

NEW SUPERFAMILY OF CALANOIDA (COPEPODA) FROM AN ANCHIALINE CAVE IN THE BAHAMAS

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ABSTRACT

A new calanoid copepod, *Fosshagenia ferrarii*, new genus, new species, was found in plankton samples collected in an anchialine cave of Caicos Islands, Bahamas. A combination of features found in this species separates it as the type of a new superfamily. The new taxon can be distinguished by a combination of several relevant taxonomic characteristics, such as the fusion of antennular segments 8 and 9, the right antennule modified in the male, less than 3 endopodal segments on the first legs, the presence of a uniramous female fifth leg, a male fifth leg forming a complex grasping organ, reduced mouthparts, and the presence of only 1 seta on the middle endopodal segment of legs 3 and 4. The new taxon appears to be more closely related to fresh- and brackish-water forms (Centropagoidea) than to any other hitherto known anchialine copepod group. The type species can be distinguished by the presence of lateral processes on the genital double-somite of the female and on the first urosomal somite of the male. It is the smallest of the known anchialine calanoid species. This small species, a predator in the water column, diverges from other anchialine copepods which are bottom-dwellers.

The term "anchialine" was coined by Holthuis (1973) to denote pools of marine or brackish waters geologically isolated from surface marine or fresh-water influence. Recently, anchialine cave faunas have been surveyed by diving (Iliffe, 1992).

Copepods are known from several anchialine environments. At least six new genera, a new family (Boholinidae), and a new order have been recorded from caves in the Bermuda region (Boxshall and Iliffe, 1986; Fosshagen and Iliffe, 1985, 1988, 1991). New copepods in these caves included specimens belonging to little known taxa such as the Misophrioida and the calanoid family Epacteriscidae, which show very primitive features. Biogeographic and taxonomic features of this fauna have raised interesting questions. The most common copepod group in caves of the Bermuda region are the Ridgewayiidae, with *Ridgewayia marki* (Esterly, 1911) being the most abundant (Sket and Iliffe, 1980; Fosshagen and Iliffe, 1985). Other anchialine species have been collected in great numbers, as the ridgewayiid *Brattstromia longicaudata* Fosshagen, 1991, in caves of Belize (Fosshagen and Iliffe, 1991) and species of the boholinid *Boholina* Fosshagen, 1989, from the Philippines (Fosshagen and Iliffe, 1989). However, the anchialine copepod fauna of several continental and insular areas of the northwestern tropical Atlantic re-

gion remains practically unknown (Iliffe, 1992).

Plankton surveys of an anchialine pool in Conch Bar, Caicos Islands, Bahamas (Fig. 1), revealed a new genus and species of the Epacteriscidae (see Fosshagen and Iliffe, 1994). Further analyses of samples from the same zone revealed several calanoid copepods of a previously unknown superfamily. Diagnosis of the new higher taxa (superfamily, family, genus) are presented. The type species is described from male and female specimens.

Caicos Islands are geographically and geologically a southeastern extension of the Bahama Banks. The Caicos Bank is composed of a flat-lying carbonate cap thicker than the surrounding ocean is deep (Dietz *et al.*, 1970). A well-developed karst topography is present both above and below present sea level. Conch Bar Cave (21°49'31"N, 71°47'32"W) is located 500 m inland from the north coast of Middle Caicos Island, about 1 km east southeast of the village of Conch Bar.

MATERIALS AND METHODS

Nineteen adult females and 6 adult male copepods of the new genus were collected at a depth of 0-0.5 m, Station 91-006, at Conch Bar cave, Middle Caicos Island, Bahamas, during May 1991. Copepods were collected by towing a plankton net with a 0.093-mm mesh in the eastern section of the cave. Specimens were fixed in a Formalin solution and then transferred to 70% ethanol. Male and female specimens, previ-

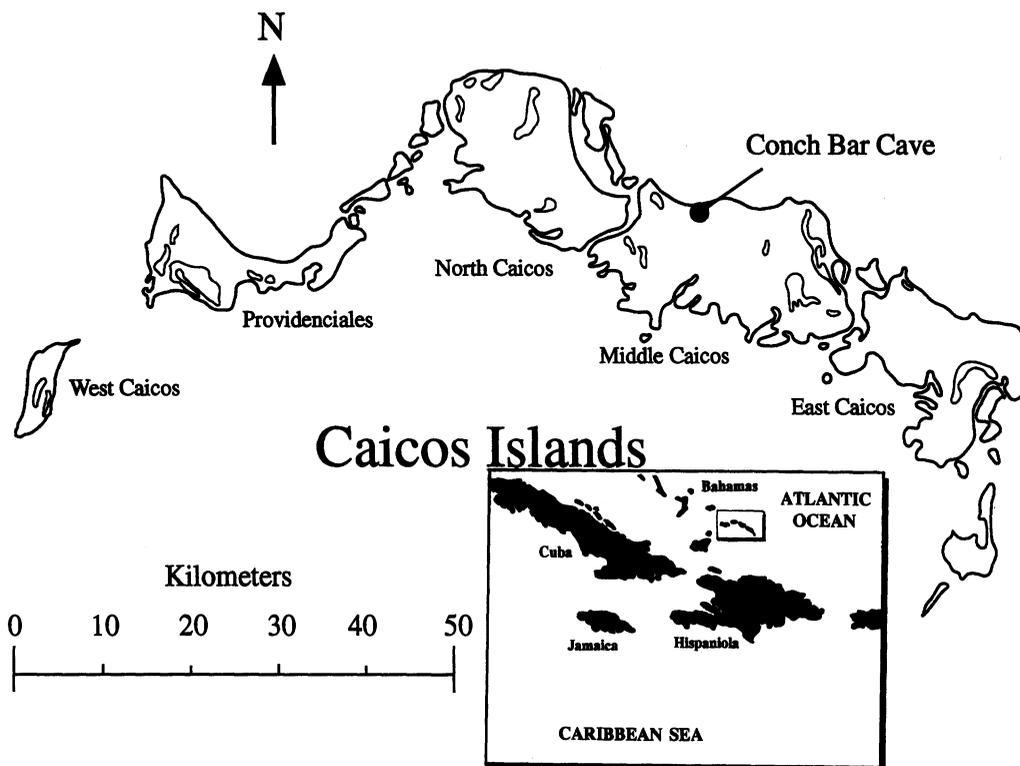


Fig. 1. Study area, showing location of Conch Bar Cave, Middle Caicos Islands, Bahamas.

ously stained with chlorazol black were completely dissected. Illustrations were made with the aid of a camera lucida.

DESCRIPTION

Fosshagenioidea, new superfamily
Fosshageniidae, new family
Fosshagenia, new genus

Until more representatives are known, the superfamily, family, and genus show the same diagnostic characters as follows. Cephalosome fused with first pediger. Rostrum blunt. Pedigers 4 and 5 partly fused. Urosome 4-segmented in female, 5-segmented in male. Caudal ramus relatively elongate in female, slightly arched on middle inner portion; short, symmetrical and straight in male. Caudal ramus with 3 long slender terminal setae in both sexes. First antenna 24-segmented with segments 8 and 9 fused. Mouthparts reduced. Endopod of first leg 2-segmented, endopod of legs 2–4 and exopod of legs 1–4, 3-segmented. Exopod of legs 2–4 with 1 long, serrate apical spine, and 3 short outer spines. Third exopodal segment of leg 1 with 5 setae. Fifth legs

apparently uniramous in females, 3-segmented, with articulated structure in middle inner margin of basipodite. Male right antennule geniculate. Fifth legs modified into complex grasping organ; right exopod with bulbous terminal segment, right endopod reduced; left exopod 2-segmented, left endopod reduced.

Fosshagenia ferrarii, new species
 Figs. 2–4

Type Material.—The species, 19 adult ♀♀, 5 adult ♂♂, no copepodids, was obtained from plankton samples taken in Conch Bar Cave (21°49'31"N, 71°47'32"W), Caicos Islands, Middle Caicos Island, Bahamas. Holotype: Adult ♀ (USNM 278042), total length 0.63 mm, from Conch Bar Cave, Caicos Islands, Bahamas. Allotype: Adult ♂ (USNM 278043), total length 0.70 mm. Paratypes: 12 adult ♀♀ and 1 dissected male (USNM 278044) from the same locality as the holotype. Five females held in the author's collection at ECOSUR. All type specimens deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Female.—Total length, measured from anterior end of cephalic somite to posterior end of anal somite, of 19 individuals ranging from 0.60–0.70 mm, with mean length

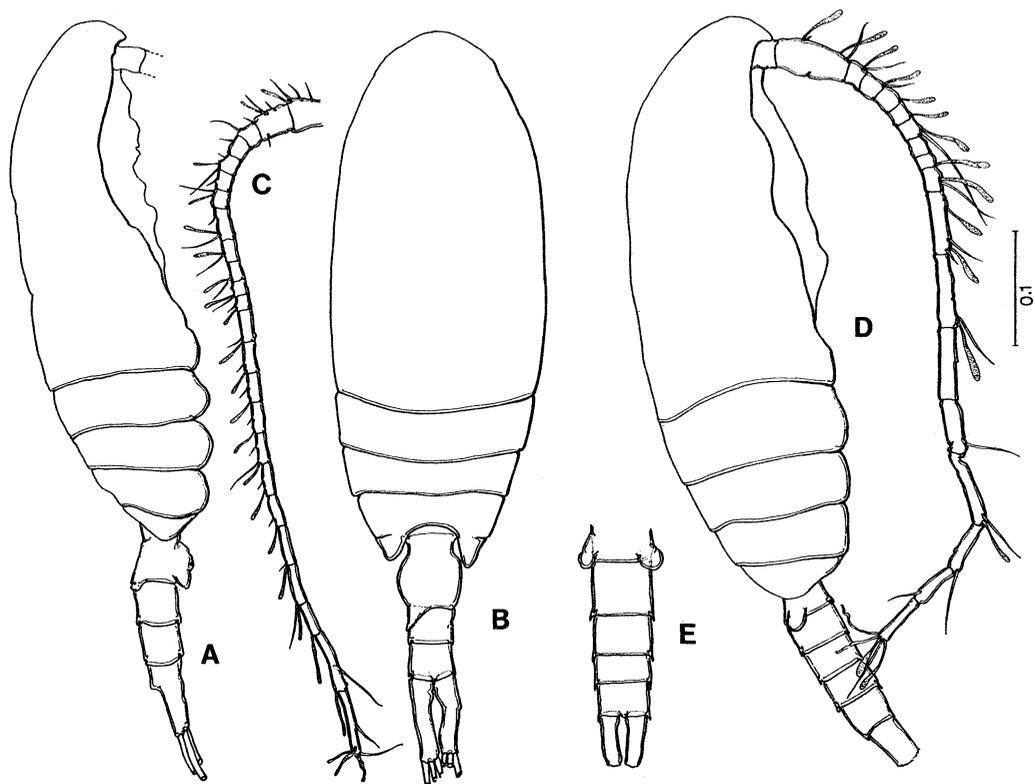


Fig. 2. *Fosshagenia ferrarii*, new genus, new species. Female. A, habitus, lateral; B, habitus, dorsal; C, antennule, dorsal. Male allotype. D, habitus, lateral; E, urosome, dorsal. Scale in mm.

of 0.64 mm. Body long, robust, cephalic somite wide, rounded anteriorly. In dorsal view, posterior corners of fifth pedigerous somite rounded, slightly asymmetrical, right side extending slightly more posteriorly than left side (Fig. 2B). Urosome measured from anterior end of genital double-somite to posterior margin of anal segment, approximately 0.21 of total body length. Urosome with 4 somites; genital double-somite, excluding triangular process, about half total length of urosome. Genital double-somite asymmetrical, produced midventrally into relatively high protuberance, also produced posteriad, with its end reaching less than one-third of ventral face of succeeding segment (Figs. 2A, B, 3A). In dorsal view, lateral margins of genital double-somite rounded, with elongate subtriangular process on left side extending to midlength of succeeding segment (Fig. 2B). Similar process present on left lateral margin of genital double-somite. Caudal ramus relatively long, about 3.5 times longer than

wide and about as long as genital double-somite, representing 0.38 of urosomal length. Each ramus with 1 small seta on middle portion of internal margin; 3 terminal setae, innermost about 20% longer than other 2, these being subequal in length and thickness (Figs. 2B, 3A).

First antenna 24-segmented, reaching to posterior margin of anal segment when stretched backward, with setae on all segments and aesthetascs on all, except on segments 3, 4, and 6. Segment 1 fused with succeeding double segment. Segments 8 and 9 fused, segments 9 and 10 partially fused; internal face-view showing segments 8–10 fused, forming large segment, but view of external face revealing 9 and 10 intersegmental division. Last segment of first antenna with 1 terminal and 2 subterminal aesthetascs and 2 setae, 1 at about midlength of segment, other terminal (Fig. 2C). Second antenna with exopod and endopod of about equal length. Basis with 2 long setae. Endopod reduced, with 2 seg-

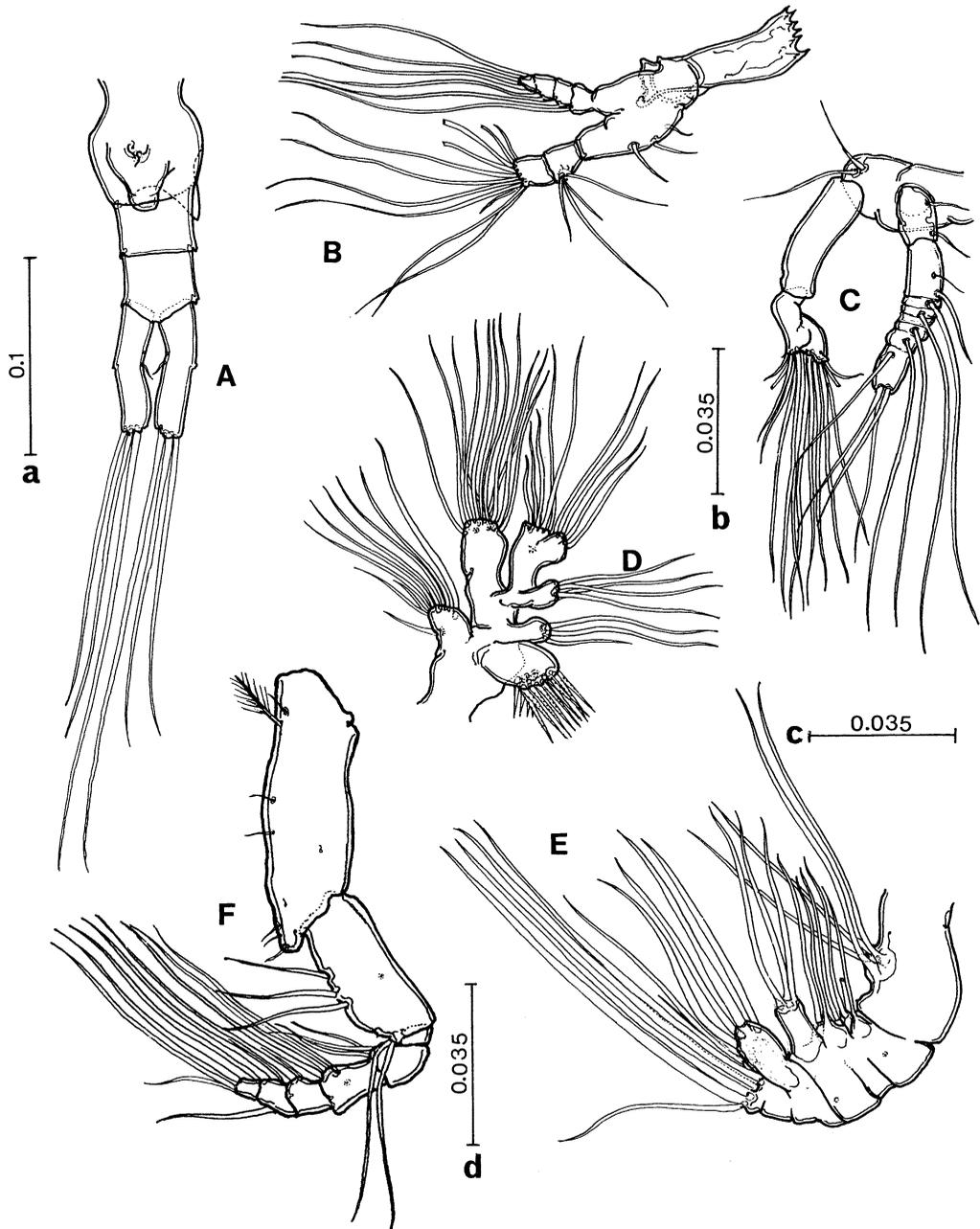


Fig. 3. *Fosshagenia ferrarii*, new genus, new species. Female. A, urosome, ventral (scale a); B, mandible and palp (b); C, antenna (b); D, first maxilla (b); E, second maxilla (c); F, maxilliped (d). Scales in mm.

ments, distal portion of terminal endopodal segment with 2 lobes, internal with 1 short posterior and 6 anterior setae; external lobe with 2 short, 2 medium-sized, and 5 long setae. Exopod indistinctly segmented, with 2 short setae on first segment, 1 short and 1 long setae on fused segments 2–4, 1 on

each segments 5–9, and 3 terminal setae on distal segment (Fig. 3C). Mandible with 5 or 6 pointed teeth on gnathobase; ventral outermost tooth relatively high and narrow, innermost 2 teeth low and wide. Basis with 3 setae; endopod with 2 segments, proximal segment with 4 setae, 2 short, 1 medium-

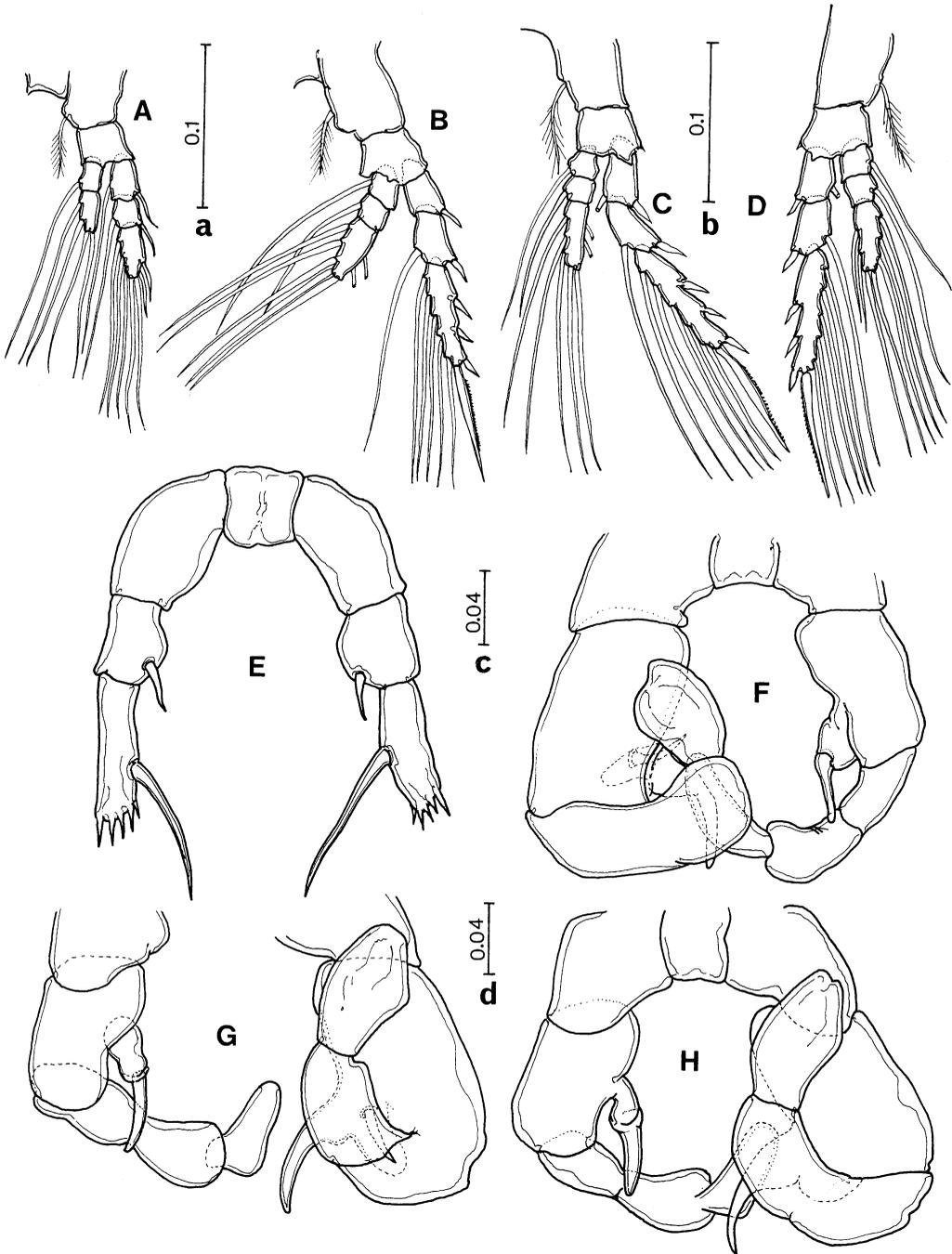


Fig. 4. *Fosszhagenia ferrarii*, new genus, new species. Female. A, first leg (scale a); B, second leg (a); C, third leg (b); D, fourth leg (b); E, fifth legs (c). Male. F, fifth legs, posterior view (c); G, fifth legs, anterior view, split (d); H, fifth legs, anterior view (d). Scales in mm.

sized, and 1 long; distal segment short, as long as wide, with 10 anterior and 1 posterior setae, outermost 2 shortest. Exopod 5-segmented, with normal 1, 1, 1, 1, 2 se-

tation pattern (Fig. 3B). First maxilla with 3 and 4 setae on coxal and first basal endites, respectively. Praecoxal arthrite with 13 spiniform setae, 9 being apical, arranged

in 2 rows with 5 and 4 setae each, plus 4 posterior setae. Coxal epipodite with 9 setae, innermost wider than others. Endopod reduced, unsegmented, articulating with basis, with 3 lobes, innermost with apical group of 5 setae and subapical group of 2; medial lobe with 2 setae and third (outer) lobe with 4 setae. Exopod with 11 setae (Fig. 3D). Second maxilla indistinctly segmented, with reduced praecoxal and coxal lobes and well-developed basal lobes. Setation pattern of the lobes as: 4, 3, 3, 3, 4, 2, 6 (Fig. 3E). Maxilliped well developed. Coxa with anterior protuberance produced over next segment, 1 short, plumose seta plus 1 smaller on proximal portion, 2 short simple setae on middle inner margin, and 3 distal, 1 on anterior protuberance. Basis with group of 3 setae placed on middle of inner margin. Endopod 6-segmented, with first segment partially fused to basis, bearing 2 subequal setae. Second endopodal segment with 3 subequal setae, third with 3, fourth with 1 long and 1 small slender setae, fifth with 2 long and 1 short, slender setae; terminal segment with 1 short and 3 long setae (Fig. 3F). First leg with 2-segmented endopods, coxa with plumose seta on internal margin. Second, third, and fourth legs with exopods and endopods 3-segmented (Fig. 4A–D). Formula for armature of swimming legs as:

	coxa	basis	exopod	endopod
leg 1	0–1	0–0	I–1; I–1; II, 5	0–1; 0–2, 2
leg 2	0–1	0–0	I–0; I–1; III, I, 5	0–1; 0–1; 0–2, 3
leg 3	0–1	0–0	I–0; I–1; III, I, 5	0–1; 0–1; 0–2, 3
leg 4	0–1	0–0	I–0; I–1; III, I, 5	0–1; 0–1; 0–2, 2, 3

Fifth leg apparently uniramous, 3-segmented (coxopodite, basipodite, plus 1 exopodal segment), with strong, short spine on inner margin of second segment, probably very reduced endopod. Terminal exopodal segment with long, slightly curved spiniform process just beyond midlength of inner margin, and 5 short apical nonarticulated processes subequal in length (Fig. 4E). Terminal segment about 3.5 times longer than wide and 1.6 times longer than second segment.

Male.—Males slightly larger than females, their length ranging from 0.687–0.705 mm, with mean of 0.697 mm. Body form and structure of cephalic and thoracic appendages similar to those of female (Fig. 2D), including similar processes on right and left margins of first urosomal somite (Fig. 2E). Male differing from female by having 5-segmented urosome, relative length (0.27 of urosome length) and shape of caudal ramus, geniculate right first antenna, and structure of fifth legs. Right antennule 18-segmented (Fig. 2D). Other cephalic appendages and swimming legs as in female. Fifth legs highly modified as grasping organ. Right fifth leg with coxopodite, basipodite, and 3-segmented exopod. Left fifth leg with 2-segmented exopod. Right endopod reduced to single segment with terminal digitiform process; from different views, segment distal margin straight or curved. Left endopod reduced to bifurcated process with 2 different projections: one long and digitiform, other diverging thumb-like process (Fig. 3F, G). Right basipod large and strong, with first segment folded over it. Left basipod with spine at midlength on inner margin. Right and left exopods with distal segment bulbous, unarmed (Fig. 4F–H).

Etymology.—The new superfamily, family, and genus are named after Dr. Audun Fosshagen, a copepodologist at the University of Bergen, Norway, in recognition of his extensive and valuable contributions to the faunal knowledge of anchialine environments. The gender is masculine. The new species is named for Dr. Frank D. Ferrari, National Museum of Natural History, Smithsonian Institution, Washington, D.C., for his outstanding work on calanoid copepods and for his encouragement and support to work in this group.

Habitat.—Conch Bar Cave is the largest known cave in the Caicos Islands. According to Gregor (1981), its length exceeds 2.5 km. The cave is situated under Conch Bar Hill, a 30-m high lithified dune running parallel to the coastline. The main entrance is a 40-m diameter, collapsed depression at the southern edge of the hill. During the 1880s, guano was mined from the cave; artifacts found in the cave provide evidence of use by the Lucayan Indians. From a

Table 1. Comparative characteristics of superfamilies of Calanoida (Andronov, 1974; Park, 1986) showing the position of Fosshagenioidea.

Superfamily	A	B	C	D	E	F	G	H
Pseudocyclopoidea	S	R	2	8, 7	5	N	—	X
Augaptiloidea	S	L	2	8, 7	5	N	—	X
Fosshagenioidea	F	R	1	7	5	Y	X	—
Centropagoidea	S	R	2	5, 8	5	Y	—	—
Megacalanoidea	S	R	2	8, 7	5	N	—	—
Bathypontoidea	F	R	2	7	5	N	X	—
Eucalanoidea	F	R	1	5	5	N	X	—
Riocalanoidea	F	R	1	6	5	N	X	X
Pseudocalanoidea	F	—	1	5	5	N	X	—
Spinocalanoidea	F	—	1	5, 6	4	N	X	—
Epacteriscoidea	S	R	2	8, 7	5	Y	—	—

A, Antennular segments 8 and 9 fused (F) or separate (S); B, Right (R) or left (L) male antennule modified; C, Number of setae on middle endopodal segment of legs 3 and 4; D, Number of setae on distal endopodal segment of legs 3 and 4; E, Number of inner setae on terminal exopodal segment of legs 3 and 4; F, Male fifth leg strongly modified (Yes, No); G, One or two segments on first leg endopod (X), or three (—); H, Extra aesthetascs on male geniculate antennule (X); without such structures (—).

large, initial breakdown chamber, partially flooded passages extend to the east and north. The clear water in these passages is generally about 0.5–1 m deep, although a section with depths to 10 m is found farther into the cave. Water levels fluctuate about 0.7 m with the tides, as indicated by stains on the cave walls. Surface salinity was 23‰, while water temperature was 24.7°C. A brown, organic-rich silt covers the floor in the flooded passageways. Other inhabitants of the cave are: the two anchialine shrimp *Barbouria cubensis* (Von Martens) and *Typhlatya garciai* Chace, the mysid *Stygiomysis clarkei* Bowman *et al.*, the amphipod *Spelaeonicippe provo* Stock and Vermeulen, the polynoid polychaete *Pelagomacellicephala iliffei* Pettibone, and the epacteriscid copepod *Erebonectes macrochaetos* Fosshagen and Iliffe.

DISCUSSION

The status of the new superfamily was defined following the phylogenetic scheme proposed by Andronov (1974) and later modified by Park (1986). In Table 1, the main diagnostic features at the superfamily level are presented for the 10 previously defined taxa, along with the characters of the new superfamily. The Fosshagenioidea shows some relationship with the Centropagoidea, which are characterized mainly by the presence of a male geniculate antennule on the right side and an extremely asymmetrical fifth pair of legs, with the

right side modified as a strong grasping organ (Andronov, 1974; Park, 1986). All these features are present in the new taxon. However, fosshagenioids diverge clearly from the centropagoid pattern by the presence of relevant taxonomic characters such as less than 3 segments in the first leg endopod and fused antennular segments 8 and 9. These features are common in five other superfamilies (Park, 1986), but in these (Bathypontoidea, Eucalanoidea, Spinocalanoidea, Ryocalanoidea, and Clausocalanoidea) the male fifth legs are not modified into a grasping organ. Therefore, the combination of characters present in the Fosshagenioidea would put this taxon close to the Centropagoidea, probably similar to the Temoridae pattern, with a highly modified male fifth leg, and the right male antennule modified. However, in temorids the female fifth leg is uniramous, while an endopod is present in *Fosshagenia*.

The fosshagenioid pattern differs also from other anchialine taxa such as the Ridgewayiidae, Epacteriscidae, and Boholinidae by several features. Ridgewayiids show biramous female fifth legs with a peculiar structure on the exopod (Fosshagen and Iliffe, 1991), clearly absent in fosshagenioids, which have a very much reduced fifth leg endopod, differing from the slight reductions present in other anchialine genera belonging to the Ridgewayiidae (3-segmented fifth leg endopod in *Brattstromia*, and *Exumella*). Sexual dimorphism of the fifth legs in Fosshagenioidea is the strongest reported among anchialine Calanoida. The new taxon shows a primitive antennular segmentation pattern with segments 2–4 completely fused, differing from ridgewayiids, such as *Ridgewayia*, with fusion of segments 2 and 3 (Fosshagen, 1970), and *Brattstromia* Fosshagen and Iliffe, 1991, with segments 2–4 only partially fused (Fosshagen and Iliffe, 1991). The Epacteriscidae show biramous female fifth legs, with an exopod bearing 3 outer spines, an unmodified biramous male fifth leg, a modified male left antennule (as in the Augaptiloidea), and very specialized mouthparts, which clearly diverge from the fosshagenioid pattern. On the other hand, boholinids have a 3-segmented first leg endopod, antennular segments 8 and 9 separated, well-developed mouthparts, and biramous fe-

male fifth legs. There are only slight similarities to the Boholinidae, with a 3-segmented endopod of the first leg and aesthetascs on all antennular segments.

Fosshagenioids show both primitive and modified structures; among the primitive: abdomen 4-segmented in the female and 5-segmented in the male; antennules 25-segmented with a setation pattern with aesthetascs and setae on most segments; antennal exopod 6-segmented, each segment with one seta; 6-lobed maxilla; maxilliped 5-segmented with a well-developed endopod; legs 1–4 with 3-segmented exopods, coxae with internal seta. Among the modified structures are: fusion of the first anterior thoracic somites and partial fusion of the posterior somites; antennular segments 8 and 9 fused; antennal exopods 2–4 and 9 and 10 fused; male antennule geniculate; basis of legs 1–4 naked. The new taxon has reduced mouthparts, with fewer setae than usual on the mandibles and first and second maxillae, and a reduced mandibular gnathobase, pointing to predatory habits. The somewhat elongate maxillipeds of the Fosshageniidae show no modified setae as in the ridgewayiids *Ridgewayia* and *Brattstromia*. Modified setae in such anchialine genera may have cutting functions to deal with carcasses deposited on the bottom (Fosshagen and Iliffe, 1991). This would support the idea of fosshageniids as predators dwelling in the water column.

The affinities of the new Fosshagenioidea with the Centropagoidea, featured by several families dwelling in brackish and freshwater environments (Park, 1986), seem to be ecologically supported, since *Fosshagenia* was found in brackish water (23‰). The Epacteriscoidea, as well as other bottom-dwelling copepod taxa, are regarded as primitive (Park, 1986). The fosshagenioids may be regarded as less primitive anchialine copepods, more closely related to brackish-water forms (Centropagoidea) than to the other anchialine groups.

The new species, *F. ferrarii*, can be easily distinguished by the lateral process of the female genital segment and by the structure of the male and female fifth legs. With a mean length of less than 0.70 mm, the new species is one of the smallest anchialine calanoids described, along with *Boholina crassicephala* Fosshagen, 1989 (0.75–

0.85 mm) and *B. purgata* Fosshagen, 1989 (0.73–0.79 mm) (Fosshagen and Iliffe, 1989).

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