



Nitocrellopsis texana n. sp. from central TX (U.S.A.) and *N. ahaggarensis* n. sp. from the central Algerian Sahara (Copepoda, Harpacticoida)

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Abstract

Nitocrellopsis texana n. sp. found in samples collected by SCUBA divers in Honey Creek Cave (Texas, U.S.A.) is described. This species is the first representative of this stygobitic taxon from a Northern American locality. The original description of *N. ioneli* (Dumont & Decraemer, 1975) is amended and the closely related *N. ahaggarensis* n. sp. is described from a well near Tamanghasset in the Ahaggar mountains in Algeria. The monophyly of *Nitocrellopsis* is discussed and its present day distribution is analyzed.

Introduction

The extended caves in the interior of Texas are inhabited with a wealth of interesting stygobiont crustacean taxa (Maguire, 1965; Holsinger et al., 1980; Holsinger, 1994). Whereas the diversity of amphipods, isopods and thermosbaenaceans and several other invertebrate and vertebrate groups is well documented, our knowledge of the copepod fauna of this region is virtually non-existent (Kroschewsky, 1990). The find of a highly specialized harpacticoid copepod of the family Ameiridae in central Texas illustrates the opinion of several researchers that the American continent is a gold mine of undiscovered species and, probably, genera, most particularly in the southern territories (Reid, in litt., 1998).

The genus *Nitocrellopsis* was defined by Petkovski (1976) for three *Nitocrella* species possessing a two-segmented endopodite in leg 4, and three-segmented endopodites in legs 2 and 3. Thus far, seven species are included in this genus. *N. intermedia* (Chappuis, 1937) is known only from its type locality near Skopje (Macedonia), whereas *N. elegans* (Chappuis & Rouch,

1959) is known from two localities in the Pyrenees (Rouch, 1964, 1986). *N. ioneli* (Dumont & Decraemer, 1974), collected in a well in the presaharan Atlas mountains of Morocco, was the first representative outside the European continent. The circum-mediterranean distribution of the genus became more evident with the addition of three more species: *N. petkovskii* Rouch, 1976 from Algeria, *N. hellenica* Cottarelli & Forniz, 1993 and *N. hippocratis* Cottarelli & Forniz, 1993, respectively from Kos and Tilos, in the Mediterranean Sporades. At last, Galassi et al. (1999) described *N. rouchi* from the Rhône River alluvium, in southern France. In the present account, a new representative of the genus, *N. texana* n. sp., collected in an inland cave in Texas, is described. This is the first record of a *Nitocrellopsis* on the American continent.

Within the last decennia, several examples of transatlantic distribution have been described for many crustacean taxa (Stock, 1994; Wagner, 1994; Wägele et al., 1995, and references therein), supporting the hypothesis of an ancestral Tethian distribution. For many of those crustacean taxa, sound phylogenetic hypotheses are available, but the phylogenetic relationships among the several copepod taxa are considerably

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obscure. This is particularly true in the case of freshwater ameirid genera such as *Nitocrella* Chappuis, 1923, *Nitocrellopsis* Petkovski, 1976, *Stygonitocrella* Petkovski, 1976 and *Parapseudoleptomesochra* Lang, 1964, where species are assembled from which crucial information on the morphology of most of their appendages is lacking, hampering analyses of their naturalness and monophyly. In the case of *Nitocrellopsis*, attempts to locate type material or additional material of several species failed for *N. intermedia* and *N. elegans*, but comparison of the type-series *N. ioneli* with additional material collected in a well at the foot of the Ahaggar Mountains in Algeria revealed the presence of a closely related species in the Central Sahara.

Material and methods

The sample from Texas, containing *N. texana* n. sp., was collected by scuba using a plankton net towed at 0–3 m in the downstream section of the cave, just above the natural entrance. Leg. T. M. Iliffe, 30th September 1990 (sample number 90-050).

The samples were fixed in formalin and specimens were transferred to either 75% ethanol (*N. texana*) or 4% formalin (*N. ioneli*) for storage. Permanent mounts were made in glycerine with sealed cover-glasses. Drawings were made at 1250 x on a Leitz Dialux 20 equipped with a drawing tube. Abbreviations made in text are: Aesth – aesthetasc; sp – spine; P1–P6, leg 1–6, Exo – exopodite; End – endopodite. The material is deposited in the collections of the Royal Belgian Institute of Natural Sciences (Brussels, labeled COP), and the United States National Museum of Natural History (Washington D.C., labeled USNM).

Taxonomic section

Nitocrellopsis texana n. sp.

Figures 1–4

Type-material: Holotype female dissected on seven slides, labeled COP 4023 A–G; male allotype dissected on five slides, labeled COP 4024 A–E; paratypes: one female and one male, preserved in ethanol, catalog number USNM 274243.

Type-locality: U.S.A., Texas, Comal County, Honey Creek Cave. Freshwater stream (see below for detailed description).

Etymology: The specific name *texana* refers to the type region.

Description

Female

Habitus (Figure 1A). Body fusiform slightly compressed, with largest width along posterior margin of cephalothorax and near middle of first pedigerous somite. Length 575 μ m (holotype; paratype: 585 μ m). Proportional lengths cephalothorax-body: 1/4.5. Rostral tip short, rounded, bearing pair of sensilla. Genital double somite with entirely fused components, squar, showing short dorso-lateral reminiscent of posterior margin of first somite. Anal somite somewhat longer than preceding somite.

Integument of cephalothorax and pedigerous somites smooth, with hyaline un-incised fringe (Figure 1B). Ventral surface of urosomal somites ornamented with few anterior short rows of minute spinules and a transversal row parallel with posterior margin. Hyaline fringe of urosomal somites minutely incised.

Anal somite with convex anal operculum, bearing five prominent spinules. Posterior margin of somite with spinules in dorsal, lateral and ventral view. Ventral surface with anterior row of long spinules, and short row of spinules on right side of anal sinus (left side without, arrow in Figure 1B). Posteriormost edge of anal sinus furnished with long bare setules.

Caudale rami slightly tapering posteriorly, twice as long as wide, with sclerified slim keel parallel with ventral inner proximal margin and bearing seven elements. Integument smooth except for 3–4 spinules along posteroventral margin and 1–2 spinules near implantation of lateral setae. Dorsal seta with basal part, arising near posterior inner edge. Three lateral setae, shorter than ramus, with distalmost one bulbous near implantation. Principal setae bipinnate (not illustrated). Inner distal seta half as long as ramus.

Antennule (Figure 2A): Eight-segmented with on each segment (Roman numerals) following number of setae (Arabic numerals) and aesthetascs: I (1)-II(10)-III(8)-IV(4+Aest)-V(2)-VI(3)-VII(4)-VIII(7+Aest). Integument of segments smooth, except for short row on inner border of segment I. Setae smooth. Setae with breaking plain in proximal part arrowed in illustration (segments III, V, VI, VIII); segments VII and VIII with two and four biarticulate setae, respectively.

Antenna (Figures 2B, C): Coxa without ornamentation. Basis and first endopodal segment without abex-

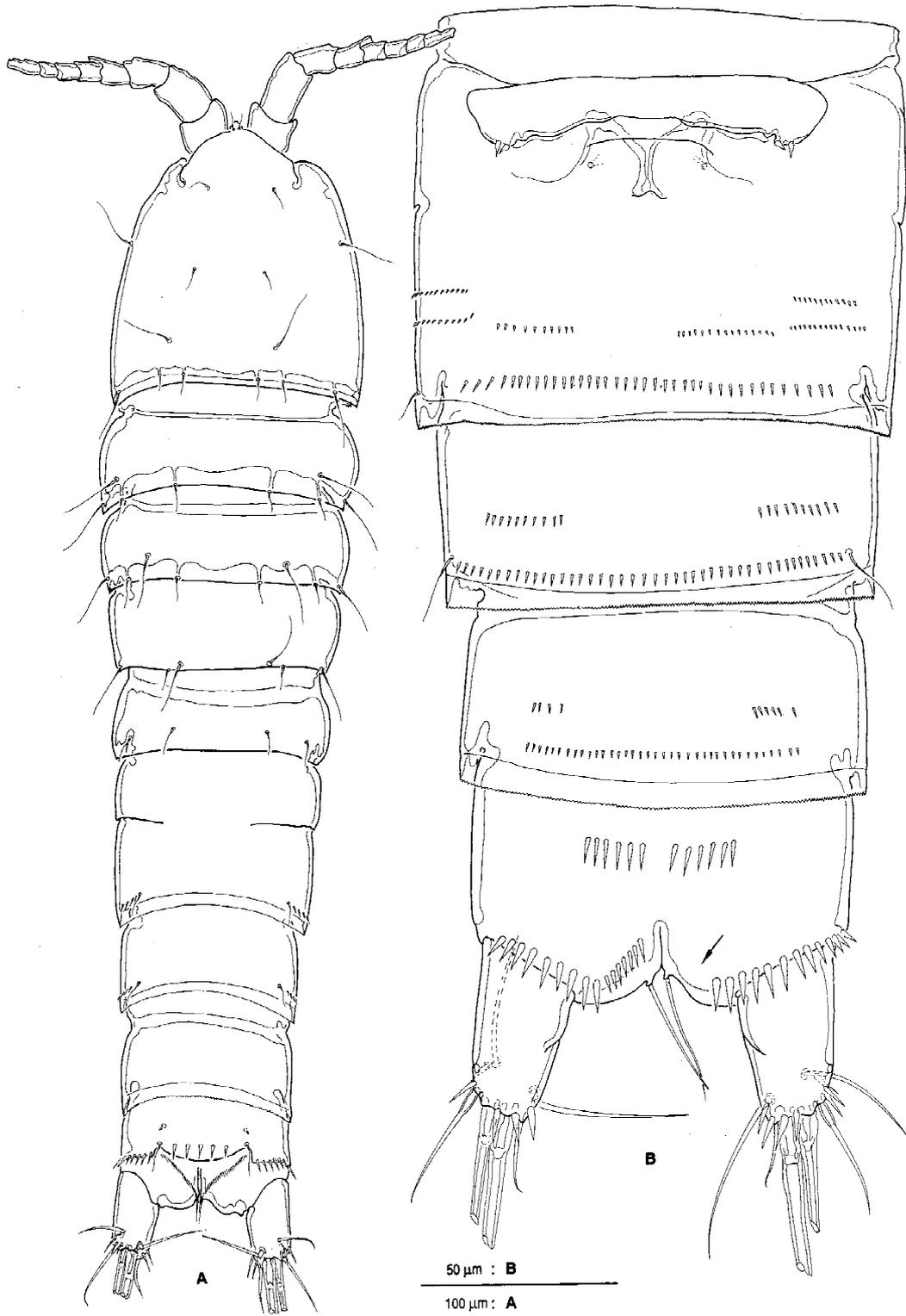


Figure 1. *Nitocrellopsis texana* n. sp.: (A) Habitus of female, dorsal; (B) Female urosome, ventral (A)–(B): holotype.



Figure 2. *Nitocrellopsis texana* n. sp.: (A) Female antennule, exploded; (B) Antenna; (C) Antennal exopodite; (D) Maxillule; (E) Maxilla; (F) Maxilliped; (G) Mandible; (H) Male antennule, segments II-VIII (A)-(E): holotype; (F)-(H): allotype.

opodal seta. Second endopodal segment with few large spinules on inner margin and two combs of spinules along outer border. Two spines and a slender seta on lateral margin, five geniculated distal setae and a pinnate seta; the latter fused at base with a distal geniculated seta on apical margin. Exopodite rather large, one-segmented, bearing three robust spines: one lateral with brush-like tip and two distal spines armed with long spinules in distal half of one side of the stem.

Mandible (Figure 2G): Gnatobasis robust with weakly developed pars molaris. Biting edge with numerous teeth, and hyaline appearance. Mandibular palp two-segmented without elements on proximal segment, and five apical setae on second segment two of them fused near base.

Maxillule (Figure 2D): Praecoxal arthrite with three uni-pinnate distal claws and two pairs of smooth setae on surface. Coxal endite with two slender setae and one geniculated seta on distal end. Basal endite somewhat shorter than coxal endite, bearing four setae on distal border. Rami vestigial represented by a single short seta.

Maxilla broken in holotype female; see description of male.

Maxilliped (Figure 2F): Syncoxa and basis equal in length, former with subdistal plumed seta but without integumental ornamentation. Basis with short row of spinules on outer distal edge and row of slender spinules parallel with inner margin of palm. Claw somewhat longer than basis, without accessorial seta or ornamentation.

P1 (Figure 3A): Praecoxa with short spinule row near anterior distal edge. Coxa with two rows of slender spinules in outer half of anterior surface and few setules along median border. Coupler rectangular, without ornamentation. Anterior surface of basis with rows of spinules near implantation of inner and medial elements and in middle of distal border. Outer and medial elements of basis spiniform, armed along outer border of stem. Exopodite and endopodite three-segmented, the latter just reaching beyond exopodite. Exopodite segments with strong spinules along outer margin and on outer distal edge. Outer spines uni-pinnate. Distal elements of third exopodal segment geniculated. Inner seta on median segment with brush-like tip. First endopodal segment 1.7 times as long as wide, just reaching beyond first exopodal segment, with spinulose outer and setulose inner border. Inner seta with brush-like tip. Median and terminal segment sub-equal, 1.9 and 2.5 times as long as wide, respectively. Inner margin setulose, outer one spin-

ulose. Inner distal seta on terminal segment shorter than segment; median seta geniculated and outer one spiniform, uni-pinnate armed.

P2 (Figure 3C), P3: Praecoxa with short row of spinules near outer distal edge of anterior surface. Surface of coxa smooth. Coupler U-shaped, with smooth surfaces. Basis with long spinules near implantation of outer element and in middle of distal border. Outer element of P2 basis short, robust and ornamented with minute spinules; of P3 basis slender and smooth. Exopodite and endopodite three-segmented, latter reaching in P2 to distal end of median exopodal segment, only to implantation of inner exopodal seta in P3. Outer margins and outer distal edges of exopodal segments ornamented with strong spinules. Outer spines of exopodite uni-pinnate. Inner seta on median segment with brush-like tip. Endopodal segments with setulose inner and spinulose outer border. Inner element on proximal and median segments with brush-like tip. Distal segment with plumose inner seta and a smooth spiniform outer element.

P4 (Figure 3D): Protopodite and coupler as in P3. Exopodite three-segmented with same ornamentation as in preceding legs. Endopodite two-segmented, not quite reaching middle of median exopodal segment. Outer border of proximal segment and inner border of distal segment smooth; inner border of proximal segment setulose and outer border of distal segment spinulose. Distal segment with inner plumose seta and outer pinnate spine.

Setal complement of the legs in Table 1.

P5 (Figure 4A): Baseoendopodites of both legs fused medially, forming an entire transversal plate with slightly raised endopodal lobes. Outer seta of baseoendopodite smooth, articulating on basal element. Endopodal elements spiniform, pinnate in distal third along outer side of stem. Exopodite small, only slightly longer than wide, bearing five smooth setae: one outer, one inner and three distal ones (middle one longest).

P6 (Figure 1B): Vestiges forming large transversal plate with only slightly raised lateral edges. Both vestiges ornamented with two minute hyaline elements. Copulatory pore rather small, located shortly posteriorly and leading to slender cylindrical copulatory duct.

Male

Habitus as in female except for separated genital somites. Length 581 μm (paratype). Integumental ornamentation on ventral surface as in female.

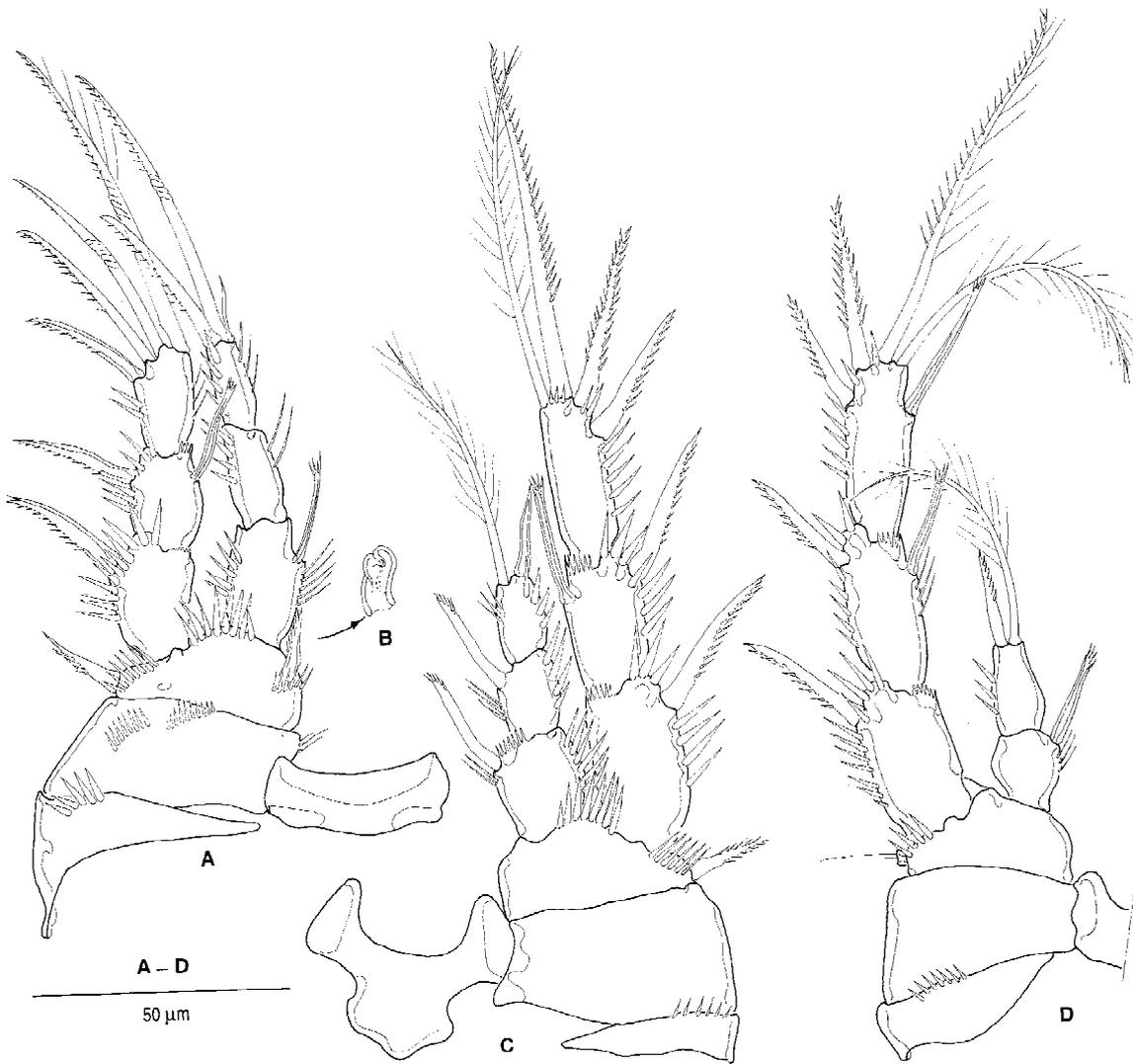


Figure 3. *Nitocrellopsis texana* n. sp.: (A) P1; (B) Medial modified spine of male P1; (C) P2; (D) P4 (A)–(D) anterior view; (A) (C)–(D): holotype; (B) allotype).

Antennule (Figure 2H): Nine-segmented, haplocerate (first and second segments broken off in allotype), with following armament: I(1)-II(8)-III(7)-IV(3+2sp)-V(2+1sp+Aest)-VI(1+1sp)-VII(3)-VIII(4)-IX(7+Aest). Original segment IV fused to segment V, with fine remnant of former separation. Spines on segments IV, V and VI robust and pinnate. Segments VIII and IX with two and four setae, respectively, articulating on basal part.

Maxilla (Figure 2E): Syncoxa with two endites: proximal one with a thick and finely plumed seta, distal one with a single brush-like element. Basis with large claw and robust additional seta, both armed

distally. Endopodite represented as a minute segment, bearing two slender and naked setae.

Medial spine on P1 basis transformed into a robust bilobed element, as long as female medial spine (Figure 3B). Exopodites and endopodites P2–P4 as in female, except for sharp attenuation of outer distal edge of median exopodal segment of P2 (Figure 4G) and the slightly stronger appearance of the outer distal spine on third endopodal segment of P2 (Figure 4E).

P5 (Figure 4C): Baseoendopodites fused as in female, with plumose outer setae implanted on basal part. Endopodal lobes vestigial, bearing one or two robust spines, armed only near tip. Exopodite small, bear-

Table 1. Chaetotaxy of the *Nitocrellopsis* species

	P1		P2		P3		P4		P5♀	P5♂
	EXO	END	EXO	END	EXO	END	EXO	END	EXO/END	EXO/END
<i>N. intermedia</i>	0-1-023	1-0-111	0-1-022	1-1-111	0-1-022	1-1-111	0-1-022	1-111	vest. ^a	vest. ^a
<i>N. elegans</i>	0-1-023	1-0-111	0-1-122	1-1-011	0-1-122	1-1-111	0-1-222	1-011	4/3	5/1
<i>N. texana</i>	0-1-022	1-0-111	0-1-022	1-1-011	0-1-022	1-1-011	0-1-122	1-011	5/2	5/1-2
<i>N. petkovskii</i>	0-1-022	1-0-011	0-1-122	0-0-011	0-1-122	0-0-011	0-1-122	0-011	4/2	4/2
<i>N. hellenica</i>	0-1-022	1-0-111	0-1-022	0-0-001	0-1-022	0-0-011	0-1-122	0-001	4/3	4/2
<i>N. hippocratis</i>	0-1-022	1-0-111	0-1-022	0-0-001	0-1-022	0-0-011	0-1-122	0-001	4/3	4/2
<i>N. ioneli</i>	0-1-022	0-0-111	0-1-022	0-0-011	0-1-022	0-0-011	0-1-122	0-011	5/4	4/2
<i>N. ahaggarensis</i>	0-1-022	0-0-111	0-1-022	0-0-011	0-1-022	0-0-011	0-1-122	0-011	5/4	5/2
<i>N. rouchi</i>	0-1-022	0-0-111	0-1-022	0-0-011	0-1-022	0-0-011	0-1-022	0-011	4/4	5/2

^aVestigial: rami represented by 2 or 3 setae only.

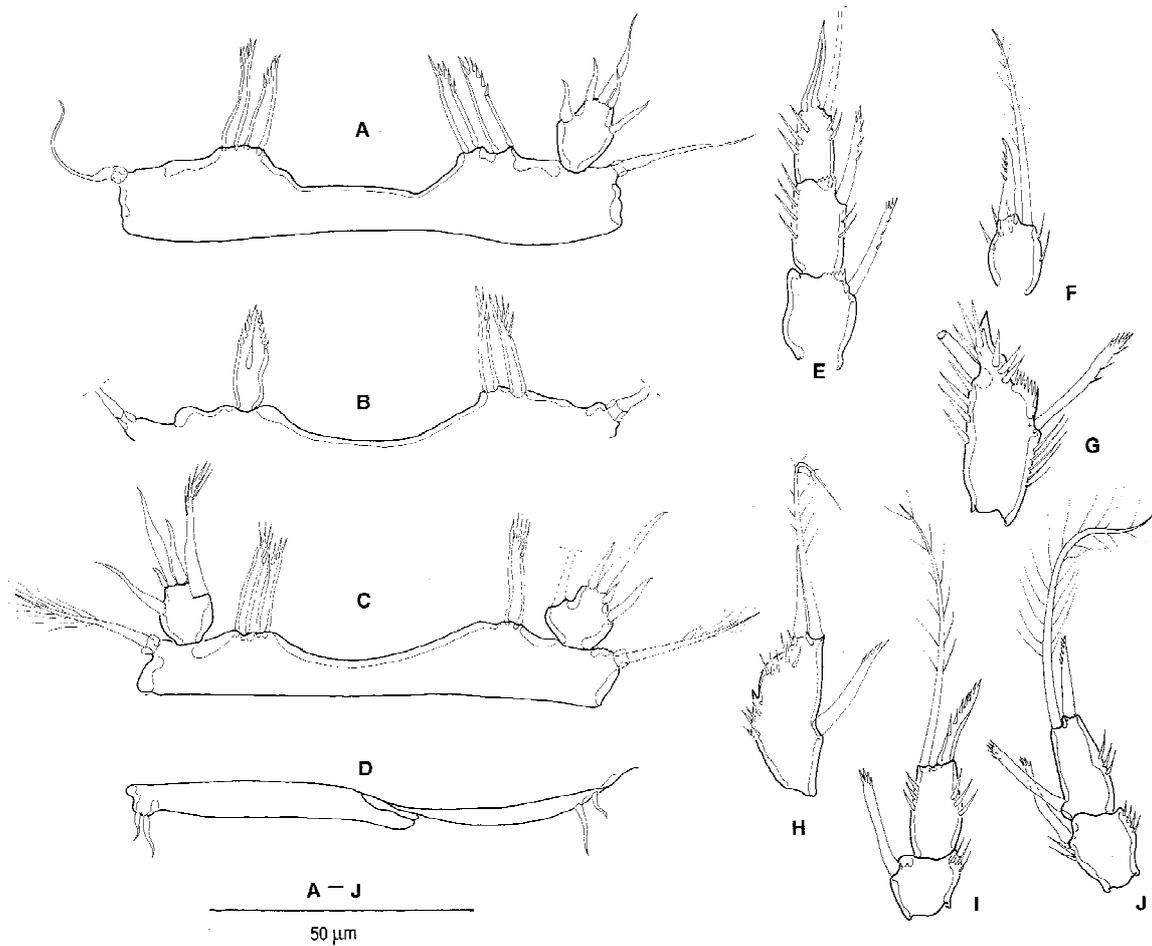


Figure 4. *Nitocrellopsis texana* n. sp.: (A) Female P5, right exopodite not illustrated; (B) Female P5 baseoendopodite; (C) Male P5; (D) Male P6; (E) Male endopodite P2; (F) Third endopodal segment male P3; (G) Median segment female exopodite P2; (H) Abberant female P4 endopodite; (I) Male P4 endopodite; (J) Abberant male P4 endopodite ((A) holotype; (B), (H): female paratype; (C)–(G), (I): allotype; (J): male paratype).

ing five elements: one outer and three apical smooth elements, and one pinnate subdistal inner spine.

P6 (Figure 4D): Vestiges each with two short naked setae. Right P6 rectangular, left one not differentiated.

Variability

In the female paratype (USNM 274243) the left endopodal lobe of P5 bears a complex bifid structure formed by the basal fusion of the two elements (Figure 4B). The left P4 endopodite of this specimen is one-segmented with one inner and two apical spines (Figure 4H). The allotype specimen bears an additional inner brush-like element on the second segment of the right P4 (Figure 4J). The left ramus of this specimen and both rami of the male paratype (USNM 274243, Figure 4I) are the same as the female.

Discussion

Among the nine known *Nitocrellopsis* species, thus including *N. ahaggarensis* described below, *N. texana* n. sp. takes an intermediary position. With its full armament on the proximal and median endopodal segments of P2 and P3, and on the basal segment of the P4 endopodite, *N. texana* n. sp. most resembles *N. intermedia* and *N. elegans*. It differs from both in the chaetotaxy of the P1 exopodite, bearing only four elements on the distal segment instead of five (see below for further discussion).

Description of type-locality

Honey Creek Cave, type locality of *N. texana* is the longest known cave in Texas with 31.26 km of surveyed passage (Elliott & Veni, 1994). It is located 340 km inland from the Gulf coast in Hill Country of Central Texas, 28 km east of Boerne. Nearly all the passages in the cave contain active streams. There are three entrances to the cave – the spring or wet entrance the nearby overflow or dry entrance, and the artificial shaft entrance located 3.5 km upstream. Between the spring and shaft entrances, the cave passage averages 4–5 m wide by 3–7 m high with most of the height occupied by water. Water temperature is 20–21 °C. The cave is formed as a spring at the base of the lower member of the Cretaceous Glen Rose Formation, a thick-bedded to massive fossiliferous limestone. The

cave originated from groundwater piracy between and within watersheds. Down cutting of a surface valley truncated the cave and formed its current entrance about 270 000 years ago. At six locations within the cave, base flow from one passage diverges and flows down two passages to different destinations. Modern discharge is substantially less than during the late Pleistocene as evidenced by mastodon and other bones encased in coarse gravel beneath recently deposited silts.

Honey Creek Cave is the type locality for the troglobitic salamander *Eurycea tridentifera* Mitchell & Reddell. The cave also contains the amphipod *Parabogidiella americana* Holsinger (in Holsinger & Longley, 1980) and is only the third record from this very rare troglobitic amphipod (John Holsinger, pers. comm. to T. Iliffe). The cirrolanid isopod *Cirolanides texensis* Benedict was also collected from this cave (Thomas Bowman, pers. comm. to T. Iliffe). This species is widespread in Texas cave and phreatic groundwater. A small bat colony roosts over the water within 100 m of the spring entrance.

Nitocrellopsis ioneli (Dumont & Decraemer, 1974)

Figures 5–7

Synonymy:

Nitocrella ioneli Dumont & Decraemer, 1974: 105–109, Figures 1–2; Dumont & Decraemer, 1977: 259; Dumont, 1984: 178.

Nitocrellopsis ioneli (Dumont & Decraemer, 1974): Petkovski, 1976: 19; Rouch, 1986: *vide* Dussart & Defaye, 1990; Rouch, 1987: 74–76; Dussart & Defaye, 1990: 73; Cottarelli & Forniz, 1993: 142. non *Nitocrella ioneli*: Van de Velde, 1982: 312. [= *Nitocrellopsis ahaggarensis*]

Material: Paratype series: one dissected female (mounted on four slides, labeled COP 4424A–D), one dissected male (mounted on four slides, labeled COP 4425A–D) and 18 ♀♀, 2 ♂♂, eight copepodites formaldehyde preserved, catalogued under number COP 4426.

Type-locality: Morocco, well close to Merzouga (31° 15' N, 04° 10' W). Leg. University of Ghent Expedition to Morocco, 27-7-71.

Amended description

Female

Habitus fusiform slightly compressed, with compon-

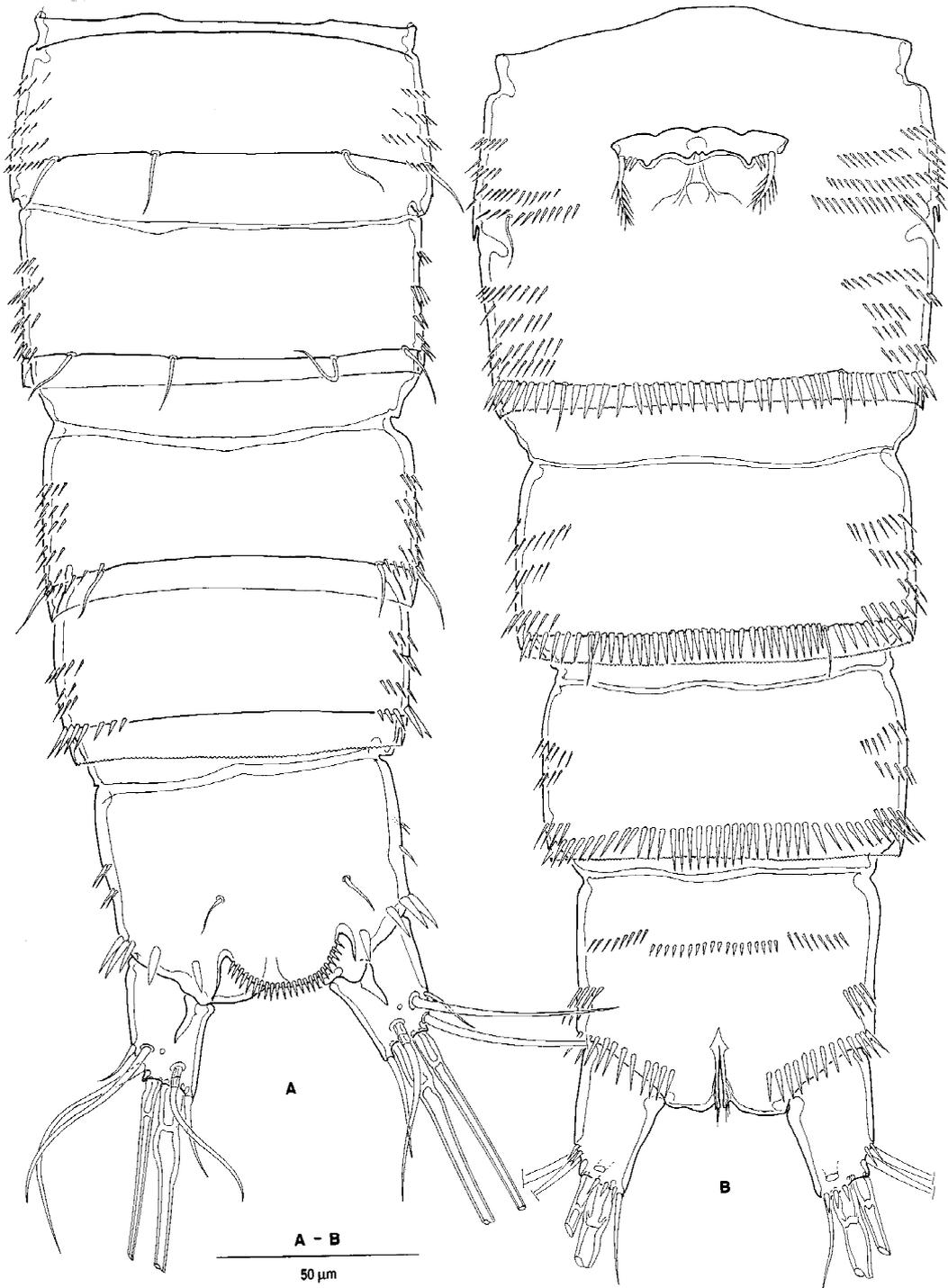


Figure 5. *Nitocrellopsis ioneli* (Dumont & Decraemer): (A) Female urosome, dorsal view; (B) Female urosome, ventral view (A)–(B): paratype female).

ents of genital double somite not fused dorsally, showing distinct posterior margin of first somite but no hyaline fringe (Figure 5A). Ventral surface of genital double somite entirely fused (Figure 5B). Length, including rostrum and caudal rami: 504 μm (492 μm –510 μm , $n=5$).

Integument of cephalothorax and pedigerous somites smooth. Urosomal somites adorned with parallel rows of slender spinules on lateral surface and with long strong spinules along posteroventral margins. Ventral and dorsal surface of urosomal somites plain.

Anal somite with convex anal operculum, garnished with 22–28 short spinules. Ventral surface with transversal rows of spinules in anterior half and near proximal outer edge. Posterior margin with two large spinules dorsally and entirely adorned laterally and ventrally (Figure 5B).

Caudale rami twice as long as wide, slightly tapering posteriorly, dorsally keeled near inner proximal corner. Lateral setae situated in distal third of ramus. Biarticulate dorsal seta implanted close to inner distal edge. Proximal lateral seta short, distal and median one 2–2.5 times as long as ramus. Inner principal seta with slightly bulbous proximal region. Integument of rami smooth, except for some spinules on ventral surface near implantation of lateral and principal setae.

Rostrum minute with rounded tip, attending only distal third of first antennular segment. One pair of sensilla.

Antennule eight-segmented (Figure 6A) with following armament: I(1)-II(8)-III(7)-IV(4+Aest)-V(2)-VI(3)-VII(4)-VIII(7+Aest). Setae smooth, some articulating on basal part on segments III, V, VI, VII and VIII. Integument of segments smooth, except for a short spinule row in proximal third of inner margin of first antennules segment.

Antenna typically with basis and one-segmented exopodite (Figure 6D). The latter with two pectinate elements and one serrate appendage. Endopodal segment with three subdistal and six terminal elements. Mandible with two-segmented palp, without setae on proximal segment and five setae on distal segment (two pairs fused near implantation). Labrum (Figure 6B) triangular with hyaline serrate apex, flanked on both sides with a series of long spinules and a median pair of serrate elements.

Maxillule (Figure 6C) with praecoxal arthrite bearing four apical serrate spines, two lateral smooth elements and two slender surface elements. Coxal endite with two, basal endite with five setae. Endopodite

(or exopodite) represented as a minute cylindrical segment, bearing two slender setae. Maxilla (Figure 7F) with two endites: proximal one bearing two thick and plumose setae, distal one with two setae and a pectinated spine. Basis with spinulose claw and pinnate seta. Endopodite obsolete, represented by two slender setae. Maxilliped (Figure 7E) with short syncoxa, bearing a distal plumose seta. Basis with a longitudinal spinule row parallel on inner margin of palm and a subdistal group of spinules on outer margin. Claw with accessorial seta, and serrate in distal half.

Setal complement of the legs in Table 1.

P1–P2 as illustrated in Dumont & Decraemer (1974).

P3 with long, slender outer seta, articulating on small basal part on basis. Exopodite as in female, without dimorphic outer spines. Endopodite (Figure 7D) with general appearance as in P2, but shorter, reaching only implantation of inner element on median exopodal segment. Third endopodal segment with inner apical plumose seta being 2.5 times as long as terminal spine.

P4 as in Dumont & Decraemer (1974), except for the short inner element on third exopodal segment having a brush-like tip and the longer inner apical plumose being somewhat longer than outer distal element.

P5 as in Dumont & Decraemer (1974), but with bipinnate innermost exopodal seta and an unarticulated outer seta on baseoendopodite.

P6 vestiges forming compact transversal single plate, not wider than 1/3 of somite width. Rami represented with an outer plumose seta and two minute hyaline elements (Figure 5B). Copulatory pore covered with integumental flap, leading to a short duct. Seminal receptacles not observed.

Male

Habitus as in the female, except for free genital somites. Length 485–500 μm . Integument of cephalothorax and pedigerous somites as in female. Ventral surface of third to fifth urosomal somites furnished with arcuate rows of spinules. Ventral surface of anal somite with a transversal anterior row of long spinules.

Antennule (Figure 6E) haplocerate, 10-segmented with following armament: I(1)-II(8)-III(6)-IV(2)-V(4+2sp+Aest)-VI(1sp+1)-VII (2sp+1)-VIII(3sp+1)-IX(4+1sp)-X(7+Aesth). General shape as illustrated in Dumont & Decraemer (1974: Figure 2B). Mouthparts as in female.

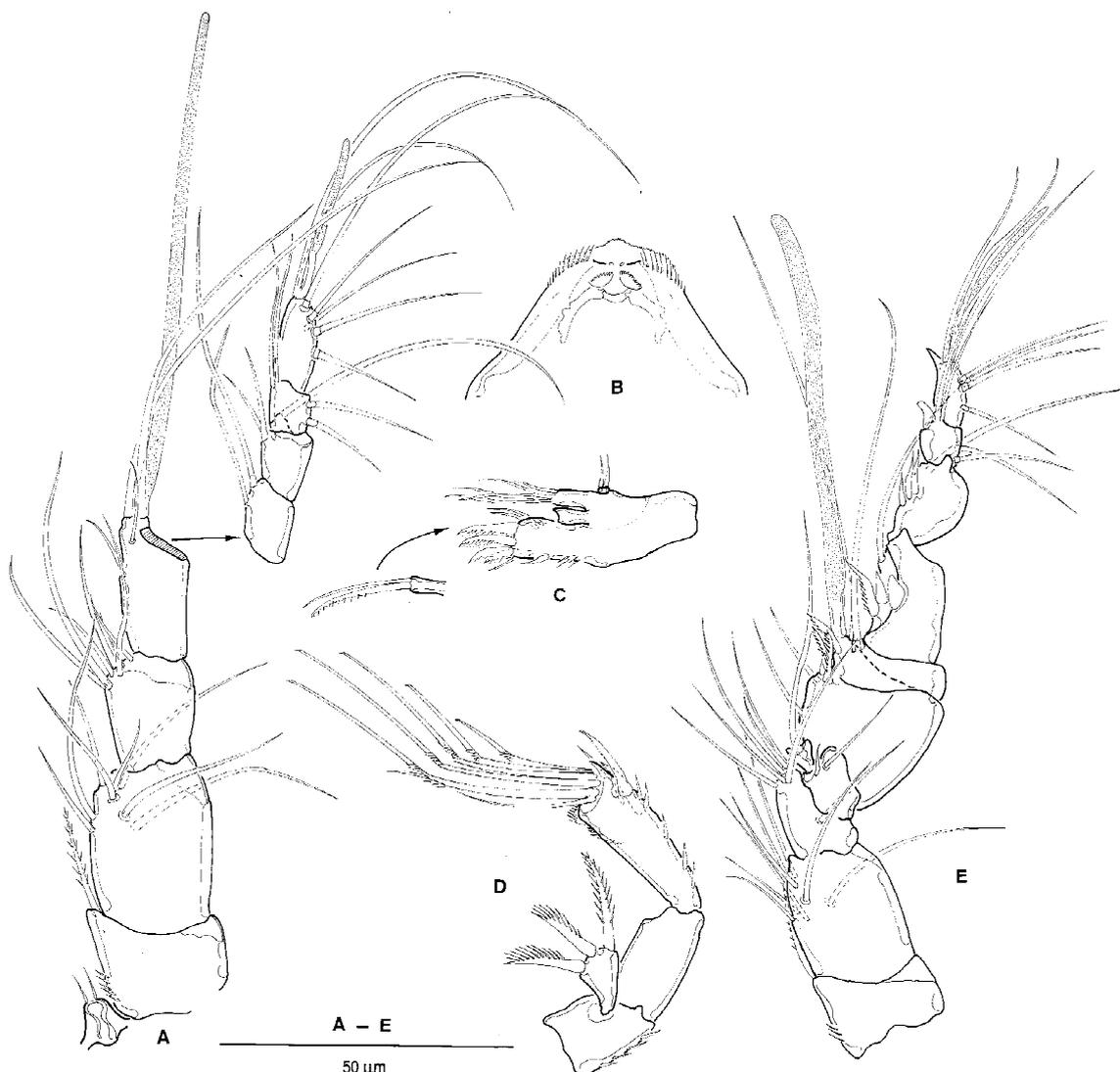


Figure 6. *Nitocrellopsis ioneli* (Dumont & Decraemer): (A) Female antennule, with rostral tip; (B) Labrum; (C) Maxillule, coxal endite detached; (D) Antenna; (E) Male antennule.

P1 (Figure 7B) with short medial bilobed dimorphic spine on basis, not reaching middle of first endopodal segment. P2 as in Dumont & Decraemer (1974: Figure 2E). P3 exopodite as in the female. Subdistal inner seta on endopodite P3 short, twice as long as distal element, at the most. The latter is somewhat grosser and stronger sclerotized than in female (Figure 7D). P4 and P5 as in Dumont and Decraemer (1974: Figure 2F).

P6 vestiges semi-ovate, both bearing two spinulose setae. Right one well distinguished from supporting somite, left one fused with somite (Figure 7A).

Nitocrellopsis ahaggarensis n. sp.

Figures 8–9.

syn. *Nitocrella ioneli* Dumont & Decraemer, 1974: Dumont, 1979: 315. [partim]; Van De Velde, 1982: 312.; Dumont, 1984: 177. [partim].

Type-material: Holotype: partially dissected female mounted on a single slide, with station-number 164 V ♀ (COP 4427); allotype: partially dissected male mounted on single slide with station number 164 V ♂ (COP 4428).

Type-locality: Algeria, near Tamanghasset. Man-made well named 'Source Hadrian' (22° 45' N, 05° 41' E). Leg. H. Dumont, 12 March 1977.

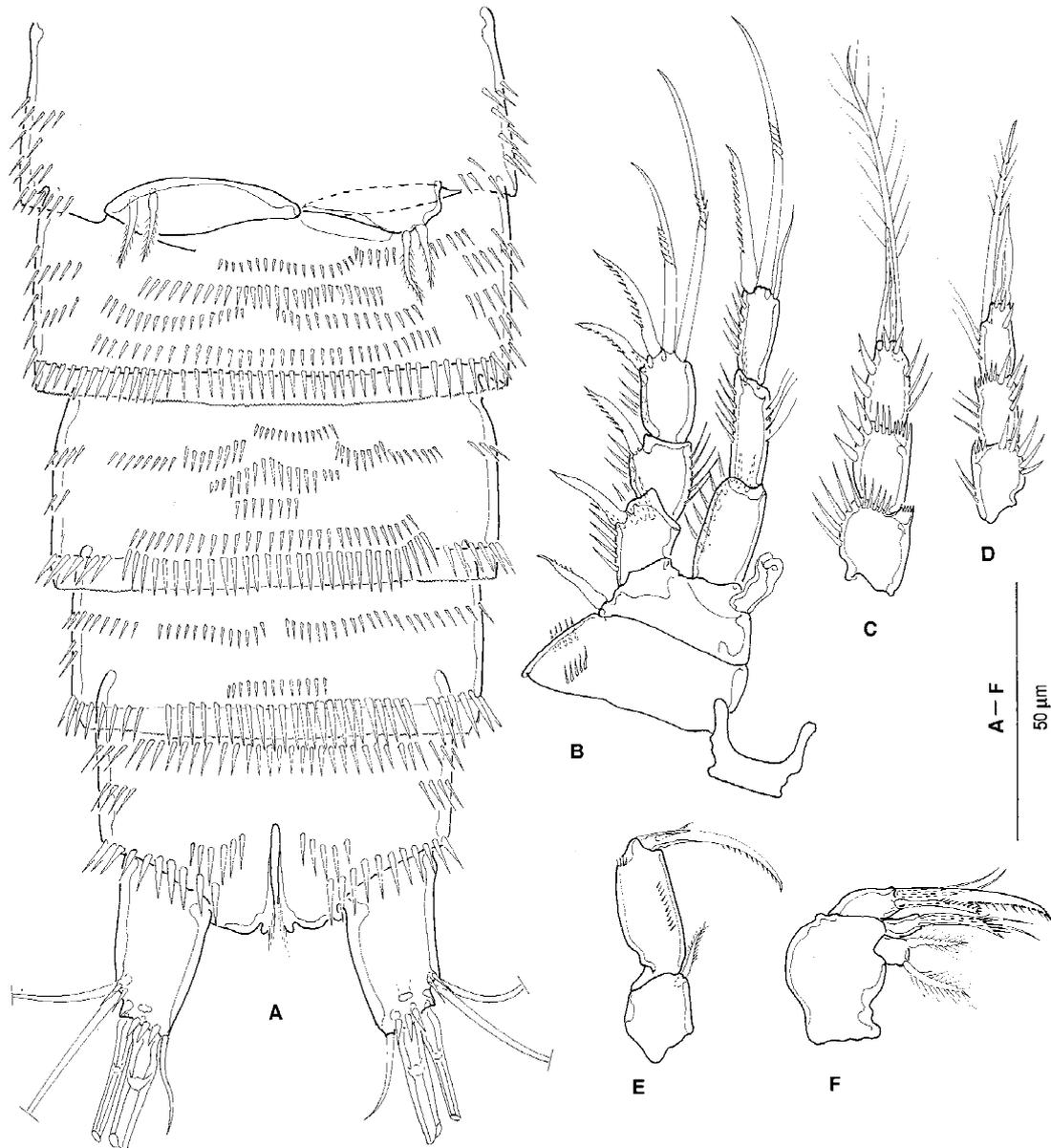


Figure 7. *Nitocrellopsis ioneli* (Dumont & Decraemer): (A) Male urosome, ventral view; (B) Abnormal male P1; (C) Female P3 endopodite; (D) Male P3 endopodite; (E) Maxilliped; (F) Maxilla (A)–(F) paratypes; (B) posterior; (C)–(D) anterior.

Etymology: The specific name *ahaggarensis* refers to the Ahaggar mountains in Niger, type-region of the species.

Description: Note: both mounted specimens are only partially dissected and are somewhat flattened. As such, it is impossible to provide accurate illustrations of urosome and buccal appendages. The description is kept to a minimum.

Female

Length from anterior margin of genital double somite to distal end of caudal rami: 305 μm , estimated total length 610 μm . Components of genital double somite not fused dorsally, with lateral reminiscents of separation, and entirely fused on ventral side.

Urosomal somites with long spinules along entire posterodorsal margin and a transversal row of

minute spinules in middle of dorsal surface. Central area of ventral surface of genital double somite smooth, lateral margins of both somites ornamented with four short transversal rows of strong spinules. Posteroventral margin with large spinules except for median smooth area. Ventral surface of fourth and fifth urosome somites as second genital component except for a single complete median transversal in fifth somite. Hyaline fringes of urosomal somites minutely sinuate.

Anal somite as in *N. ioneli* except for a transversal row of spinules in anterior third of dorsal surface and six large spinules along posterodorsal margin. Anal operculum convex, furnished with about 40 very slim spinules along margin. Anal sinus with short terminal hairs.

Caudale rami (Figure 9A: somewhat flattened) at the most as long as wide, keel not observed. Dorsal seta biarticulate. Proximal lateral and inner distal seta as long as ramus, distal one 1.5 times as long as ramus. Principal setae bipinnate. Integument smooth, except for seven spinules along posteroventral margin and two spinules near implantation of lateral setae.

Antennule, antenna and buccal appendages with general appearance and armature as in *N. ioneli*.

P1 protopodal segments garnished with several rows of spinules (Figure 8A). Outer and medial spine of basis bipinnate with short attenuated tip. Rami three-segmented, with endopodite reaching shortly beyond exopodite. Chaetotaxy and ornamentation of segments as in *N. ioneli*.

P2–P4 with chaetotaxy and general morphology as in *N. ioneli*, but differ from the latter in the following aspects: P2 (Figure 8B) and P3 (Figure 8C) with distal endopodal seta more than three times as long as distal spine.

P5 (Figure 9D) with slightly produced endopodal lobe, not reaching to middle of exopodite and bearing four bifid spines. Outermost endopodal spine reaching beyond middle outer median spine. Outer seta of basis articulating on short cylindrical extension. Exopodite ovate, 1.25 times as long as wide, with five elements: middle one and outermost one smooth, remaining ones spinulose. Integument smooth except for few spinules on inner margin of exopodite.

P6 vestiges (Figure 9C) forming a rigid, concave, median plate, not longer than 1/3 of somite

width. Vestiges represented only by a pinnate seta. Copulatory orifice wide, leading to short duct.

Male

Ventral ornamentation of urosomal somites resembling pattern in *N. ioneli* but composed by shorter spinules and less dense. Dorsal ornamentation of somites unknown.

P1 (Figure 9B) with medial modified spine reaching far beyond middle of first endopodal segment. P2–P4 as in female, without marked dimorphism of exopodal spines. Distal spine on endopodite P2 more robust than in female, armed along both sides and somewhat curved proximally (Figure 8E). Distal seta on P2 endopodite only 1.5 times as long as spine, furnished with stout setules along stem. P3 endopodite with smooth and curved distal spine (Figure 8E). Endopodite P4 as in female.

P5 (Figure 9E) with distinct baseoendopodite and ovate exopodite. Two endopodal bifid spines and five exopodal elements. Outer seta of basis broken off in specimens at hand. P6 as in *N. ioneli*.

Discussion

It is apparent that *N. ahaggarensis* is more closely related to *N. ioneli* than to any other species of the genus, as both species share the reduced chaetotaxy of the P1 endopodite (without an inner seta on the proximal endopodal segment). However, *N. ahaggarensis* is a distinctly larger species than its congener. Although its body length could only be estimated because the specimens examined were dissected, it seems that *N. ahaggarensis* is at least 100 μm longer than *N. ioneli*.

Other features distinguishing both species are the length/width proportions of the caudal rami (2/1 in *N. ioneli*, 1/1 in *N. ahaggarensis*) and the lengths of the lateral setae of the caudal rami (twice as long as the rami in *N. ioneli*, at the most 1.5 times in *N. ahaggarensis*). Males of both species are distinguishable by the chaetotaxy of the P5 exopodite, bearing five elements in *N. ahaggarensis* and four in *N. ioneli*, and the length of the medial spine on the P1 basis which reaches far beyond the middle of the first endopodal segment in the former.

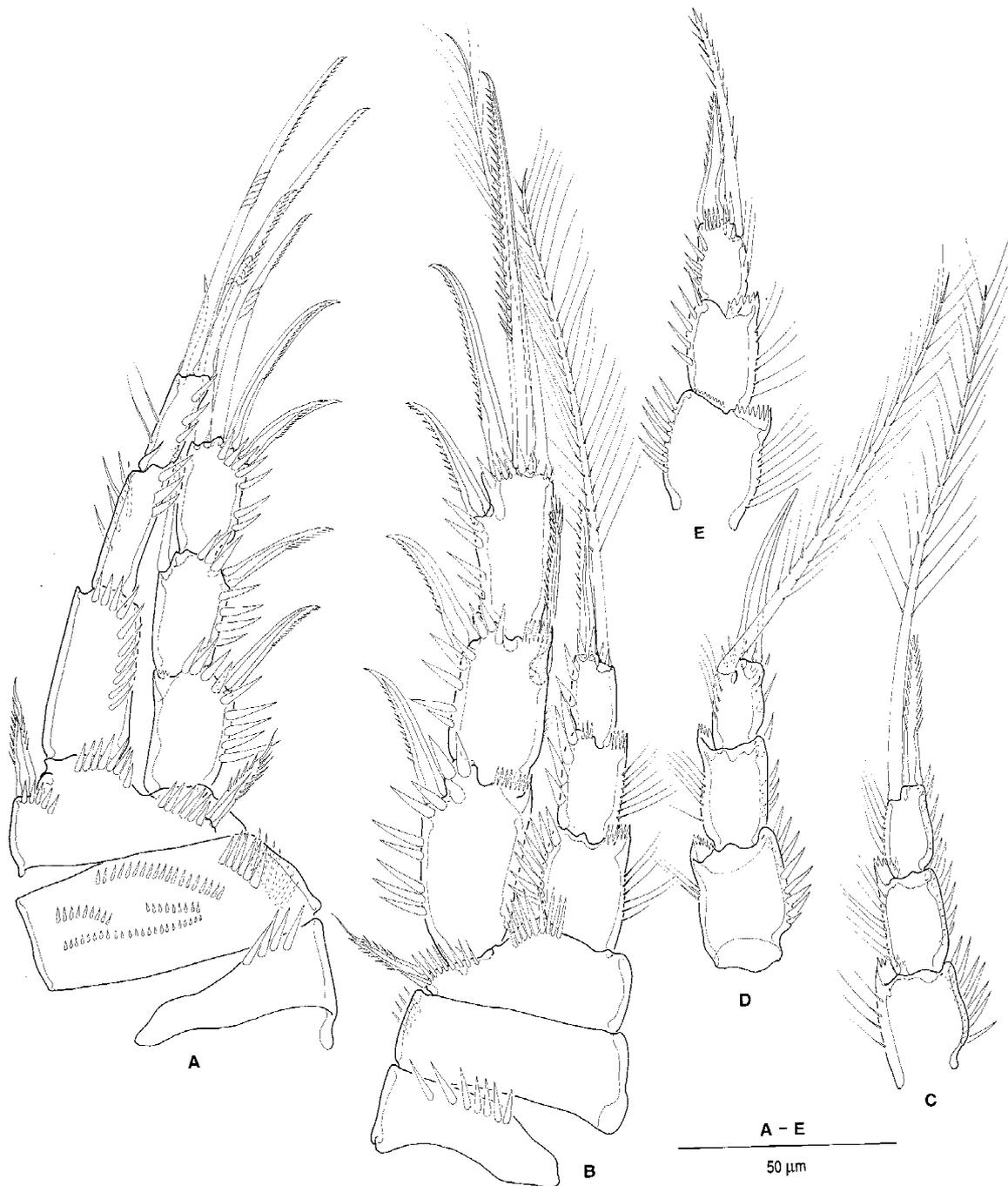


Figure 8. *Nitocrellopsis ahaggarensis* n. sp.: (A) Female P1; (B) Female P2; (C) Female endopodite P3; (D) Male P2 endopodite; (E) Male P3 endopodite (A)–(C), holotype female; (D)–(E), allotype male).

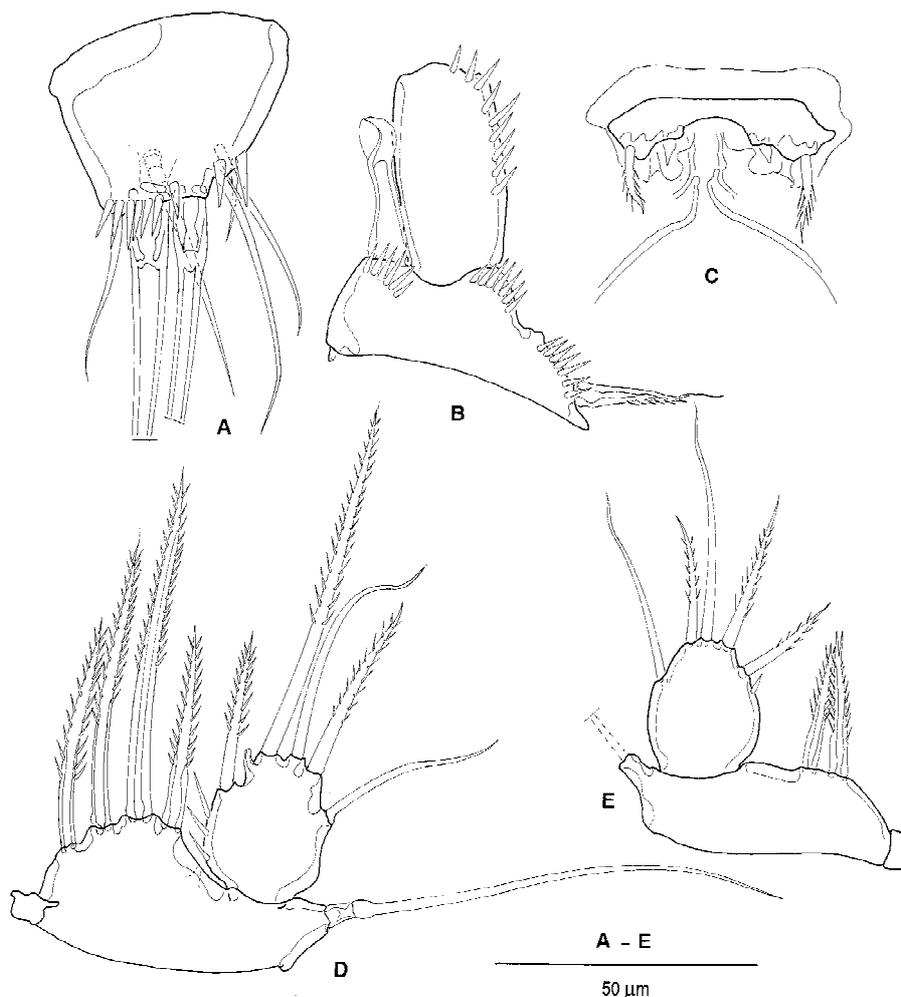


Figure 9. *Nitocrellopsis ahaggarensis* n. sp.: (A) Left female caudal ramus, ventral (slightly flattened), (B) Basis and first endopodal segment of male P1; (C) Female genital field; (D) Female P5; (E) Male P5 (A), (C)–(D), holotype female; (B), (E), allotype male.

General discussion

The genus Nitocrellopsis Petkovski, 1976

With the increased interest on the interstitial and hypogean realm, the number of interstitial and stygobitic harpacticoid copepods described in the second half of the present century grew exponentially. Common to all those taxa are the strong reductions of the setal complements and segmentation of the appendages which are generally considered as adaptations to their environment.

The variety of reduction patterns, mainly those observed in the natatorial legs, have been the stepping stone to clustering species together in genera. However, Lang (1965) stressed explicitly that in the

case of the Ameiridae Monard (1927, partim) et Lang (1936), the generic definitions are arbitrary groupings which do not represent the true phylogenetical relationships. These groupings have to be seen as a practical division of the morphological diversity displayed in this world wide distributed family. In the same discussion, however, Lang (1965) suggested to distribute the species of the genus *Nitocrella* over four different genera on the basis of the segmentation of the endopodite of the natatorial legs. His advice was followed by Petkovski (1976) who sub-divided the genus *Nitocrella* in three species groups according to their chaetotaxy of the leg 4 exopodite, and defined the genera *Nitocrellopsis* and *Stygonitocrella* primarily on the basis of their reduced endopodal segmentation of the legs.

The genus *Nitocrellopsis*, which at present assembles nine species (including the two described above), might be a typical example of such a non-natural assemblage. Unfortunately, we lack fundamental information on the exact morphology of the head appendages and of the body somites for two key species of the genus: *N. intermedia* (Chappuis, 1937) and *N. elegans* (Chappuis & Rouch, 1959). Attempts to locate type-material or topotypic material failed, so that we can only rely upon the limited information given in the original descriptions.

Thus far, we have indications for most of the species about the degree of fusion of the female genital somites (Galassi et al., 1999). For *N. elegans*, we have only indirect evidence, but when Chappuis & Rouch (1959) stated in the original description that the separation between the genital segment and the third urosomal one is indistinct, we assume that the fusion of this complex has to be fairly complete. Thus, three out of nine species actually assigned to the genus possess a genital double somite, which may be an indication that the Northern American representative, *N. texana*, and the south European species, *N. elegans* and *N. intermedia* are more close to each other than to the six other species. This assumption is corroborated by the fact that the three species have a comparable setal complement on the proximal and median endopodal segments of the legs 2–4 (see Table 1).

The three species known from northern Africa, the two from the eastern Mediterranean Isles and the recently described species from southern France seems to form a second cluster. All lack an inner element on the proximal endopodal segments of legs 2–4 and the median one of legs 2 and 3. Solely based on the chaetotaxy of the first leg, this peri-mediterranean group can be subdivided into two groups with *N. ioneli*, *N. rouchi* and *N. ahaggarensis* lacking an inner element on the first endopodal segment, and *N. hellenica*, *N. hippocratis* and *N. petkovskii* still possessing an inner seta on this endopodal segment. However, the sub-division of the peri-mediterranean group is not corroborated by the degree of fusion of the genital complex. Where *N. ioneli* and *N. ahaggarensis* have a ventrally firmly fused genital double somite (dorsally unfused), the four other species are characterised by a complete separation between pediger six and the third urosomite.

If it is assumed that *Nitocrellopsis* represents a monophyletic group, than represents the degree of fusion of the second and third urosomite a morphocline with the trans-atlantic species cluster as most

plesiomorphic (with a genital double somite) and the perimediterranean cluster as most derived (with a partially or entirely separated genital complex). However, whether the genus *Nitocrellopsis*, like several other ameirid genera, is a natural assemblage remains hypothetical because of our inadequate knowledge of so many ameirids.

Tethyan relict distribution?

The harpacticoid family Ameiridae is a complex assemblage of several genera living in a wide array of habitats ranging from pure marine to freshwater. There are indications that the wealth of phreatic ameirid freshwater species have their origin from marine – estuarine ancestors. Genera as *Nitocra* Boeck, 1864, *Nitocrella* Chappuis, 1923 and *Parapseudoleptomesochra* Lang, 1965 of which most of their species are known from inland waters, still have marine-aestuarine representatives.

The distribution of *Nitocrellopsis* as defined nowadays is reminiscent of that of the thermosbenacean genus *Tethysbaena* Wagner, 1994. Species of *Tethysbaena* have three general areas of distribution: Central Texas, Caribbean (Hispaniola, Cuba, Puerto Rico, the British and U.S. Virgin Islands) and Mediterranean and East African (Israel, Somalia, Morocco, Spain, Italy, Croatia, Greece and the Balearic Islands). Similar distribution patterns are known for several other crustacean taxa (see Botosaneanu et al., 1989; Notenboom, 1991; Coineau, 1994; Sanz et al., 1995). In all those cases, a Tethyan distribution pattern with main center in southern north America, the Caribbean, and the perimediterranean regions is obvious (Holsinger et al., 1994). Moreover, for some of these groups (i.e. cirrolanid isopods, atyid shrimps), sister taxa still roam the shallow continental waters.

Relying on the interpretation of the present day distribution of the several other crustacean taxa, we infer that the genus *Nitocrellopsis* displays a typical Tethyan distribution pattern, with a trans-Atlantic range of the most ancestral cluster of species (*N. intermedia*, *N. elegans* and *N. texana*).

If *Nitocrellopsis* is considered as derived from a marine ancestor (thallasobiont), inhabiting the interstitial of Tethyan shallow waters, the amphi-Atlantic distribution of the genus and its penetration of the Sahara can be an indication that the ancestral range of *Nitocrellopsis* should be situated between the late Cretaceous Turonian (90 mY) and the Paleocene (65–

55 mY) when large, Tethyan connected seaways over the western saharian region and over large parts of the North American continent were established (Smith et al., 1994).

However, not all taxa which have representatives in estuarine environments and which apparently show a comparable Tethyan distribution are unequivocally of marine origin. Wägele (1983) and Wägele et al. (1995) on phylogenetical grounds oppose the marine origin of interstitial living microcerberid isopods and claim that these animals were derived from freshwater ancestors, which subsequently invaded the interstitial realm of the coastal mesopsammal.

Unfortunately, and again because of the absence of sound hypotheses on the phylogenetic relationships between ameirid genera, we are unable to advance a comparable profoundly documented reasoning. This not only applies to the case of *Nitocrellopsis*, but also to the several highly advanced species and genera of the hyporeal of continental waters.

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