ONTOGENY OF AN ANCHIALINE OSTRACOD FROM WESTERN AUSTRALIA AND COMMENTS ON THE ORIGIN AND DISTRIBUTION OF HALOCYPRIDIDAE

BY

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ABSTRACT

Juvenile instars II, IV, and V of the anchialine halocyprid ostracod *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000 (Thaumatocyprididae) are described and illustrated. In addition, a supplementary description of the adult male is presented. Specimens had been collected in Bundera Sinkhole, the type locality of the species in Western Australia. Also, juvenile instars I and II of the deep-sea species *Thaumatoconcha radiata* Kornicker & Sohn, 1976, which is in the same family as members of the genus *Danielopolina*, are described and illustrated. It is tentatively concluded that during its ontogeny, *D. kornickeri* has 6 growth stages; morphological characters useful in identifying the stage and sex of juveniles of *D. kornickeri* are presented. Finally, the hypothesis is proposed for an anchialine cave ancestor to the present-day planktonic Halocyprididae, now widely spread in the oceans.

RÉSUMÉ

Les stades juvéniles II, IV et V de l'ostracode anchihalin de la famille des Halocyprididae, *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000 sont décrits et illustrés. Une description complémentaire du mâle adulte est également présentée. Les spécimens ont été collectés à Bundera Sinkhole, la localité-type de l'espèce en Australie occidentale. De même, les stades

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juvéniles I et II de l'espèce d'eaux profondes *Thaumatoconcha radiata* Kornicker & Sohn, 1976, taxon attribué à la même famille comme membres du genre *Danielopolina* sont décrits et illustrés. La conclusion provisoire est que, au cours de son ontogénie, *D. kornickeri* montre 6 stades de croissance; les caractères morphologiques utiles pour l'identification du stade et du sexe des stades juvéniles de *D. kornickeri* sont présentés. Enfin, l'hypothèse d'un ancêtre vivant dans des grottes anchihalines est proposée pour les Halocyprididae, aujourd'hui planctoniques et largement répandus dans les océans.

INTRODUCTION

Danielopol, Baltanas & Humphreys (2000) described a new species, *Danielopolina kornickeri* from Bundera Sinkhole in Western Australia. It was the first species of the genus reported from an anchialine cave in the Southern Hemisphere and the Indo-west Pacific region. The present collection from the type locality of *D. kornickeri* contains juveniles as well as adults, thus presenting the opportunity to investigate the ontogeny of the species. Also included is an illustrated supplementary description of the adult male.

The anchialine fauna of Bundera Sinkhole includes the genera *Sphaerosyllis* (Syllidae), *Prionospio* (Spionidae), *Lasionectes* (Remipedia), *Liagoceradocus* (Hadziidae), *Stygiocaris* (Atyidae), *Bunderia* (Epacteriscidae), *Stygocyclopia* (Pseudocyclopiidae), *Speleophria* (Speleophriidae), and *Milyeringa* (Eleotridae). Fuller details and context are provided by Humphreys (1999), Wilson & Humphreys (2001), and Page et al. (2008).

When identifying species, or describing a new species, it is important to identify the sex and age of specimens under study, because the morphologies generally differ with sex and age. Unfortunately, collections of specimens of *Danielopolina* in anchialine caves generally contain relatively few specimens; e.g., not all instars are in the present collection of *D. kornickeri* from Bundera Sinkhole. Based on the morphology of the appendages, the senior author estimates that *D. kornickeri* has 6 instars, and that the juveniles in the collection are instars II, IV, and V, and that instars I and III were not yet collected (see Appendix).

In order to elucidate morphological changes in the mandible of early instars of species in the family Thaumatocyprididae, instars I and II of the deep-sea *Thaumatoconcha radiata* Kornicker & Sohn, 1976 were examined, and supplementary descriptions of these are presented.

Finally, we will propose our view on the possible origin of the planktonic Halocyprididae. This latter family is represented by oceanic ostracods, the origin of which could be found in anchialine lineages, such as representatives of the subfamily Spelaeoeciinae Kornicker, Iliffe & Harrison-Nelson, 2007. Our discussion on this topic is aimed, firstly, to raise the potential of subterranean fauna for elucidation of evolutionary and/or biogeographic aspects of present-day animal groups, and, secondly, to stimulate ostracodologists to concentrate their research interest on the phylogenetic reconstructions of the Halocyprida, and to include in their data sets taxa from both oceanic and anchialine habitats.

MATERIAL AND METHODS

Samples were collected by divers using a plankton net (Lots BES 9160, BES 9161) or a slurp gun (Lot 4292), and the ostracods were then preserved in 75% alcohol. The specimens were collected from 20-30 m depth in the marine part of the anchialine system with water salinity ∼ 35 psu, temperature ∼ 26°C, and dissolved oxygen less than 0.5 mg l^{-1}. Physico-chemical profiles were provided in Humphreys (1999) and Seymour et al. (2007), and microbiological profiles in the latter work. Collecting methods are also described in Danielopol et al. (2000). Specimens were transferred to 25% alcohol for air transport to the Smithsonian.

In order to preserve the specimens in close to their original condition only 2 specimens (specimens M and W) were dissected and mounted in glycerine on a glass slide and sealed. The remaining specimens were examined in a drop of glycerine. Some of these were partly dissected, and appendages along with the body and valves put in the same vial.

USNM, National Museum of Natural History, Washington, D.C.; WAM, Western Australian Museum, Perth. Capital letters have been used to identify described specimens in the text and Appendix. The WAM numbers assigned to the capital letters are given in the “Material” paragraph in the section on “Systematics”. Specimen L was lost after it was described and, therefore, was not assigned a WAM number.

KEY TO INSTARS OF *D. KORNICKERI*

1 – Basis of mandible with 4 teeth[1]) .... Instar I
– Basis of mandible with 5 teeth........ 2

2 – 6th limb without bristles, or absent[2]) .... Instar II
– 6th limb with bristles[2]) 3

3 – 6th limb does not extend posteriorly past 5th limb, and 7th limb absent[3]) .... Instar III
– 6th limb extends posteriorly past 5th limb; 7th limb present........ 4-7

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[1]) The presence of 4 teeth is a prediction based on other species, because no instar I of *D. kornickeri* is known.

[2]) Note: If present, the 6th limb on instar II may be obscured and overlooked because of the small size of the bare lobe.

[3]) These characters are predictions based on other species, because no instar III of *D. kornickeri* is known.

4 – Furca with 6 claws .... Instar IV
5 – Furca with 7 claws .... Instar V
6 – Furca with 8 claws .... Instar VI (adult)

IDENTIFICATION OF SEX OF SPECIMENS OF *D. KORNICKERI* DESCRIBED HEREIN

1. Female genitalia are obscure and have not been used herein for identifying females. On the other hand, two-lobed copulatory organs are quite visible on male instars IV and V as well as the adults, and the presence of the organ was used to identify specimen B (instar IV) as a male. The male copulatory organ was not observed on other juvenile instars. The absence of copulatory organs on specimen M (instar IV), and specimens N and F (instar V) was used to identify them as females.
2. The first antenna of the adult female differs from that of the adult male in having no bristles on the 4th article compared to 2 on the adult male. Specimen B (instar IV), which was identified as a male on the basis of having a copulatory organ, has 1 ventral bristle on the 4th article; whereas specimen M (instar IV), which is without a copulatory organ, has no ventral bristles on the 4th article. This supported the identification of specimen M as a female. No other juveniles in the collection have bristles on the 4th article.
3. The 3rd article of the endopod of the 2nd antenna bears a hook in the adult male (specimen A) and a small node with 1 short bristle in the adult female. A hook is present only in the adult male, and a single bristle is present only in the adult female.
4. A node with 2 short bristles is present on both male instar IV (specimen B) and female instar IV (specimen M). The 2 bristles are shorter than the length of the node in the male, and longer than the node in the female. Also, the node in the instar IV male (fig. 6C) is much larger than that on the instar IV female (fig. 8G). This suggests that the size of the node and the relative lengths of the terminal bristles may be useful for identifying the sex of juveniles.
5. The sexes of specimens W and L (instars II), were not determined.

CLASSIFICATION OF HALOCYPRIDA MAINLY CONFINED TO ANCHIALINE CAVES

Order HALOCYPRIDA
  Suborder HALOCYPRIDINA
    Superfamily HALOCYPRIDOIDEA
      Family HALOCYPRIDIDAE (open ocean)
      Family DEEVEYIDAE (anchialine)
        Subfamily DEEVEYINAE
          Genus *Deeveya*
        Subfamily SPELAEOECIINAE

Genus *Spelaeoecia*
Superfamily THAUMATOCYPRIDOIDEA
Family THAUMATOCYPRIDIDAE
Genus *Danielopolina*
Subgenus *Danielopolina* (anchialine and deep ocean)
Subgenus *Humphreysella* (anchialine)
Genus *Thaumatocypris* (open ocean)
Genus *Thaumatoconcha* (open ocean)

SYSTEMATICS

Class OSTRACODA
Subclass MYODOCOPA
Order HALOCYPRIDA
Suborder HALOCYPRIDINA
Superfamily THAUMATOCYPRIDOIDEA
Family THAUMATOCYPRIDIDAE

Genus *Danielopolina* Kornicker & Sohn, 1976

Type species. — *Danielopolina carolynae* Kornicker & Sohn, 1976.

Composition. — This genus contains two subgenera: *Danielopolina* and *Humphreysella*.

Subgenus *Danielopolina* Kornicker & Sohn, 1976

Type species. — *Danielopolina carolynae* Kornicker & Sohn, 1976.

Composition and distribution. — *D.* (*D.*) *carolynae* Kornicker & Sohn, 1976, South Atlantic deep sea; *D.* (*D.*) *kornickeri* Danielopol, Baltanas & Humphreys, 2000, Australia; *D.* (*D.*) *phalanx* Kornicker & Iliffe, 1995, Canary Islands; and *D.* (*D.*) *mexicana* Kornicker & Iliffe, 1989, Mexico.

Diagnosis. — Protopod of 2nd antenna with posterior bristle. The bristle not present in early juveniles of some species, but present in instar II of *D. kornickeri*.

KEY TO ADULTS OF SPECIES IN SUBGENUS *DANIELOPOLINA*

1 – Carapace longer than 1.5 mm . . . . . *D. carolynae*
– Carapace shorter than 1.0 mm 2

2 – Endopod of 2nd antenna with 4 bristles on 1st article . . . . . *D. kornickeri*
– Endopod of 2nd antenna with fewer than 4 bristles on 1st article 3

3 – Carapace with posterior process on valves . . . . . *D. mexicana*
– Carapace without posterior process on valves . . . . . *D. phalanx*

Danielopolina kornickeri Danielopol, Baltanas & Humphreys, 2000 (figs. 1-11)

Danielopolina kornickeri Danielopol, Baltanas & Humphreys, 2000: 3-8, figs. 2, 3.
Not *Danielopolina* sp. cf. *D.* (*D.*) *kornickeri* — Humphreys & Danielopol, 2006: 1340. — Kornicker et al., 2006: 83-84, figs. 2-4.

Holotype. — Dissected adult female (WAM C24366). Carapace destroyed.

Type locality. — Bundera Sinkhole (Karst index C-28), Cape Range peninsula, Western Australia (22°25′S 113°46′E), in saline water, 7 August 1993 (date corrected by W. F. Humphreys in litt., 2009). (See Yager & Humphreys, 1996; Danielopol et al., 2000: 8; for details about location of the cave.)

Material. — Bundera Sinkhole (Karst index C-28). Lot BES 9160, 29 April 2002, deep plankton net trawl by divers: WAM C 40320, spm. M, dissected instar IV female on slide; WAM C 40321, 5 undissected adults in ethanol (2 males, 1 female, 2 ?females); WAM C 40322, spm. A, dissected adult male in ethanol. Lot BES 9161, 29 April 2002, deep plankton net trawl by divers at sediment: WAM C 40323, spm. B, undissected instar IV male in ethanol; WAM C 40324, spm. W, instar II on slide; WAM C 40325, spm. N, undissected instar V female in ethanol; WAM C 40326, spm. F, undissected instar V female in ethanol; WAM C 40327, 1 adult male and 2 late juveniles in ethanol; spm. L, instar II (specimen lost after initial description). Lot BES 4292, 26 May 1995, slurp gun in remipede area: WAM C 40328, 5 adults (probably females) in ethanol; WAM C 40329, spm. Y, undissected adult male in ethanol; WAM C 40330, spm. Z. undissected adult male in ethanol.

Descriptions. — Adult male, instar VI, WAM 40322, spm. A (most appendages drawn while attached to body). Carapace an elongate oval in lateral view, with upper and lower anterior processes (fig. 1A). Dorsal margin linear; ventral and posterior margins convex; upper and lower anterior processes each terminating in single prong. Surface with numerous reticulations.

Carapace size (mm). WAM C 40322, spm. A: length of separated left valve including upper anterior process 0.78; length without upper anterior process 0.71; height 0.47; height as percent of length with anterior process excluded 66%; height as percent of length with anterior process included 60%. Additional specimens: WAM C 40329, spm. Y: length including upper anterior process 0.81; length without upper anterior process 0.75; height 0.55; height as percent of length with upper process excluded 82%; with upper process included 80%. WAM C 40330, spm. Z: length including upper anterior process 0.85; length without anterior process 0.71; height 0.50. Range of length excluding anterior process 0.71-0.75.

Central adductor muscle attachments (fig. 1A). Consisting of about 7 wedge-shaped scars.

First antenna (fig. 1B). Article 1 with 2 bristles (1 lateral, 1 dorsal); article 2 with 2 bristles (1 ventral, 1 dorsal). Articles 3 and 4 fused; article 3 with ventral spines; article 4 with 2 terminal ventral bristles (1 long, 1 shorter). Article 5 with 3 terminal ventral bristles (outer bristle long, ringed, with 3 hook-like filaments near tip (fig. 1B); adjacent bristle thinner and filament-like; inner bristle shorter); article 6 bare; article 7 with short dorsal a-bristle and long ventral b- and c-bristles. Article 8 with long d-, e-, and f-bristles.

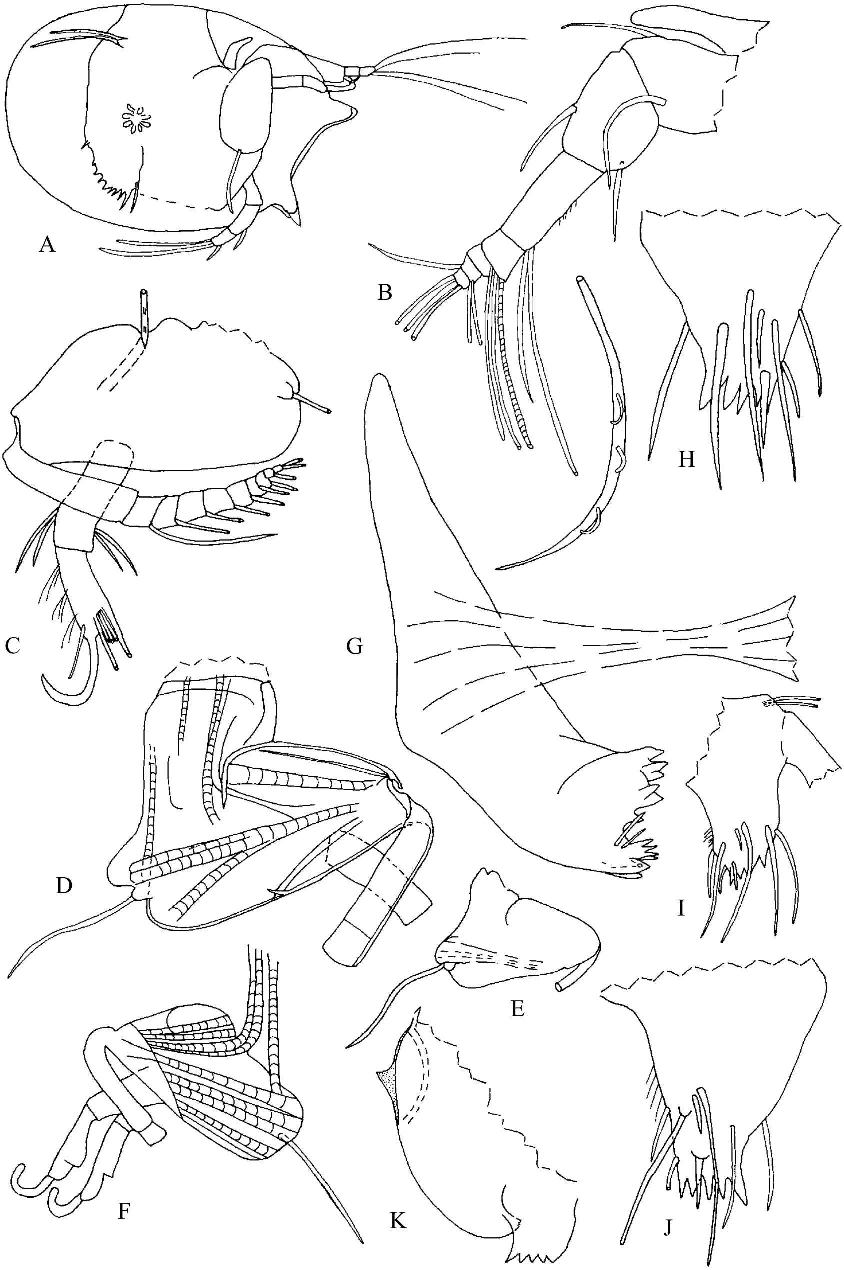

Fig. 1. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. A, C40322, adult male: A, complete specimen from right side, length 0.71 mm; B, left 1st antenna, lv; C, left 2nd antenna, lv; D, part right 2nd antenna, lv; E, part left 2nd antenna, mv; F, part left 2nd antenna, lv, and endopod right limb, mv; G, coxa of right mandible and muscle connecting it to left mandible, av; H, distal part of basis of right mandible, lv; I, basis left mandible, lv; J, distal part of basis of right mandible, lv; K, anterior of body showing location of distal teeth of basis of mandible, from left side. av, anterior view; lv, lateral view; mv, medial view.

Second antenna (fig. 1C–F). Protopod with long bristle on posterior margin. Endopod with 3 articles (articles 2 and 3 fused); article 1 with 4 marginal bristles (2 ventral, 2 dorsal); article 2 with long dorsal spines and 5 lateral bristles (4 long near ventral edge, 1 short near dorsal edge); article 3 short, with long hook-like process with forked tip. Exopod with 9 articles; article 1 divided into long proximal and short distal parts (distal part with bristle not reaching 9th article); articles 2 to 8 with long ventral bristle with indistinct distal marginal hairs; article 9 small and with 2 terminal bristles.

Mandible (figs. 1G–K, 2A, B). Coxa with proximal and distal sets of teeth separated by space containing small triangular process; proximal set of teeth consisting of row of teeth; distal set of teeth (ip) consisting of 2 rows of teeth; 1 slender bristle (ap) adjacent to anterior set of distal teeth. Basis: medial side near distal dorsal corner with 2 bristles; distal lateral surface with 6 bristles; anterior margin with 1 long bristle; posterior margin with 2 short bristles (distal of these with tubular tip); ventral edge of basis with 5 triangular teeth. Endopod: article 1 with lateral spines and long anterior bristle near midlength; article 2 with 2 anterior bristles, 1 distal posterior bristle, 3 medial bristles near posterior margin, and spines on anterior margin; 3rd article with long terminal claw-like bristle, 1 bristle of medium length, and 5 short bristles.

Maxilla (fig. 2C, D). Endite I with 2 proximal and about 8 terminal bristles; endites II and III each with about 6 obscured bristles. Dorsal margin of coxa with long bristle. Basis: with terminal medial exopodal bristle on ventral margin. Endopod: article 1 with 6 bristles: 3 bristles on anterior margin, 2 bristles on posterior margin, and 1 short distal medial bristle; article 2 with terminal bare claw without rings or basal suture and 5 bristles.

Fifth limb (fig. 2E). Epipod with long bristles forming 3 groups, each with 4 or 5 bristles. Precoxa and coxa with 13 bristles and small triangular tooth. Basis with indentation on ventral margin and article broader in proximal part (proximal half with 3 bristles; distal half with 2 or 3 bristles). Exopod represented by long bare terminal bristle on dorsal margin of basis. Endopod with 2 articles: article 1 with 2 ventral bristles near midlength; article 2 with 3 terminal bristles (1 long, 2 short).

Sixth limb (fig. 2F). Epipod with long hirsute bristles forming 3 groups: middle group with 4 bristles, proximal and distal groups with 5 bristles. Precoxa and coxa fused; precoxa with 2 ventral bristles; coxa with 3 ventral bristles. Basis not separated from coxa by suture and with 4 ventral bristles (2 at midlength, 2 terminal). Exopod lobe small with 2 long terminal bristles (outer bristle stouter and longer than inner bristle). Endopod: articles 1 and 2 fused, with 2 ventral bristles at midlength; article 3 with 3 bristles (1 long terminal and 2 short ventral).

Seventh limb (fig. 2H). Elongate lobe with 2 terminal bristles.

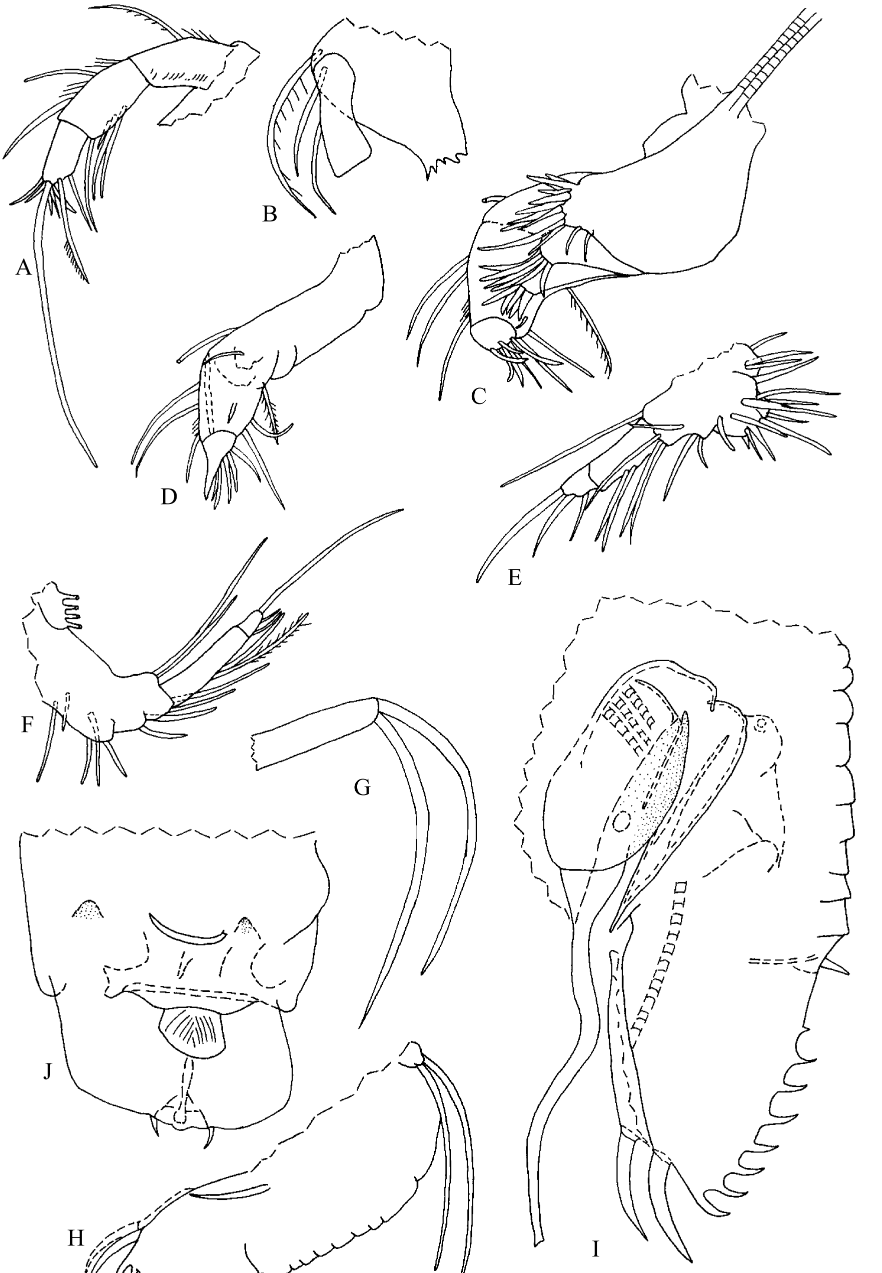

Fig. 2. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. A, C40322, adult male: A, endopod right mandible, mv; B, dorsal bristles of basis of left mandible, lv; C, right maxilla, mv; D, left maxilla, lv; E, left 5th limb, mv; F, right 6th limb, lv; G, 7th limb; H, posterior of body from left side showing 7th limb, furca, unpaired bristle, and posterior article; I, posterior of body from left side showing copulatory organ; J, upper lip. lv, lateral view; mv, medial view.

Furca (fig. 2H). Each lamella with 1 long articulated anterior claw, 1 shorter unarticulated claw on anteroventral corner, and 6 smaller unarticulated claws followed by smaller undeveloped unarticulated triangular claw on ventral margin (triangular claw not present on all specimens). Bare, pointed, unpaired process present on posterior of body following lamellae.

Bellonci Organ (fig. 1B). Elongate with rounded tip.

Lips (fig. 2J). Upper lip with 2 small ventral teeth.

Anterior of body (fig. 1K).With anterior triangular process on each side dorsal to upper lip.

Copulatory organ (fig. 2I). Organ on left side of body medial to left 5th and 6th limbs. Anterior branch with long slender tubular process; posterior branch tapered and less than half length of anterior branch.

Posterior of body (fig. 2H). Segmented.

Instar V female, WAM C 40325, spm. N. Carapace represented by small, nonreticulated, anterior fragment with 1 bare process.

Carapace size (mm). Unknown.

Central adductor muscle attachments. Part of valve bearing muscle attachments missing.

First antenna (fig. 3A, B). Article 1 with 1 dorsal and 1 lateral bristle. Article 2 with 1 dorsal bristle. Articles 3 and 4 fused and without bristles; article 4 with ventral spines. Articles 5 and 6 fused; article 5 with 2 long terminal ventral bristles; article 6 bare. Article 7 with short dorsal a-bristle and long ventral b- and c-bristles. Article 8 with long d-, e-, and f-bristles.

Second antenna (fig. 3C-E). Protopod with long bristle on posterior margin of each limb. Endopod with 3 articles; article 1 with 4 short bristles (2 ventral, 2 dorsal); articles 2 and 3 fused; article 2 with 4 bristles (3 long ventral, 1 short dorsal), and dorsal spines; article 3 forming a small dorsal process with 2 short terminal bristles longer than process forming article 3. Exopod with 9 articles; article 1 with minute distal indentation on dorsal margin and 1 short terminal bristle; articles 2 to 8 with long bristles (marginal hairs not observed); article 9 small with 2 terminal bristles.

Mandible (figs. 3F, G, 4A). Coxa with 1 proximal row and 2 distal rows of teeth. Proximal and distal sets of teeth separated by space containing small triangular process. Lateral bristle adjacent to distal sets of teeth. Basis: medial surface near dorsal margin with 2 long bristles near anterior corner; lateral surface of left limb with 4 bristles (2 long, 2 short); lateral surface of right limb with 6 bristles (3 long, 3 short); posterior margin with 2 short bristles (distal short bristle with tubular tip); anterior margin with 1 bristle at midlength; ventral edge of basis with 5 triangular teeth. Endopod: article 1 with 1 dorsal bristle; article 2 with 2 anterior bristles

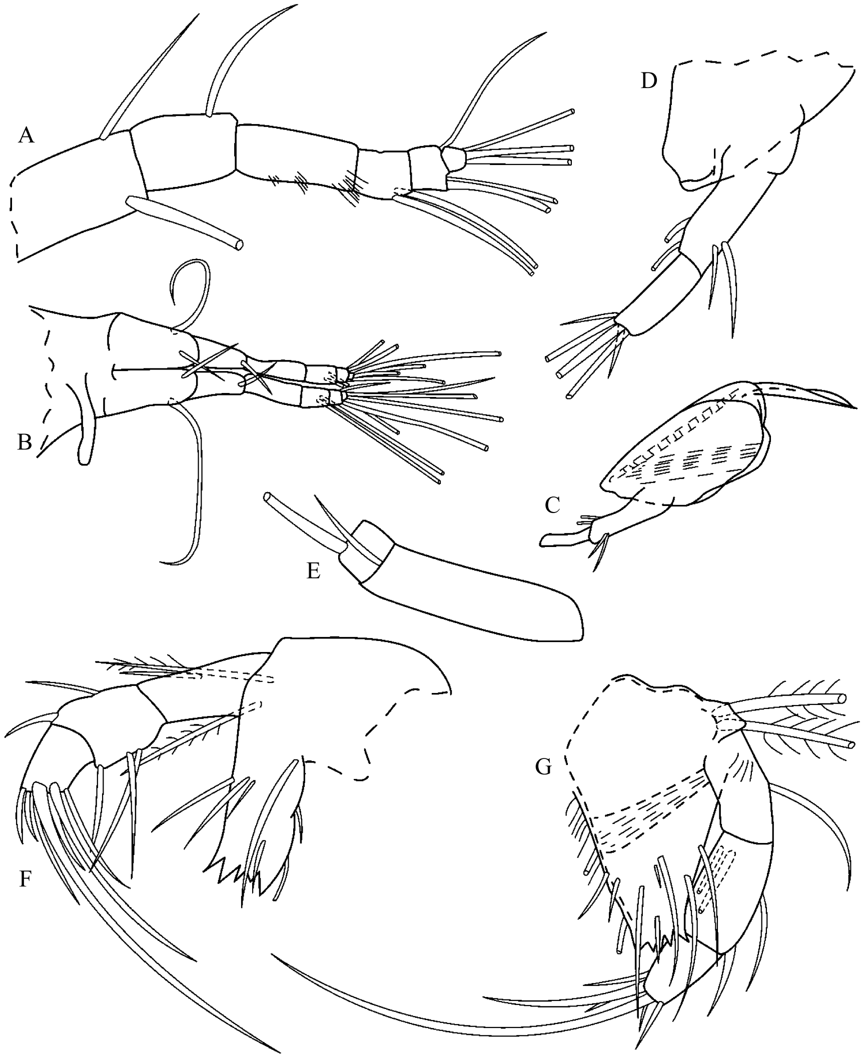

Fig. 3. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. N, C40325, instar V female: A, right 1st antenna, lv; B, 1st antennae and Bellonci Organ, dv (drawn on body). Left 2nd antenna: C, protopod, endopod (nabs), and posterior sclerite on protopod (long posterior bristle broken off), mv; D, protopod and endopod, mv; E, articles 1 and 2 of exopod, mv. Mandible: F, left limb (drawn on body), lv; G, right limb, lv. dv, dorsal view; lv, lateral view; mv, medial view; nabs, not all bristles shown.

and 3 posterior bristles; 3rd article with long terminal claw-like bristle, 1 medium length bristle, and 5 short bristles.

Maxilla (fig. 4A, B). Precoxa endite I bristles obscured. Coxa: endites II and III bristles obscured. Dorsal margin of coxa with long bristle. Basis: with terminal exopodial bristle on ventral margin. Endopod: article 1 with 3 bristles on anterior

Fig. 4. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. N, C40325, instar V female: A, anterior of body showing left mandible and maxilla and marginal teeth of basis of right mandible (nabs) vv; B, left maxilla (endites not shown), lv (drawn on body); C, distal left 5th and 6th limbs (nabs) vv (drawn on body); D, left 5th limb, lv (drawn on body); E, distal right 6th limb (drawn on body, nabs) vv; F, right 7th limb; G, left 7th limb and furca, drawn on body, ventral-left view; H, posterior of body from left side showing left 7th limb, part of left lamella of furca, lv; I, left lamella of furca, lv. lv, lateral view; nabs, not all bristles shown; vv, ventral view.

margin and 2 bristles on posterior margin; article 2 with terminal bare claw without rings or basal suture and 4 bristles.

Fifth limb (fig. 4C, D). Epipod with long bristles forming 3 groups, each with about 4 bristles. Precoxa with about 5 bristles; coxa with about 5 bristles and triangular process. Basis with about 7 bristles. Exopod represented by long bare terminal bristle on dorsal margin of basis. Endopod with 2 articles: article 1 with 1 dorsal and 2 ventral bristles near midlength; article 2 with 1 long and 2 shorter bristles.

Sixth limb (fig. 4C, E). Extends past 5th limb. Epipod with long hirsute bristles forming 3 groups, each with 5 bristles. Precoxa and coxa fused (precoxa with 1 ventral bristle, coxa with 2). Basis not separated from coxa by suture and with 4 ventral bristles (2 at midlength, 2 terminal). Exopod lobe small with 2 long terminal bristles. Endopod: articles 1 and 2 fused, with 2 ventral bristles at midlength; article 3 with 3 bristles (1 long terminal and 2 short ventral).

Seventh limb (fig. 4F–H). With 2 long terminal bristles.

Furca (fig. 4G–I). Each lamella with 1 long articulated anterior claw, 1 shorter unarticulated claw on anteroventral corner, and 5 smaller unarticulated ventral claws followed by minute triangular process. Bare, pointed, unpaired bristle on posterior of body following lamellae.

Bellonci Organ (fig. 3B). Elongate with rounded tip.

Lips (fig. 4A). Upper lip with posterior spines. Lower lip with triangular process on each side.

Anterior of body (fig. 4A). With triangular process on each side dorsal to upper lip.

Genitalia. Absent.

Posterior of body (fig. 4H). Segmented.

Gut content. Two food balls with unrecognized particles.

Instar V female, WAM C 40326, spm. F. Carapace shape (fig. 5A) similar to that of adult male. Carapace decalcified (camera lucida drawings of appendages mainly made through transparent left valve of specimen).

Carapace ornamentation. Present only on anterior processes.

Carapace size (mm). Specimen F: length of right valve including upper anterior process 0.75; length without upper anterior process 0.64; height 0.50; height as percent of length with anterior process excluded 78%; height as percent of length with anterior process included 67%.

Central adductor muscle attachments (fig. 5A). About 7 adjacent scars within oval.

First antenna. Article 2 with 2 bristles, 1 ventral, 1 dorsal. Limb otherwise same as on spm. N.

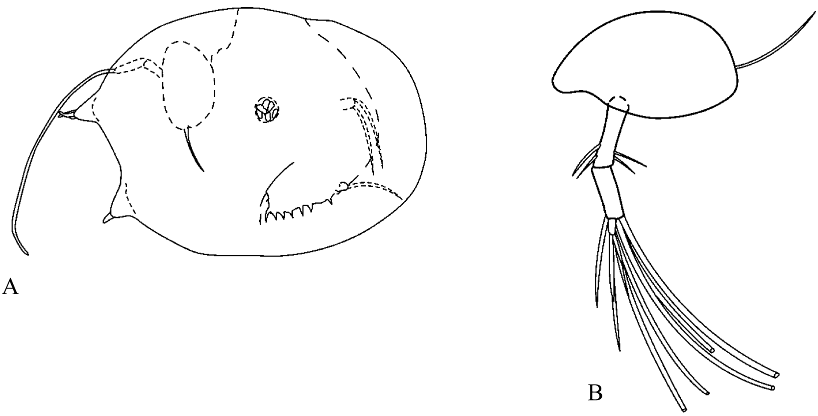

Fig. 5. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. F, C40325, instar V female: A, complete specimen from left side showing central adductor muscle scars, left 2nd antenna, 7th limb, and furca; length of carapace 0.64 mm; B, left 2nd antenna showing protopod and endopod.

Second antenna (figs. 5A, B). Limb same as on spm. N.

Mandible. Coxa obscured. Basis: lateral surface with 5 bristles. Endopod: 3rd article with long terminal claw-like bristle, and 5 shorter bristles. Basis and endopod otherwise same as that of spm. N.

Maxilla. Endites I–III obscured. Coxa and basis same as on spm. N. Endopod: article 1 with 5 bristles (4 bristles on anterior margin, 1 bristle on or near posterior margin); article 2 with terminal bare claw without rings or basal suture and 5 bristles.

Fifth limb. Epipod with long bristles forming 3 groups: 4 bristles in end groups, 5 in middle group. Precoxa and coxa with 11 bristles and small triangular tooth. Basis with indentation on ventral margin and article broader in proximal part (proximal half with 3 bristles; distal half with 2 bristles). Exopod represented by long, bare terminal bristle on dorsal margin of basis. Endopod with 2 articles: article 1 with 2 ventral bristles near midlength; article 2 with 3 terminal bristles (1 long, 2 short).

Sixth limb. Limb same as on spm. N.

Seventh limb (fig. 5A). Elongate lobe with 2 terminal bristles.

Furca (fig. 5A). Furca and unpaired bristle same as on spm. N.

Bellonci Organ. Same as on spm. N.

Lips. Upper lip obscured.

Anterior and posterior of body. Same as on spm. N.

Genitalia. Not observed.

Gut content. Containing 4 balls that contain brown particles.

Instar IV male, WAM C 40323, spm. B. Carapace decalcified, represented by posterior end of valves (camera lucida drawings made from undissected specimen and through transparent left valve).

Carapace ornamentation. Absent in decalcified valve fragment.

Carapace size (mm). Height ca. 0.50 (based on measurement of posterior half of specimen). Rough estimate of length without anterior process 0.66, with anterior process 0.73. (Rough estimate of length based on relative heights and lengths of other specimens.)

Central adductor muscle attachments. Not observed.

First antenna (fig. 6B). Article 1 with 1 dorsal bristle and 1 long lateral bristle; article 2 with 2 bristles, 1 ventral, 1 dorsal. Articles 3 and 4 fused; article 4 with 1 short terminal ventral bristle. Article 5 with 2 long terminal ventral bristles. Article 6 bare; article 7 with dorsal a-bristle and long ventral b- and c-bristles. Article 8 with long d-, e-, and f-bristles.

Second antenna (fig. 6C, D). Protopod with long bristle on posterior margin. Endopod with 3 articles; article 1 with 4 marginal bristles (2 ventral, 2 dorsal); article 2 with 4 bristles (3 long near ventral edge, 1 short near dorsal edge); article 3 stout, nodelike, with rounded tip with 2 short terminal bristles; articles 2 and 3 fused. Exopod with 9 articles; article 1 divided into long proximal and short distal parts; with short terminal ventral bristle; articles 2 to 7 with long ventral bristle with indistinct distal marginal hairs; article 9 small and with 2 terminal bristles.

Mandible (figs. 6E, 7E). Coxa obscured. Basis: medial side near distal dorsal corner with 2 long bristles; lateral surface with 6 bristles; anterior margin with 1 long bristle; posterior margin with 2 short bristles (distal of these with tubular tip); ventral edge of basis with 5 triangular teeth. Endopod: article 1 anterior bristle near midlength; article 2 with 2 anterior bristles, and 3 posterior bristles (1 distal, 2 near midlength); 3rd article with long terminal claw-like bristle, and 5 shorter bristles.

Maxilla (fig. 6F). Bristles of endites I–III obscured. Dorsal margin of coxa with long bristle. Basis: medial side with bristle near midwidth and terminal exopodial bristle near ventral margin. Endopod: article 1 with 4 or 5 bristles: 3-4 bristles on anterior margin, 2 bristles on or near posterior margin; article 2 with terminal bare claw without rings or basal suture and 5 bristles.

Fifth limb (figs. 6G, H, 7A). Epipod with long bristles forming 3 groups: 4 bristles in end groups, 5 in middle group. Precoxa endite with 9 bristles. Coxa endite with 5 bristles and small triangular tooth. Basis with indentation on ventral margin and article broader in proximal part (proximal half with 3 bristles; distal half with 2 bristles). Exopod represented by long bare terminal bristle on dorsal

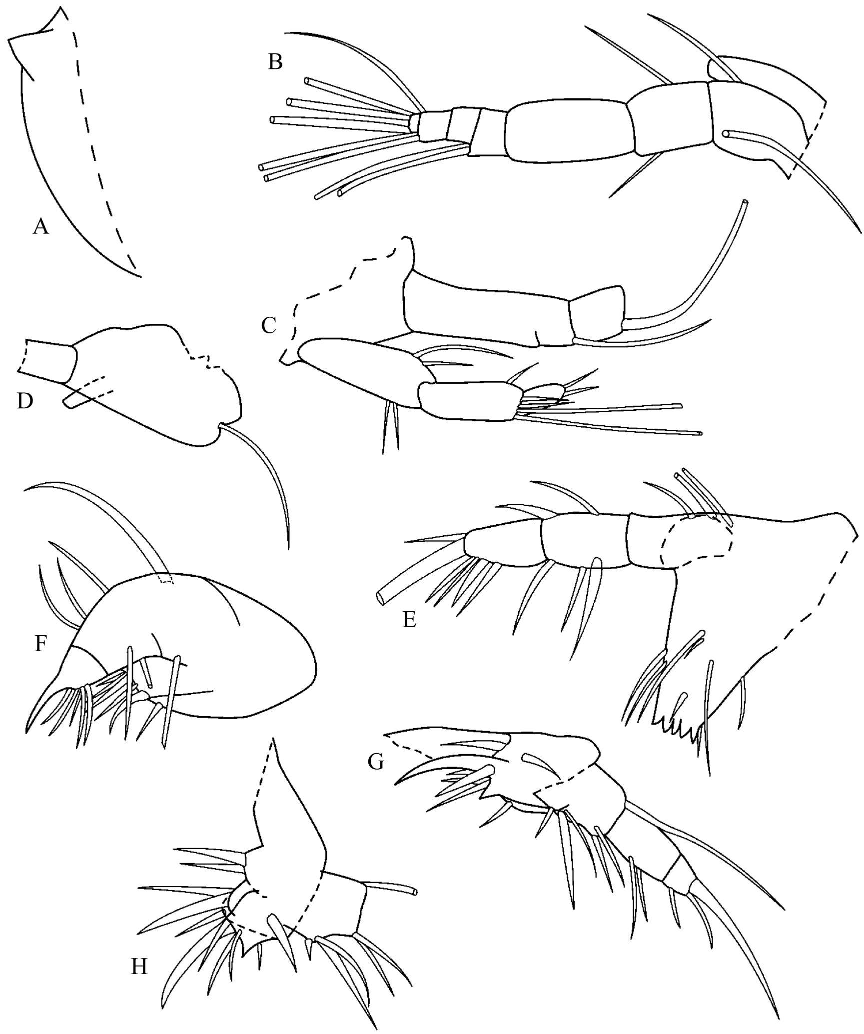

Fig. 6. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. B, C40323, instar IV male (all drawings from appendages on undissected specimen not under cover slip): A, part of anterior of body from left side; B, left 1st antenna and Bellonci Organ, lv; C, part of right 2nd antenna, vv; D, protopod of left 2nd antenna (endopod dashed), lv; E, left mandible, lv (coxa not shown); F, left maxilla, lv (endites I and II not shown). Left 5th limb: G, complete limb, (nabs; epipod not shown) vv; H, proximal part of limb, lv (epipod not shown). lv, lateral view; nabs, not all bristles shown; vv, ventral view.

margin of basis. Endopod with 2 articles: article 1 with 2 ventral bristles near midlength; article 2 with 3 terminal bristles (1 long, 2 short). The 6th limb extends past the 5th.

Sixth limb (fig. 7A, D). Epipod with long hirsute bristles forming 3 groups: 4 bristles in end groups, 5 in middle group. Precoxa and coxa fused; precoxa with

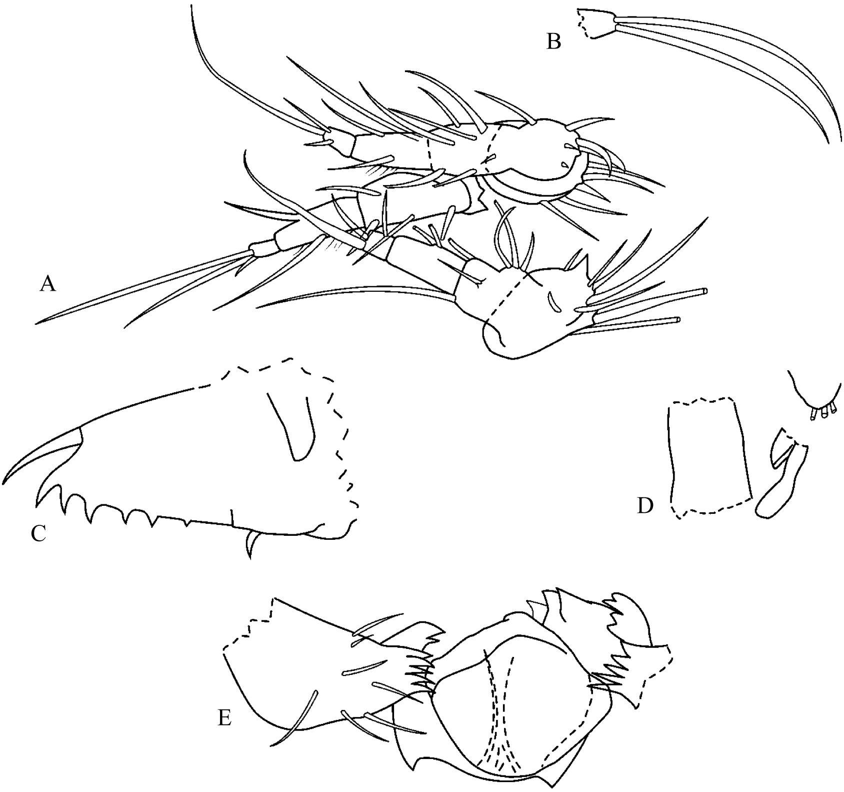

Fig. 7. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. B, C40323, instar IV male (all drawings from appendages on undissected specimen not under cover slip): A, posterior of body showing both 5th limbs and right 6th limb (nabs) vv; B, left 7th limb; C, left lamella of furca and copulatory organ; D, ventral view of left side of posterior of body showing part of epipod of 6th limb, furca, and copulatory organ; E, ventral view of anterior of body showing upper lip and parts of coxa and basis of mandibles, vv. av, anterior view; dv, dorsal view; lv, lateral view; mv, medial view; nabs, not all bristles shown; vv, ventral view.

2 ventral bristles; coxa with 3 ventral bristles. Basis not separated from coxa by suture and with 4 ventral bristles (2 at midlength, 2 terminal). Exopod lobe small with 2 long terminal bristles. Endopod: articles 1 and 2 fused, with 2 ventral bristles at midlength; article 3 with 3 bristles (1 long terminal and 2 short ventral).

Seventh limb (fig. 7B). Elongate lobe with 2 terminal bristles.

Furca (fig. 7C, D). Each lamella with 1 long articulated anterior claw, 1 shorter unarticulated claw on anteroventral corner, and 4 smaller unarticulated claws followed by smaller unarticulated triangular process on ventral margin. Bare, pointed, unpaired process present on posterior of body following lamellae.

Bellonci Organ (fig. 6B). Elongate with rounded tip.

Lips (fig. 7E). Upper lip obscured.

Anterior of body (fig. 6A). With anterior triangular process on each side dorsal to upper lip.

Copulatory organ (fig. 7C, D). Organ on left side of body medial to left 5th and 6th limbs. Anterior branch either absent or represented by small lobe; posterior branch represented by elongate lobe.

Posterior of body. Segmented.

Gut. Containing 4 balls that contain brown particles.

Instar IV female, WAM C 40320, spm. M. Carapace an elongate oval in lateral view with upper and lower anterior processes (fig. 8A–C). Dorsal margin linear; ventral and posterior margins convex; upper and lower anterior processes terminating in elongate prong.

Carapace ornamentation. Without reticulations. Minute hairs along anteroventral margin.

Carapace size (mm). Length of right valve including upper anterior process 0.59; length without upper anterior process 0.53; height 0.41; height as percent of length with anterior process excluded 77%; height as percent of length with anterior process included 69%.

Central adductor muscle attachments (fig. 8B). Present as 7 wedge-shaped attachments.

First antenna (fig. 8D). Article 1 with 1 long lateral bristle near ventral margin; article 2 with 2 bristles (1 ventral, 1 dorsal). Articles 3 and 4 fused, bare. Article 5 with 2 terminal ventral bristles. Article 6 bare; article 7 with short dorsal a-bristle and long ventral b- and c-bristles. Article 8 with long d-, e-, and f-bristles.

Second antenna (fig. 8E–I). Protopod with long bristle on posterior margin. Endopod with 3 articles (articles 2 and 3 fused); article 1 with 3 or 4 marginal bristles (2 ventral, 2 dorsal on left limb; 2 ventral, 1 dorsal on right limb); article 2 with 4 bristles (2 long and 1 medium length near ventral edge, 1 short near dorsal edge); article 3 short, narrow, with 2 short terminal bristles. Exopod with 9 articles; article 1 divided into long proximal and short distal parts by slight indentations in margins (distal part with short terminal bristle); articles 2 to 8 with long ventral bristle (marginal hairs not observed); article 9 small and with 2 terminal bristles.

Mandible (figs. 8I, 9A–C). Coxa with proximal and distal sets of teeth separated by space containing small triangular process; proximal set of teeth consisting of row of teeth and spines; distal set of teeth consisting of 2 rows of teeth; 2 slender bristles medial to distal teeth. Basis: medial side near anterior dorsal corner with 2 long bristles; distal lateral surface with 6 bristles; anterior margin with 1 long bristle; posterior margin with marginal spines and 2 short bristles (distal of these with tubular tip); ventral edge of basis with 5 triangular teeth. Endopod: article 1

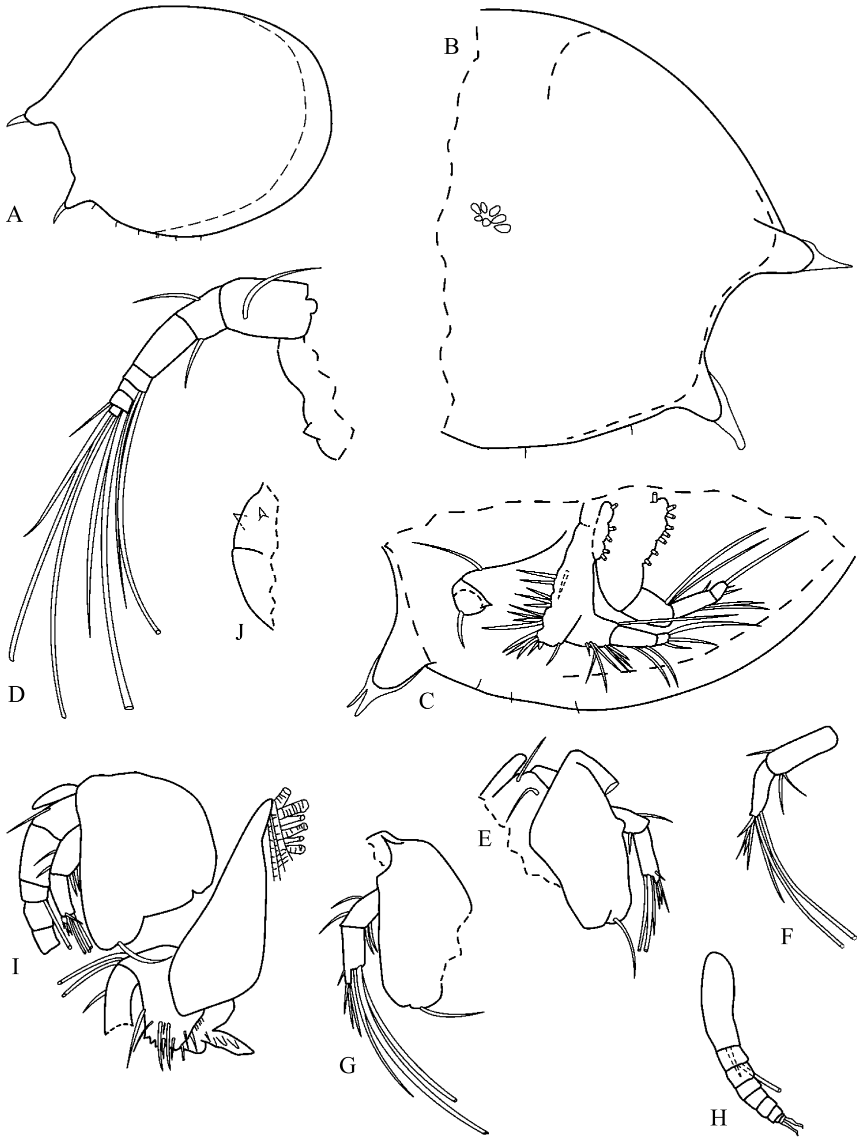

Fig. 8. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. M, C40320, instar IV female: A–C, carapace: A, complete carapace (posterior edge of right valve dashed) length with anterior process 0.59 mm, without process 0.53 mm; B, anterior of right valve with central adductor muscle scars; C, part of right valve containing 3 left limbs (maxilla, 5th and 6th limbs) (nabs); D, left 1st antenna and outline of anterior edge of body; E, anterior of body from right side showing Bellonci Organ, article 1 of right 1st antenna, and protopod and endopod of right 2nd antenna, lv; F, endopod of right 2nd antenna, mv. Left 2nd antenna: G, protopod and endopod, lv; H, exopod, (nabs) lv; I, Bellonci Organ, left 1st antenna, left 2nd antenna and left mandible in place on body, (nabs) lv; J, anterior margin of body. lv, lateral view; mv, medial view; nabs, not all bristles shown.

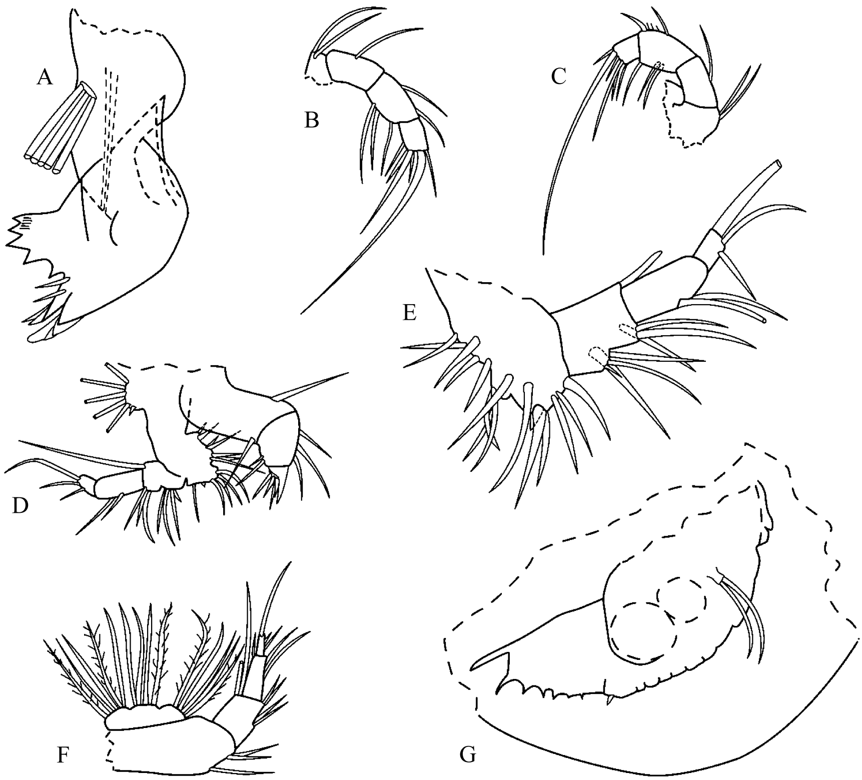

Fig. 9. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. M, C40320, instar IV female: A–C, left mandible: A, coxa, mv; B, dorsal corner of basis and endopod, mv; C, dorsal corner of basis and endopod, lv; D, right maxilla and 5th limb, lv; E, left 5th limb, lv; F, left 6th limb, lv; G, posterior of body from left side with 7th limb, left lamella of furca, and 2 food balls (drawn inside carapace). lv, lateral view; mv, medial view.

with lateral spines and long anterior bristle near midlength; article 2 with 2 anterior bristles, 1 distal posterior bristle, 2 medial bristles (1 short with base almost on posterior margin, 1 long with base a small distance from posterior margin and proximal to short bristle), and spines on medial surface and anterior margin; 3rd article with long terminal claw-like bristle, 1 medium length bristle, and 4 short bristles.

Maxilla (figs. 8C, 9D). Endites I–III obscured. Dorsal margin of coxa with long bristle. Basis: with terminal medial exopodal bristle on ventral margin. Endopod: article 1 with 5 bristles: 3 bristles on anterior margin, 2 bristles on posterior margin; article 2 with terminal bare claw without rings or basal suture and 4 short bristles.

Fifth limb (figs. 8C, 9D, E). Epipod with long bristles forming 3 groups, each with 4 or 5 bristles. Precoxa endite with 9 bristles; coxa endite with 5 bristles and small triangular tooth. Basis with indentation on ventral margin and article broader in proximal part (proximal half with 4 bristles; distal half with 3 bristles). Exopod represented by long bare terminal bristle on dorsal margin of basis. Endopod with 2 articles: article 1 with 2 ventral bristles near midlength; article 2 with 3 terminal bristles (1 long, 2 short).

Sixth limb (figs. 8C, 9F). Epipod with long hirsute bristles forming 3 groups: middle group with 4 bristles, proximal and distal groups with 5 bristles. Precoxa and coxa fused; precoxa with 2 ventral bristles; coxa with 3 ventral bristles. Basis not separated from coxa by suture and with 4 ventral bristles (2 at midlength, 2 terminal). Exopod lobe small with 2 long terminal bristles (outer bristle stouter and longer than inner bristle). Endopod: articles 1 and 2 fused, with 2 ventral bristles at midlength; article 3 with 3 bristles (1 long terminal and 2 short ventral).

Seventh limb (fig. 9G). Elongate lobe with 2 terminal bristles.

Furca (fig. 9G). Each lamella with 1 long articulated anterior claw, 1 shorter unarticulated claw on anteroventral corner, and 4 smaller unarticulated claws followed by smaller unarticulated triangular process on ventral margin. Bare, pointed, unpaired process present on posterior of body following lamellae.

Bellonci Organ (fig. 8E, I). Elongate with rounded tip.

Lips. Obscured.

Anterior of body (fig. 8J). With anterior triangular process on each side dorsal to upper lip.

Genitalia. Not observed.

Posterior of body (fig. 9G). Segmented.

Gut (fig. 9G). With 4 ovals containing unidentified brown particles.

Instar II (sex unknown), WAM C 40324, spm. W. Carapace an elongate oval in lateral view with upper and lower anterior processes (fig. 10A). Dorsal margin linear; ventral and posterior margins convex; upper and lower anterior processes without prongs (prongs interpreted to have broken off).

Carapace ornamentation. Without reticulations.

Carapace size (mm). Length including upper anterior process 0.42; length without upper anterior process 0.40; height 0.30; height as percent of length with anterior process excluded 75%; height as percent of length with anterior process included 71%.

Central adductor muscle attachments. Consisting of wedge-shaped scars.

First antenna (fig. 10B). Article 1 with 1 dorsal bristle; article 2 bare. Articles 3 and 4 fused and without bristles. Article 5 with 1 terminal ventral bristle; Article 6 bare; article 7 with short dorsal a-bristle and 1 long ventral b- or c-bristle. Article 8 with 2 long bristles (d-, e-, or f-).

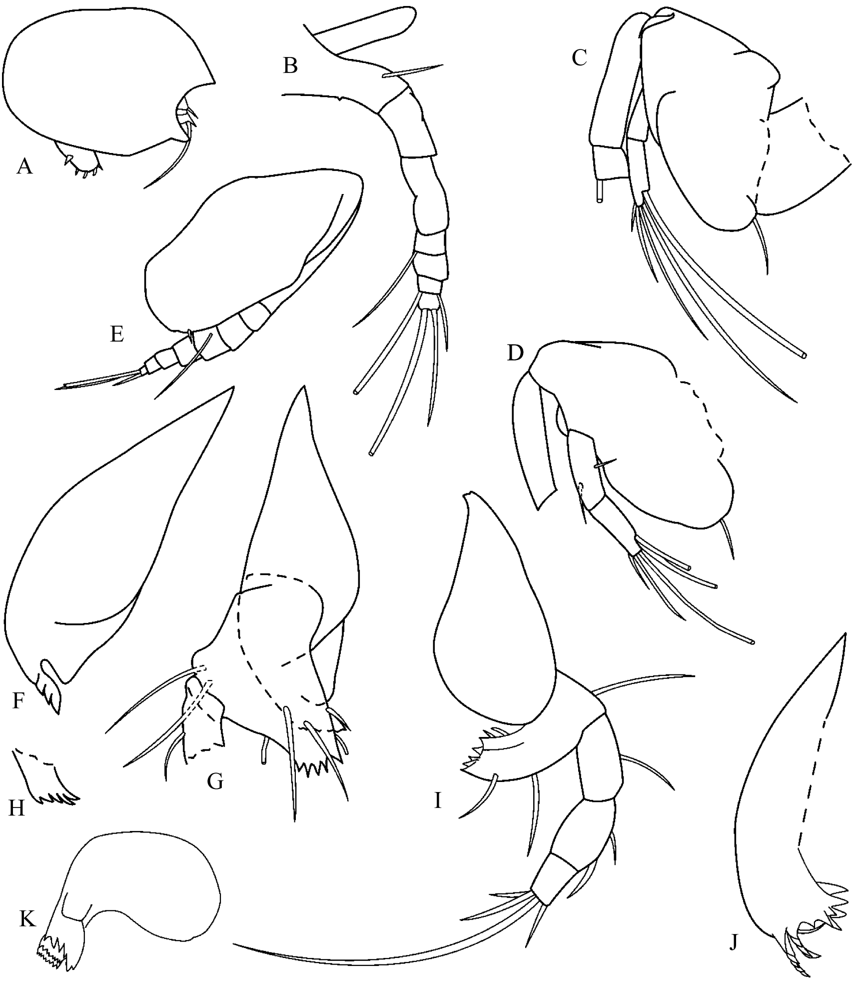

Fig. 10. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. W, C40324, instar II, sex unknown: A, complete specimen with projecting right mandible and furca, length of carapace including anterior process 0.42 mm, without process 0.40 mm; B, right 1st antenna (nabs) and Bellonci Organ; C, left 2nd antenna (nabs) lv. Right 2nd antenna: D, protopod and endopod (nabs) mv; E, protopod and exopod (nabs) lv. Left mandible, limb, lv (on body): F, aberrant coxa, lv; G, basis (nabs) lv; H, teeth of basis, mv. Right mandible: I, limb on body (nabs) lv; J, coxa, mv (on body); K, coxa drawn on body, vv. lv, lateral view; mv, medial view; nabs, not all bristles shown; vv, ventral view.

Second antenna (fig. 10C–E). Protopod with bristle on posterior margin (broke off). Endopod with 3 articles (2 and 3 fused); article 1 with 1 or 2 short bristles; article 2 with 3 bristles; article 3 short, same width as 2nd article, with 2 bristles longer than 3rd article. Exopod with 8 articles; article 1 undivided, bare; articles 2 to 7 each with a long bristle; article 8 small, with 2 terminal bristles; hairs not observed on exopodal bristles.

Mandible (fig. 10F–K). Coxa with 1 proximal row and 2 distal rows of teeth. Proximal and distal sets of teeth separated by space containing small triangular process. Lateral bristle adjacent to distal sets of teeth. Basis: medial surface near dorsal margin with 2 long bristles near anterior corner; lateral surface with 2 distal bristles; posterior margin with proximal long bristle and distal short bristle with tubular tip; anterior margin with 1 bristle at midlength; ventral edge of basis with 5 triangular teeth. Endopod: article 1 with 1 dorsal bristle; article 2 with 2 anterior bristles; 3rd article with long terminal claw-like bristle, 1 medium length bristle, and 2 short.

Maxilla (fig. 11A–C). Precoxa endite I bristles obscured, with 5 or 6 bristles. Coxa: endites II and III bristles obscured, each with 3 or 4 bristles. Dorsal margin of coxa with long bristle. Basis: with terminal medial exopodal bristle on ventral margin. Endopod: article 1 with 2 bristles on anterior margin and 1 or 2 bristles on posterior margin; article 2 with terminal bare claw without rings or basal suture and 4 short bristles.

Fifth limb (fig. 11D, E). Epipod with long bristles forming 3 groups, each with about 4 bristles. Precoxa with 4 bristles; coxa with 6 bristles including claw-like bristle and minute process with rounded tip. Basis with 2 bristles. Exopod represented by long bare terminal bristle on dorsal margin of basis. Endopod with 2 articles: article 1 with 1 dorsal bristle near midlength; article 2 with 2 bristles (1 long and 1 short).

Sixth limb (fig. 11E). Elongate bare lobe.

Seventh limb. Absent.

Furca (fig. 11F). Some claws missing on both lamellae. From uneven ventral edges of lamellae it is deducted that each lamella had 1 long articulated anterior claw, 1 shorter unarticulated claw on anteroventral corner, and 2 smaller unarticulated claws followed by smaller unarticulated triangular process on ventral margin. Bare, pointed, unpaired process present on posterior of body following lamellae.

Bellonci Organ (fig. 10B). Elongate with rounded tip.

Lips (fig. 11G, H). Upper lip with posterior spines. Lower lip with triangular process on each side.

Anterior of body (fig. 11G). With triangular process on each side dorsal to upper lip.

Genitalia. Absent.

Posterior of body (fig. 11F). Segmented.

Gut content. Unrecognized particles.

Instar II (sex unknown), spm. L (specimen lost after initial description). Carapace shape, ornamentation, and central adductor muscle attachments same as those of spm. W.

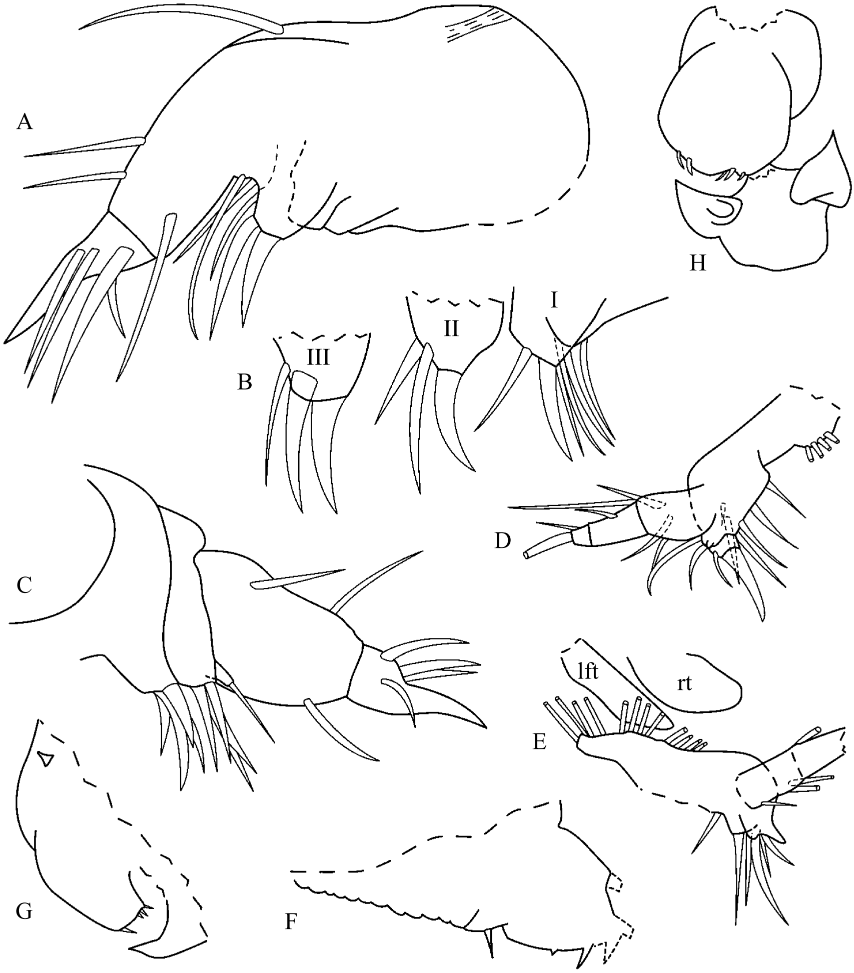

Fig. 11. *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000, spm. W, C40324, instar II sex unknown. A, right maxilla, mv; B, endites of right maxilla, mv; C, left maxilla (nabs) mv; D, right 5th limb, lv (viewed through right valve); E, left 5th limb, mv, and left 6th limb, lv, and right 6th limb, mv; F, right lamella of furca, lv; G, anterior of body from left side; H, upper and lower lips, vv. lv, lateral view; mv, medial view; vv, ventral view.

Carapace size (mm). Length including upper anterior process 0.51; length without upper anterior process 0.46; height 0.38; height as percent of length with anterior process excluded 83%; height as percent of length with anterior process included 75%.

First antenna. Article 2 with 1 dorsal bristle. Limb otherwise similar to that of spm. W.

Second antenna. Protopod with long bristle on posterior margin. Endopod with 3 articles; article 1 with 1 bristle; articles 2 and 3 same as in spm. W. Exopod same as in spm. W.

Mandible. Coxa obscured. Basis: lateral surface with 3 distal bristles; anterior margin with proximal long bristle and distal short bristle; posterior margin with 1 short bristle; ventral edge of basis with 5 triangular teeth. Endopod: article 1 bare; article 2 with 2 anterior bristles; 3rd article with long terminal claw-like bristle, 1 medium length bristle, and 1 short bristle.

Maxilla. Precoxa and coxa endite bristles obscured. Dorsal margin of coxa with long bristle. Basis: with terminal medial exopodal bristle on ventral margin. Endopod: article 1 with 3 bristles on anterior margin, 2 bristles on posterior margin, and 1 short distal medial bristle; article 2 with terminal bare claw without rings or basal suture and 5 short indistinct bristles.

Fifth limb. Epipod with long bristles forming 3 groups, each with 3 or 5 bristles. Precoxa with 4 bristles; coxa with 5 bristles including claw-like bristle. Basis with 1 terminal ventral bristle. Exopod represented by long bare terminal bristle on dorsal margin of basis. Endopod with 2 articles: article 1 with 2 bristles near midlength (1 ventral, 1 dorsal); article 2 with 2 bristles (1 long and 1 short).

Sixth and seventh limbs. Absent.

Furca. Each lamella with 1 long articulated claw, 1 shorter unarticulated claw on anteroventral corner, and 2 smaller unarticulated claws followed by smaller unarticulated triangular process on ventral margin. Bare, pointed, unpaired process present on posterior of body following lamellae.

Bellonci Organ, anterior and posterior of body, and genitalia. Same as in spm. W.

Lips. Not observed.

Genus *Thaumatoconcha* Kornicker & Sohn, 1976

Type species. — *Thaumatoconcha radiata* Kornicker & Sohn, 1976.

Thaumatoconcha radiata Kornicker & Sohn, 1976
(figs. 12-14)

Thaumatoconcha radiata Kornicker & Sohn, 1976: 40-58. — Kornicker & Iliffe, 1998: 62.

Holotype. — USNM 143794, adult female.

Type locality. — USCGC Glacier station 0022, Weddell Sea, 3035 m.

Material. — Paratypes USNM 143753SS, instar I in alcohol; USNM 143753G, instar II in alcohol.

Descriptions. — Instar I (sex unknown), USNM 143753SS.

Second antenna (fig. 12A). Endopod with 3 articles: 1st and 2nd articles separated by suture; 1st article bare; 2nd article with 1 long and 1 short bristle near dorsal edge; article 3 with 3 terminal bristles. Exopod with 8 articles; article 1 bare; article 8 with 2 bristles.

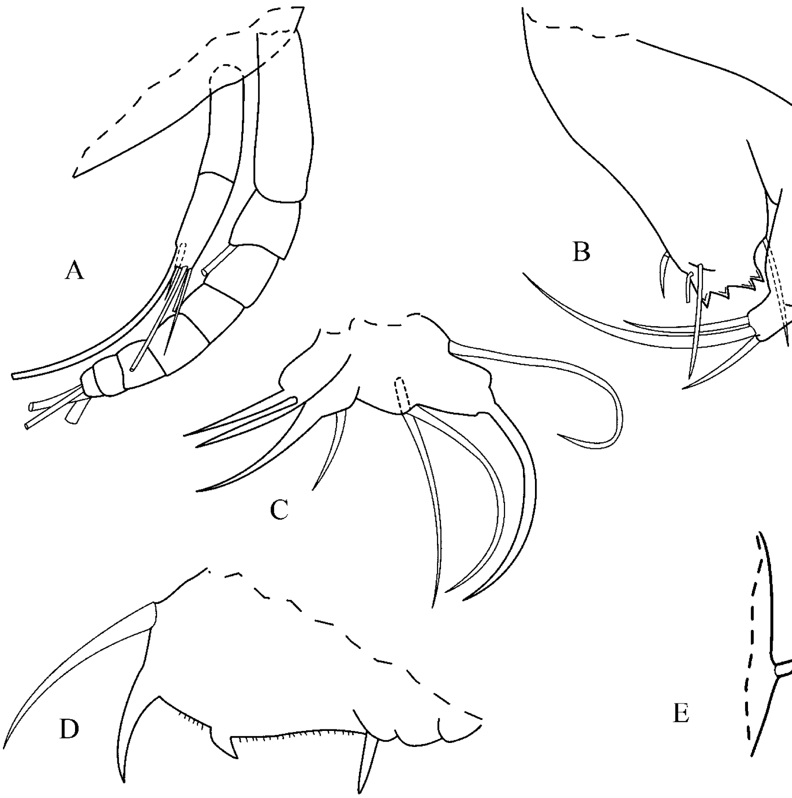

Fig. 12. *Thaumatoconcha radiata* Kornicker & Sohn, 1976, USNM 143753SS, instar I, sex unknown: A, right 2nd antenna (nabs) lv; B, coxa and endopod of right mandible, lv; C, left 5th limb (nabs) lv; D, left lamella of furca; E, profile of anterior of body from right side. All limbs drawn while attached to body. lv, lateral view; nabs, not all bristles shown.

Mandible (fig. 12B). Basis with 4 triangular marginal teeth. Endopod: end article with 5 bristles including 1 long claw-like bristle.

Fifth limb (fig. 12C). Exopod present. Endopod with 1 stout terminal bristle.

Sixth and seventh limbs. Absent.

Furca (fig. 12D). Each lamella with long anterior claw with suture at base, 1 shorter claw on corner without suture at base followed by space and then 1 small triangular process without suture at base. Ventral margin of lamellae with minute spines anterior and posterior to triangular process.

Unpaired process (fig. 12D). Stout unpaired process just posterior to posterior corner of lamella.

Anterior of body (fig. 12E). With anterior process.

Posterior of body (fig. 12D). With weakly developed scallops.

Instar II (sex unknown) USNM 143753G.

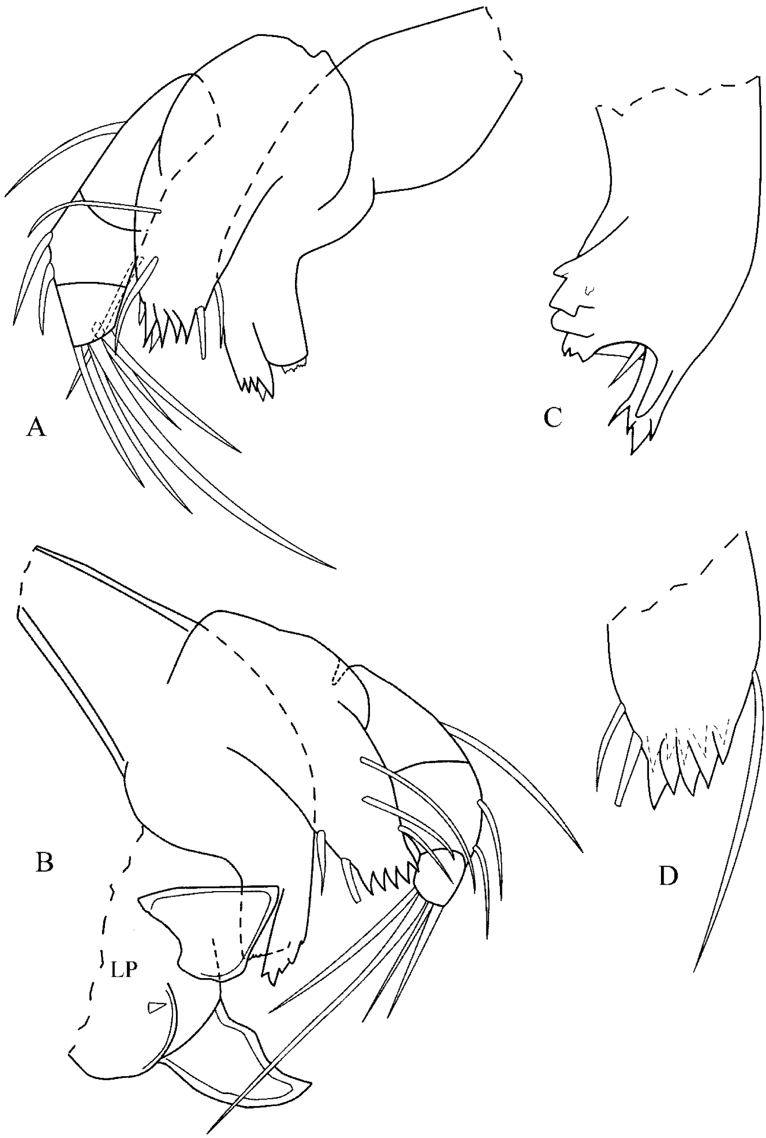

Fig. 13. *Thaumatoconcha radiata* Kornicker & Sohn, 1976, USNM 143753G, instar II, sex unknown: A, right mandible, mv; B, ventral view of lower lip and medial view of left mandible; C, ventral margin of coxa of right mandible, lv; D, ventral margin of basis of right mandible, lv. lv, lateral view; mv, medial view.

Mandible (fig. 13). Coxa with 2 sets of marginal teeth: anterior set with 5 stout teeth, posterior set with 4 flat-tipped teeth (proximal tooth small); short bristle with fuzzy tip on margin between the two sets of teeth. Basis: endite with 5 triangular marginal teeth (anterior tooth small); anterior margin with 1 distal bristle; posterior

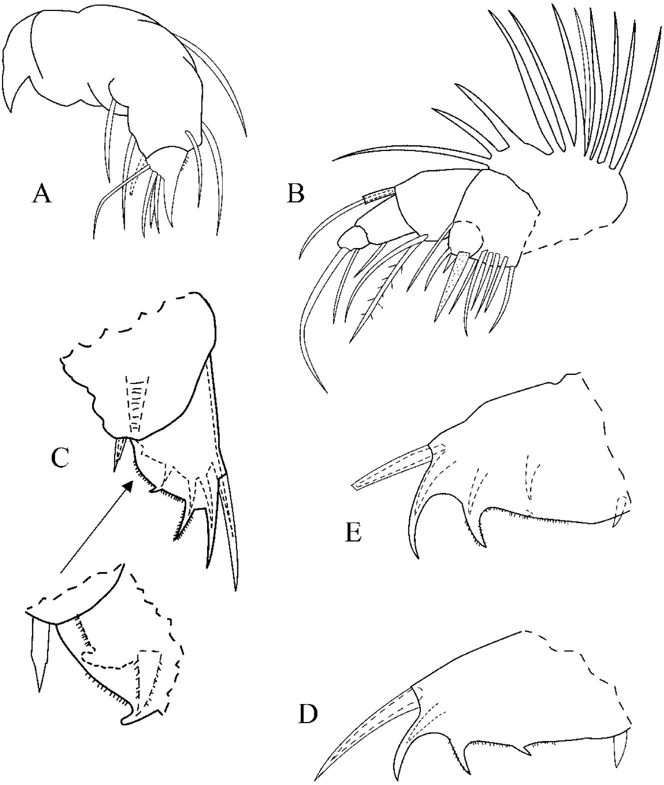

Fig. 14. *Thaumatoconcha radiata* Kornicker & Sohn, 1976, USNM 143753G, instar II, sex unknown: A, right maxilla (nabs), lv-vv; B, right 5th limb, vv; C, right lamella of furca, lv; D, right lamella of furca, mv; E, left lamella of furca, lv. lv, lateral view; mv, medial view; vv, ventral view.

margin with 2 distal bristles (distal of these with tubular tip); medial surface with 2 long bristles closer to anterior margin than to posterior margin. Endopod: 1st segment with long anterior bristle; segment 2 with 2 anterior bristles; endite 3 with 1 long claw-like bristle, and 3 medium length bristles. Instar III mandible visible inside instar mandible: 5 teeth of basis of instar III visible inside 5 teeth of instar II.

Maxilla (fig. 14A). Endites obscured. Coxa with long dorsal bristle. Basis with long ventral bristle. Endopod with 2 segments: segment 1 with 2 ventral and 2 dorsal bristles; segment 2 with stout unarticulated terminal claw, 3 slender bristles, and minute spines along anterior edge.

Fifth limb (fig. 14B). Epipod with 3 lobes with a total of 12 bristles (4 on proximal lobe, 5 on middle lobe, 3 on distal lobe). Precoxa with about 6 slender ventral bristles. Coxa well defined, with 2 long slender bristles, 1 long stout ventral claw-like bristle, and 1 short ventral triangular process. Basis with 2 long ventral bristles (stouter of these with long marginal spines). Exopod bristle long, bare.

Endopod with 2 segments: segment 1 with 1 short bristle near ventral margin; segment 2 with 1 short bristle and 1 long claw-like bristle.

Sixth limb. Rudimentary and without bristles (Kornicker & Sohn, 1975, fig. 34d). Note: we did not observe 6^{th} limb of instar III inside instar II of USNM 143753G; however, specimen is in pieces, and 6^{th} limb possibly lost.

Seventh limb. Absent.

Furca (fig. 14C–E). Each lamella with long anterior articulated claw, 1 shorter unarticulated claw on corner, 1 short ventral unarticulated claw with minute spines or teeth along both edges, and 1 small unarticulated triangular process. Ventral margin of lamellae with minute spines or teeth anterior and posterior to triangular process. Furca of instar III visible within that of instar II (USNM 143753G). Additional, short ventral claw of instar III visible just proximal to triangular process of instar II. One triangular process visible on each lamella of instar III. Spines or teeth visible on posterior ventral claw and on ventral margin of each lamella of instar III.

Unpaired process (fig. 14C–E). — Stout unpaired process just posterior to posterior corner of left lamella, and unpaired process of instar III visible inside that of instar II.

Posterior of body (fig. 14C). With weakly developed scallops.

Discussion of furcal lamellae

The instar II (USNM 143753G) body of *T. radiata* with carapace removed had been retained in a vial of alcohol for several years. It was examined in glycerine immediately after having been removed from the alcohol. The appendages of instar III were clearly visible inside the body of instar II. Each lamella of the furca of the species of *Thaumatoconcha* has a small triangular process posterior to the short ventral claws of instars II–VII (example, fig. 14C, D), and posterior to the corner bristle in instar I, which has no short bristles (example, fig. 12D). In descriptions of the furca in the literature, the process has generally been called "small triangular process", and infrequently has been called a "claw". The present senior author thought the process may be an "incipient claw" representing the location of a claw to be added in the following instar.

Each furcal lamella of instar II (USNM 143753G) of *T. radiata* has 1 short ventral claw followed by the triangular process (fig. 14C–E). The internal instar III has a furcal lamella with 2 short ventral claws, and the 2^{nd} claw is just proximal to the small triangular process on the furcal lamella of instar II. Each furcal lamella of the internal instar III has a small triangular process following the 2^{nd} bristle. The location of the 2^{nd} short claw on instar III was initially interpreted to indicate that the triangular process was indeed an incipient claw that became a large claw on the following instar. However, the adults of species of *Thaumatoconcha* bear a well-developed triangular process following the last ventral claw, despite the fact that no additional claws are to be added (e.g., *Thaumatoconcha pix* Kornicker, 1992, which bears a prominent triangular process on the furca of the adult male (see Kornicker, 1992, fig. 2g). Based on this, it is concluded that the triangular processes on the furcae of species of *Thaumatoconcha* are not incipient claws, but are structures unrelated to claws. It is probable that the triangular process is also unrelated to claws in species of the genus *Danielopolina*.

COMMENTS ON THE ORIGIN AND DISTRIBUTION OF PLANKTONIC HALOCYPRIDIDAE

As an extension of this morphological study we re-examine the bold hypothesis on the origin of the planktonic Halocyprididae inhabiting the domain of oceanic waters, especially those of the Atlantic, that "the phylogeny of the halocyprid family seems likely to have involved species inhabiting either abyssal or anchialine habitats" (Angel, 1993: 6).

Our development data, especially those on the high number of segments of the first antenna and of the endopodite of the second antenna, indicate that representatives of the Thaumatocypridoidea, as in the Halocypridoidea: Deeveyidae (cf. Kornicker et al., 2007), display primitive traits compared to those of the Halocyprididae, and that these traits are already expressed in the early stages of the post-embryonic development. The proposition that the planktonic oceanic halocypridids "evolved either in abyssal waters or in caves" (Angel & Iliffe, 1987) was based mainly on the observation of the lack of visible ocular structures in the Halocyprididae and in the peculiarity of the halocypridoid antennae, namely, that both deep-sea and cavernicolous species display a more primitive limb structure than the oceanic forms, and that they are blind.

At the time when the putative cavernicolous origin of oceanic halocypridid species was proposed it appeared implausible to many biospeleologists, because of the established view in subterranean biology that stygobiotic (hypogean) species are so closely specialized to their environment that they can not successfully recolonize the surface (epigean) environment, then considered the more dynamic (cf. inter alia Jeannel, 1943; Vandel, 1965). This established view is a variant of Dollo's and Arber's laws (Lincoln et al., 1982) of the irreversibility of evolution, but, in some cases this now appears contradicted (Domes et al., 2007) including cases amongst ostracods (cf. Dingle, 2009).

The ostracod family Deeveyidae, which includes 12 species belonging to the genus *Spelaeoecia* Angel & Iliffe, 1987 (subfamily Spelaeoecinae) and 7 species of *Deeveya* Kornicker & Iliffe 1985 (subfamily Deeveyinae), comprises exclusively troglobiotic species living in the Caribbean, Gulf of Mexico, and Bermuda (Kornicker et al., 2007). *Spelaeoecia*, which has a carapace similar in shape to those of present day oceanic Halocyprididae, is tentatively concluded to be an ancestor of the latter. This conclusion is based on its similar carapace shape, as well as on having both more articles in the first antenna, and 2 instead of 1 lobes forming the male copulatory organ (Kornicker et al., 2007, fig. 9).

Thus, the hypothesis that blind cavernicolous species related to *Spelaeoecia* could, during past geologic time, have invaded the oceanic environment now appears plausible. We proffer three fields of argument that potentially strengthen this idea: stygobionts are often flushed from karst; flushed fauna can survive at the surface and re-establish; the concentration of caves with myodocopid ostracods in the greater Caribbean region may not be fortuitous, but be related to the events associated with the end-Cretaceous mass extinction event.

Karst systems can support very large populations of crustaceans (Rouch, 1986). Some individuals are flushed from the karst at springs, and, periodically, in response to various hydrologic cycles, karst waters exfiltrate enormous numbers of invertebrates, such as 45 individuals per hour of *Niphargus rhenorhodanensis* Schellenberg, 1937 (cf. Gibert, 1986) and annually, thousands and millions of copepods, ostracods, amphipods, and isopods (Rouch, 1970; Gibert & Laurent, 1982), releasing them to surface waters. Some of these crustaceans can survive in surface water habitats. Forel (1884) and more recently Henry (1976) mention the case of the stygobiotic isopod *Proasellus cavaticus* (Leydig, 1871), which lives commonly also on the bottom of alpine lakes (e.g., at greater depths of Lake Geneva). Moreover, accepted stygobiotic species like the copepod *Graeteriella unisetigera* (Graeter, 1908) can spread in Europe through epigean (cryptozoic) habitats (Fiers & Ghenne, 2000). It is also likely that anchialine *Danielopolina*, present on a seamount rising from abyssal depths in the Indian Ocean, may have survived ocean passage (Humphreys et al., 2009).

A suggestion by the senior author, that halocyprids with eyes may have once lived in the open ocean, but were exterminated as a result of deleterious conditions resulting from the Chicxulub impact occurring at or near the end of the Cretaceous, stimulated the following discussion. We propose that halocypridids living in caves prior to the impact eventually re-established themselves in the ocean. Loss of eyes is a typical adaptation to life in caves and so the occurrence of eyeless halocyprids in the present oceans is a consequence of the Chicxulub impact.

In the case of the halocypridids related to *Spelaeoecia*, during a strong dewatering event of the marine karst in the Caribbean and the Gulf of Mexico, a high number of stygobiotic ostracods could be released in the open ocean. Exfiltrated halocypridids could continue to live in surface waters and evolve to the present day planktonic ostracods (cf. Angel, 1972 for the morphological and ecological adaptation to the planktonic life of two halocypridid species). Such a major dewatering event could have occurred at the end of the Cretaceous (K-T boundary) as a consequence of tsunamis following the Chicxulub impact (MacLeod et al., 2007), or the subsequent eustatic lowering of sea-level (Keller et al., 2009). However, because very fast and variable tidal currents are typical of anchialine systems in small carbonate platform islands (Schwabe, 2008), widespread and sustained leakage of anchialine fauna to the ocean is to be expected, even in the absence of a catastrophic event, much as occurs from freshwater springs. Under either scenario, following the asteroid impact at or near the K-T boundary (Keller et al., 2004, 2009; MacLeod et al., 2007), mass extinction took place of planktonic species, such as the Foraminifera documented, for example, by MacLeod et al. (2007), but also for the ostracods.

The Chicxulub impact occurred in the sea, including deep water at the edge of the continental shelf (Gulick et al., 2008). The trajectory of the Chicxulub impactor (Wittmann et al., 2007) concentrated ejecta over south east North America, where, at the time, most of south eastern U.S.A. and the Caribbean were covered by shallow epicontinental seas (Kiessling & Claeys, 2002). Sedimentary processes throughout the Gulf of Mexico, were interrupted by massive debris flows and failure of platform margins or significant erosion of Upper Cretaceous (Claeys et al., 2002). The mass extinction event with a pronounced collapse of the pelagic ecosystem and a 50% loss of plankton biomass, possibly resulting from the very acid rain, and SO_x and NO_x poisoning (Kiessling & Claeys, 2002) severe temperature change, and deoxygenation of surface ocean waters (Pope et al., 1997; Buffetaut & Koeberl, 2002), effects that would be buffered within carbonate substrates. Jablonski (2008), considering bivalve molluscs, showed that this region was subject to significantly more intense invasion, although not survival, following the K-T mass extinction event than three other regions of the world with which is was compared, suggesting that the recovery of the local fauna was impeded by proximity to the impact. Jablonski (2005) argued, that following a mass extinction event, taxa would enter a phase during which competition was much reduced as a result of severe reduction of population density and biodiversity. During such times of competitive vacuum survivors may be able to expand into regions and habitats formerly closed to them, and evolve life styles previously marginal to them, or, as stated by Jablonski (2008: 11530) 'the removal of incumbents and the subsequent diversification of formerly marginal taxa are essential elements of the evolutionary dynamic fuelled by mass extinctions'.

Ostracod Halocyprididae are seldom recorded in the upper Cretaceous layers (Colin & Andreu, 1982) and there is only one halocyprid species, *Conchoecia cretacea* Pokorný, 1964 that occurs in the Coniacian stage but disappears thereafter. No fossil planktonic halocypridids are recorded from oceanic Tertiary sediments.

Finally, our comments should be viewed as an invitation to a more intense comparative investigation of the possibilities that present-day successful organismic groups could originate from subterranean fauna. Such a possibility was foreseen by Racovitza (1907), discussed in the context of the K-T boundary in central America (Humphreys, 2000: 428) and later supported by data for troglobiontic scorpions in Mexico (Volschenk & Prendini, 2008). Stygobiontic animals have the same capacity to evolve as those living in surface waters, and therefore such a scenario is now plausible.

Note added in proof. — Two papers of particular pertinence to this paper have been published recently. Schulte et al. (2010) provide a comprehensive synthesis of the evidence and find overwhelming support for the thesis that the Chicxulub meteorite impact caused the end-Cretaceous mass extinctions. Prendini et al. (2010) provide further independent support that cave adapted species can repopulate surface habitats.

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APPENDIX

Morphology of instars and adults of *Danielopolina kornickeri* Danielopol, Baltanas & Humphreys, 2000. Abbreviations: A, anterior; Ab, absent; B, bristles; C, claw; D, dorsal; L, long; M, medial; mm, millimetres; nd, no data; P, posterior; Prb, present but bare; Pr, present; S, short; V, ventral; ? = unknown; + = present; − = not applicable (limb absent)

Specimen	W	L	M	B	N	F	A	K*	K*
Sex	?	?	F	M	F	F	M	F	M
Instar	II	II	IV	IV	V	V	VI	VI	VI
Carapace									
Length (mm)									
Without process	0.40	0.46	?	nd	?	0.64	0.71	nd	nd
With process	0.42	0.51	?	nd	?	0.75	0.78	0.85	0.85
Height (mm)	0.30	0.38	?	nd	?	0.50	0.47	0.56	0.56
Reticulations	ab	ab	ab	ab	ab	P	P	P	P
1st antenna articles B									
1st	1	1	1	2	2	2	2	2	2
2nd V/D	0	1D	1/1	1/1	1D	1/1	1/1	1/1	1/1
3rd V	0	0	0	0	0	0	0	0	0
4th V	0	0	0	1	0	0	2	0	2
5th V	1	1	2	2	2	2	3	2	3
7th V/D	1/1	1/1	2/1	2/1	2/1	2/1	2/1	2/1	2/1
8th	2	2	3	3	3	3	3	3	3
2nd antenna									
Protopod PB	L	L	L	L	L	L	L	L	L
Endopod articles B									
1st V/D	1/1	0/1	2/1-2	2/2	2/2	2/2	2/2	2/2	2/2
2nd V/D	3	3	3/1	3/1	3/1	3/1	4/1	3/1	4/1
3rd	2	2	2	2	2	2	hook	1	hook
Exopod articles B									
1st S	0	0	1	1	1	1	1	1	1
2nd-7th L	6	6	6	6	6	6	6	6	6
8th	2	1	1	1	1	1	1	1	1
9th	–	2	2	2	2	2	2	2	2
Mandible									
Basis B									
Dorsal + Medial	2	1	2	2	2	2	2	2	2
Anterior edge	1	1	1	1	1	1	1	1	1
Posterior edge	2	2	2	2	2	2	2	2	2
Lateral side	2	3	6	6	4-6	5	5	6	6
Terminal teeth	5	5	5	5	5	5	5	5	5
Endopod articles B									
1st A	1	0	1	1	1	1	1	1	1
2nd A/P/M	2A	2/1P	2/1/2	2/3P	2/3P	2/3P	2/1/3	2/1/2	2/1/2
3rd C/B	1/3	1/2	1/5	1/5	1/6	1/5	1/7	1/6	1/6

APPENDIX
(Continued)

Specimen	W	L	M	B	N	F	A	K*	K*
Sex	?	?	F	M	F	F	M	F	M
Instar	II	II	IV	IV	V	V	VI	VI	VI
Maxilla B									
Precoxa endite I	5-6	?	?	?	?	?	13	?	?
Coxa D	1	1	1	1	1	1	1	1	1
Coxa endites II/III	4/4	4/4	?	?	?	?	?	ca. 6/5	ca. 6/5
Basis M	1	0	0	1	?	?	0	1	1
Exopod	1	1	1	1	1	1	1	1	1
Endopod articles									
1st A/P	2/1-2	2/3	3/2	3-4/2	3/2	4/1	3/3	4/3	4/3
2nd C/B	1/4	1/5	1/5	1/5	1/4	1/5	1/5	1/5	1/5
5th limb B									
Epipod (3 groups)	12	12	13	13	12	13	14	14	14
Precoxa-Coxa									
VB + tooth	11	9	15	15	11	12	14	14	14
Basis V	2	1	7	6	7	5	5-6	7	7
Exopod	1	1	1	1	1	1	1	1	1
Endopod articles									
1st V	1	2	2	2	2	5	2	2	2
2nd	2	2	3	3	3	3	3	3	3
6th limb									
Ab/Pr/Prb	Prb	Ab	Pr	Pr	Pr	Pr	Pr	Pr	Pr
Extends past 5th limb	–	–	+	+	+	+	+	+	+
Epipod B (3 groups)	–	–	5/4/5	4/5/4	5/5/5	5/5/5	5/4/5	5/4/5	5/4/5
Precoxa B, V	–	–	2	2	1	1	2	2	2
Coxa B, V	–	–	3	3	2	2	3	2	2
Basis B, V	–	–	4	4	4	4	4	5	5
Exopod B	–	–	2	2	2	2	2	2	2
Endopod articles B									
1 + 2	–	–	2	2	2	2	2	3	3
3rd	–	–	3	3	3	3	3	3	3
7th limb	A	A	P	P	P	P	P	P	P
7th limb B	–	–	2	2	2	2	2	2	2
Furcal ventral claws**	2	2	4	4	5	5	6	6	6
Unpaired process	+	+	+	+	+	+	+	+	+
Bellonci Organ	+	+	+	+	+	+	+	+	+
Anterior of body									
Triangular processes	+	+	+	+	+	+	+	?	?
Genitalia	ab	ab	ab	+	ab	ab	+	ab	+
Posterior of body									
Segmented	+	+	+	+	+	+	+	?	?

* = Female and male described by Danielopol et al. (1999).
** = Number of ventral claws does not include 2 anterior claws, nor posterior triangular process, if present.

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