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The North American Continental Copepods in Chappuis' Legacy and Redescription of Three Species of the Genus *Moraria* T. & A. Scott 1893 (Crustacea: Copepoda: Harpacticoida)

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Frank Fiers and Oana T. Moldovan (2012) The North American continental copepods in Chappuis' legacy and redescription of three species of the genus *Moraria* T. & A. Scott 1893 (Crustacea: Copepoda: Harpacticoida). *Zoological Studies* **51**(8): 1549-1573. In the process of inventorying the copepod collection assembled by P.A. Chappuis and hosted at the "Emil Racoviţă" Institute of Speleology (Cluj, Romania), part of his material originating from the US was located. In 5 vials and on 6 slides are representatives of 9 different species: 7 Harpacticoida and 2 Cyclopoida. A list of the species, numbers of specimens available, and their condition is presented. Some of them had to be annotated as syntypes. Most of the cyclopids mentioned were donated to F. Kiefer and are currently hosted in the collection at Karlsruhe, Germany. Three representatives of the genus *Moraria* T. & A. Scott 1893, namely *M. cristata* Chappuis 1929, *M. affinis* Chappuis 1927, and *M. americana* Chappuis 1927, the latter currently known as *M. laurentica* Willey 1927, are reexamined and redescribed. Their diagnostic features, compared to the other known New World *Moraria* species, are summarized in tabular form to facilitate identification. http://zoolstud.sinica.edu.tw/Journals/51.8/1549.pdf

Key words: Chappuis' collection, Species list, *Moraria*, Redescription, North America.

Chappuis contributed to the study of the North American continental copepod fauna on several occasions (Chappuis 1927 1929a 1931 1932 1933 1937, Chappuis and Delamare Deboutteville 1958). His earliest contributions to the New World fauna were copepods found among mosses and in caves (Chappuis 1927 1929a 1931). Among the 19 copepod species he reported from those localities, a considerable number of new ones, including 2 cyclopoids and 7 harpacticoids, were detected and subsequently described.

In the process of cataloguing the copepod collection compiled by Chappuis in the period he was affiliated with the "Emil Racoviţă" Institute of Speleology at Cluj, Romania, slides and vials referring to his contributions to the North American continental copepod fauna were recovered. Although not all the vials from each locality or sample he dealt with were located, those which could successfully be linked to his work appeared to contain sufficient and fairly well-preserved material.

This contribution provides information on the species present and their condition encountered in 5 vials and on 6 slides. Since Chappuis did not indicate any reference to the status of the animals on the slides or on the labels in the vials, certain of the specimens mentioned here are eligible to become syntypes. In the following pages, 3 *Moraria* species, *M. americana* Chappuis 1927 (currently referred to as *M. laurentica* Willey 1927), *M. cristata* Chappuis 1929, and *M. affinis*

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Chappuis 1927 are redescribed. The redescription of *M. cristata* is based on material obtained near Columbus, OH, USA, and it is compared to a single female specimen still present from the type locality, Donnaldson Cave, IN, USA. Specimens of *M. affinis* Chappuis 1927 were unexpectedly found intermixed with specimens of *M. americana* from New Jersey; the vial from its type locality, Pelham Park, NY, USA, could not be located.

MATERIALS AND METHODS

The material hosted at the "Emil Racoviţă" Institute of Speleology (Cluj, Romania) and attributed to Chappuis consists of a number of slides (ca. 300) and vials with spirit-preserved animals (ca. 200). In the current condition, the collection is difficult to access because of the sparse and cryptic labeling of slides and vials. An archive (field notes, correspondence, etc.) related to the collection and/or the activities of Chappuis is not available. The work on a complete and annotated catalog of the materials present in the Chappuis collection at Cluj is currently in progress.

Vials dealt with here and holding alcohol-preserved material were grouped in a jar with the label, "U.S.A." During the years, animals in the vials have become compacted within a fine-grained sediment. Repeatedly washing and stirring the contents with a mixture of ethyl alcohol and glycerol allowed the separation of the copepods from the sediment. Minute particles remain fixed on the body and appendages, in particular on buccal ones, making observations of details impossible in some cases. Slides with dry remnants of specimens were rehydrated (first with ethyl alcohol, which was progressively replaced by glycerol) and sealed (with a polyurethane varnish) after all air bubbles had been removed. Information on the slide labels and in vials was carefully compared to that published by Chappuis and their contents to ascertain the origin of the animals present. Vials with labels with insufficient information were not used in the present work. The different species recovered from a vial were separated and stored individually in 75% ethyl alcohol (with a drop of glycerol). Each of them was labeled with the original indication, and an additional label was annotated with the species name and its origin, and eventually with its nomenclatural status.

Specimens were examined using temporary mounts. Specimens that were dissected for the present contribution were mounted in glycerol, and the cover glasses were sealed. All material is deposited at the "Emil Racoviţă" Institute of Speleology, Cluj, Romania. The harpacticoid classification adopted herein is basically that introduced by Lang (1948), but in its most recent presentation according to Wells (2007). In the synonymy lists, pagination to the 1964 translation of Borutzky's 1952 work is indicated between parentheses. Abbreviations used throughout the text include P1-P4, legs 1-4; Aesth, aesthetasc; EXO, exopodite; END, endopodite. Abbreviations used in table 1 are explained in its caption.

RESULTS

Annotated list of the North American material in the Chappuis collection

(1) Vial labeled: "South Orange, N.J. 15.IV.25". Chappuis (1927: 302) referred to a moss sample in which 2 species were present: *Viguierella paludosa* Mrz and *Moraria americana* n. sp. The date on the label (15 Apr. 1925) differs from that communicated by Chappuis (12 Apr. 1925). However, the vial contains both species mentioned in Chappuis' contribution, and the published date is assumed to be a typographic error. The animals were found in a sample (collected by M. Marcel Chappuis) of wet mosses in small seeps on stony outcrops in a young deciduous forest along a western hill slope at South Orange, NJ, USA. According to present-day topographic maps, the locality seems to have been situated in the township limits between South and West Orange (see Reid and Lesko 2003). Closer examination of the contents revealed the presence of a 3rd species, *M. affinis* Chappuis 1927. The latter, also a moss-inhabiting species and described in the same paper (Chappuis 1927), has its type locality in the "public park near Pelham Bay, New York". Animals in the "South Orange N.J." vial are fairly well preserved and rather abundant but transparent and very fragile. Manipulation was limited to a minimum. The collection is now preserved as follows: 1 vial containing 70 specimens (females and males) of a mixture of *Phyllognathopus paludosus* Mrázek 1894, *Moraria americana*, and *M. affinis*; 1 vial with 5 specimens (3 females and 2 males) of *P. paludosus*; 1 vial with the remains of the original sample (containing nematodes and some ostracods); and 8 series of slides with the dissected parts of *M. americana*

and *M. affinis* (details given below).

(2) Vial labeled "Cop. Donnaldson" undoubtedly refers to the sample collected in Donnaldson Cave, IN, USA on 26 Aug. 1928 during the Bolivar and Jeannel field trip to North America. This was confirmed by its contents. Chappuis (1929a 1931) mentioned the receipt of 2 vials from this locality, but only one could be located in the collection at Cluj. Four species were described from the cave: 1 cyclopid, *Cyclops* (*Megacyclops*) *donnaldsoni* (= *Megacyclops donnaldsoni* (Chappuis 1929)) and 3 harpacticoids: *Attheyella* (*Brehmiella*) *pilosa* (= *Attheyella* (*Ryloviella*) *pilosa* (Chappuis 1929)), *Echinocamptus* (*Limocamptus*) *Morrisoni* (= *Bryocamptus* (*Limocamptus*) *morrisoni morrisoni* (Chappuis 1929)), and *Moraria cristata* Chappuis 1929. The vial contents were a single male specimen of *M. donnaldsoni* (spirit preserved), 13 specimens of *A.* (*R.*) *pilosa* (5 females and 5 males, spirit-preserved, and 2 females and 1 male, dissected), 5 specimens of *B.* (*L.*) *morrisoni morrisoni* (4 females and 1 CIV female juvenile, all spirit-preserved), and 1 female specimen of *M. cristata*. Both the latter are considered to be syntypes and were left undissected. *Moraria cristata* was compared to specimens encountered in the vial from Ohio (vial 4, see below). The condition of specimens from Donnaldson Cave is not optimal. Additional material of *M. donnaldsoni* is hosted at the F. Kiefer collection in Karlsruhe, Germany. The catalog of the collection (Franke 1989) lists 2 slides with the dissected parts of a female urosome (slide #1147) and a partially dissected female prosome and legs (slide #1148) from "Donaldson-Höhle, USA" [sic]. They form part of the type series.

(3) Vial labeled "Marengo cave" is clearly from Marengo Cave (Crawford County, IN, USA) and was also collected on 26 Aug. 1928 during the Bolivar and Jeannel field trips. Chappuis (1929) described "*Cyclops* (*Diacyclops*) *Jeanneli*" from this cave. The 33 specimens (18 females, 11 males, and 4 juveniles) of this cyclopid, currently named *D. jeanneli* (Chappuis 1929) are in fairly good condition and are to be considered as the syntypes. Two additional slides (#1138 and #1139), respectively with a dissected female and male and originating from the cave sample, are present in the F. Kiefer collection at Karlsruhe and belong to the type series. A vial (#492: Franke 1989) labeled "Marengohöhle, USA" is in the Kiefer collection but was not examined for the present paper. Marengo Cave still hosts a viable population of this species, and *D. jeanneli* was recently redescribed in detail on the basis of topotypic material by Reid (2004).

(4) Vial labeled "Ohio, Harp." appears to be the sample which Chappuis (1931) referred to as "Ohio, humid mosses from near Colombus, May, 1929". The vial contains few specimens; besides 8 specimens of *M. cristata*, there are a few remains of unidentifiable juvenile harpacticoids and a cyclopid. Some of the specimens are fairly well preserved which allowed a redescription of *M. cristata*.

(5) Vial labeled "Spring in Battle Park, Chapman Hill, N.C., Cocker". Chappuis (1932) described *Attheyella* (*Brehmiella*) *carolinensis* from a spring in Battle Park. The label in the vial coincides perfectly with the locality information given in Chappuis (1932), but contrary to his statement that only 1 specimen of each gender was available, the vial contains more material attributable to the species. The 4 additional specimens encountered (2 males, 1 CV female juvenile, and 1 CIII juvenile) are spirit-preserved and should not be considered type material. The species, currently named *Attheyella* (*Ryloviella*) *carolinensis*, was redescribed and compared to *A.* (*R.*) *pilosa* Chappuis 1929 in Bowman et al. 1968.

The slides, although dry for quite some time, appear after restoration to still contain the mounted body parts, of which the general structure is visible. Specimens were partially dissected by Chappuis, and not every body part seems to be present. Examination of slides was almost useless to discern structural details.

The 3 slides with remnants of *M. cristata* are labeled "*cristata*" and "Ohio" and are specimens featuring in Chappuis (1931). They served to expand the original description of *M. cristata* with the formerly unknown male characteristics. One slide bears the indication 2 females and the other 1 male. They cannot be considered type material, but are nevertheless important (see discussion below). No slides of *M. cristata* from the type locality (Donnaldson Cave) were found. Two slides bear the indication "donnalds". One has the additional indication, "Canth n. sp.", and contains the urosome of *Attheyella pilosa* Chappuis 1929; the contents of the 2nd one, labeled "*Cyclops* (*Megacyclops*) *donnaldsoni* 1F, Donaldson", is obvious. Two slides each containing remnants of a *D. jeanneli* female bear the indication, "Marengo", but are in bad shape and rather useless.

So far, copepods from a moss sample collected at Pelham Park, NY, USA have not been encountered at Cluj. Chappuis (1927) reported 6 harpacticoids and 1 cyclopoid in the

sample: *Canthocamptus illinoisensis* Forbes 1876 (= *A.* (*Neomrazekiella*) *illinoisensis* (Forbes 1876), *C. minutus minnesotensis* Herrick 1884 (= *Bryocamptus* (*Bryocamptus*) *minutus* (Claus 1863)), *C. pygmaeus* Sars 1863 (= *Bryocamptus pygmaeus* (Sars 1863)), *Epactophanes Richardi muscicola* Richters (= *Epactophanes muscicolus* (Richters 1900)), *Canthocamptus newyorkensis* (= *Bryocamptus* (*Bryocamptus*) *newyorkensis* (Chappuis 1927)), and *Moraria affinis* Chappuis 1927. Type materials of the last 2 species are yet to be located. Specimens of the cyclopid mentioned by Chappuis, *D. crassicaudis brachycercus* Kiefer 1927, are still present in the F. Kiefer collection hosted at Karlsruhe, Germany (Franke 1989). The type series of the species consists of 7 slides labeled "*Cyclops crassicaudis*" (4 slides: #747-#750) and "*Cyclops crassicaudis nearticus*" (3 slides: #762, #763, #766) and 1 vial (coll. # 0431). The subspecific status of *C. c. brachycercus* Kiefer 1927 was discussed at length in Reid (1992) on the basis of observations made on slides #762, #763, and #766, additional material from various localities, and literature data. Currently, *brachycercus* is considered a mere variation of the nominate subspecies (Reid 1992, Reid and Williamson 2010).

Specimens from Horse Cave and Mammoth Cave, KY, USA were not encountered in the Cluj collection. The unique specimen of *Echinocamptus* (*Limocamptus*) *morrisoni elegans* Chappuis 1929 (type locality: Horse Cave) and males of *Attheyella* (*Brehmiella*) *pilosa* mentioned as occurring in Mammoth Cave remain to be located. According to Franke (1989), a vial from Mammoth Cave is available in the F. Kiefer collection at Karlsruhe (labeled "Mammuthöhle, USA": vial #493). The contents were not examined in the process of the present contribution, but the vial is expected to contain at least some of the 6 Cyclopidae mentioned by Chappuis (1929a): (with the current nomenclature) *Eucyclops serrulatus* (Fischer 1851), *E. elegans* (Herrick 1884), *Paracyclops chiltoni* (Thomson 1882), *Tropocyclops prasinus* (Fischer 1860), *Acanthocyclops robustus* (Sars 1863), *Mesocyclops edax* (Forbes 1891), and *Cyclops* sp. Apparently Kiefer made no attempt to examine them closely, as no slides of these are listed in his slide collection.

Species account: redescription of 3 *Moraria* species

Family Canthocamptidae Brady 1880

Genus *Moraria* T. & A. Scott 1893

Moraria cristata Chappuis 1929

(Figs. 1-3)

Moraria cristata n. sp. - Chappuis 1929a: 56-57, figs 16-18 [key].
Moraria cristata Chappuis 1929 - Chappuis 1929c: 485, 504 [key]; Chappuis 1931: 353, figs. 16-22; Chappuis 1933: 18, 31; Lang 1948: 1033, 1047, fig 418(4), [key]; Wilson 1956a: 297; Wilson and Yeatman 1959: 835-836, fig. 29.180 [key]; Dussart and Defaye 1990: 135; Reid and Lesko 2003: 11-12, table 1; Reid and Williamson 2010: 896 [key].
Moraria (s. str.) *cristata* Chappuis 1929 - Borutzky 1952 (1964): 323 (298), 325 (300), 332 (307), figs. 88(1-2), 91(15-18) [key].

Material observed: (1) 1 ♀ from Donnaldson Cave, Lawrence Co, IN, syntype (spirit-preserved); (2) 6 ♀♀, 1 ♂, and 1 copepodid from Columbus, OH (2 ♀♀ and 1 ♂ dissected, mounted on 2, 3 and 1 slide, respectively), 4 ♂♂ and 1 copepodid spirit-preserved).

Description of female (based on Ohio specimens, except where stated otherwise): Body fusiform, somewhat depressed (Fig. 1A). Metasome nearly parallel-sided, urosome smoothly tapering caudally. Prosome and urosome of equal lengths with indistinct major body articulation. Genital double-somite considerably wider than long (with a length: width ratio of about 0.6) with faint remnants of ancestral articulations along the lateral margin. Body length (Ohio specimens) 335 μm (compact) to 450 μm (expanded) (*n* = 4); (Donnaldson specimens) 510 μm (expanded specimen).

Dorsomedian cephalic window keyhole-shaped, with broad border, located centrally on head shield. Lateral integumental window present on pedigers 2 (Fig. 1C) and 3 (presence obvious in Ohio specimens, unclear in Donnaldson specimen). Integument of all somites showing refractile points (details in Fig. 1C). Posterior margin of all somites irregularly serrate. Structural ornament absent from cephalothorax, metasomites, 1st urosomite, and dorsal and lateral surfaces of urosomites 2-5. Genital double-somite with short row of long spinules on posteroventral corner (specimens from Ohio, Fig. 1B), without spinule row in Donnaldson Cave specimen (not illustrated). Ventral surface of urosomites 4 and 5 with median row of short, narrowly spaced, spinules in anterior half. Posteroventral margin

of urosomites 4 and 5 with widely spaced long spinules, and lateral interruption on urosomite 4, but uninterrupted on urosomite 5.

Anal somite with prominent rounded anal operculum, expanded beyond anal sinus in Ohio specimens (Fig. 1A), far less expanded in Donnaldson Cave specimen (Fig. 3A). Opercular margin smooth. Posterodorsal margin of anal somite with small, transparent triangular spinules (Figs. 1A, 3A, D). Lateral and ventral caudal borders with uninterrupted girdle of long spinules (Fig. 1B). Caudal rami (Fig. 3A) truncate, twice

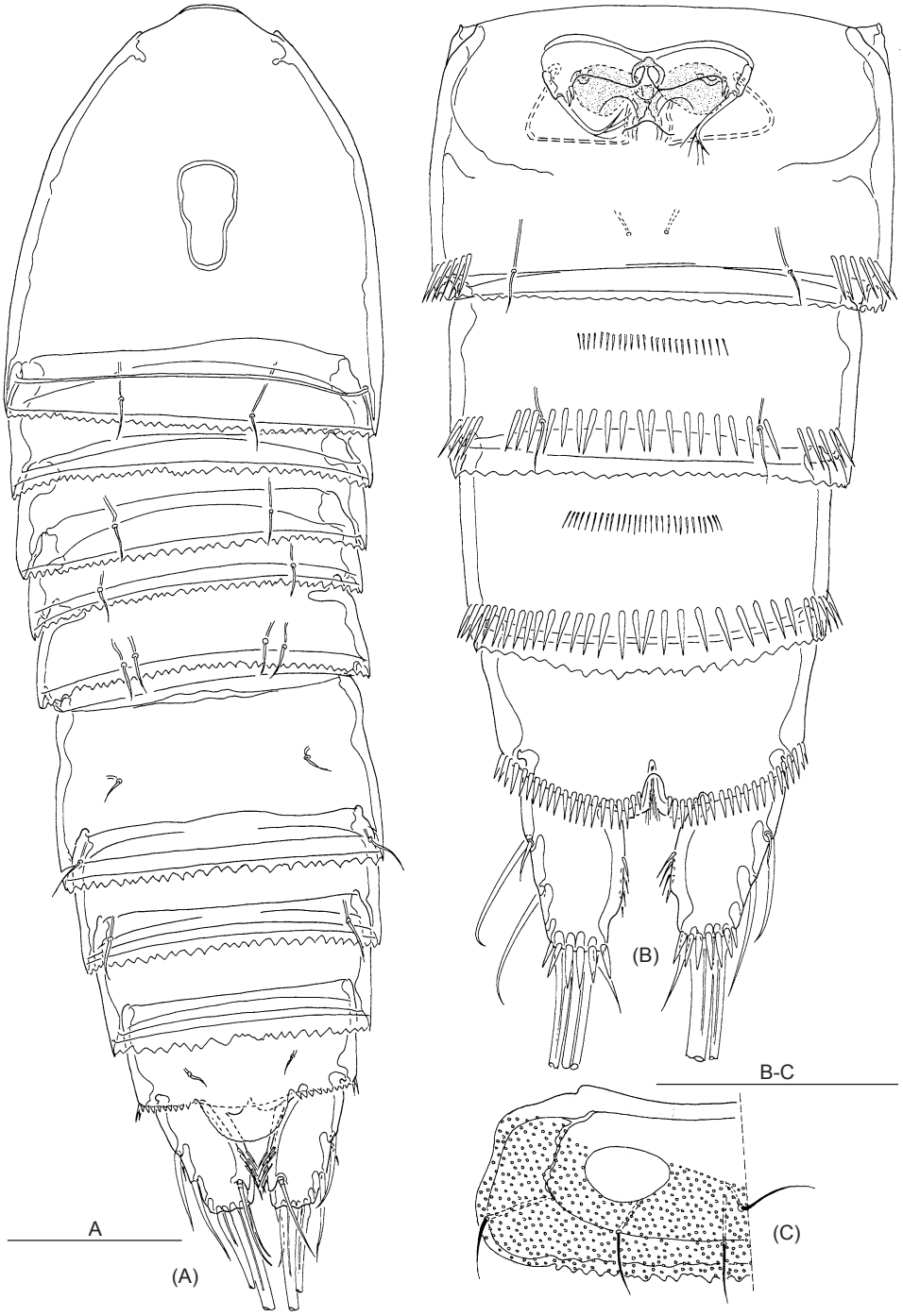

Fig. 1. *Moraria cristata* Chappuis 1929, female (A-C, from Columbus, OH). (A) Habitus, dorsal (pattern of sensilla incomplete); (B) abdomen, ventral; (C) details of pleurotergite, 2nd pediger. Scale bars: A = 50 μm, B-C = 50 μm.

as long as wide (females from Ohio), 2.4-times longer than wide (female from Donnaldson Cave), with distinct longitudinal dorsal crest located near medial margin and parallel to it. Crest terminating in sharp point that extends beyond insertion of dorsal seta. Medial surface with row of long, slender spinules, arranged along oblique line, perpendicularly on medial axis. Posterior margin smooth dorsally, with long spinules ventrally. Anterolateral and distolateral setae equally long. Accessorial lateral seta short. Terminal setae without breaking plane, both with widely spaced and rigid setules along outer margin. Outer terminal seta as long as caudal ramus (Donnaldson Cave specimen, Fig. 3B) or nearly twice as long as ramus (Ohio specimens, Fig. 3C). Medial terminal seta short, smooth, wide at insertion. Dorsal seta shorter than ramus, inserted on 2 basal parts.

Rostrum large and triangular with blunt apex and small hyaline truncate extension at tip. One pair of sensilae in proximal third of outer margin. Antennule (Fig. 2A) 7-segmented. First segment with spinule comb on frontally directed border. Second segment with rigid ventral rim parallel to inner and frontal border. Armament: 1(1)-2(9)-3(6)-4(2+Aesth)-5(1)-6(3)-7(9+Aesth). Aesthetasc on segment 4 linguiform, reaching middle of terminal segment. Aesthetasc on segment 7 tubiform.

Antenna (broken) with 2 setae on abexopodal margin of allobasis, proximal one shortest. Exopodite 1-segmented with 4 setae: 2 apical and 2 lateral. Proximalmost lateral element pinnate, other setae smooth. Exopodite segment smooth. Endopodite segment with normal armature (3 lateral and 6 terminal) and spinular pattern along lateral and distal border. Mandible, maxillule, maxilla, and maxilliped broken, covered by dirt, not illustrated. Mandibular palp 2-segmented with 1 outer seta on basal segment and 4 long spinules/setules on medial margin. Second segment quadrangular with 3 apical setae. Maxillulary arthrite not observed, coxa and basis with rigid medial element bearing serrate/spatulate tip, and slender setae. Maxillulary rami obsolete. Maxilla with 2 endites, each with 2 robust elements furnished along 1 side with long and slender setules. Maxillary basis with claw, serrate in medial 1/2, and obsolete endopodite. Basis of maxilliped with long, rigid spinules along medial margin and serrate claw.

Legs 1-4 (Fig. 2B-F) with wide, smooth intercoxal sclerite, concave along distal border. Praecoxal fold obvious, rigid. Exopodites 3-segmented, endopodites 2-segmented. Leg 1 (Fig. 2B) with medial spine on basis and spiniform flagellum-bearing outer element. Endopodite short, not extending beyond exopodite, with proximal segment 1.5-times longer than distal one, with medial pectinate element and robust spinules along outer margin. Distal endopodite segment with single robust spinule in proximal half of medial margin. Medial element short, inner terminal element long and slender, and outer terminal claw long (as long as entire endopodite) with flagel. Leg 2 basis with flagellated spiniform outer element. Basis of legs 3 and 4 with long setiform outer element. Proximal endopodite segment in legs 2-4 with pectinate medial element, extending beyond distal segment. Distal and medial elements on distal endopodite segments setiform. Distal endopodite segment as long as proximal one (legs 2 and 4) or slightly longer (leg 3). Outer margins of endopodite segments with 1-3 large spinules, inner margin with a single spinule at insertion of medial element. Leg armament distribution as follows:

	EXO	END
P1	I.0-I.0-II.2.0	0.1-I.1.1
P2	I.0- I.0-II.2.0	0.1-I.2.0
P3	I.0- I.0-II.2.0	0.1-I.2.0/1
P4	I.0- I.0-II.2.1	0.1-I.2.0

Leg 5 (Fig. 3H, I) prominent with ovate exopodite and expanded endopodite lobe, the former extending slightly beyond distal margin of inner lobe of baseoendopodite. Coupler distinct, smooth, and with prominent convex distal margin. Exopodite bearing 5 setae, apicalmost one longest and innermost one robust with widely spaced rigid setules. Baseoendopodite with outer seta and 6 endopodite armature elements. Outer proximal element on endopodal lobe with a comb of long rigid setules in proximal third. Both proximal inner elements on endopodal lobe pectinate (Fig. 3H) or pectinate and setiform (Fig. 3I). Medial margin of exopodite with long, sturdy spinules. Proximal margin of endopodite lobe with 2 triangular processes caudally and a pair of minute spinules at insertion of outer proximal element. Surface of both rami smooth.

Leg 6 (Fig. 1B) represented as relatively large semi-ovate plate, with 3 elements: a long, sparsely pinnate outer element and 2 dwarf elements medially. Genital complex with short copulatory duct with orifice in anterior half of genital double-somite leading to large ovate seminal receptacles.

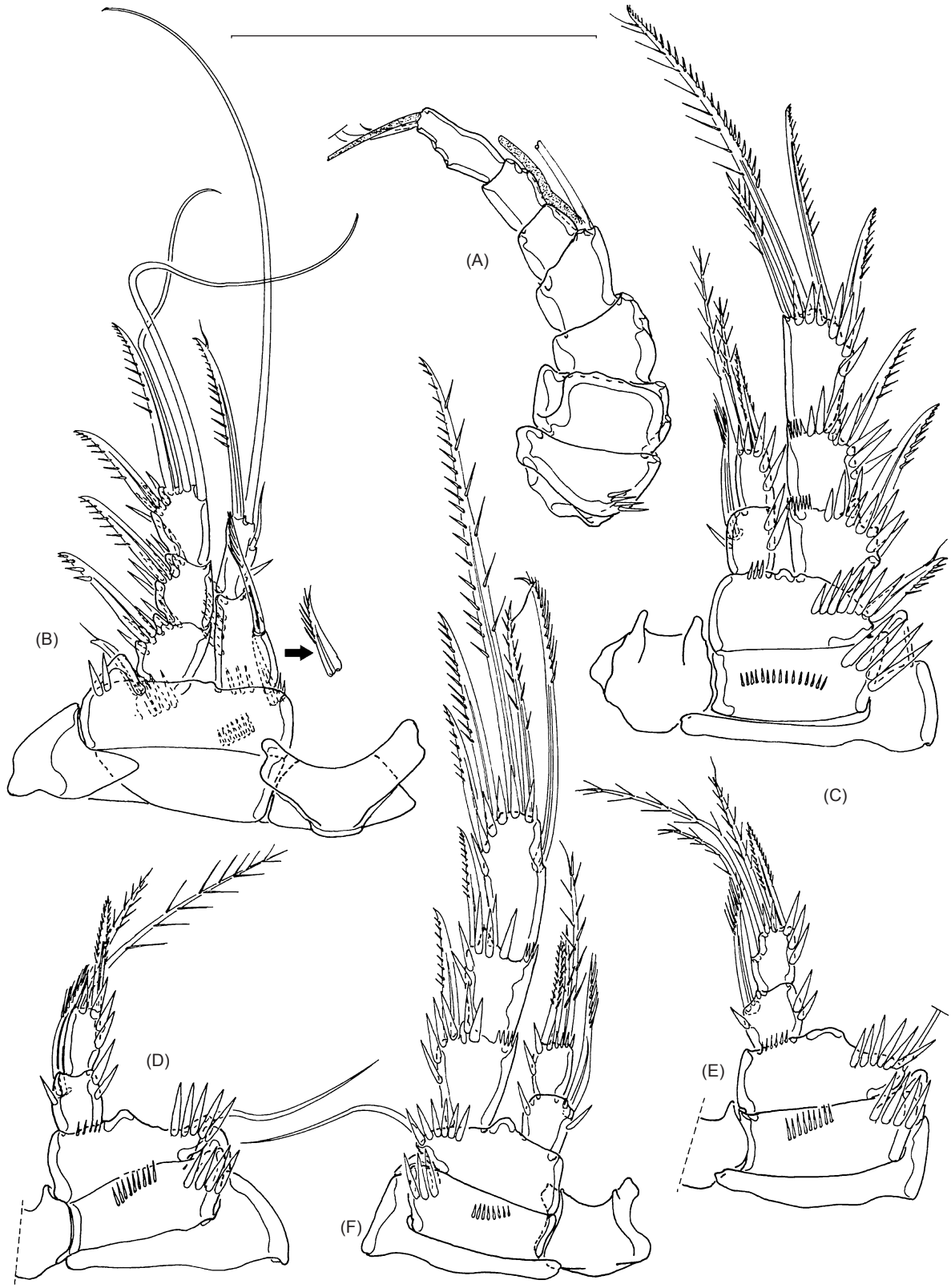

Fig. 2. *Moraria cristata* Chappuis 1929, female (A-F, from Columbus, OH). (A) Antennule contour, dorsal view; (B) leg 1, caudal view; (C) leg 2, frontal view; (D) leg 3 protopodite and endopodite, frontal view: aberrant setal armament; (E) idem, normal setal armament; (F) leg 4, frontal view. Scale bar = 50 μm.

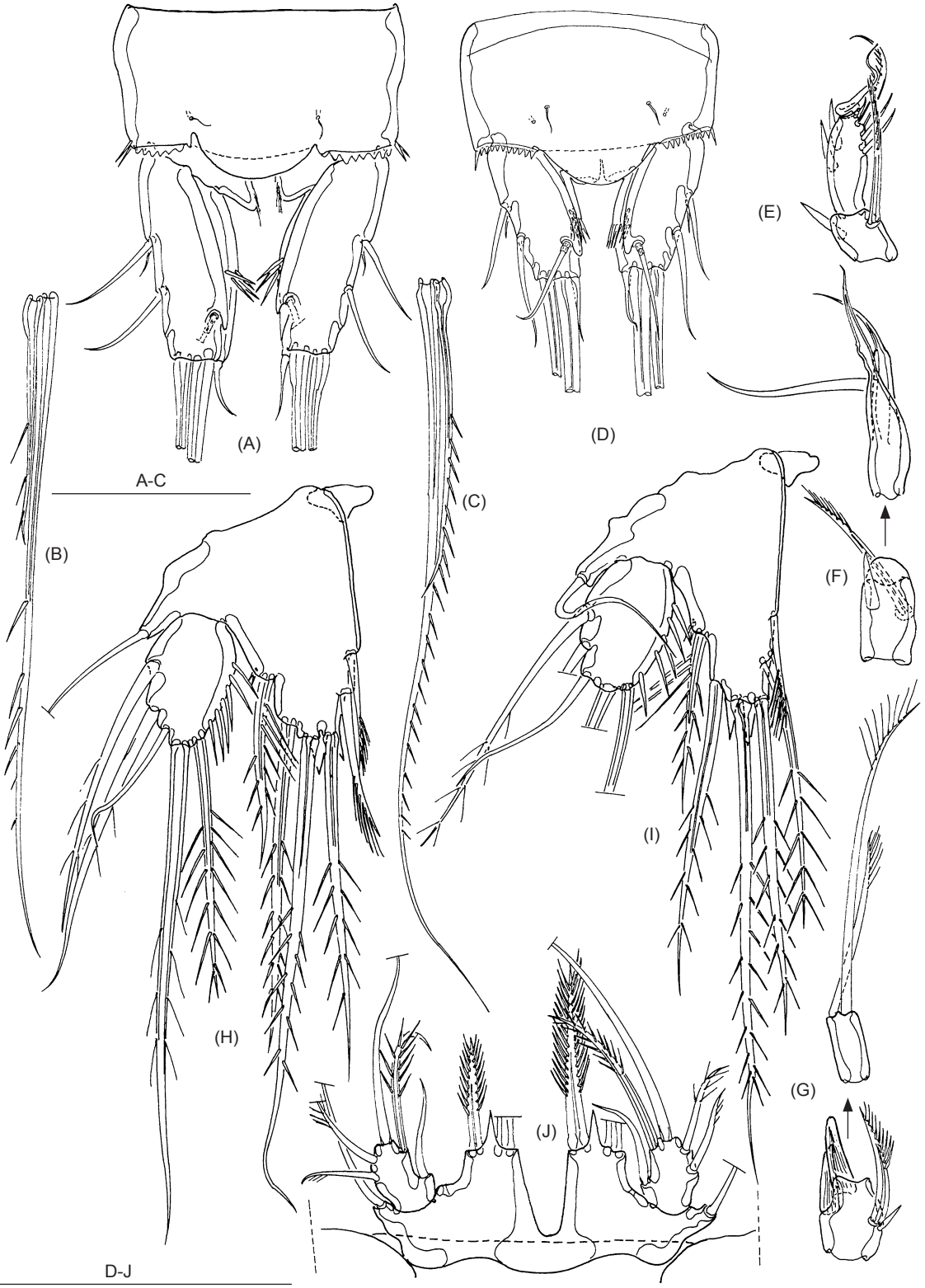

Fig. 3. *Moraria cristata* Chappuis 1929, female (A-C, H-I), male (D-G, J) (A, B, specimen from Donnaldson Cave, IN; C-J, specimens from Columbus, OH). (A) Anal somite and caudal rami, dorsal view; (B) principal terminal setae caudal rami; (C) principal terminal setae caudal rami; (D) anal somite and caudal rami, dorsal view; (E) leg 4 endopodite, caudal view; (F) male leg 3 endopodite, frontal view; (G) leg 2 endopodite, frontal view; (H) leg 5, frontal view; (I) leg 5, frontal view; (J) leg 5, frontal view. Scale bars: A-C = 50 μm, D-J = 50 μm.

Description of male (Ohio specimen only). Body as in female, except for separate 2nd and 3rd urosomites. Body length 360 μm (*n* = 1). Integument structure and ornamentation of prosome as in female. Urosome 1 (leg 5 pediger) and 2 (leg 6 pediger) without ornamentation. Posteroventral margin of urosomites 3-5 with uninterrupted row of long, slender spinules. Ventral surface of urosomites 3 and 5 smooth, urosomite 4 with a median row of narrowly spaced short spinules in frontal half (as in female). Anal somite and caudal rami as in female, inclusive of spinule cluster on medial surface of rami (Fig. 3D).

Antennule (broken), mouthparts as in female in so far as they could be observed. Leg 1 as in female. Legs 2-4 with protopodites and exopodites as in female. Both outer spinules on proximal segment of leg 2 endopodite larger and more robust than those in female, both with blunt apex (Fig. 3G). Second leg 2 endopodite segment narrow, 1.5-times longer than wide, bearing 2 sparsely pinnate apical setae distally. Leg 3 endopodite 2-segmented with crescentic and expanded posterodistal margin of proximal segment, and with a single subdistal spinule on outer margin (Fig. 3F). Medial element pinnate. Second segment with 2 lanceolate elements confluent with segment. Lateral element rather wide in proximal half, narrow in distal half. Medial terminal element naked, slightly longer than outer confluent element, apparently inserted perpendicularly on ramal longitudinal axis. Proximal segment of leg 4 endopodite as in female (Fig. 3E). Distal segment twice as long as proximal one with 2 spinules on outer margin in distal half, and 4 armature elements along inner margin. Distal structure corkscrew-shaped and hyaline. Proximal and next to proximal medial elements

Table 1. 1, Urosomal hyaline membrane border is either serrate, weakly crenate, or straight; 2, in ventral view, border of genital double-somite (GDS) has either a lateral cluster of spinules while the medial region does not, is completely smooth, or is completely with spinules; 3, in dorsal view, GDS is either smooth along the caudal border or has a complete row of spinules; 4, posteroventral border of urosomites (UROs) 4 and 5 are either furnished with a spinular border interrupted at the insertion of the posteroventral sensillae, or with a complete (i.e., uninterrupted) row of spinules; 5, presence of a spinule cluster on medial surface of caudal rami (CR), being present in ♀ and ♂, present in ♀ but absent from ♂, or absent from both (note that the spinule cluster in *M. arctica* is situated dorsally, not along the medial surface as in other species); 6, crescentic = sickle-shaped resembling a waxing or waning moon (dixit "lunar" in Wells 2007), round-triangular when the length > width and the apex is truncate, or triangular in cases with a sharp apex; 7, not produced, when caudal margin of operculum does not extend beyond anal area, produced, when operculum distinctly extends beyond; 8, number of elements on distal endopodite segment of legs 2-4 (note that the armature number can differ on the 2 sides of animal)

	1 urosome membrane	2 border GDS ventral view	3 border GDS dorsal view	4 URO 4-5 ornament	5 CR medial spines	6 anal operc. shape	7 anal operc. size	8 P2-P4 endopodite
M. cristata Chappuis	serrate	spine cluster lateral or smooth	smooth	4: interrupted 5: complete	present (♀ & ♂)	crescentic	not produced or produced	3,3,3
M. hudsoni Reid & Lesko	crenate	smooth	complete uninterrupted	encircling complete	present (♀ & ♂)	crescentic	not produced	2,3,3
M. mrazeki T. Scott	straight	smooth	smooth	4: interrupted 5: complete	♀: present ♂: absent	crescentic	not produced	3,3-4,3-4
M. duthiei (T.& A. Scott)	straight	complete uninterrupted?	smooth	4: complete 5: complete	absent (♀ & ♂)	triangular	not produced	4,5,4
M. laurentica Willey	straight	spinule cluster lateral	smooth	4: interrupted 5: complete	♀: present ♂: absent	round-triangular	produced	3,4,4
M. viriginana Carter	straight	smooth	smooth	4: interrupted 5: complete	present (♀ & ♂)	triangular-round triangular*	produced	3,3,3
M. affinis Chappuis	straight	complete uninterrupted?	smooth	4: complete 5: complete	absent (♀ & ♂)	crescent	produced	3,3,3-4
M. arctica Flössner	straight	unknown	smooth?	4-5 complete?	♀: dorsal	serrate	produced?	3,3,3

*personal observations: specimens from Bland County, Virginia (coll. Museum d'Histoire Naturelle de Genève, CH).

slender and smooth. Subdistal element dwarfed, filiform. Next to subdistal element most prominent, twice as long as proximal ones, serrate along outer margin, smooth along medial margin. Leg 5 (Fig. 3J) of both sides fused medially. Exopodite semi-rectangular with 5 elements, apicalmost element longest, subapical medial one rigid and armed with rigid setules. Inner lobe of baseoendopodite bearing 2 spines with triangular process between their insertion. Outer armature spine 1/2 as long as medial one. Exopodite reaching slightly beyond apical margin of baseoendopodite. Medial margin of exopodite naked. Surface of both rami smooth.

Leg 6 pair asymmetrical. Both ovate with operational (right) one wider than non-operational opposite (left) valve. Armament consisting of 3 elements, outer one longer. Lengths of middle and medial elements not observed (broken and lost). Surface of valves naked.

Moraria laurentica **Willey 1927**
(Figs. 4-7)

Moraria laurentica - Willey 1927: 2-9, figs. 1-21 [*partim*], [6-IV-1927].
Moraria americana n. sp. - Chappuis 1927: 309-310, figs. 12-15 [XII-1927].
Moraria americana Chappuis 1927 - Chappuis 1928: 125 [key]; Chappuis 1929c: 485, 504 [key].
Moraria laurentica laurentica Willey 1927 - Chappuis 1931: 60; Gurney 1932: 218; Carter 1944: 164 [key]; Wilson 1956a: 297.
Moraria laurentica americana Chappuis 1927 - Chappuis 1931: 360; Carter 1944: 164 [key]; Wilson 1956a: 297.
Moraria (s. str.) *laurentica* Chappuis 1927 - Borutzky 1952 (1964): 323 (298), 325 (301), figs. 91(1-5) [key].
Moraria laurentica Willey 1927 - Gurney 1932: 218; Wilson and Yeatman 1959: 836, fig. 29.182 [key]; Dussart and Defaye 1990: 135; Reid and Lesko 2003: 11, table 1; Wells 2007: 45, 312 [key]; Reid and Williamson 2010: 896 [key].
Moraria laurentiaca Willey 1927 - Lang 1948: 1029-1033, 1045-1046, fig. 418(2) [key]; Wells 2007: 312, 314-315 [key].
non *Moraria laurentica* - Willey 1927: 9-11, figs. 22-29 [= *Epactophanes* spec.].

Material examined: (1) from "South Orange, N.J., U.S.A. 15.IV.25", considered to be syntypes of *M. americana*: 2 ♀♀ and 2 ♂♂ dissected and several females and males examined on temporary mounts, spirit-preserved afterwards; (2) 13 ♀♀, 8 ♂♂ from Floyd County, VA, USA: seepage area near top of Willis Ridge, ca 1000 m, 6 km west of Floyd. (leg. R.L. Hoffman, 5/9/1982, Coll. Museum d'Histoire naturelle de Genève); (3) 1 ♂ from Mount Michel, Yancey Co., NC, USA: litter at 1800 m in mixed *Pices-Fagus-Rhododendron* forest (leg. H.L. Hoffman, 23 Dec. 1984, Coll. Museum d'Histoire naturelle de Genève).

Description of female: Body fusiform with prosome and urosome of equal length, without obvious major body articulation (Fig. 4A). Genital double-somite wide, about 0.65 times wider than long. Internal remnants of ancestral articulation vaguely visible laterally (Fig. 4D). Body length 330-355 μm (*n* = 3).

Mediodorsal integumental window on cephalothorax semi-oval and wide, located in caudal half of head, with very noticeable border. Lateral integumental windows on pedigers 2 and 3 present, semicircular (not illustrated). Integument of all somites showing refractile points. Posterior margin of each somite straight. Structural ornamentation on cephalothorax and pedigers 2-5 absent, except for (barely visible) dorsal transverse spinule rows in, anterior half of pleurotergites (not completely observed, only partially illustrated). Genital double-somite with a short lateral row of long spinules (Fig. 4D). Urosomites 4 and 5 with median row of short spinules in anterior half of ventral surface and row of long narrow spinules along posterior margin, interrupted laterally (urosomite 4) or entire (urosomite 5). Anal somite with rounded operculum covering anal sinus. Opercular border smooth. Posterodorsal margin with short, triangular, hyaline spinules. Posterolateral and posteroventral margins bordered with an uninterrupted row of long, slender spinules.

Caudal rami 1.5-times longer than wide, with dorsal crest parallel to and near medial margin. Crest extending sharply beyond insertion of dorsal seta. Medial surface with cluster of 2-4 slender spinules. Posterodorsal margin without ornamentation, posteroventral border with spinules. Anterolateral and posterolateral setae of equal size. Accessorial lateral seta present and short. Principal terminal setae without breaking plane, not particularly modified near insertion, and sparsely pinnate along outer side. Outer principal seta 1.5-times longer than ramus. Medialmost terminal seta shorter than ramus. Dorsal seta articulating on 2 basal parts.

Rostrum triangular, with blunt tip. Apical hyaline extension absent. Sensilla in caudal half of outer margin.

Antennule (Fig. 5D) 7-segmented with spinule comb on 1st segment (Fig. 5E). Armament as in *M. cristata* (see above). Aesthetascs broken, though clearly linguiform on segment 4, tubiform on segment 7.

Antenna with 2 setae on abexopodal

margin of allobasis. Antennary exopodite (Fig. 5C) 1-segmented with 4 elements: 2 lateral and 2 apical; proximalmost lateral one pinnate. Endopodite segment with normal complement (3 lateral and 6 apical setae/spines) and spinules along margin.

Mandible (not illustrated) with 2-segmented palp. Proximal one with 1 outer and 1 medial setae, distal segment rectangular, bearing 3 apical setae.

Maxillule and maxilla (not illustrated): see description of *M. cristata*. Maxilliped (Fig. 5B) with comb-like syncoxal medial seta, armed with long setules along inner margin. Basis with noticeable row of medially directed spinules along inner margin. Claw indistinctly articulating on basal segment and serrate in distal half. Accessorial seta present, nearly half as long as claw.

Legs 1-4 with large coupler with deep distal crescent groove. Praecoxa large and robust. Outer element on basis either spiniform (legs 1 and 2) or setiform (legs 3 and 4). Medial element

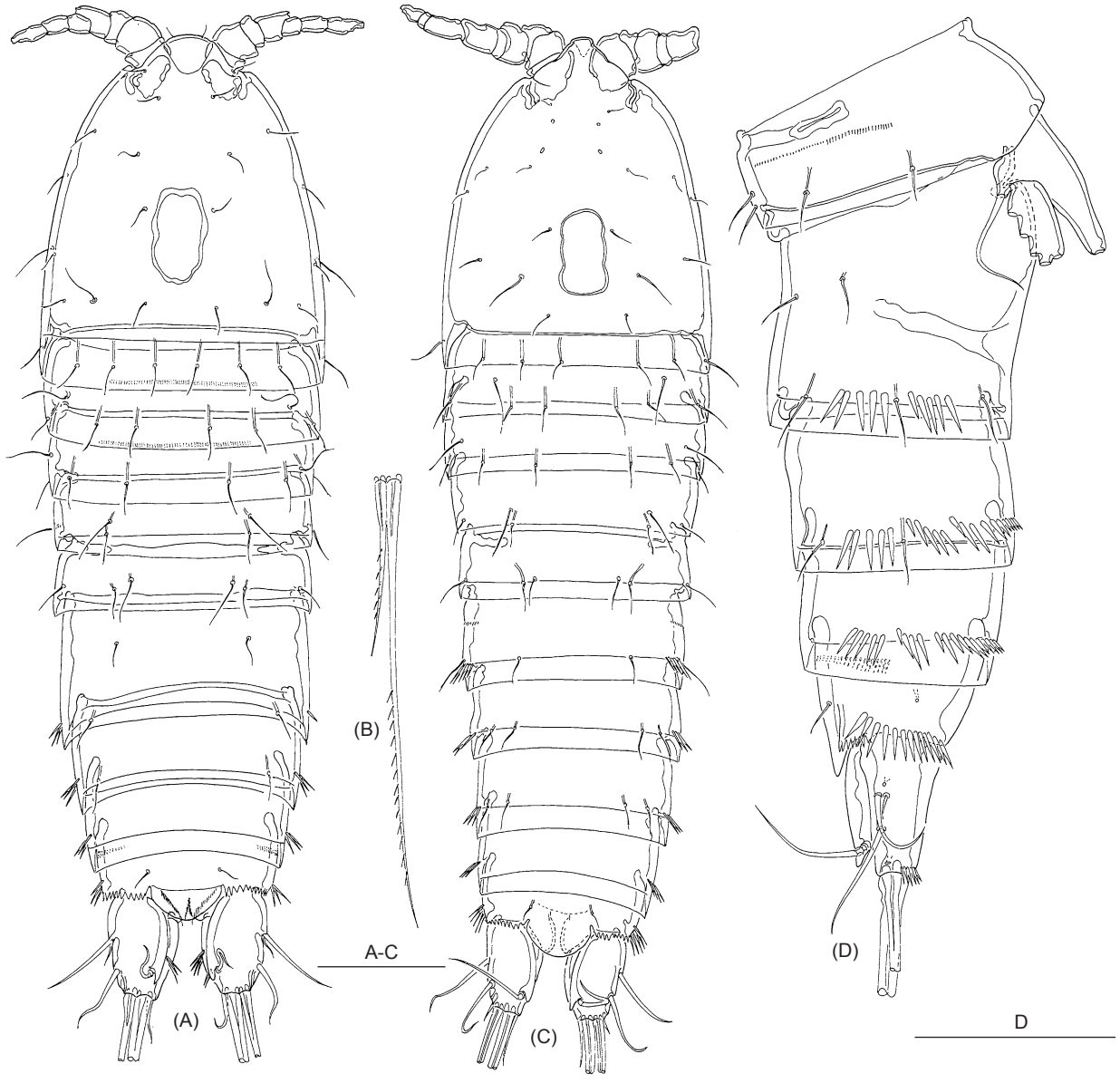

Fig. 4. *Moraria laurentica* Willey1927, female (A, B, D), male (C) (all from South Orange, NJ). (A) Habitus, dorsal view; (B) principal terminal seta of caudal rami, (C) habitus, dorsal view; (D) urosome, lateral view. Scale bars: A-C = 50 μm, D = 50 μm.

on leg 1 basis spiniform and serrate along outer margin only. Exopodites 3-segmented, endopodites 2-segmented. Endopodite of leg 1 (Fig. 6A) shorter than exopodite. Proximal segment twice as long as distal one. Medial element on proximal segment and proximalmost medial element on 2nd segment pectinate, the latter longer than entire endopodite. Outer subdistal spine on 2nd segment as long as endopodite, serrate. Endopodite segments of legs 2-4 (Fig. 6B-D) of equal size, armed with robust spinules along outer margin. Medial element on proximal (in legs 2-4), and on distal segment (in legs 3 and 4), and medial element on terminal

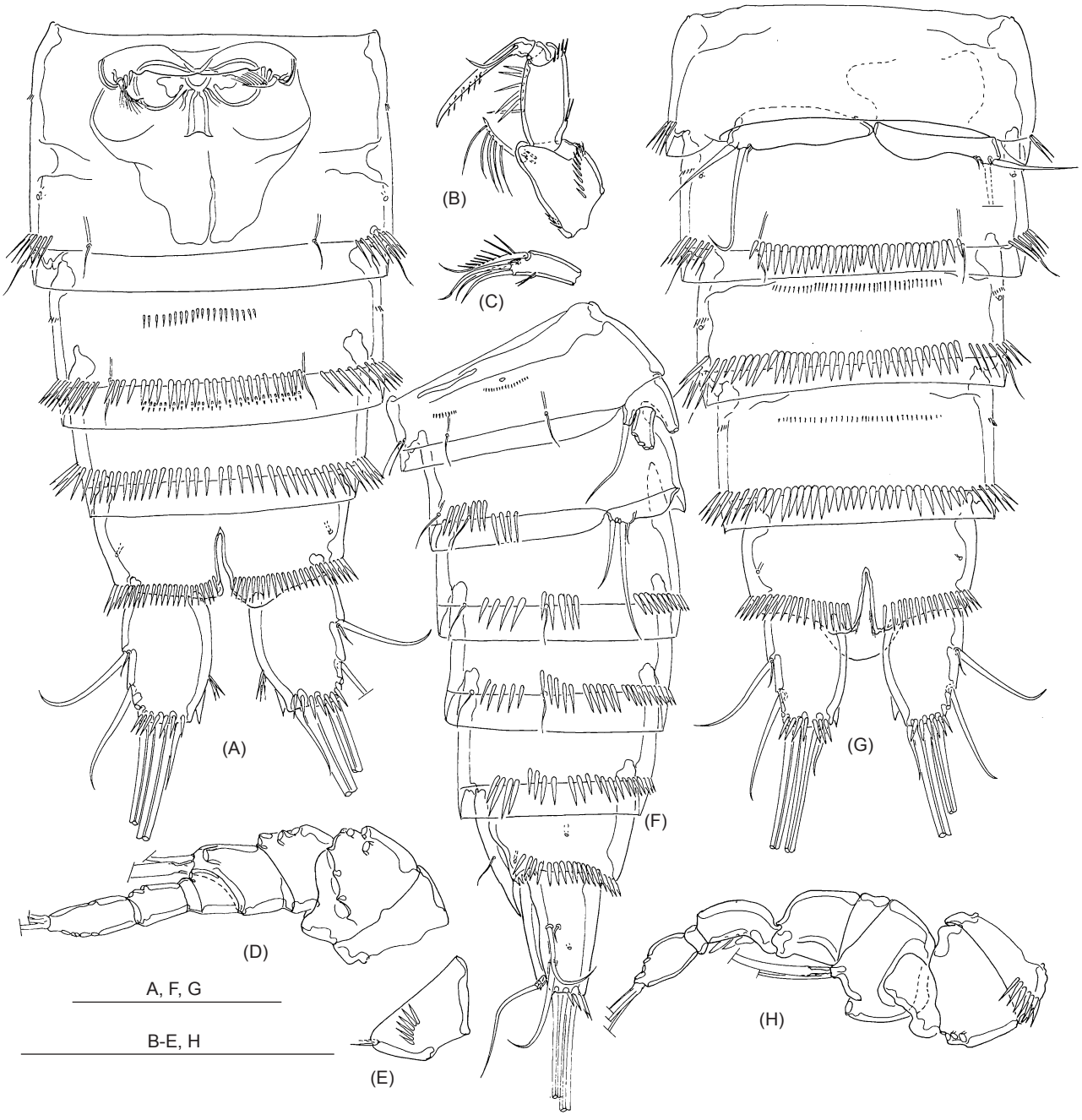

Fig. 5. *Moraria laurentica* Willey 1927, female (A-E), male (F-H) (all from South Orange, NJ). (A) Abdomen, ventral view; (B) maxilliped; (C) antennary exopodite; (D) antennule contour, ventral view; E, 1st antennulary segment, dorsal view; F, urosome, lateral; G, abdomen, ventral view; (H) antennule contour, dorsal view. Scale bars: A, F, G = 50 μm, B-E and H = 50 μm.

Fig. 6. *Moraria laurentica* Willey 1927, female (A-F), male (G-J) (all specimens from South Orange, NJ). (A) Leg 1, frontal vies; (B) leg 2, caudal view; (C) leg 3 endopodite, frontal view; (D) leg 4, caudal view; (E) leg 5, caudal view; (F) aberrant terminal exopodite segment of leg 3, frontal view; (G) leg 2 endopodite, caudal view; (H) leg 3 endopodite, frontal view; (I) leg 5, frontal view; (J) pair of leg 4 endopodites, frontal view. Scale bar = 50 μm.

exopodite segment of leg 4 pectinate. Leg armament distribution as follows:

	EXO	END
P1	I.0-I.0-II.2.0	0.1-I.1.2
P2	I.0-I.0-II.2.0	0.1-I.2.0
P3	I.0-I.0-II.2.0	0.1-I.2.1
P4	I.0-I.0-II.2.1	0.1-I.2.1

Leg 5 (Fig. 6E) prominent, with semicircular exopodite and large endopodal lobe, both with setiform armament, except for 2 pectinate elements along medial margin of baseoendopodite. Exopodite not extending beyond distal border of endopodal lobe. Coupler rectangular. Endopodal lobe with 6 (normal situation) or 5 setae (less 1 pectinate element on medial side). Exopodite with 5 setae. All setae either sparsely pinnate or smooth. Exopodite devoid of ornamentation. Baseoendopodite with 2 large spinules near apex and 1 along outer margin of endopodal lobe, near insertion of proximalmost seta.

Leg 6 (Fig. 5A) with 3 elements. Outer one long and densely pinnate along outer margin, middle and medial ones minute with hyaline appearance. Valve smooth. Genital complex with moderately long copulatory tube and large ovate seminal receptacles.

Description of male: Body (Fig. 4C) as in female, except somites 2 and 3 separate and urosome narrower. Body length 330-340 μm (*n* = 2). Anal somite and operculum as in female. Caudal rami without spinular cluster on medial surface.

Antennule (Fig. 5H) 9-segmented, chirocer with spinule comb on segment 1 and aesthetasc (partially broken) on segments 4 and 9.

Mouthparts, leg 1, and protopodites and exopodites of legs 2-4 as in female.

Leg 2 endopodite (Fig. 6G) 2-segmented with 2 large spinules and a pectinate element on proximal segment. Distal segment narrow, shorter than proximal segment, bearing 2 apical, sparsely pinnate, setae. Proximal segment of leg 3 endopodite (Fig. 6H) as in female. Distal segment with 2 confluent elements and 1 articulating seta. Medialmost element with tooth in distal half. Seta robust, extending far beyond confluent elements, and serrate along distal third of outer margin. Leg 4 endopodite (Fig. 6J) 2-segmented with pectinate medial element on proximal segment. Distal segment with 2 robust spines along outer border, a corkscrew-shaped distal structure, and 4 elements along medial border: distalmost one filiform; proximal pair minuscule, visible only by perforation of integument; subdistal one long and well developed, serrate along outer margin only.

Leg 5 (Fig. 6I) with semi-quadrate exopodite and moderately expanded endopodal lobe, the former extending beyond the latter. Exopodite with 5 setae, baseoendopodite with 2 endopodal spines. Distal margin of endopodal lobe with triangular expansion between apical spines.

Leg 6 (Fig. 5G) with 3 setiform elements: middle one longest, medial one dwarfed and filiform. Operational valve (left one) wider than opposite, non-operational one and slightly expanded medially. Surface of valves smooth.

Variability

Willey (1927) mentioned the occurrence of "round markings" on the rostrum which are assumed herein to refer to the refractile points in the integument (which are not restricted to the rostrum) and not illustrated here.

Instead of a single spinular comb on the inner surface of the caudal rami, females possess 2 combs on each ramus (Fig. 7A) or are asymmetrical with 2 rows on the right ramus and a single comb on left one (Fig. 7B, C). Aberrations from the normal morphology observed included (1) a female leg 5 setal armament with 5 instead of 6 endopodite elements (Fig. 6E) and (2) a terminal exopodite segment of leg 3 lacking one of the outer spines (Fig. 6F).

***Moraria affinis* Chappuis 1927**

(Figs. 8-11)

Moraria affinis n. sp. - Chappuis 1927: 310-312, figs. 16-20.

Moraria affinis Chappuis 1927 - Chappuis 1928: 125 [key]; Chappuis 1929a: 58 [key]; Chappuis 1929c: 485, 504 [key]; Lang 1948: 1032-1033, 1047, fig. 418(3) [key]; Wilson 1956a: 297; Wilson and Yeatman 1959: 836, fig. 28.181 [key]; Dussart & Defaye 1990: 134; Reid and Lesko 2003: 11, table 1; Wells 2007: 45, 312 [key]; Reid and Williamson 2010: 896 [key].

Moraria (s. str.) *affinis* Chappuis 1927 - Borutzky 1952 (1964): 322 (297), 330 (305)-331 (307), figs. 91(6-10) [key].

non *Moraria affinis* Chappuis 1927 - Damian-Georgescu 1970: 201-202, fig. 94a-f [*species inquirenda*].

Type locality: Public park at Pelham-Bay, NY, USA.

Material observed: from "South Orange, N.J. 15.IV.25": 2 ♀♀ and 2 ♂♂ dissected and several females and males examined on temporary mounts, spirit-preserved afterwards.

Description of female: Body fusiform with discrete major body articulation (Fig. 8A, B). Prosome and urosome of equal lengths. Metasome parallel-sided. Genital double-somite cylindrical, wider than long (L: W of 1: 3) with ventrolateral internal remnants of ancestral division (Fig. 9A). Body length 405-415 μm (*n* = 3). Structure of integument of cephalothorax, pedigers, and urosomites with refractile points. Dorsal integumental window on cephalothorax keyhole-shaped, with delicate border, centrally located. Pedigers 2 and 3 each with lateral

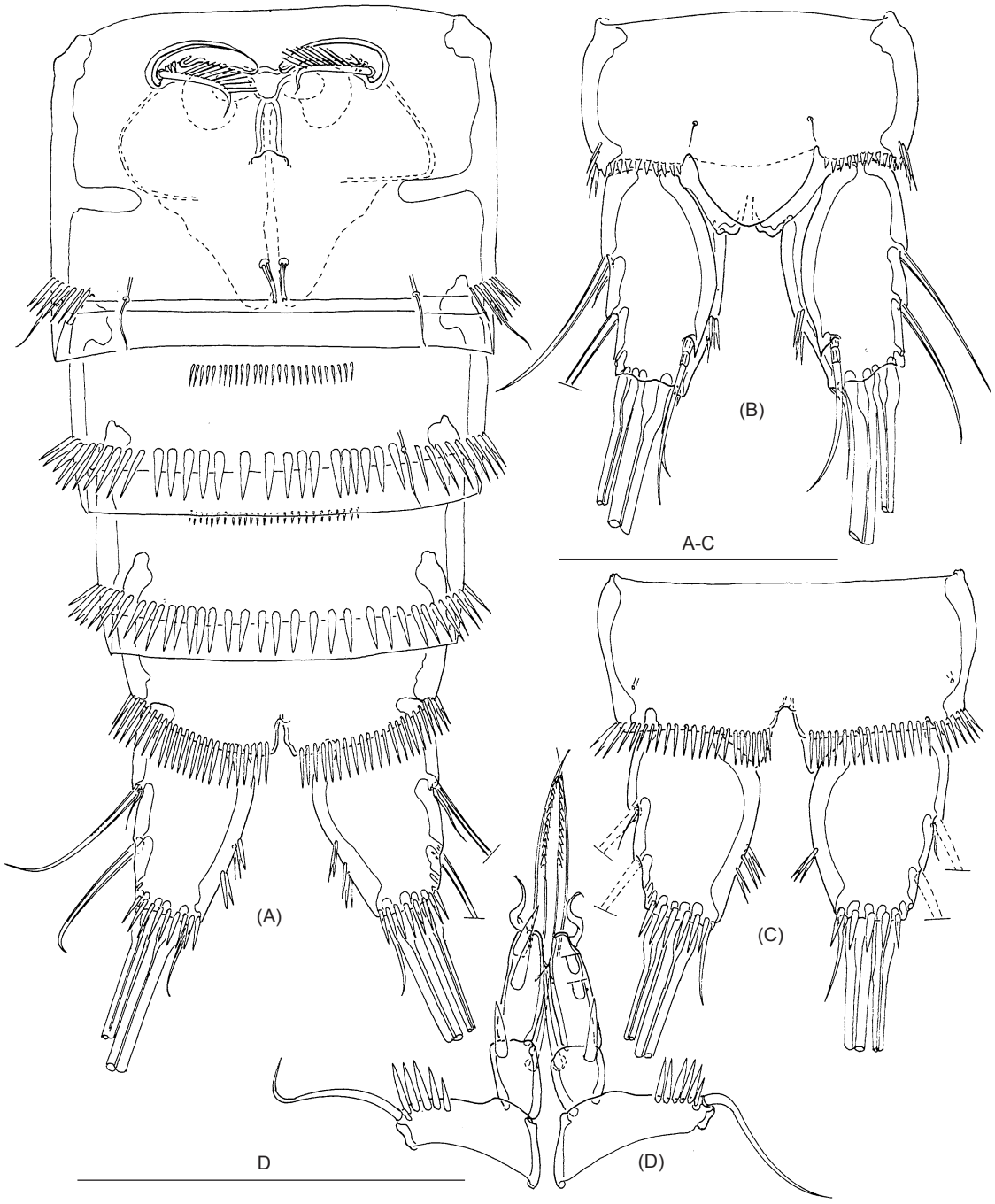

Fig. 7. *Moraria laurentica* Willey 1927, female (A-C), male (D) (A, B, female from Floyd Co., VA; C, female from South Orange, NJ; D, male from Floyd Co.). (A) Abdomen, ventral view; (B) anal somite and caudal rami, dorsal view; (C) idem, ventral view; (D), pair of leg 4 basis and endopodites. Scale bars: A-C = 50 μm, D = 50 μm.

ovate integumental window. Posterior margins of all somites straight. Cephalothorax without ornamentation, pedigers 2-4 with anterolateral row(s) of minute spinules. Pediger 5 with a short comb of long, slender spinules laterally (Fig. 8B). Genital double-somite with short row of minute spinules in anterior half of ventral surface on either side of genital field, urosomites 4 and 5 with a complete anteroventral row. Posteroventral margin of genital double-somite and urosomites 4 and 5 with an uninterrupted row of long spinules (Fig. 9A).

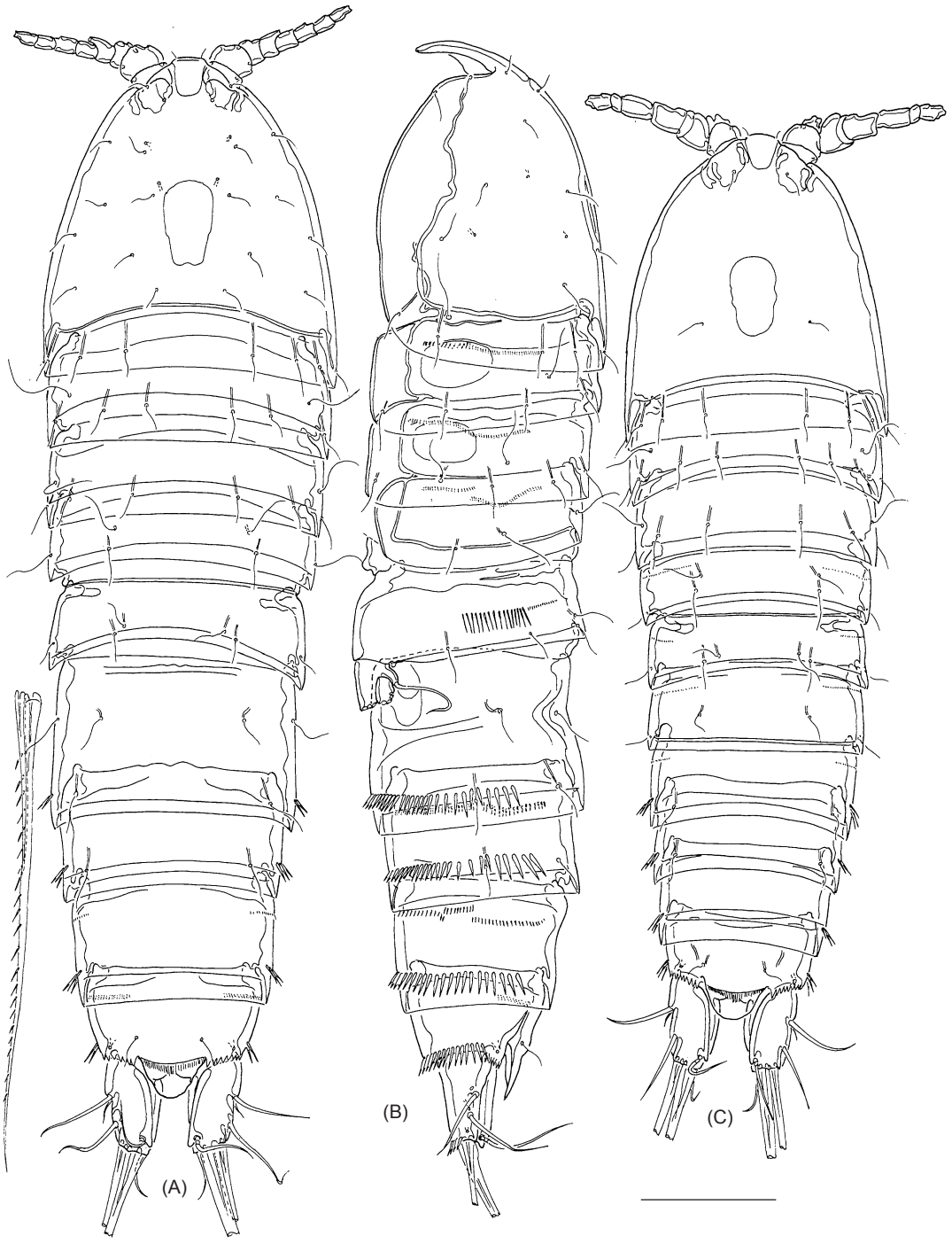

Fig. 8. *Moraria affinis* Chappuis 1927, female (A-B), male (C) (all specimens from South Orange, NJ). (A) Habitus, dorsal view; (B) idem, lateral view; (C) habitus, dorsal view. Scale bar = 50 μm.

Anal somite with prominent and rounded operculum. The latter rather thin and transparent allowing observation of spinular ornamentation along anal sinus (Fig. 8A). Posterodorsal margin of segment bordered with triangular hyaline teeth. Posterolateral and posteroventral margins with an uninterrupted row of spinules. Caudal rami about twice as long as wide, tapering distally. Dorsal crest near and parallel to medial border and extending caudally from insertion of dorsal seta, with blunt tip. Anterolateral and distolateral setae of equal length. Accessorial lateral seta present.

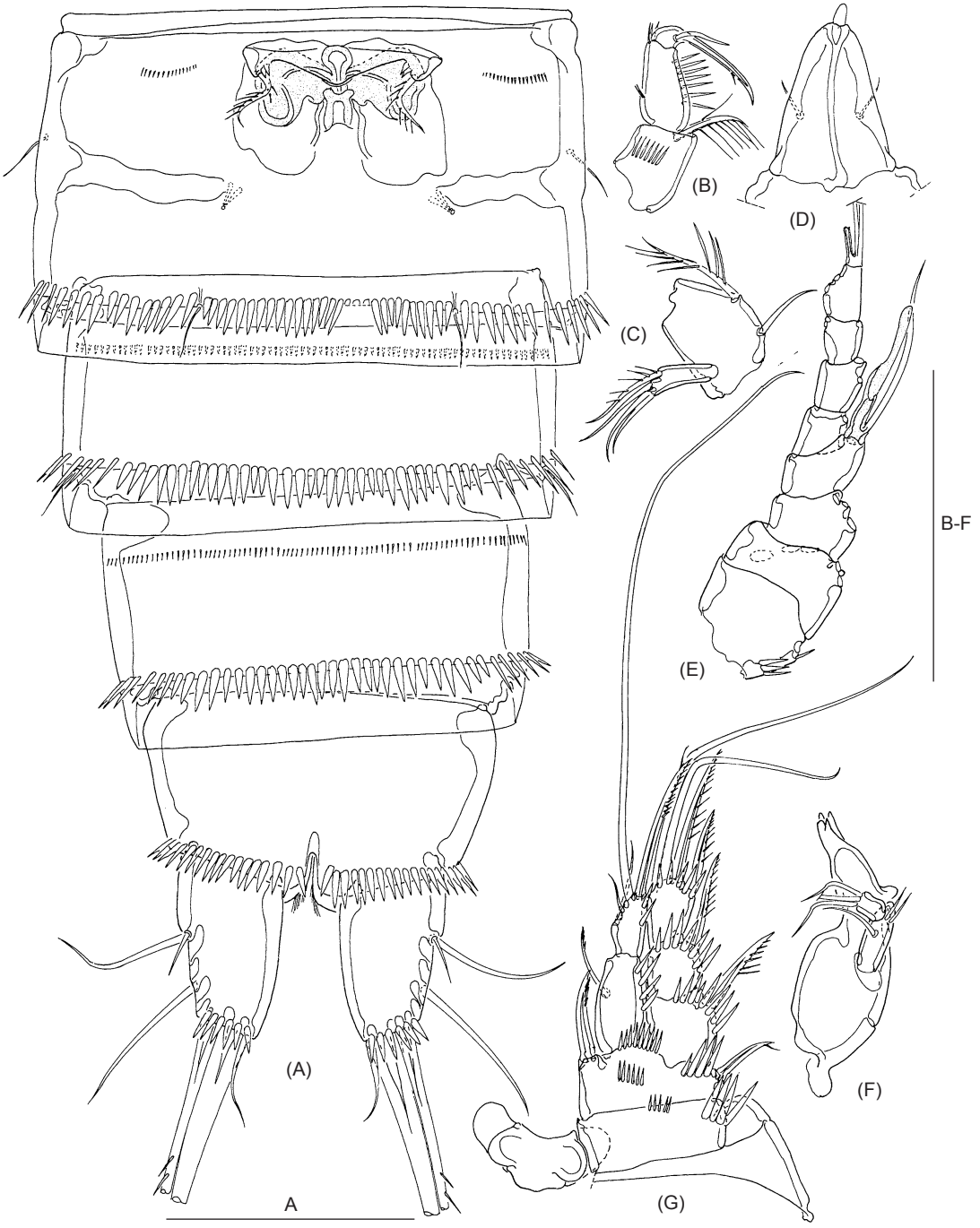

Fig. 9. *Moraria affinis* Chappuis 1927, female (A-E, G), male (F) (all specimens from South Orange, NJ). (A) Abdomen, ventral view; (B) maxilliped; (C) antennary allobasis and exopodite; (D) rostrum, ventral view; (E) antennule, contour and aesthetascs (terminal one broken); (F) mandible; (G) leg 1, frontal. Scale bar = 50 μm.

Principal terminal elements without breaking plane, not particularly modified at basis; outer one 1.5-times longer than ramus. Medial terminal element short. Rami lacking ornamentation except for a posteroventral spinular row (Fig. 9A).

Rostrum (Fig. 9D) large, triangular, with rounded apex and hyaline structure at apex. One pair of sensillae. Integument structure with refractile points.

Antennule (Fig. 9E) 8-segmented with spinular comb along frontal margin and single tooth near insertion of distal seta on 1st segment. Antennulary complement as in *M. cristata* (see above: terminal segments 7 and 8 separated, with 2 and 7+ Aesth, respectively). Principal aesthetasc linguiform with distinct expansion in proximal half, fused with accompanying seta at base, and not extending beyond terminal segment. Terminal aesthetasc tubular (broken in examined specimens), fused with 2 setae at base.

Antenna (Fig. 9C) with distinct exopodite bearing 4 elements: 2 apical and 2 lateral ones. Proximalmost seta pinnate. Allobasis with 2 abexopodal setae: proximal one smooth, distally pinnate. Single endopodite segment with 2 spines and 1 seta laterally, with 3 spines, 2 geniculated setae, and 1 slender seta distally. Spinular ornamentation present along both sides of endo-

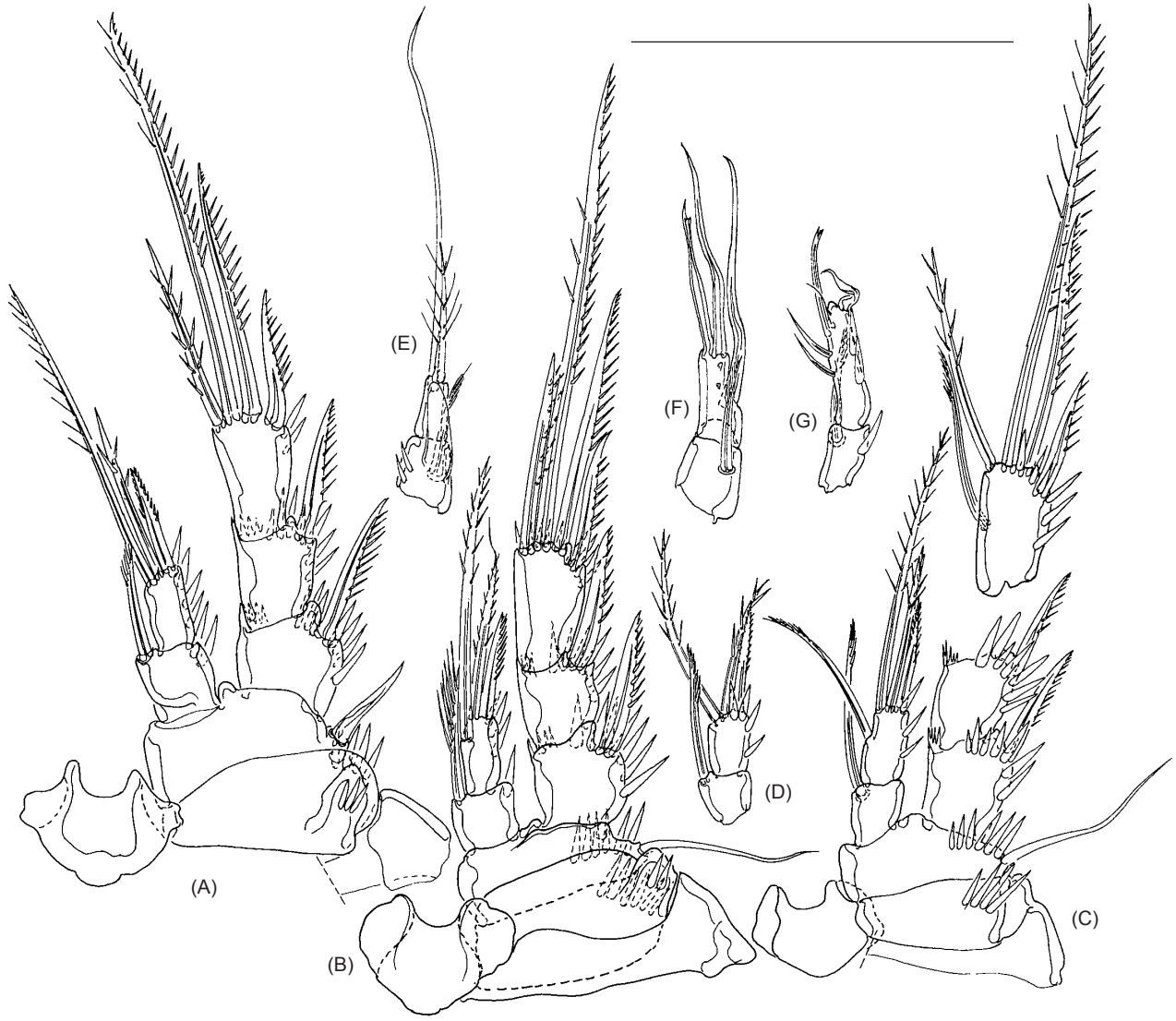

Fig. 10. *Moraria affinis* Chappuis 1927, female (A-D), male (E-G) (all specimens from South Orange, NJ). (A) Leg 2, caudal view; (B) leg 3, caudal view; (C) leg 4, frontal view (terminal exopodite segment detached); (D) leg 4 endopodite with normal complement, frontal view; (E) leg 2 endopodite, lateral/frontal view; (F) leg 3 endopodite, caudal view; (G) leg 4 endopodite, frontal view. Scale bar = 50 μm.

podite segment.

Mandible (Fig. 9F) with 2-segmented palp bearing 1 outer seta and 2 medial spinules on basal segment, 3 setae on distal segment. Maxillule, maxilla, and maxilliped (not illustrated) each with basic shape as described for *M. cristata* (see above).

Legs 1-4 with wide, smooth, intercoxal sclerite with deeply invaginated distal border. Praecoxa rigid and prominent. Basis of leg 1 with long medial spine (± 3/4-times 1st endopodite segment length). Outer element on basis of legs 1 and 2

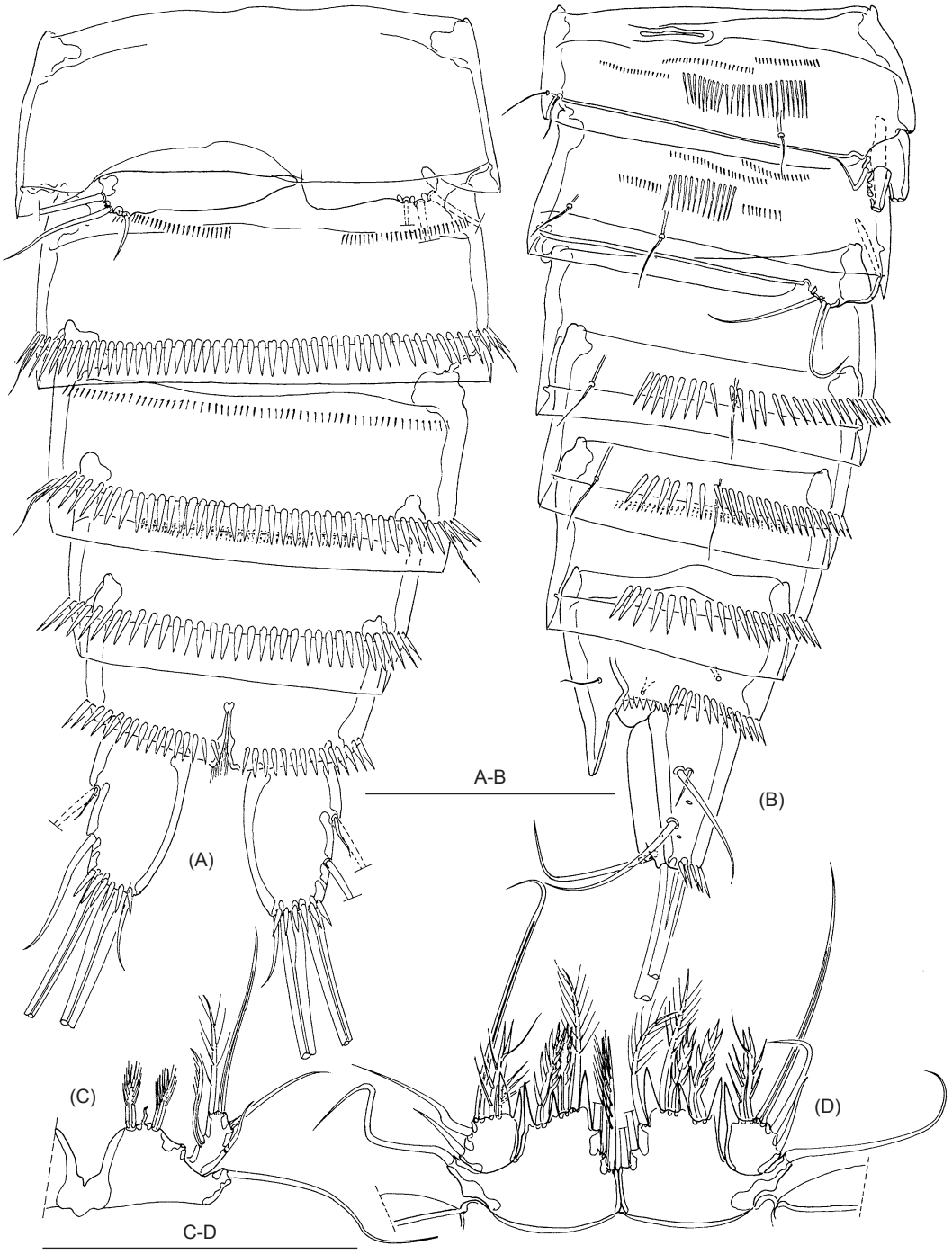

Fig. 11. *Moraria affinis* Chappuis 1927, female (D), male (A-C) (all specimens from South Orange, NJ). (A) Abdomen, ventral view; (B) urosome, lateral view; (C) leg 5, caudal view; (D) leg 5, frontal view. Scale bars: A-B = 50 μm; C-D = 50 μm.

spiniform, of legs 3 and 4 setiform. Exopodites 3-segmented, endopodites 2-segmented.

Leg 1 (Fig. 9G) endopodite slightly shorter than exopodite, with proximal segment twice as long as distal one. Proximal segment with medial pectinate element and spinular armament along outer margin. Medial elements on distal segment short, as long as segment. Outer terminal spine as long as entire endopodite. Endopodites of legs 2-4 (Fig. 10A-D) with proximal and distal segments of equal lengths. Each proximal segment with pectinate medial element. Outer margin of endopodite segments with spinular armament, except for proximal segment of leg 4. Medial element on distal segment of leg 4 exopodite pectinate. Leg armature distribution as follows:

	EXO	END
P1	I.0-I.0-II.2.0	0.1-I.1.2
P2	I.0-I.0-II.2.0	0.1-I.2.0
P3	I.0-I.0-II.2.0	0.1-I.2.0
P4	I.0-I.0-II.2.1	0.1-I.2.0/1

Leg 5 (Fig. 11D) compact, with 4 elements on exopodite, 6 on endopodal lobe of baseoendopodite. Exopodite quadrangular to semicircular, not extending beyond endopodal lobe of baseoendopodite. Mediodistal corner of exopodite extended in 1 or 2 sharp, obvious processes. Distal margin of endopodal lobe with 3 sharp, distinct extensions; one located at outer and inner corners and one between outermost and next to outermost setae. Medial element on exopodite robust, with bifid and flagellated tip. Both outermost elements of endopodal lobe robust, spiniform, and both medialmost elements pectinate. Surface of rami smooth, coupler absent (?) or minute.

Leg 6 (Fig. 9A) with 3 elements on narrow, concave valve. Outer seta well developed and pinnate along 1 side. Middle and median elements dwared, with hyaline appearance. Genital complex with copulatory tube orifice in anterior half of double-somite, leading to large ovate seminal receptacles.

Description of male: Habitus as in female, except for individual urosomites 2 and 3. Length 340-350 μm. Urosomites 1-5 and anal somite (Fig. 11B) adorned as in female, with an additional lateral comb of long spinules between several rows of short spinules on urosomite 2 (leg 6 bearing somite).

Antennule broken, so not observed in detail.

Legs 1-4 with protopodites and exopodites as in female. Leg 2 endopodite (Fig. 10E) with pectinate inner element and subdistal prominent large spine-shaped process on outer margin, reaching distal margin of distal segment. The latter narrow, slightly longer than wide, bearing 2 apical setae. Leg 3 endopodite (Fig. 10F) 2-segmented with inner pectinate (caudal) element and crescentic distal margin (frontal). Distal segment typically modified with 3 smooth elements: median elements (lateral and distal ones) articulating and lanceolate, outer bifid terminal one confluent with segment. Medial margin with 2 dwarfed structures (pores or remnant seta) between lateral element and distal corner. Leg 4 endopodite (Fig. 10G) 2-segmented. Proximal segment with medial pectinate element and single spinule near distal outer corner. Medial margin of distal segment with 4 setae: 2 short (proximal ones), 1 long and bifid element, and 1 filiform seta (subdistal one). Distal border of segment with corkscrew-shaped hyaline structure. Outer margin of segment with 2 spinules in distal half.

Leg 5 (Fig. 11C) with narrow rectangular exopodite, bearing 5 setae, and extending beyond distal margin of endopodal expansion. Medialmost exopodite element pectinate. Endopodal lobe with 2 apical, equally sized spines. Distalmost pore orifice with hyaline tubular extension. Surface of rami smooth. Opposite legs confluent medially.

Leg 6 (Fig. 11A) with crescentic operational (right) leg, wider and larger than non-operational one; the latter concave. Each valve with 3 elements: outer one longest, middle one 1/2 as long, and medial one shortest but well-developed. Valves smooth.

Variability. Leg 4 with an additional medial pectinate element on distal endopodite segment on both sides (Fig. 10C).

DISCUSSION

In a recent update, Reid and Lesko (2003) listed 8 different *Moraria* species for the North American continent. Besides the introduction of a new member from the Laurentian Great Lakes district, *M. hudsoni* Reid and Lesko 2003, considerable range extensions for certain species previously reported from the North American continent were included. The principal diagnostic characteristics were summarized and tabulated in order to facilitate identification.

Many earlier descriptions only highlighted

the most obvious diagnostic characteristics of the species introduced in order to differentiate them from their congeners. Structural details which are now considered important in species identification or may turn out in the future to be highly diagnostic were left unnoted and remain to be documented. In the absence of such information, misidentifications can readily occur as was demonstrated by Reid and Lesko (2003), who recalled their initial confusion when studying the presence of *M. mrazeki* T. Scott 1903, *M. laurentica* Willey 1927, and *M. hudsoni* Reid & Lesko 2003 in samples from the Laurentian Lake District. The redescriptions presented here based on material examined by Chappuis are an attempt to complete the picture on each species. Each of them has been subsequently reported from other localities, but the identifications were very rarely substantiated. Identification keys, in whatever form, are only tools providing guidance to identify specimens under study. Unless there is the possibility to compare the identification against a detailed description, the outcome will remain, up to a certain degree, subject to doubt. The redescriptions of the 3 *Moraria* species should be seen within this context.

The original description of *M. cristata* was based on an unspecified number of female specimens collected in Donnaldson Cave, IN. Details of the male morphology from which specimens were found in a moss sample obtained near Columbus, OH were subsequently added (Chappuis 1931). Text and illustrations dealing with the female morphology are completely identical in both contributions. However, the Ohio females differ in some aspects from the original description of *M. cristata*. Examination of the sole female specimen found in the vial labeled "Donnaldson Cave" confirms the discrepancies.

The most apparent differences between the animals from the 2 localities are the anal operculum and caudal ramus and its armament. Specimens in both localities have a prominent crescentic anal operculum. The extension, however, rather differs. In the Donnaldson Cave specimen, the proximal border of the operculum does not extend beyond the anal sinus. In contrast, the Columbus specimens invariably posses an operculum which is distinctly more expanded caudally and extends well beyond the caudal margins of the somite and completely covers the anal sinus.

Second, the caudal rami of the Donnaldson Cave female are slimmer in appearance (with an L: W ratio of 2.4: 1) than those of Columbus specimens (with an L: W ratio of 2: 1). The shape of the rami in the Donnaldson Cave female coincides completely with the illustration in the original description (Chappuis 1929a: fig. 16) but contrasts with the text stating that the rami are only twice as long as wide. A comparable discrepancy is seen in the outer terminal seta of the rami. In the remaining Donnaldson Cave specimens, the seta is only as long as the caudal ramus (as stated by Chappuis (1929a) but incompletely illustrated) but is considerably longer (nearly twice the length of the ramus) in the Columbus specimens. Specimens reported from the Great Lakes resemble the Columbus specimens in each of these aspects (see Lesko et al. 2003).

Other differences observed are the body shape (slender and cylindrical in the Donnaldson Cave specimen but compact and depressed in Columbus specimens), the absence of a lateral spinule cluster near the posteroventral corner of the female genital double-somite in the Donnaldson Cave specimen (present in Columbus specimens), and the dorsal integumental window (large and wide in Donnaldson Cave but narrow in Columbus specimens). Unfortunately, several structural details of the remaining female from Donnaldson Cave are either hidden by dirt or seem to be broken off, but the spinule ornamentation along the urosomal posteroventral margins appears to be more-robust and less-dense than in the Ohio specimens.

Whether these differences have a particular taxonomical value or are just expressions of the morphologic variability of the species collected in 2 different habitats (cave vs. wet moss) has to be clarified. The "produced anal operculum" considered to be a differential feature for *M. cristata* in Reid and Lesko (2003: table 1) may be confusing, as this is the case for the Columbus population (and those from the Great Lakes) but not in the female from Donnaldson Cave, the type locality. The unique combination of the serrate nature of the urosomal membrane and the presence of spinules on the medial surface of the caudal rami (in both genders) is a sound indication of a close affinity. However, additional specimens, including males, from Donnaldson Cave have to be analyzed in order to establish the taxonomic importance of the anal operculum structure and caudal rami and its armature.

Willey (1927) refrained from introducing the name of the species described from the Laurentian Mountains in a formal way. The name *M. laurentica* appeared only in the captions of the

text figures. The introduction of a new species is extractable from the text and specifically from the notation (Willey 1927: p. 11): "The types of this species …. They bear the numbers 59850 (female holotype) and 59851 (male paratype) in the United States National Museum." The "junior form" described (Willey 1927: 9-11, figs. 22-30) is the description of an adult female member of the genus *Epactophanes* Mrázek 1894) (according to Gurney 1932: *Epactophanes richardi* Mrázek 1894). Lang (1948) misspelled the specific epithet as "*laurentiaca*" followed only by Wells (2007: 45, 312-315).

Moraria americana and *M. laurentica* Willey 1927 were almost simultaneously introduced but soon turned out to largely coincide. *Moraria laurentica* received priority by precedence. At first, *M. americana* was attributed a subspecific rank (Chappuis 1929a, Carter 1944, Wilson 1956a) but is nowadays perceived as a junior synonym of *M. laurentica* (Lang 1948, Wilson and Yeatman 1959, Reid and Lesko 2003, Wells 2007). Apart from its type locality (Laurentian Mountains near Quebec, Canada) and New Jersey (with *M. americana*), the species has only been found in 2 additional places: near New York (Strayer 1989) and in Huron Lake (Hudson et al. 1998).

Moraria americana and *M. laurentica* are similar in almost every aspect which justifies the assumption that they are conspecific. However, the New Jersey specimens (*M. americana*) differ from *M. laurentica* in the appearance of the leg 5 of both males and females. In the specimen(s) featured in the original description of *M. americana*, and in specimens examined here, the leg 5 exopodite is invariably a semicircular article (curiously described as "long-ovate" although illustrated as being semicircular). The leg 5 described for *M. laurentica* clearly differs in having a rather-narrow appearance with a long-ovate exopodite (at least twice as long as wide). The male leg 5 exopodite shows equal differences: square in the New Jersey specimens and rectangular in the Laurentian ones. The prolonged aspect of the female leg 5 exopodite was assumed to be a consequence of the oblique position of the appendage during observation (Lang 1948: 1030). Whether this difference has systematic value has to be confirmed with observations on additional material.

Moraria laurentica resembles *M. mrazeki* Scott 1903 in many aspects, and both are unique among the other members of the genus by the spinular ornamentation on the medial surface of the caudal rami being present in females but absent in males. Chappuis (1927) overlooked the spines on the rami in his description of the species (see discussion of *M. affinis*, below), and recently, Reid and Lesko (2003: table 1) omitted to remark on the dimorphic aspect of the caudal rami armature of *M. mrazeki*. *Moraria laurentica* is mainly distinguishable from *M. mrazeki* by the much-larger anal operculum, which is distinctly expanded beyond the caudal margin of the anal sinus (in *M. mrazeki* the operculum does not cover the anal area) and the armature of the endopodites of legs 2-4 which is 3.4.4 in *M. laurentica* and 3.3.4 in *M. mrazeki*. However, specimens of *M. mrazeki* with different armature numbers on both sides were reported (3 or 4 in leg 3 and/or leg 4 in Gurney 1932). The absence of a spinular adornment along the medial margin of the female leg 5 exopodite in *M. laurentica*, the number of armature elements on the distal endopodite segment of leg 1 (4 in *M. laurentica* and 3 in *M. mrazeki*), and the reduced aspect, or near absence, of the proximal elements on the endopodite of the male's leg 4 (slender but clearly present in *M. mrazeki*) are additional discriminating characteristics.

The distributional ranges of both species overlap with a significant larger number of records for *M. mrazeki* on the North American continent (i.e. Canada, Alaska, Greenland and in the US from Michigan, North Carolina, and Colorado: Reid and Lesko 2003 and references therein). The sole illustrated record of *M. mrazeki* on the North American continent is from Alaska (Wilson and Yeatman 1959). In Europe, *M. mrazeki* is reported to cohabit with other *Moraria* species (pers. observ.) which is assumed to occur in North America as well.

Gurney (1932) found 2 types of female leg 5 exopodites in *M. mrazeki*: a semi-rectangular form (approximately twice as long as wide) and a compact ovate or "narrow" one (approximately 1.4-times longer than wide). The exopodite in both morphs reaches the distal margin of the inner lobe of leg 5. Apparently, leg 5 in *M. laurentica* females displays similar variability. It is possible that Willey (1927) intermixed both species in his description, as *M. mrazeki* often co-occurs with other *Moraria* species. However, that seems improbable, since he clearly addressed the absence of spinular ornamentation along the median margin of the leg 5 exopodite in *M. laurentica*.

The presence of 2 different species, *M. americana* (= *M. laurentica*) and *M. affinis*, in the South Orange sample (= West Orange, NJ)

passed unnoticed by Chappuis (1927). *Moraria affinis* was only known to Chappuis from a wet moss sample obtained in Pelham Park located along the northern shores of Long Island Sound, NY. The original description is rather brief, but *M. affinis* is distinguished by the particularly compact female leg 5 and armature of endopodites of legs 2-4.

It seems reasonable to assume that Chappuis unintentionally intermixed specimens of *M. affinis* and "*M. americana*" in the course of his examination of the New Jersey sample. According to Chappuis (1927), the spinule adornment along the posteroventral margin of the urosomites (called "abdominal segments") and the morphology of the caudal rami are identical in the 2 species. However, ornamentation of the urosomites and caudal rami significantly differ. Leaving aside the unnoted presence of a midlateral spinular comb on the leg 5 pediger in both sexes and on the leg 6 pediger of the male, the urosome of *M. affinis* is distinctly more hirsute than that of "*M. americana*". *Moraria affinis* possesses an uninterrupted spinular posteroventral margin of the genital double-somite in the female and on the 3rd urosomite of the male. In "*M. americana*", only the posteroventral edges of the genital double somite are furnished with a cluster of spinules, whereas the midventral region is devoid of ornamentation. In males of "*M. americana*", there is a distinct lateroventral interruption of the posteroventral spinule row on the 3rd urosomite. In addition, *M. affinis* possesses an anterior row of spinules on the ventral surface of the urosomites which spans the entire width instead of being limited medially as in "*M. americana*".

The female caudal rami of *M. affinis* lack a medial spinular cluster and coincide as such with the description by Chappuis of the caudal rami of "*M. americana*". This feature and the contradictory description of urosomal spinular ornament support the assumption that certain parts of the description of "*M. americana*" (body, caudal rami, and urosomal ornament) in fact refer to the cohabiting *M. affinis*.

Most important is Chappuis' interpretation of the female leg 5 morphology, since this appendage is a key feature for identification purposes (Lang 1948, Wells 2007). The general aspect of the leg as initially depicted is correct: a compact baseoendopodite with a semicircular exopodite. However, the presence of 7 armature elements on the medial lobe of the baseoendopodite and of 5 elements on the exopodite is erroneous since the triangular extension of the distal edge of the baseoendopodite and of the medial edge of the exopodite are counted as armature elements. The cornute aspect of the rami and their armament was correctly depicted for Alaskan specimens by Wilson and Yeatman (1959). However, the diagnosis summarized in Lang (1948) should be amended accordingly and the key (KG 47 in Wells 2007) corrected with 6: 4 in the second column instead of 6: 5.

The assumption that *M. laurentica* and *M. affinis* are closely related species cannot be subscribed to. Although both are unquestionably members of the "*Moraria*" lineage as currently accepted, they do not share a common ancestry. Detailed analysis within a phylogenetic context is impossible at this point as too many species ascribed to the genus are insufficiently known to perform a sound evaluation of their characters. However, based on the general shape of the leg 5 of females, *M. laurentica* is obviously related to a lineage including *M. mrazeki*, whereas the roots of *M. affinis* are embedded in a lineage including, among others, *M. varica* (Graeter 1911), *M. stankovitchi* (Chappuis 1924), and *M. fontinalis* Flössner 1970.

Moraria affinis is now known from Alaska (Wilson 1956b), Lake Huron in the Great Lake District (Hudson et al. 1998), New York (Chappuis 1927, Strayer 1989), New Jersey (present contribution), and south-central Virginia (Reid and Lesko 2003). The occurrence of *M. affinis* in tap water in Bucharest (Romania) as reported by Damian-Georgescu (1970) has to be referred to with caution. Re-identification of the specimen(?) featured in Damian-Georgescu's description was not possible. Although the ventral spinule pattern of the urosomal somites and the leg 2-4 armament resemble the North American species, *M. affinis* sensu Damian-Georgescu cannot be considered conspecific with *M. affinis* Chappuis. The absence of the manifestly cornute aspect of leg 5 and the armament of its exopodite clearly differ. The Bucharest specimen appears to be closer to *M. stankovitchi* and *M. varica*, but differs from both by the female leg 5 armature with 5 elements on the exopodite and 6 on the inner lobe (4 exopodite elements in both other species, 5 on the inner lobe of *M. stankovitchi* and 6 in *M. varica*). In the absence of the original specimens and additional material from Bucharest, *M. affinis* sensu Damian-Georgescu 1970 should be treated as a doubtful identification.

Supplementary morphological data extracted

from the materials studied by Chappuis allow certain adjustments in the diagnostic table compiled by Reid and Lesko (2003). In the table included herein, the terminology is slightly adapted (as explained in the caption of the table), and the information on spinule ornamentation of the urosomites is subdivided with data on the genital double-somite and succeeding somites presented separately.

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