	0.012	0.02	0.04
9676 sl.2 #1	1.3	0.066	0.02	0.078	0.054	0.02	0.022	0.102	0.014	0.01	0.02	0.066
9676 sl.2 #2	1.38	0.06	0.022	0.08	0.056	0.018	0.026	0.092	?	0.01	0.02	0.054
9675	?	0.06	0.022	0.108	?	?	0.044	0.12	0.014	0.012	0.028	0.054
9661	1.84	0.084	0.034	0.09	0.06	0.024	0.04	0.122	0.016	0.016	0.032	0.076
						fousheensis						
3890 spec. 1	1.5	0.066	0.018	0.08	0.058	0.02	0.048	0.1	0.02	0.01	0.03	0.106
3890 spec. 2	1.54	0.068	0.02	0.071	0.06	0.022	0.04	0.11	0.02	0.012	0.034	0.1
9782 spec. 1	1.7	0.058	0.02	0.056	0.066	0.024	0.044	0.11	0.022	0.014	0.028	0.124
9782 spec. 5	1.4	0.056	0.02	0.06	0.052	0.022	0.04	0.1	0.02	0.012	0.02	0.098
9782 spec. 2	1.4	0.044	0.018	0.05	0.052	0.018	0.04	0.108	0.018	0.016	0.028	0.088
9782 spec. 3	1.04	0.032	0.012	0.024	0.03	0.022	0.03	0.1	0.02	0.01	0.022	0.092
						helleri						
9276 sl.1 #1 (holotype)	1.4	0.06	0.038	0.082	0.068	0.028	0.04	0.16	0.024	0.012	0.036	0.11?
9276 sl.1 #2	2	0.084	0.05	0.1	0.088	0.026	0.048	?	0.03	0.012	0.04	?
9276 sl.2 #1 (allotype)	2.08	0.086	?	0.1	0.072	0.032	0.056	0.208	0.03	0.014	0.036	0.164
9276 sl.2 #2	1.64	0.07	0.026	0.08	0.07	0.022	0.054	0.196	0.026	0.014	0.038	0.134
						steinmanni						
9677 sl.1 #2	2.26	0.084	0.02	0.09	0.08	0.032	0.044	0.144	0.02	0.02	0.034	0.084
9677 sl.1 #1	1.98	0.09	0.032	0.08	0.074	0.028	0.04	0.12	0.02	0.022	0.03	0.096
9677 sl.2	2.1	0.086	0.03	0.1	0.09	0.032	0.04	0.166	0.02	0.02	0.03	0.082
9677 sl.4 #2	1.86	0.08	0.024	0.1	0.09	0.03	0.048	0.152	0.024	0.022	0.032	0.082
9677 sl.4 #1	2.12	0.078	0.024	0.104	0.11	0.034	0.038	0.126	0.022	…	…	0.09
						unica						
9737 sl.2 #1	0.96	0.044	0.022	0.052	0.042	0.016	0.028	0.088	0.02	0.012	0.03	0.06
9737 sl.2 #2	1.08	0.042	0.02	0.048	0.04	0.016	0.036	0.09	0.018	0.008	0.026	0.074
9737 sl.1 #1	1.44	0.05	0.024	0.07	0.04	0.016	0.03	0.09	0.02	0.01	0.03	0.078
9737 sl.1 #2	1.2	0.056	0.024	0.08	0.06	0.02	0.058	0.1	?	0.008	0.028	0.09

Species descriptions and comments

All measurement of the new species herein described are given in Table 3.

Typhlogastrura alabamensis Thibaud 1975 (Fig. 7A–D)
This species is unique among the Nearctic *Typhlogastrura* in having 3–4 A setae between the levels of the P1 setae on abdominal segment 5 (Fig. 7C). It also has the most sharply angled A1 and M1 setae on abdominal segment 4 (Fig. 7C). The apical organ of the fourth antennal segment consists of several elements, similar to those of *T. christianseni* and *T. valentini*. (Fig. 7A). All of the 11 verifiable specimens, including four type specimens, are from Swaim Cave in Morgan Co., Alabama. Thibaud also recorded a specimen from a salamander stomach in Bryant Cave in Blount Co., but this record is very questionable (for fuller description see Thibaud 1980).

Typhlogastrura asymmetrica new species (Fig. 8A–J)
Description: Color slightly tan in life, white in alcohol. Apical bulb of fourth antennal segment when expanded small and weakly trilobed, but when withdrawn appearing as a single structure, sometimes with an apical indentation. Longest setae ~0.7 as long as maximum width of segment. Dorsal surface with six blunt setae, which are not clearly distinguished from normal setae. Ventral surface without "file" but with 9–10 short, acuminate, straight or weakly curved setae. Apical organ of third antennal segment with two very short curved blunt rods and lateral sensillae not clearly differentiated from other setae. Second antennal segment with 4–5 cylindrical, apically blunt or pointed, ciliate setae. Large specimens with 1–2 such also on third segment. First antennal segment with five dorsal and one (or possibly two) ventral setae. Three or four of the dorsal setae are cylindrical and similar to those on second segment with the remaining setae acuminate. Eyes usually 6 + 6 and moderately to weakly pigmented. PAO with 4–6 lobes and ~2 times nearest eye. Maxillae with 2 large lamellae, reaching apex of teeth and without ciliations or teeth along edge. Other lamellae unclear. Six clear labral papillae. Area verticalis, with 2 + 2 setae, outer setae 4–5 times as long as the inner, thick, cylindrical, coarsely ciliate and truncate. On the posterior margin P3 and P4 are similar and ~2–3 times as long as P1 & P2 which are sparsely ciliate and acuminate. First thoracic segment with all setae thick and ciliate. Seta 2 is 0.51–0.71 seta 3. Setae 1 usually asymmetrical with one 1.5–1.7 times the other. One of these setae is usually ~seta 2. Remaining thoracic and abdominal chaetotaxy as shown in Table 1 and Fig. 8E–G. Large setae all cylindrical, coarsely ciliate (Fig. 8N), and apically blunt or conical. Small setae vary from slender, acuminate and smooth to cylindrical and coarsely ciliate. Sensory setae slender, smooth and clearly differentiated from normal setae. Cuticle coarsely granulate, Yosii A measure 14–21, average 18.5. Tenaculum with four teeth and no setae. Dens with seven slender, straight, dorsal setae. Mucro with lateral basal flap-like tooth absent or reduced. Tibiotarsi with 16–16–17 setae. Unguis with strong inner tooth. Unguiculus varying from having a simple basal lamella to having a distinct tooth-like structure on the lamellar apex.

Holotype: Colorado, Custer Co., 1 adult female, White Marble Halls Cave, August 11, 2000, at 3,566 m., 3.33° C, on moist mud and scat. Locality 9676. Paratypes 1 immature female and 1 subadult male same locality, 1 adult female Burns Cave, August 11, 2000, altitude 3,429 m, on mud and scat; also same locality 9675 & 9661 David Steinmann coll., Biogeographic zone 8.

Derivatio nominis: Named for the large degree of asymmetry found in the species.

Remarks: The PAO is compacted and difficult to analyze. All specimens show some degree of asymmetry. Three specimens have seta P4 on only one side of the fifth abdominal segment while two have it on both sides and one on neither. Three specimens have the setae 1 on the first thoracic segment very different in length and many other features show bilateral asymmetry. This asymmetry is far greater than any other species we have seen. In addition the unguiculus shows unusual states. In some legs the inner margin, which appears to be thickened, is entire; however on most legs it does not reach the shaft of the unguiculus resulting in a tooth-like projection (Fig. 8I). In collection 9675 from Burns Cave this reaches an extreme with the unguiculus shortened and the unguis showing

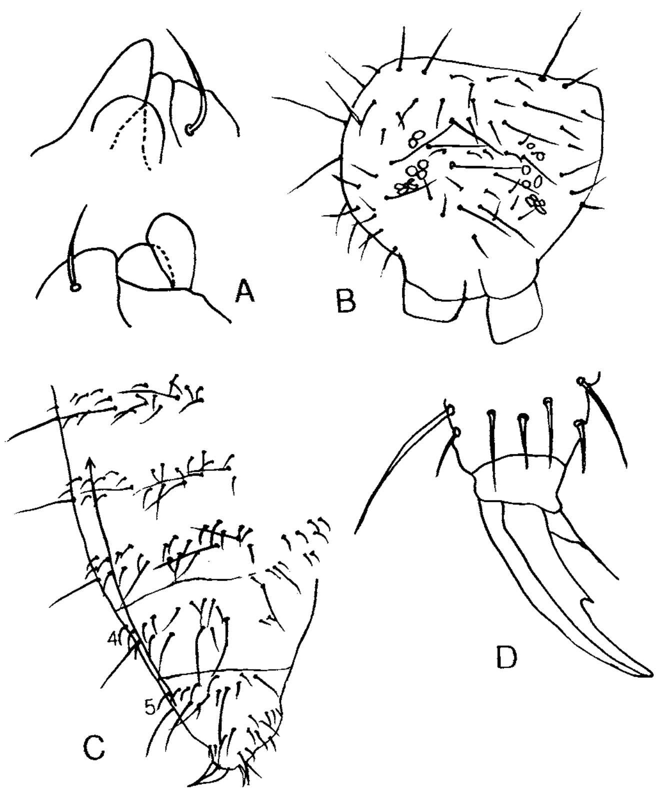


Figure 7. *Typhlogastrura alabamensis* Thibaud. All figures of specimens from type locality. A, apical organs of fourth antennal segment; B, dorsum of head; C, dorsal chaetotaxy abdominal segments 1–6; D, hind foot complex.

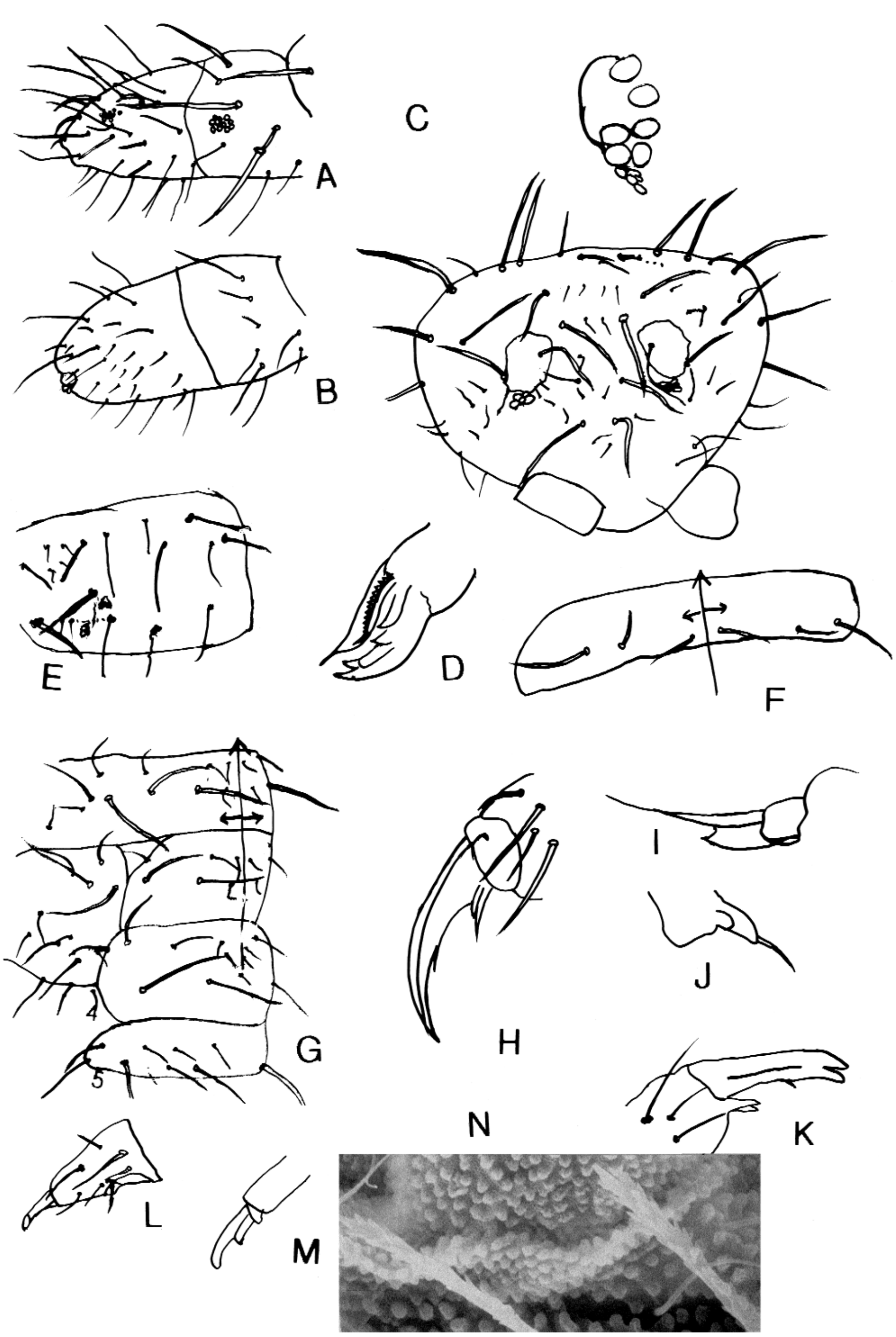


Figure 8. *Typhlogastrura asymmetrica* n. sp. Figures A-C, E, I & L holotype. Others paratypes. Microchatae serrations not shown. A, dorsum of antennal segments 3–4; B, venter of same; C, cephalic chaetotaxy with enlargement of eyepatch and PAO; D, maxilla; E, chaetotaxy second thoracic segment; F, chaetotaxy first abdominal segment; G, chaetotaxy abdominal segments 2–5; H, fore foot complex of holotype; I, unguiculus of holotype; J, unguiculus of paratype; K, abnormal unguis and unguiculus from Burns Cave; L, dens and mucro, dorsal view; M, mucro lateral view; N, electron micrograph of base of antenna showing serrations seen on most macrochaetae.

a separation between the outer unguis margin and the inner margin (Fig. 8K). White Marble Halls and Burns Cave are on the same mountain and are both much colder and higher (1,350 m and 1,213 m) than any other U.S. *Typhlogastrura* caves. It is possible that the unusual features of this species are an ecomorphic response to these conditions.

This species is similar to *T. steinmanni* but differs in seta P4 normally on the fifth abdominal and chaetotaxy of third thoracic segment, They also differ in the chatotaxy of thorcic segment 1 where seta 1 is much shorter than 3 whereas they are similar in length in *steinmani*. The much smaller and unlobed apical antennal bulb and the structure of the macrochaetae, particularly on the antennae, are the most striking differences.

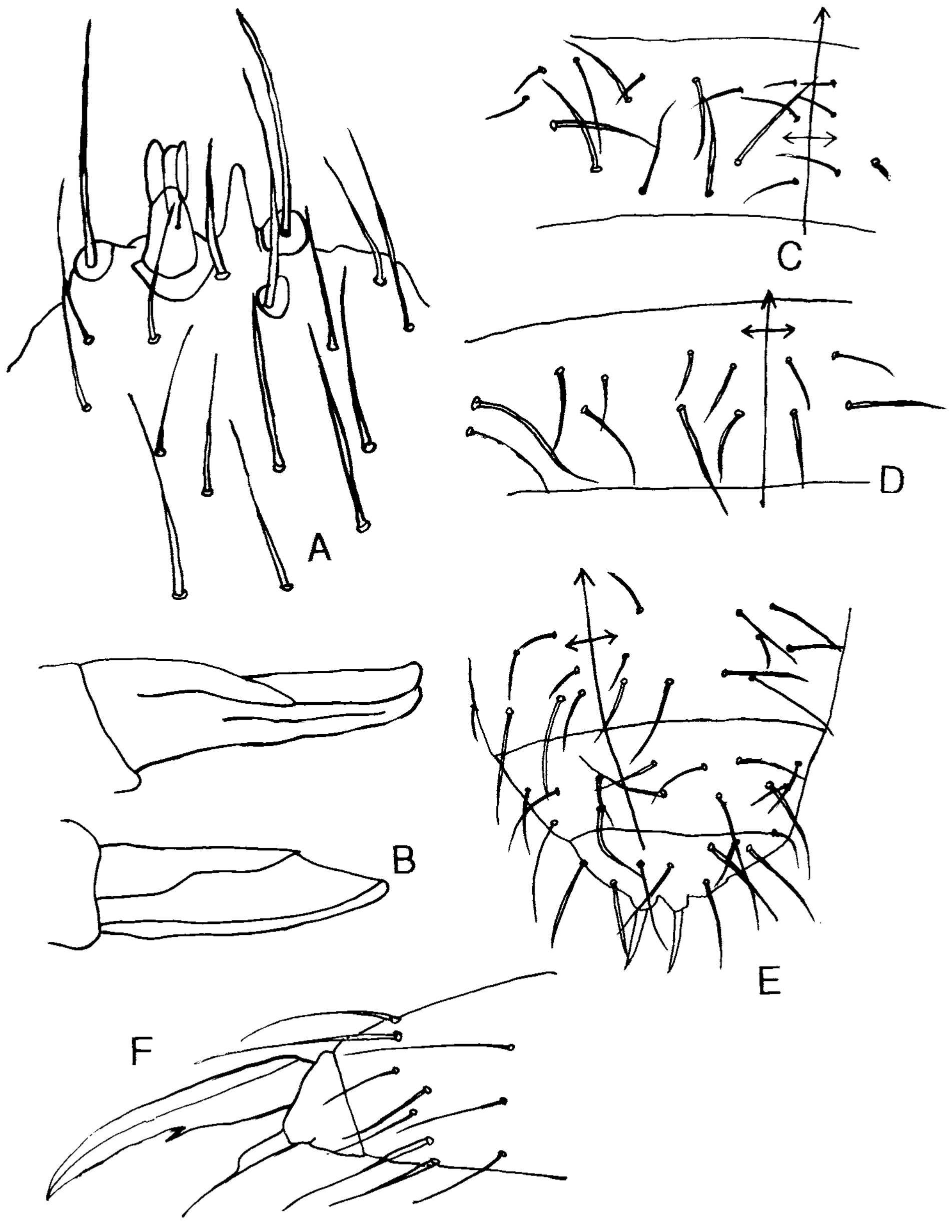
Typhlogastrura christianseni
Thibaud 1975 (Fig. 9A–F)

This species has two unusual features. First, the mucro shows no basal unilateral lamella or flap-like tooth (Fig. 9B); second, the apical antennal bulb shows no sac-like exsertile bulb but rather two or three triangular or conical projections (Fig. 9A). In the latter it is somewhat similar to *T. valentini* but differs in that the latter is exsertile. They differ in fifth abdominal segment chaetotaxy. It is probable they both evolved from the same *Ceratophysella* ancestor (for a fuller description see Thibaud 1980).

Typhlogastrura fousheensis new species (Fig. 10A–I)

Description: Color light brown to white with dark eyespots. Fourth antennal segment apical bulb simple without apical indentation (Fig. 10A). Longest setae about as long as maximum width of segment. Dorsal surface with seven blunt setae moderately distinguished from normal setae. Ventral surface without clear file, with 13–15 short, straight acuminate setae. Apical organ of third antennal segment with two very short blunt curved pegs and lateral sensillae slightly differentiated from normal setae. All antennal setae smooth, acuminate,

Figure 9. *Typhlogastrura christianseni* Thibaud. All figures of type specimens. A, apex of antenna; B, mucrones, lateral view; C, chaetotaxy second thoracic segment, left side; D, chaetotaxy third abdominal segment, left side; E, chaetotaxy abdominal segments 4–6; F, hind foot complex.



straight or weakly curved and smooth. First antennal segment with seven setae. Eyes 4 + 4, PAO with 4–5 lobes. Maxillae similar to *Ceratophysella pecki*. Labral papillae weakly developed. Area verticalis, with 2 + 2 setae with outer setae 3.5–6 times as long as inner. On the posterior margin seta 1 is ~2 times seta 2 and 0.4–0.5 times seta 3. First thoracic segment with all setae acuminate and smooth. Seta 1 only a little longer than seta 2 and 0.4–0.6 as long as seta 3. All pairs subequal in length. Remaining thoracic and abdominal chaetotaxy as shown in Table 1 and Fig. 10E–H. All large setae acuminate and smooth or very finely granulate. Sensory setae clearly differentiated from normal setae. Ventral tube with 4 + 4 setae. Cuticle finely granulate on head and appendages but coarsely granulate on the body dorsum particularly on abdominal segments 4–6. Yosii A measure 11–14. Tenaculum with four teeth and no setae. Dens with seven straight acuminate dorsal setae. Mucro with a very small flap-like lateral tooth, visible only from the side. Unguis with one clear inner tooth.

Holotype: Adult female USA, Arkansas, Independence Co., Foushee Cave. March 18, 2005, Locality 9782, slide 1 specimen 1. Norman & Jean Youngsteadt colls. Paratypes 1 subadult female and 4 adult females same slide and five specimens in alcohol plus 1 adult female and 1 subadult same locality May 1978 with same collector and site data. Biogeographic zone 7B.

Derivatio nominis: Named after the type locality, Foushee Cave.

Remarks: Larger specimens are sometimes pale brown but the smaller specimens are white. The former all have full guts whereas guts of the latter are sometimes empty. This species is one of the few having thoracic segment 2 B/A ratio greater than 2.0. (Fig. 10E). It, along with *alabamensis*, has a range of values for this bridging *christianseni* and *valentini* with ratios greater than 3.1 and the other species all with ratios below 1.8; however the two ranges barely overlap (Table 1). This also is one of the few species having well developed pigment and the only species we have seen with a projecting slender ciliate or weakly serrate lamella 1 of the maxilla (Fig. 10C).

All specimens were collected from bat guano. We were very fortunate that the Youngsteadts were able and willing to go back to the same cave after 27 years and collect more specimens since the first collection contained only one adult specimen.

Typhlogastrura helleri new species (Fig. 11A–H)

Description: Color tan with black eye spots. Fourth antennal segment apical bulb simple without apical indentation.

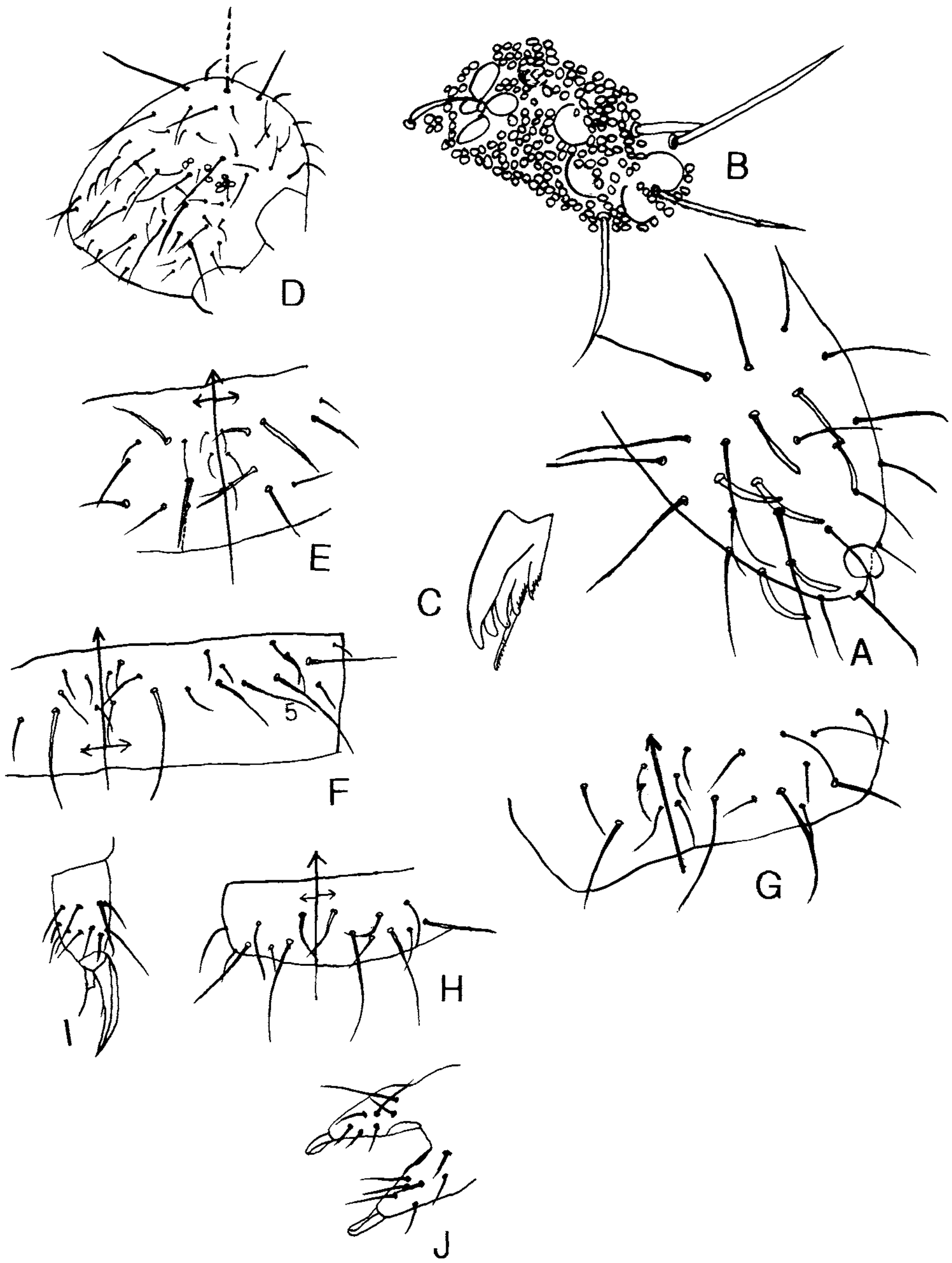


Figure 10. *Typhlogastrura fousheensis* n. sp. All figures of type specimens. A, fourth antennal segment, dorsal view; B, eyepatch and PAO; C, maxilla; D, cephalic chaetotaxy; E, chaetotaxy second thoracic segment; F, chaetotaxy third abdominal segment; G, chaetotaxy fourth abdominal segment; H, chaetotaxy fifth abdominal segment; I, fore foot complex, dentes and mucrones.

Longest setae about as long as maximum width of segment. Dorsal surface with seven blunt setae poorly distinguished from normal setae. Ventral surface without clear file with 23–25 short, acuminate, mostly straight setae. Apical organ of third antennal segment with two short straight blunt rods and lateral sensillae slightly differentiated from normal setae. All antennal setae smooth, acuminate, straight or weakly curved and smooth. First antennal segment not seen clearly. Eyes usually 5 + 5, PAO with 4–5 lobes and 2.5–3.2 times nearest eye. Maxillae not clearly seen but appear similar to that of *T. unica*. Labral papillae weakly developed. Area verticalis, with 2 + 2 setae with outer setae ~4 times as long as inner. On the posterior margin seta 1 is 1.2–0.15 times seta 2 and 0.2–0.42 as long as P3. First thoracic segment with all setae acuminate and smooth. Seta 2 is 0.36–0.34 seta 3 and 0.54–0.42 setae. All pairs subequal in length. Remaining thoracic and abdominal chaetotaxy as shown in Table 1 and Fig. 11E–F. All large setae acuminate and smooth or very finely granulate. Sensory setae weakly differentiated from normal setae except at their thinner apices. Cuticle mostly finely granulate except on the dorsum of abdominal segments 4–6. Yosii A measure 12–20. Tenaculum with four teeth and no setae. Dens with seven straight acuminate dorsal setae. Mucro without clear flap-like lateral tooth. Tibiotarsi with 16–16–17 setae. Unguis with one clear inner tooth.

Holotype: Adult male USA, Pennsylvania, Huntingdon Co., Heller Cave, January 1997, on pool surface, Locality 9276. Keith Christenson coll. Allotype adult female, and 2 paratypes, subadult females, all with same collection data. Biogeographic zone 7A.

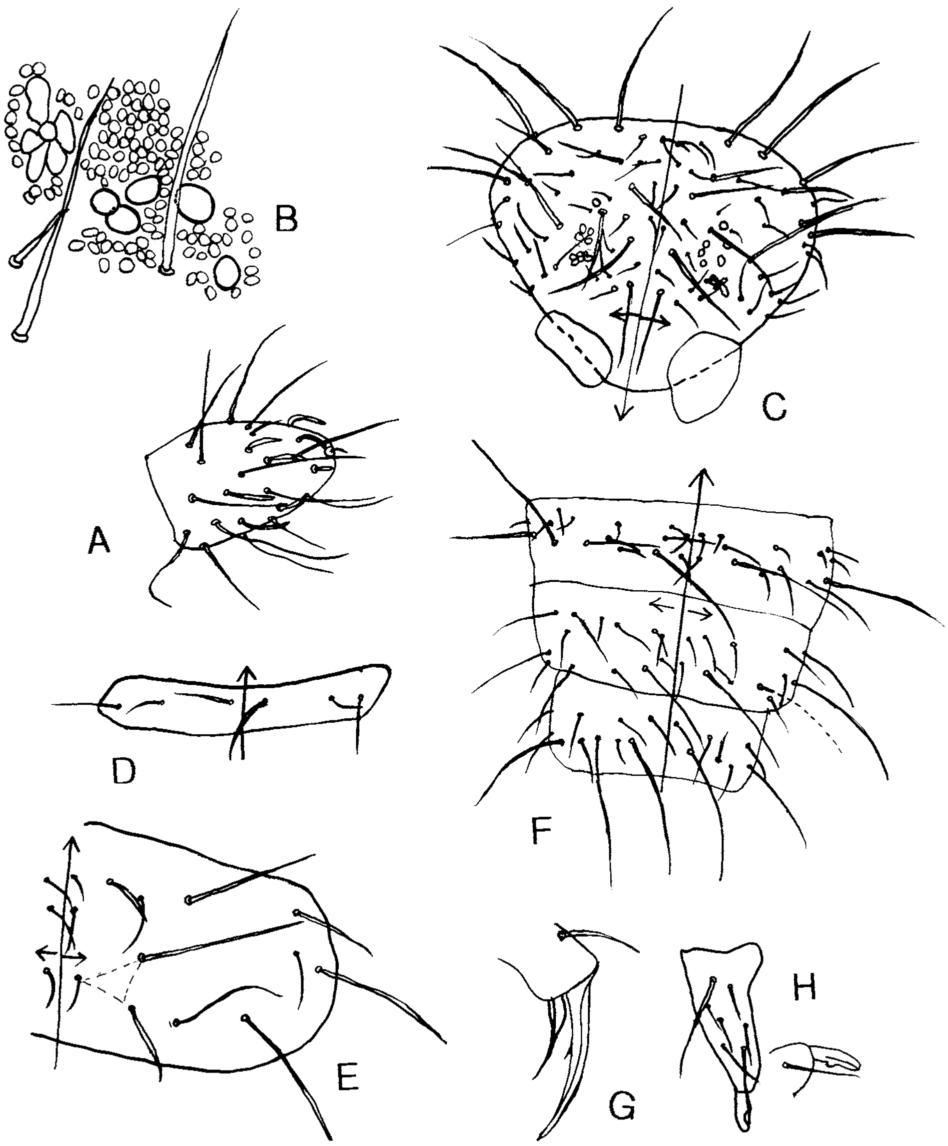
Derivatio nominis: Named after the type locality, Heller cave, and in honor of the owners, the Heller family.

Remarks: This is by far the most Northeastern Nearctic species of the genus. It is somewhat similar to *T. alabamensis* but differs in mucronal structure, apical antennal bulb, and chaetotaxy (Table 1). The specimens display a considerable degree of asymmetry. It is possible that one or two specimens have only four ocelli on one side as the outlines of the ocelli are often obscured by the eye pigment.

Typhlogastrura steinmanni new species (Fig. 12A–G)

Description: Color white except for black ocelli. Fourth antennal segment apical bulb when expanded large and clearly double (Fig. 12A) but when withdrawn appearing as a single structure. Longest setae about as long as maximum width

Figure 11. *Typhlogastrura helleri* n. sp. All figures of type specimens. A, fourth antennal segment; B, ocelli and PAO right side; C, cephalic chaetotaxy; D, chaetotaxy first thoracic segment; E, chaetotaxy right half of second thoracic segment; F, chaetotaxy abdominal segments 3–5; G, hind foot complex; H, mucrones and dens.



of segment. Dorsal surface with six blunt setae with only apical two clearly distinguished from normal setae. Ventral surface without file but with eight short, acuminate setae. Apical organ of third antennal segment with two very short curved blunt rods and lateral sensillae not clearly differentiated from other setae. First antennal segment with seven setae. 6 + 6 usually well-pigmented eyes. PAO with 4–6 lobes and ~1.5 times nearest eye. Maxillae not seen clearly but not having any lamellae surpassing the apical maxillary tooth. Labral papillae 4 and weakly developed. Area verticalis, with 2 + 2 setae, outer setae 4–5 times the inner, thick, weakly tapered and rugose or finely ciliate and blunt. On the posterior margin P3 are similar and ~4 times P1 & P2 which are smooth and acuminate. First thoracic segment with all setae thick and rugose or sparsely ciliate. Seta 1 is 1.1–1.5 seta 2, which is 0.59–0.74 seta 3, which is 1.7–2.6 seta 1. Thoracic and abdominal chaetotaxy as shown in Table 1 and Fig. 12C–E. Large setae varying from acuminate to almost cylindrical and blunt. Sensory setae with long filamentous apices and clearly differentiated from normal setae. All large setae are rugose or very sparsely ciliate. Cuticle granulations moderate, Yosii A measure 23–28. Tenaculum with four teeth and no setae. Dens with 7–8 slender, straight, dorsal setae. Mucro with lateral basal flap-like tooth absent or reduced. Tibiotarsi with 16–16–17 setae. Unguis with strong inner tooth and sometimes with a minute outer tooth.

Holotype: Adult male USA, Colorado, Eagle Co., Fulford Cave. August 22, 2000, altitude 3,139 m, temp. 1.67° C, on rotted wood and pool surfaces. Allotype: same data Locality 9677. Paratypes: same data as holotype, three adult or subadult females and one immature specimen. Biogeographic zone 8. Found only in type locality.

Derivatio nominis: Named in honor of David Steinmann who discovered most of the new species described in this work.

Remarks Most of the specimens have seven dorsal dental setae but at least two specimens have eight on one or both sides. The allotype and all but one paratype are females, apparently adult with a well-developed genital plate but poorly developed genital opening. The mucro is quite varied in structure but never has the typical flap-like lateral tooth typical of *Ceratophysella*. While this species resembles *T. asymmetrica* in some respects, it differs stringly in having the antennal apical bulb large and double versus small and single as well as many other features (see remarks under *asymmetrica*).

Typhlogastrura unica new species (Fig. 13A–H)

Description: Color white. Fourth antennal segment apical bulb when expanded small and clearly trilobed (Fig. 13A), but when withdrawn appearing as a single structure sometimes with apical indentations visible. Longest setae ~0.9 as long as maximum width of segment. Dorsal surface with seven blunt setae. Ventral surface with weakly developed file but with ~20

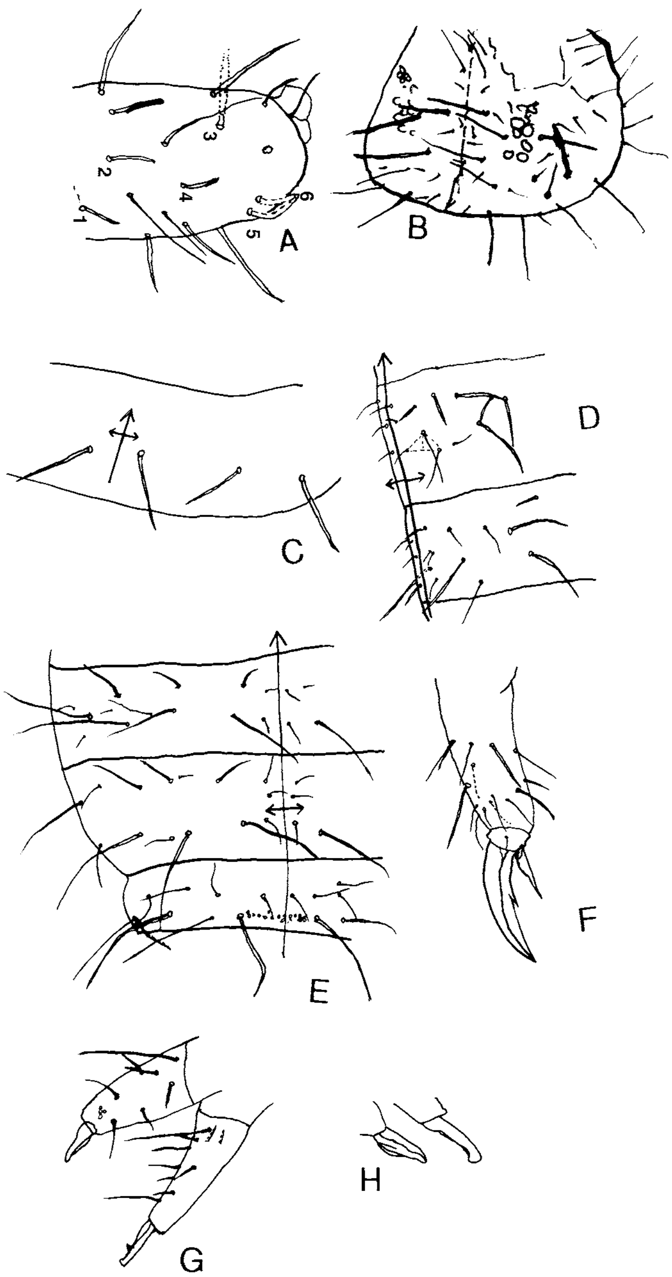


Figure 12. *Typhlogastrura steinmanni* n. sp. Figures A–C holotype, others paratypes. A, fourth antennal segment, dorsal view; B, dorsum of head; C, chaetotaxy first thoracic segment; D, chaetotaxy right half of thoracic segments 2–3; E, chaetotaxy right half of abdominal segments 3–5; F, hind tibiotarsus and foot complex; G, dentes and mucrones.

short, acuminate, straight or weakly curved setae. Apical organ of third antennal segment with two very short curved blunt rods and lateral two slightly basally enlarged, acuminate sensillae. Large setae of antennal segments 1–3 acuminate, heavy and rugose. First antennal segment with five dorsal and two ventral setae. Four labral papillae. Maxilla of *denticulata* type with lamella 1 clearly surpassing the apex of the teeth but without visible inner serrations. Eyes 5 + 5 and moderately pigmented. PAO usually with seven lobes. Area verticalis, with 2 + 2 setae, outer setae 3.5–5 times the inner. On the posterior margin, seta P1 is 2.5–3 times P2 and 0.52–0.80 times P3. First thoracic segment with seta 2 ~½ as long as seta 3 and 0.55–0.64 as long as seta 1. Remaining thoracic and abdominal chaetotaxy as shown in Table 1 and Fig. 13D–F. Small setae all acuminate and varying from smooth to ciliate. Large setae all acuminate, straight to slightly curved and sparsely ciliate. Sensory setae slender, smooth and clearly differentiated from normal setae. A well-developed hump occurs between the P1 setae on abdomen 5. Integument moderately granulate but coarsely granulate on the posterior part of abdomen 5 and abdomen 6. Yosii A measure 14–17. Tenaculum with 4–5 teeth and no setae. Dens with 6–7 slender, straight, dorsal setae. Mucro with a small lateral basal flap-like tooth. Tibiotarsi with 16–16–17 setae. Unguis with strong inner tooth.

Holotype: Adult male USA, Colorado, Gunnison Co., Hunters Camp Cave. ?- August 11, 2000, altitude 3050 m, 12.2 m from entrance, on scat; Locality 9737, David Steinmann coll. Allotype adult female, same data as holotype. Paratypes 1 adult and 1 subadult females, same data. Known only from type locality.

Derivatio nominis: Latin unica = only, in view of the fact that it is the only member of the genus having a fifth abdominal hump.

Remarks: This is the most striking member of the genus from the northern Nearctic. The combination of fifth abdominal segment hump, many-lobed PAO, and trilobed apical bulb make it easy to identify. Both the tenacular teeth and dental chaetotaxy are variable.

Typhlogastrura valentini Thibaud 1996 (Fig. 14A–I)
Ref.: Revue Franc. Ent. (N.S.) 18:11-12

Redescription: Color pale brown to white. Eyespots usually black. Fourth antennal segment apical bulb when unexpanded appearing like a broad peg or pair of pegs more or less conjoined. When fully expanded it is single, with a larger or smaller apical indentation. Intermediate stages of expansion show a variety of forms. Longest setae about as long as maximum width of segment. Dorsal surface with 6–7 blunt setae. Ventral surface without clear file but with 16–22 short, acuminate or slightly truncate setae. Apical organ of third antennal segment with two very short blunt pegs and lateral sensillae not clearly differentiated from other setae. First antennal segment with seven setae. 3 + 3 (rarely 2, 4, 5 or 6) usually well-pigmented eyes. PAO with four lobes (one specimen with five) ~1.4–2.5 times nearest eye. Maxillae similar to those of *Ceratophysella pecki*. Labral papillae weakly developed but apparently with six lobes. Area verticalis, with 2 + 2 setae, outer setae 2.2–2.7, all setae acuminate and smooth. On the posterior margin setae P1 & P2 are subequal and seta 3 is 2.0 to 2.3 times these. All are smooth and acuminate. First thoracic segment with setae 1 & 3 usually thick and straight but seta 2 curved and slender.

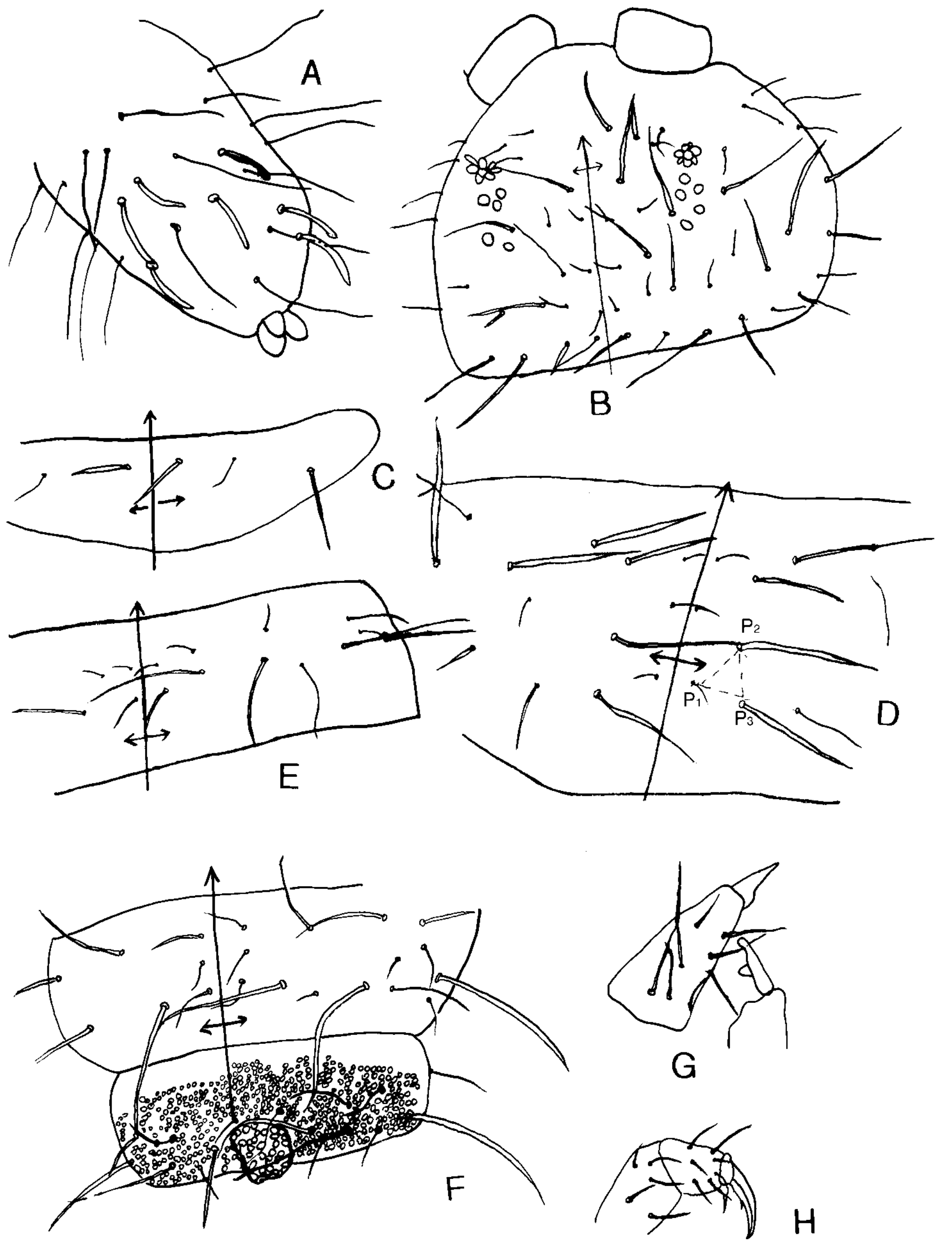


Figure 13. *Typhlogastrura unica* n. sp. All figures of paratypes. A, fourth antennal segment, dorsal view; B, dorsum of head; C, first thoracic segment; D, left side of second thoracic segment; E, left side of third abdominal segment; F, left side of abdominal segments 4–5; G, dentes and mucrones; H, foot complex.

Seta 1 is 1.5–2.25 seta 2, and 0.48–0.84 seta 3. Thoracic and abdominal chaetotaxy as shown in Table 1 and Fig. 14D–G. Large setae varying from acuminate to almost cylindrical and blunt. Sensory setae with long filamentous apices and clearly differentiated from normal setae. All large setae are rugose or very sparsely ciliate. Cuticle granulations moderate, heavier on the last three abdominal segments, Yosii A measure 23–28. Tenaculum with four teeth and no setae. Dens with 7–8 slender, straight, dorsal setae. Mucro with lateral basal flap-like tooth absent but with a clear basal expansion. Tibiotarsi with 16–16–17 setae. Unguis with strong inner tooth and sometimes with a minute outer tooth.

Holotype: USA, Virginia, Scott Co., Grigsby Cave, August 8, 1995, and Herons Echo Hall Cave August 9, 1996. D. Hubbard coll. on rotted wood and pool surfaces; 14 paratypes same localities.

Also collected from many other Virginia caves: Scott County: six additional caves; Wythe County: nine caves; Russell County: four caves; Pulaski County: two caves; and Washington, Smyth and Giles County: one cave each.

Remarks: The apical bulb of the fourth antennal segment is very confusing. At first it appears that there are several different types of organ, but one sample shows that this is due to different levels of expansion of the exsertile bulb. In the unexpanded condition it is similar to the apical organ of *T. christianseni*. *T. valentini* is quite similar to *christianseni*, appearing to differ primarily in the non- exsertile nature of the apical bulb in the latter and the fifth abdominal chaetotaxy and the shape of the mucro. Thibaud in his original description says there are nine cylindrical setae on the fourth antennal segment but we were never able to see more than seven.

This species has the most remarkable distribution of any species of the genus. It occurs over the western third of the State of Virginia. This is in striking contrast to almost all other species of the genus, which occur in one or two close-by caves, or at most three such. It is almost impossible that these Virginia caves are presently connected by cave passages, although it is possible that there are connections through the MSS, which has not been studied in the state. The chaetotaxy is remarkably constant throughout its range. There is some variation in eye number and relative sizes of organs, but these occur largely in isolated specimens in the two counties with the greatest number of collections. As far as we can see there are several possible explanations:

1) The present distribution reflects geological changes in the cave systems and the various caves were at one time linked; 2) there actually are MSS linkages between the various cave systems; or 3) this represents a series of invasions of

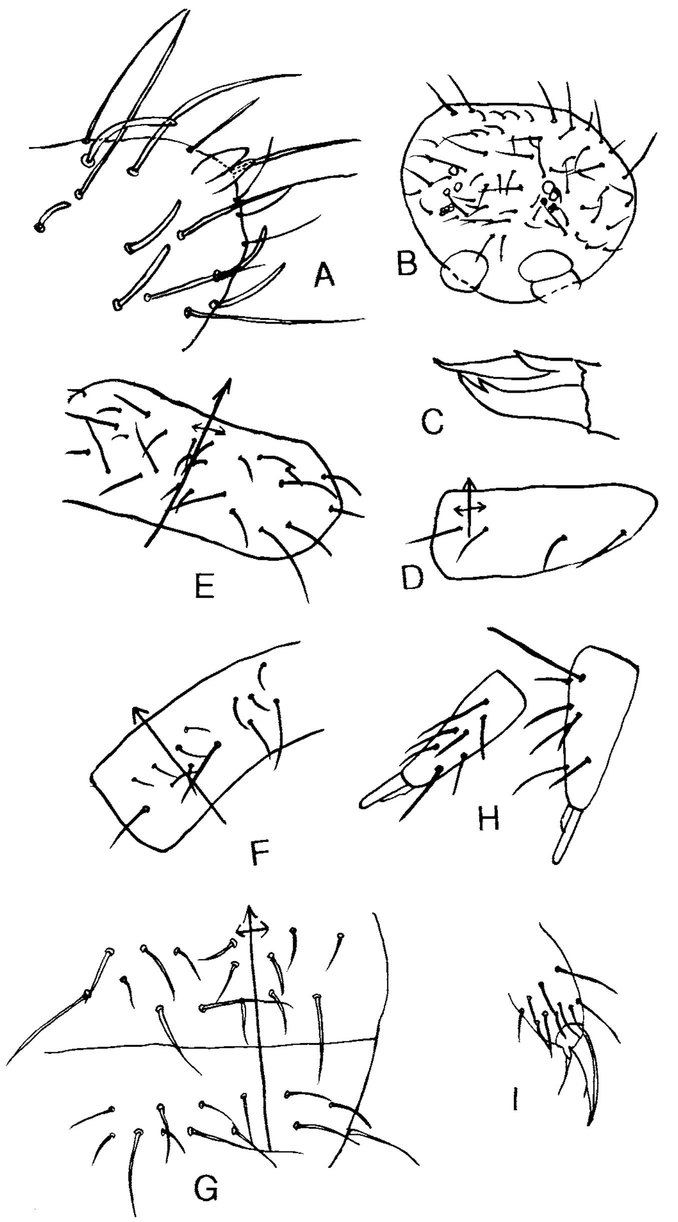


Figure 14. ***Typhlogastrura valentini*** **Thibaud. A, fourth antennal segment, dorsal view (Giles County); B, dorsum of head (Wythe County); C, maxilla (Wythe County); D, chaetotaxy first thoracic segment (Washington County); E, chaetotaxy second thoracic segment (Wythe County); F, right side of third abdominal segment (Wythe County); G, chaetotaxy abdominal segments 4–5 (Wythe County); H, dentes and mucrones (Wythe County); I, foot complex (Wythe County).**

caves followed by parallel morpho-speciation. The latter hypothesis could be readily tested by genetic analysis.

Discussion

The three new species from Colorado come from three cave regions, which are both topographically and geologically separated. Each also comes from a very high-altitude cold cave or caves (3,048 m or over). It would appear to be ideal for a series of glacial relict species; however, while it is possible that *T. steinmanni* and *T. asymmetrica* arose from a common ancestor, *T. unica* clearly arose from a different group. We have seen no clear candidates for putative ancestors to either group from arctic species of *Ceratophysella.*

There are a number of mysterious features about this polyphyletic genus. First, all described species are exclusively or almost exclusively troglobitic, yet most show only slight troglomorphy, usually limited to eye and pigment reduction. The exceptions to this are two European species: *T. mendizabili* from Spain and *T. morozovi* from Georgia. Both are eyeless and have the troglomorphic feature of elongate ungues and the putatively troglomorphic hypertrophy of the PAO. It is possible but not certain that loss of the mucronal tooth is also a troglomorphic feature. This is supported by the fact that the two Mexican species, which show the greatest troglomorphy in the American species, show the most reduced mucronal structure. The other frequent Collembola troglomorphic features — elongation of antennae, hypertrophy of third antennal segment sense organ, elongation of furcula, and elongation of unguis or other appendages, gracilization, increase of size (Christiansen, 2004) — are absent. That such increase in troglomorphy is possible in the Hypogastruridae is clearly shown by the highly troglomorphic genus *Ongulogastrura* (Thibaud & Massoud, 1983); however this genus is virtually impossible to associate with any species of *Typhlogastrura*.

Second, we have the rarity of their occurrence. We have only one species from the very heavily collected Missouri–Arkansas region, two each from the very thoroughly collected Virginia and Alabama–Georgia regions, and none from the heartland of cave Collembola collections — the Southeast of the U.S., nor from the also heavily collected Iowa, Indiana and Illinois regions, nor the also heavily collected California region. In contrast, three species are known from poorly collected Colorado and one from poorly collected Pennsylvania caves. An explanation for this may be that there are no troglophile species, which allow invasions of caves over wider regions. Another possible explanation is that the cave invasions were not successful where there were pre-existing troglomorphic Collembola.

This brings up the third mystery: why no troglophiles? The simplest explanation would be that the physiological and reproductive and/or behavioral changes required to succeed in the caves prevents survival outside them. If so, this raises another question: why does the analogous genus *Bonetogastrura*, which differs only in the ancestral group of species of *Ceratophysella,* have both edaphic and troglophilic forms? If the undescribed edaphic species should turn out to be a member of *Typhlogastrura,* this would make even more mysterious the absence of troglophilic forms.

Fourth: why is it that the species, after invading the caves, show no evidence of evolving into progressively more troglomorphic species as do most cavernicole lineages (Christiansen and Culver, 1987; Christiansen, op. cit.)? All these puzzles furnish an ample source of future interesting scientific investigations.

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