

Amphi-Atlantic distribution of the subterranean amphipod family Metacrangonyctidae (Crustacea, Gammaridea)

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Abstract

Members of the strictly stygobiont, continental subterranean amphipod family Metacrangonyctidae are reported for the first time outside the Old World. Two new species of *Metacrangonyx* are described from two widely separated localities in the Dominican Republic (Hispaniola), one facing the Caribbean and the other the Atlantic ocean. The discovery of metacrangonyctids in the western Atlantic suggests that they are an ancient subterranean lineage tied to the shores of the Tethys belt, and thus weakens previous biogeographic arguments raised to favour their separate and independent family status with respect to the Hadziidae. The discovery in the Mediterranean of marine populations of metacrangonyctids is reported as well, and both findings are used to test the reliability of the scenario currently held for the origin and evolution of this peculiar group of stygobiont amphipods. It is concluded that *Metacrangonyx* is a thalassoid lineage already present in the shores of the western Tethys before the complete aperture of the central North Atlantic (circa 110 Myr BP), and with marine populations persisting at both shores of this ocean until some time in the Quaternary, in case they have not yet disappeared. Evidence derived from Hispaniolan and Balearic *Metacrangonyx* does not support the correspondence between species-groups and the time at which precise waves of colonization of continental ground waters took place (after Turonian and Senonian marine regressions, respectively) as is assumed to occur for Old World taxa.

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Introduction

The metacrangonyctidae Boutin & Messouli, 1988 is a strictly stygobiont taxon displaying a broad peri-Mediterranean distribution. Sixteen species in two genera, one of them monotypic, have been described thus far, most from ground waters in Morocco (12 species in two genera; see Balazuc & Ruffo, 1953; Ruffo, 1954; Karaman & Pesce, 1980; Boutin & Messouli, 1988a; b; Messouli et al., 1991; Oulbaz et al., 1998), with others occurring as solitary outliers in the Sinai Peninsula (near the Red Sea; Ruffo, 1982) and the Dead Sea depression (Karaman, 1989) to the East, Fuerteventura (Canary Islands; Stock & Rondé-Broekhuizen, 1986) to the West, and Mallorca and Minorca (Balearic Islands; Chevreux, 1909; Margalef, 1952), and Elba (Tuscan Archipelago; Stoch, 1987) to the North. Most are freshwater interstitial taxa gathered in springs, wells, or alluvial sediments, but the taxon from Elba was caught in a slightly brackish well, whereas the Balearic taxon occurs in a wide range of salinities, from fully marine (D.J., pers. obs.) to completely fresh waters. The species from the Dead Sea depression is athalassohaline. Only the Balearic species seems to be an ordinary cave-dweller.

The mainly limnicoid habits and the peculiar morphology (especially their reduced, uncleft telson and reduced third uropods) of metacrangonyctids have made their taxonomic placement – and underlying alternative freshwater or thalassoid origin – a matter of debate. Their early assignment to the (primarily freshwater, Holarctic) crangonyctids (Schellenberg, 1936) was convincingly dis-

carded by Holsinger (1977). Their inclusion in the (marine / thalassoid stygobiont, Tethyan) hadziids (Barnard, 1976; Bousfield, 1977) was not supported by Stock (1977), by Barnard & Karaman (1982), or by Ruffo (1982), the latter considering metacrangonyctids as an isolated intermediate between the crangonyctids and the hadziids. The conservative expression of the diagnostic morphological traits, the relatively high number of species comprising the group (many not yet formally described; see Boutin, 1994), plus their apparent restriction to the Old World only, led Boutin & Messouli (1988b) to propose distinct family status for this taxon, although "closely allied to the essentially marine family Hadziidae" (see Boutin, 1994: 50).

In this paper we describe two new species of *Metacrangonyx* Chevreux, 1909 from widely separated localities in the Dominican Republic (Hispaniola), one facing towards the Caribbean and the other to the Atlantic ocean (see Fig. 1). These new taxa, together with the discovery in the Mediterranean of marine populations of metacrangonyctids, allow the testing of the currently held scenario for the origin and evolution of this peculiar group of stygobiont amphipods (Boutin, 1994). The presence of metacrangonyctids in the western Atlantic is remarkable since it suggests they are an ancient subterranean lineage tied to the shores of the Tethys belt, and weakens previous biogeographic arguments made to support their separate and independent family status with respect to the Hadziidae S. Karaman, 1932 (see Boutin, 1994: 50, 59 and fig. 7).

Material and methods

The amphipods were gathered using a hand-held plankton net attached to an extensible (to 3 m) handle. Baited traps left in the lakes for several days did not produce any specimens. Specimens were coloured by Black Chlorazol B cuticular staining following the procedure described in Wagner (1994). Drawings were prepared using a camera lucida on an Olympus BH-2 microscope equipped with Nomarski differential interference contrast. Body measurements were derived from the sum of the maximum dorsal distances of somites. Ma-

terials are deposited in Museo Nacional de Historia Natural, Sto. Domingo, Museo de la Naturalesa de les Illes Balears, Palma de Mallorca [MNCM], and in the Crustacea collection of the Zoologisch Museum, University of Amsterdam [ZMA]. Positioning of the caves was determined with a MAGELLAN GPS Blazer12 receiver.

The caves

"Cueva Seca" (= Dry Cave; Fig. 1) contains 717 m of traversable passage, and has a vertical extent of 30 m. Being formed along a fracture, it is mostly linear with average cross-sectional dimensions of 15 m wide and 5 m high. The entrance is a collapse sink, with a talus pile leading down to the water table. However, beyond this low point is a large breakdown chamber with two small skylights to the surface. At the far side of this large room the floor of the cave again drops down to water table, and the cave continues for just over 200 m. Swimming or boating is required to reach the end of the cave.

The cave is formed in Quaternary age limestone, with the overlying land surface relatively flat-lying. The primary vegetation above the cave is thorn scrub/pasture, although it is likely that the cave watershed extends beneath sugar cane fields to the north. The lower levels are phreatic in origin, with higher areas existing due to ceiling collapse. Stalactites and stalagmites are common in the upper levels, and generally absent in the lower levels. The groundwater flows through the cave southward, toward the Caribbean Sea, which is three km away. Seven caves have been discovered along the same fracture as Cueva Seca, with three being deep enough to encounter the groundwater. At the upstream end of Cueva Seca is a bat colony (10,000+), which deposits large amounts of guano in the water. *Phyllonycteris poeyi* Gundlach, 1860, *Artibeus jamaicensis* Leach, 1821, *Brachyphylla nana* Miller, 1902, *Pteronotus parnellii* (Gray, 1843) and *Mormoops blainvilleii* Leach, 1821 are known from this roost. Additionally, *Eptesicus fuscus* (Palisot de Beauvois, 1796) and *Macrotus waterhousii* Gray, 1843 are known from the cave entrance area.

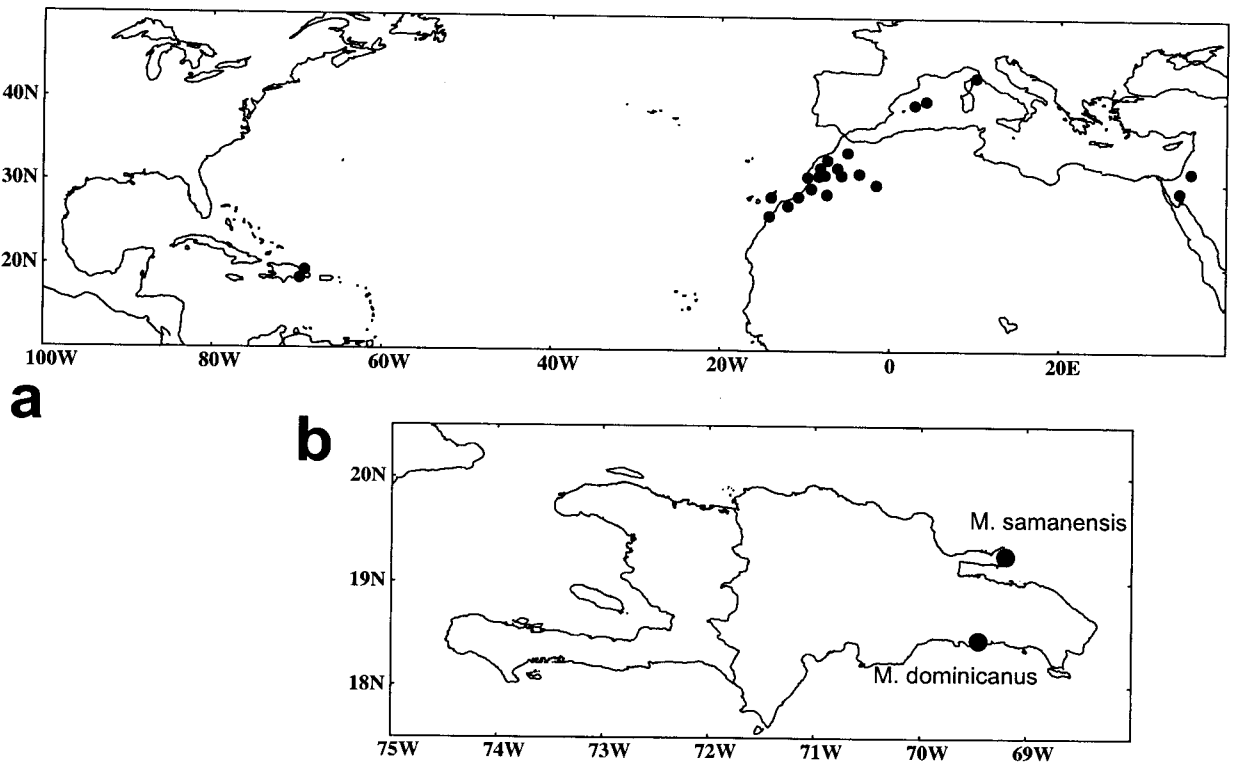


Fig. 1. a, amphi-Atlantic distribution of *Metacrangonyx*; b, map of Hispaniola showing the localities for the two new *Metacrangonyx* species.

“Cueva del Agua de Saturnino” opens less than 500 m inland from the shore line. It is excavated in the Quaternary terrace extending from the base of the cliffs of metamorphosed dolomites facing the sea on the trail to Playa Frontón (Cabo Samaná; Fig. 1). It consists of a single chamber of about 40 × 20 m, with a still, slightly brackish water lake of 10 × 3.5 m occupying the lower reaches of the cave (the cave is 27 m deep to the water line, the latter corresponding to the sea level). This cave is used as an emergency watering point for the people living along the cliffs; getting their permission to enter is recommended before undertaking any sampling.

Systematics

Order Amphipoda Latreille, 1816
 Suborder Gammaridea Latreille, 1803
 Family Metacrangonyctidae Boutin & Messouli, 1988
 Genus *Metacrangonyx* Chevreux, 1909

Metacrangonyx dominicanus sp. nov. (Figs. 2-9)

Material examined. – San Pedro de Macoris province, near Juan Dolio (southern Dominican Republic): “Cueva Seca”. UTM coordinates: 2038475N 448421E. HOLOTYPE: disarticulated adult female (oöstegites developed) 9.69 mm, in 70% ethanol vial deposited in the collection of the Museo Nacional de Historia Natural, Sto. Domingo. PARATYPES: thirteen adult females in 70% ethanol vial [ZMA reg. no. AMPH. 204933 b], two partially disarticulated adult males (penile papillae developed) in 70% ethanol vial [ZMA reg. no. AMPH. 204933 a], plus two females lacking oöstegites in 70% ethanol vial [MNCM reg. no. 363]. Collected by authors, 28 October 1999. Accompanying fauna: *Macrobrachium lucifugum* Holthuis, 1974, *Stygiomysis* sp., cyclopoid copepods. Fresh water.

Description of female. – Body length of 10 specimens 9.69, 7.68, 8.47, 8.96, 8.66, 8.46, 7.55, 7.47, 8.80, and 7.12 mm. Blind and unpigmented. Troglolitization manifest also in elongation of first and second antennae (especially of peduncle segments of both limbs, and main flagellum of antenna 1), and of pereopods 5 to 7 (Fig. 2A). Terg-

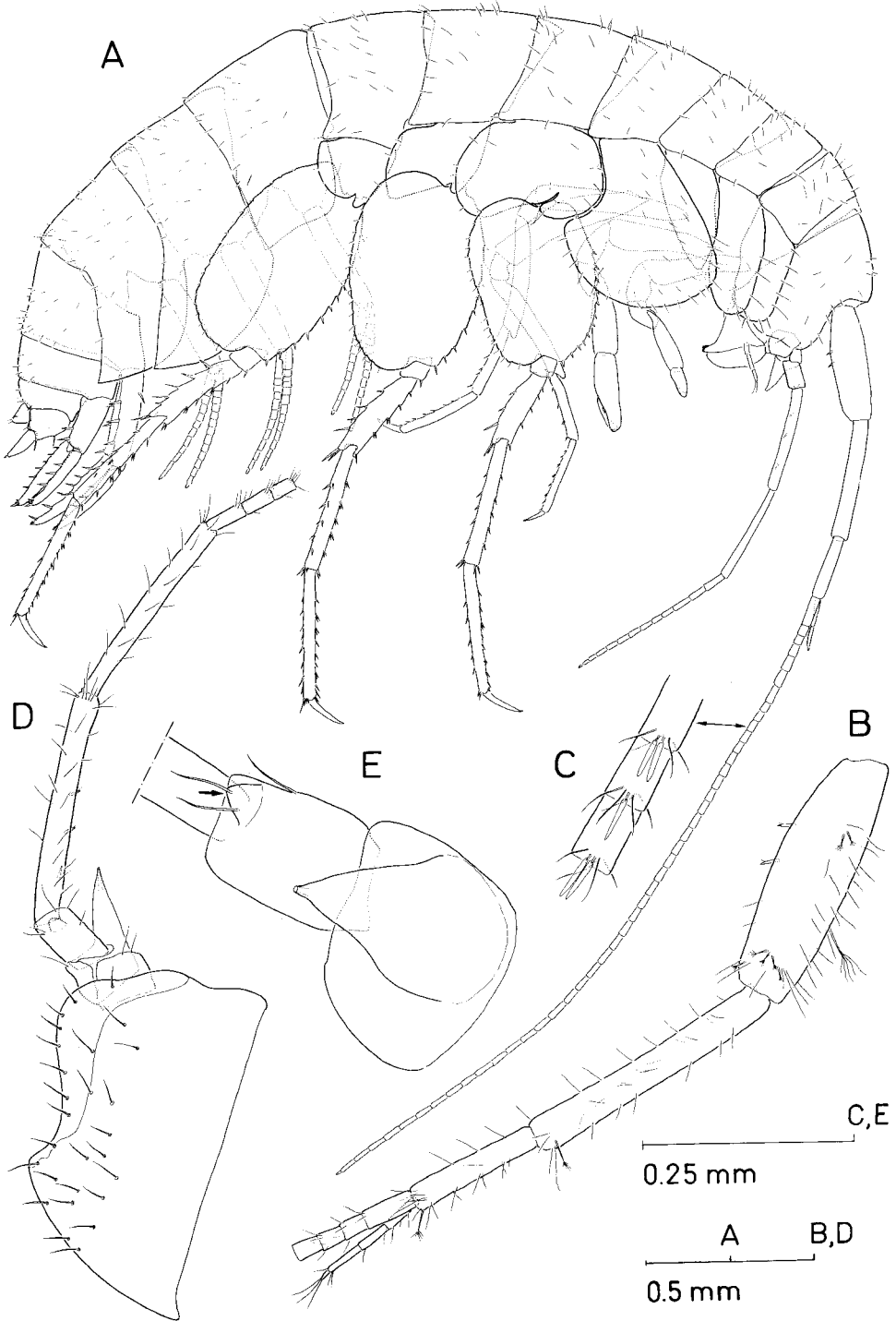


Fig. 2. *Metacrangonyx dominicanus* sp. nov., adult female. A, body, lateral view; B, detail of proximal part of right antenna 1, lateral; C, detail of articles 10-12 of main flagellum of latter; D, head and right antenna 2, lateral; E, detail of second and third peduncle segments of right antenna 2, medial (arrow indicating distomedial scar on third segment).

ites of body somites with sparsely set long setules distributed as in Fig. 2A, D. Integument of somites and all limb segments uniformly covered with densely set microsetules, not represented in figures.

Head (Fig. 2D) lacking rostrum. Lateral lobes well developed, evenly rounded, extending beyond anterior margin of head; post-antennal sinus not developed.

Antenna 1 elongate, about 69% of body length (Fig. 2A). Peduncle segments (Fig. 2B) elongate, slender, first and second of similar length, third about half length of preceding segment. First segment with 2-3 short flagellate spines along posterior margin; other armature on segments as figured. Main flagellum composed of 38-53 articles, each displaying 1 or 2 aesthetascs (Fig. 2C) except proximal 8 (exceptionally 9) and distal article, which lack aesthetascs; proximal article about twice length of forthcoming articles. Accessory flagellum 4-segmented (exceptionally 3- or 5-segmented), reaching distal margin of fourth article of main flagellum; distal article reduced.

Second antenna (Fig. 2D) short, about 47% length of antenna 1, with first and second peduncle segments incompletely separated, short; gland cone long and slender, reaching beyond distal margin of third peduncle segment. Latter about as long as two preceding segments together, rectangular, 1.6 times longer than wide; scar with two setae subdistally on medial surface of segment (Fig. 2E). Fourth and fifth peduncle segments elongate, slender, fourth of similar length to proximal segments of antennular peduncle, fifth somewhat shorter. Fourth segment with 3-4 flagellate spines on medial surface. Flagellum shorter than peduncle, with 11-19 articles.

Upper lip (Fig. 3A) globose, with defined epistome; two patches of densely set, short setules on posterodistal surface.

Left mandible (Fig. 3E) with incisor 5-cuspidate, lacinia mobilis 4-cuspidate; cusps rounded. Spine row composed of 8 multi-denticulate elements along medial surface; spines slightly bowed inwards; parallel row of 8 slender plumose setae lying lateral to spine row. Molar well developed, fungiform, with three short plumose setae basally on distal surface; molar seta short, spinulose; or-

namentation of grinding plate as figured. Mandibular palp 3-segmented, not reaching incisor tip; distal segment with two pinnate setae distally.

Right mandible (Fig. 3B) with 5-cuspidate incisor (Fig. 3C) and 6-cuspidate lacinia (Fig. 3D), latter with patch of long, flattened spinules along lateral margin. Spine row composed of 8 elements, two proximal slender and somewhat reduced; row of plumose setae running parallel to spine row composed of only 5 elements. Molar seta longer and stronger than left counterpart, three plumose setae basally on margin of molar process reduced compared to left mandible counterparts. Palp similar to left counterpart except for shorter distal setae.

Lower lip (Fig. 4A) asymmetrical, with left lobe larger than right counterpart; inner lobes wanting. Lobes covered distally with densely set, stout spinules directed inwards, some of them bifid or trifid. Other setulation as figured.

Maxilla 1 (Fig. 4C) with lanceolate inner plate covered with sparsely set, long setules. Twelve stout, hirsute setae along medial margin. Outer plate slightly curved, slender, with subparallel margins covered with sparsely set setules; eleven stout spines with heterogeneously serrated distomedial margin disposed terminally on plate. Palp 2-segmented, with curved distal segment bearing 7 clavate spines terminally, each furnished with row of tiny denticles, plus three setae with rounded tip subdistally on posterior surface of segment, distalmost seta smooth, other two pinnate. Palp asymmetrical only in having more slender spines and sometimes additional seta on distal segment of left branch.

Maxilla 2 (Fig. 4B) with outer plate slightly longer than inner counterpart, with subdistal row of 9 + 1 stout setae with striated hyaline frill on anterior surface of plate; distal margin of plate with 16 smooth setae with expanded tip, reduced bifid seta, plus single seta pinnate along distomedial margin only. Inner plate with submarginal row of 14-15 stout, finely pinnate setae on anterior surface along medial margin; rest of armature on plate as figured.

Maxillipeds (Fig. 5A) inserted on U-shaped pedestal representing fused coxae, with two submarginal setae at each side on posterior surface. Basis expanded distally, about 1.8 times longer than wide, with row of three setae near medial margin,

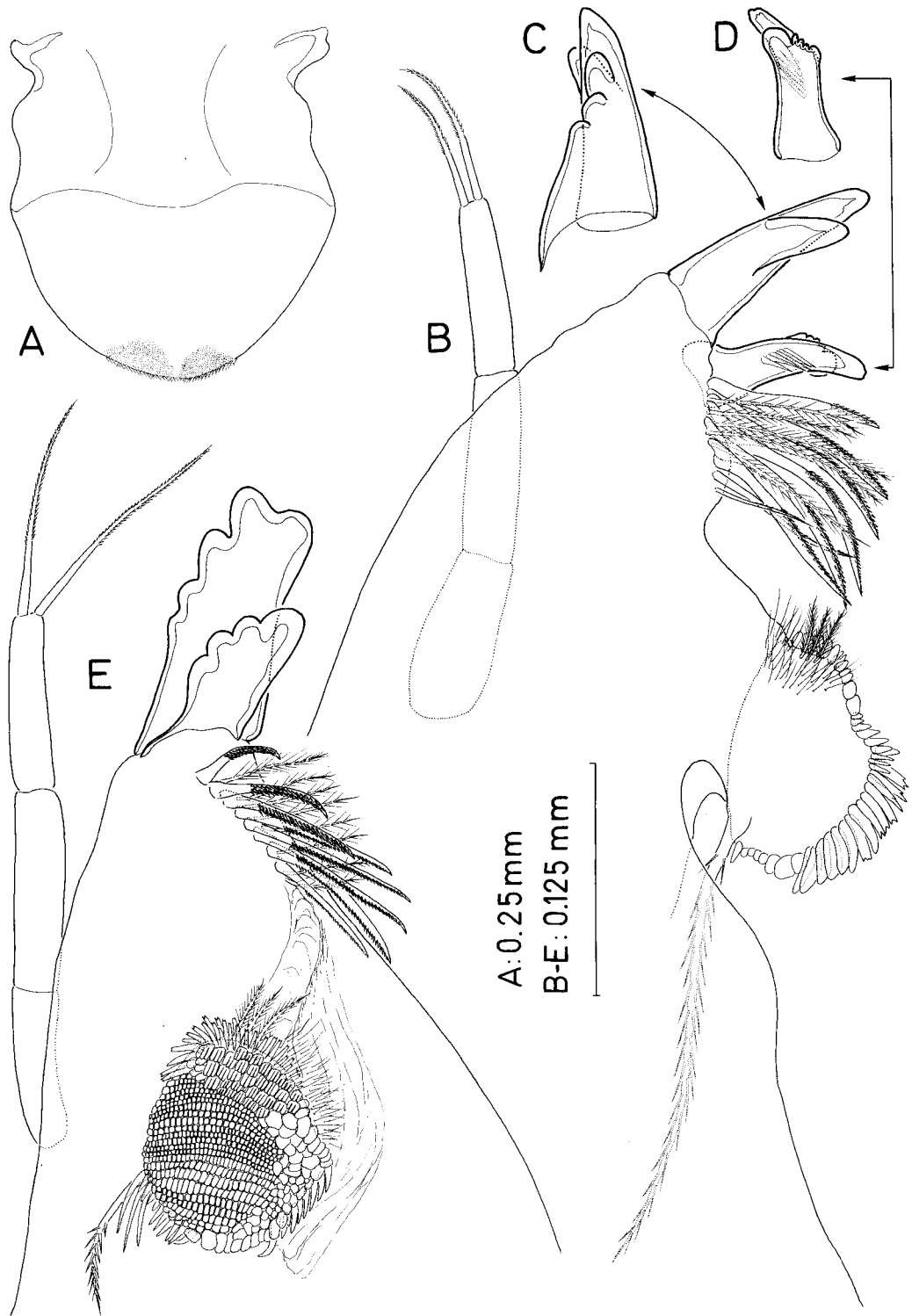


Fig. 3. *Metacrangonyx dominicanus* sp. nov., adult female. A, upper lip, anterior; B, right mandible, lateral; C, detail of incisor, medial; D, detail of lacinia, medial; E, left mandible, medial.

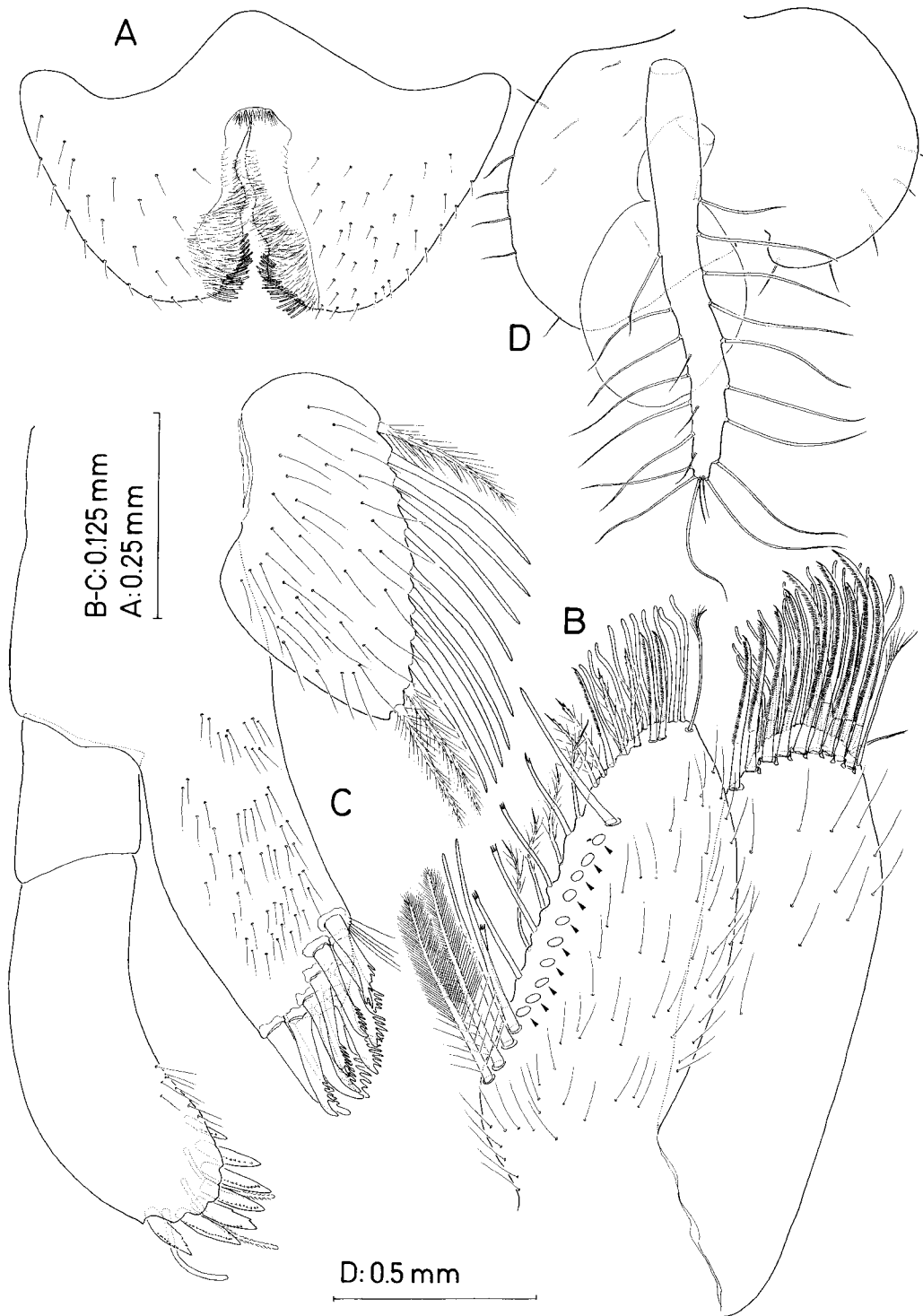


Fig. 4. *Metacranonyx dominicanus* sp. nov., adult female. A, lower lip, anterior; B, right maxilla 2, anterior (arrowheads pointing to insertions of setae omitted in figure; ornamentation on posterodistal surface of inner plate omitted); C, right maxilla 1, anterior (arrowheads indicating insertion of some setae on inner plate omitted in figure); D, left pereiopod 5 coxa with attached oostegite and coxal gill, medial.

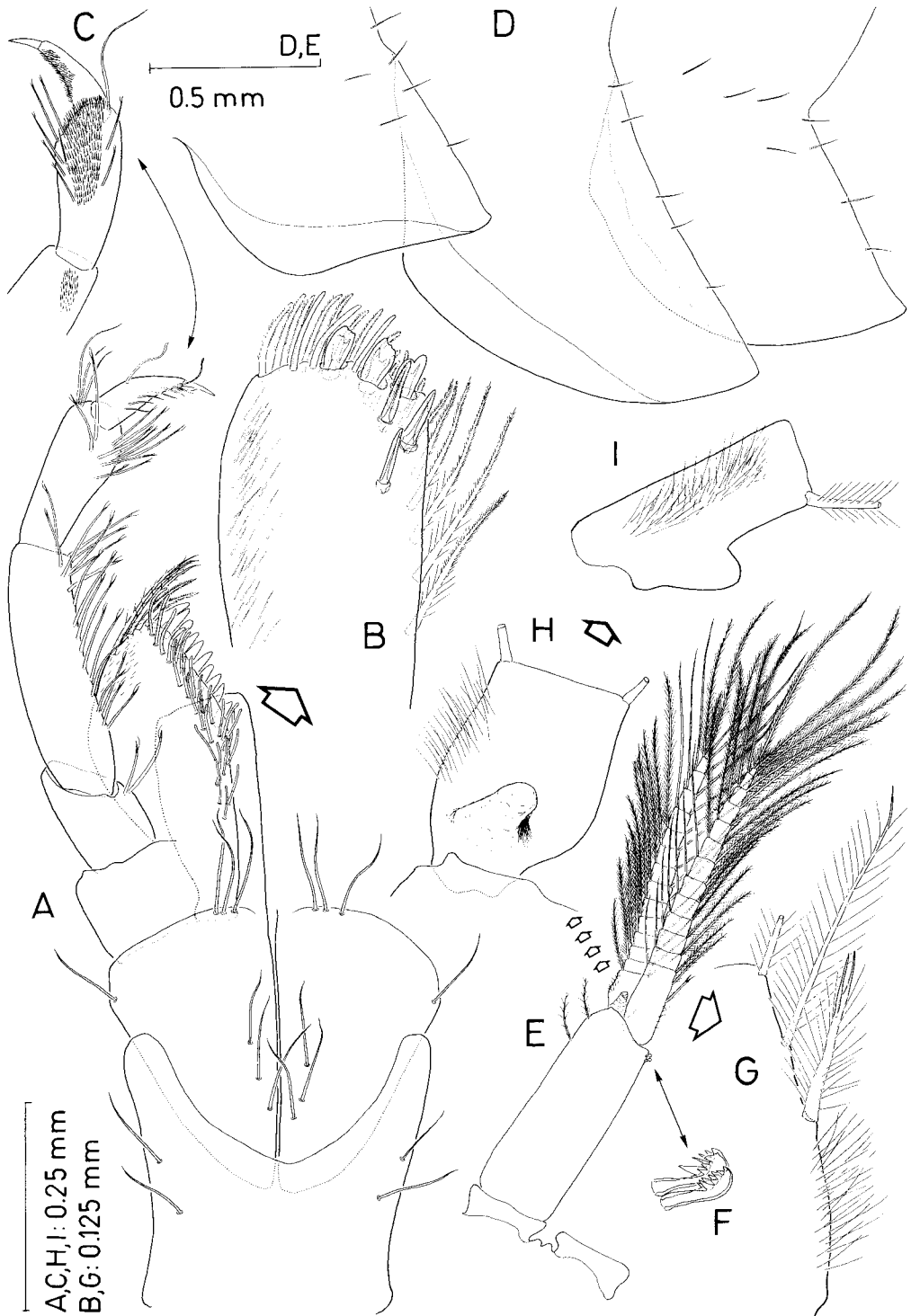


Fig. 5. *Metacrangonyx dominicanus* sp. nov., adult female. A, right maxilliped, posterior; B, detail of maxilliped inner plate, posterior; C, detail of distal segments of maxilliped palp, anterior; D, left epimeral plates; E, right first pleopod, posterior; F, detail of retinacles of latter; G, detail of lateral margin of proximal article of inner ramus of pleopod; H, detail of proximal article of outer ramus of pleopod, posterior; I, same, lateral.

one distal seta on lateral margin, and row of three setae on distal margin; foregoing setae placed on posterior surface of segment. Inner plate (Fig. 5B) spatulate, about 2.2 times longer than wide, with 5 long pectinate setae submarginally on anterior surface close to medial margin; distal margin with three stout spines partially embedded into plate, two of them tricuspidate, other bicuspidate, and three smooth setae with blunt tip; submarginal row of 12 short pectinate setae with blunt tip close to distal margin on anterior surface of plate, and three stout, pointed spines, two of them smooth, other pectinate, near distomedial corner on posterior surface; spinules submarginally on anterior surface of plate close to medial margin, as figured. Ischium short, unarmed; outer plate rhomboid, with tip not reaching two-thirds length of second palp segment; armature of plate consisting of three plumose and two pinnate setae distally, row of 10 thick, smooth clavate spines along distal half of medial margin, and cluster of short, smooth setae with blunt tip submarginally on posterior surface of plate near to medial margin. Palp 4-segmented, with second, third, and fourth segments (= carpus to dactylus) each with patch of densely set, short spinules on anterior surface (Fig. 5C). Second segment elongate, 3.5 times longer than wide, slender. Palp segments ornamented with flagellate and blunt-tip setae as figured.

Coxal plates 1-4 of unequal length (Fig. 2A): coxae 1 and 2 subsimilar, coxa 3 clearly shortest, coxa 4 longest. Coxae 1-3 anteroventrally-directed. Coxa 1 (Fig. 6A) slender, about 1.8 times longer than wide, with anterior and posterior margins subparallel, distal margin evenly rounded; two flagellate spines on posterodistal margin as figured. Coxa 2 (Fig. 7A) slender, about 2.4 times longer than wide, linguiform, with anterior and posterior margins subparallel, anterior slightly convex, posterior shallowly excavate; distal margin rounded, but more produced than in preceding plate, also with two flagellate spines on posterodistal margin. Coxa 3 (Fig. 8C) lanceolate, 1.9 times longer than wide. Coxa 4 (Fig. 8E) axe-shaped, slightly longer than wide, with posterior margin deeply excavate. Coxal plates 5-7 bilobed, with anterior lobes progressively produced and curved from coxa 5 to 7 until reaching digitiform aspect

on latter. Posterior lobe hardly developed on coxa 7 (Fig. 9C), lobe rounded and slightly overreaching anterior lobe on coxa 5 (Fig. 9A), and postero-distally-produced, clearly overreaching anterior lobe on coxa 6 (Fig. 9B). Anterior margin of coxa 5 convex, evenly rounded; those of coxae 6-7 nearly straight.

Coxal gills (Figs. 4D; 8C, E; 9B) on second gnathopod and on pereopods 2-6, ovoid, with long stalk except that on pereopod 6, sacculiform with stalk not well defined.

Oöstegites (Figs. 4D; 8C) on second gnathopod and on pereopods 2-5 sinuous, elongate, furnished with long smooth marginal setae and sparsely set tiny submarginal setae.

First gnathopod (Fig. 6A) basis slightly expanded distally, about 3.7 times longer than wide, with long setae sparsely set along posterior margin, and two setae near posterior margin on medial surface, at about one-quarter of distance along segment. Ischium subrectangular, short, about 1.8 times longer than wide. Basis and ischium each with patch of densely set scutellated scales (scutelles coalescent at base; see Fig. 6B) on medial surface. Setae on basis and ischium simple, smooth. Merus rhomboid, about 1.3 times longer than wide, with distal half of medial surface covered with densely set, not coalescent spinules (see Fig. 6C); transverse row of stout flagellate setae (as in Fig. 6D) along distal half of posterior margin of segment. Carpus elongate, about 3.8 times longer than wide and about 81% of basis length, with parallel margins; four transverse rows of flagellate setae on medial surface, and 8 similar rows on posterior margin; patch of densely set spinules similar to those on preceding segment on distomedial surface of segment. Propodus of melitoid type (Fig. 6E), about 1.8 times longer than wide and 48% of propodus length. Palm angle with three similar, short bifid flagellate spines on medial side and another three, one of them twice length of others, on lateral side (Fig. 6G). Palm margin microspinulate, with submarginal row composed of short flagellate spine plus three smooth setae with expanded tip on medial side, and submarginal row composed of two short flagellate spines and two short, stiff setae along lateral side of segment. Long, stout flagellate seta and long smooth seta with expanded tip inserted on lateral

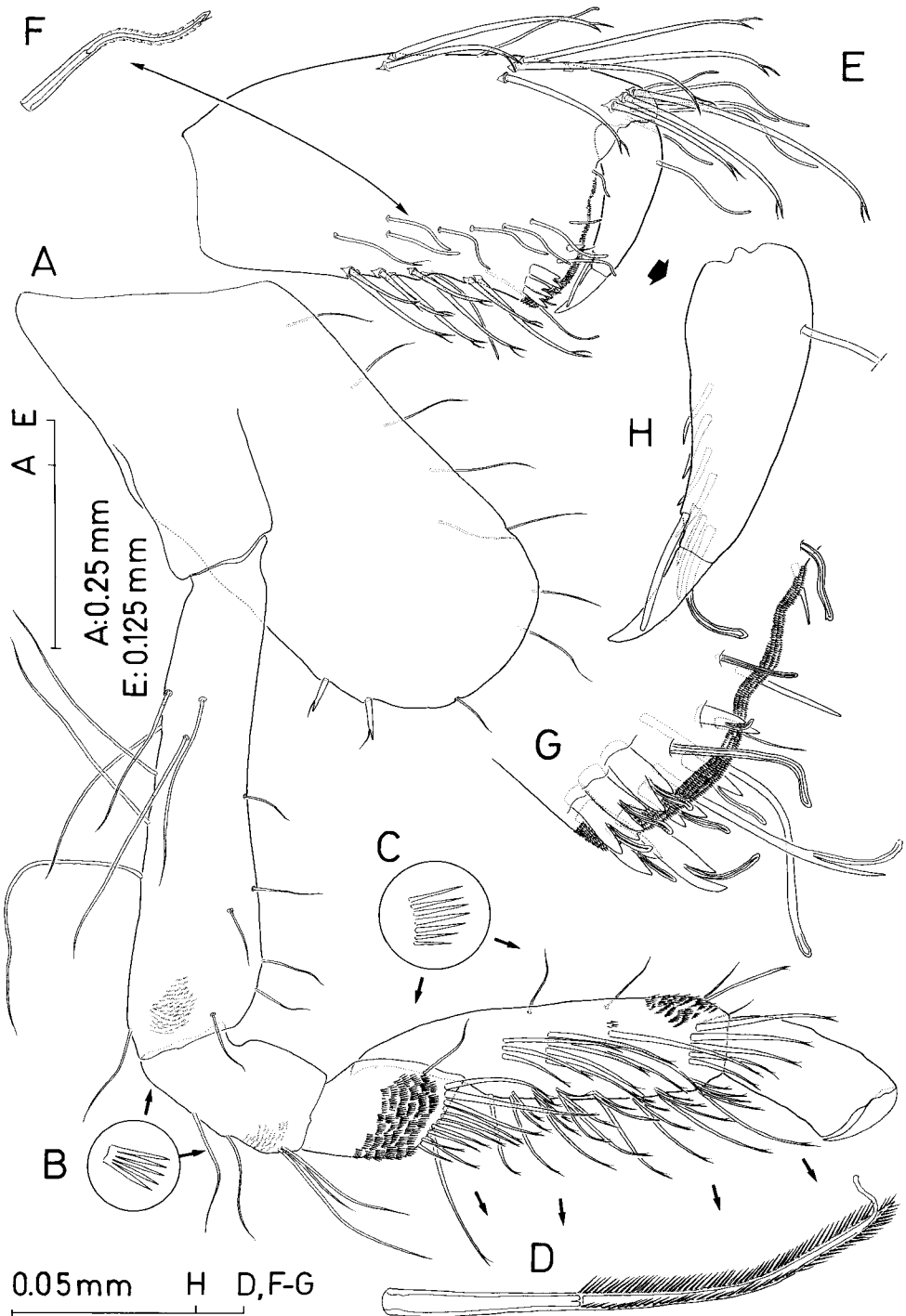


Fig. 6. *Metacrangonyx dominicanus* sp. nov., adult female left first gnathopod. A, medial view (propodus-dactylus outlined only); B, detail of one of scutellated scales on medial surface of basis and ischium; C, detail of row of spinules on medial surface of merus and carpus; D, detail of one of stout flagellate setae on merus, carpus, and propodus; E, detail of propodus-dactylus, medial (armature on lateral side of palm margin and on lateral side of dactylus omitted); F, detail of seta on medial surface of propodus; G, detail of armature on palm angle and palm margin of propodus, medial; H, detail of dactylus, medial.

surface of segment near to palm margin. Anterior and posterior margins of propodus each with 4 transverse rows of stout flagellate setae; medial surface of segment with 7 setae, proximal flagellate, rest as in Fig. 6F. Dactylus not extending beyond palm angle, with row of 6 short smooth setae plus longer distal seta with expanded tip on medial surface, stiff seta with rounded tip on posterior margin near insertion of nail, and smooth seta with expanded tip proximally on anterior margin of segment (Fig. 6H).

Second gnathopod (Fig. 7A) with basis similar, but longer than corresponding counterpart in preceding limb (about 1.2 times longer), 3.3 times longer than wide, lacking submarginal long setae on medial surface. Ischium and merus short, of similar length, former about 2.0 times, latter about 2.9 times longer than wide. Carpus elongate, about 84% of basis length, 3.3 times longer than wide; six clusters of stout flagellate setae (as in Fig. 6D) along posterior margin. Propodus elongated, 94% of carpus length, about three times longer than wide. Posterior margin with 5 clusters of stout flagellate setae; anterior margin with 7 clusters of stout flagellate setae located submarginally on medial surface of segment. Palm angle positioned at 58% of segment length, with short, bifid flagellate stout spine on medial side and similar, but elongate, spine plus long, stout flagellate seta and cluster of slender smooth setae with rounded tip on lateral side (Fig. 7B). Palm margin oblique, slightly convex, with row of 6 stout, bifid flagellate spines and two short smooth setae with rounded tip along medial side, and two long and three short bifid flagellate spines, two short unicuspid flagellate spines, and two short smooth setae with rounded tip along lateral side (Fig. 7B). Dactylus not extending beyond palm angle, slender, with similar armature as counterpart of preceding limb (Fig. 7B).

Third (Fig. 8C) and fourth (Fig. 8E) pereopods subsimilar, with basis slender, elongate, about 5.8 times longer than wide, with long setae along posterior margin. Propodus elongate, slightly longer than carpus. Carpus and propodus with row of short flagellate spines along posterior margin. Dactylus (Fig. 8D, F) similar, slender, about 4.8 times longer than wide (including nail), with two spines (distalmost fused at base to segment) and smooth

tiny seta with rounded tip near insertion of nail on posterior margin of segment; posterior margin finely pectinate along distal half; seta with brush-like tip proximally on anterior margin; scale covering proximal half of anterior margin of nail.

Pereopods 5-7 elongate, P5 shorter than P6-P7, last two of similar length (Fig. 2A). Ischium-to-dactylus similar except in P5, with propodus clearly shorter than carpus (Fig. 9A; propodus about as long as carpus in P6-P7, see Fig. 9C, D), and P6, with longer dactylus (Fig. 8F). Margins of segments with numerous short flagellate spines. Merus of each limb with distal corner of both anterior and posterior margins produced into process crowned with spines. Dactylus of each pereopod with armature similar to that of pereopods 3-4 (Fig. 9D, E). Basis of P5 (Fig. 9A) 1.5 times longer than wide, anterior margin convex, with numerous short, flagellate spines, posterior margin nearly straight, serrated, with numerous short setae; postero-proximal lobe well developed, evenly rounded, posterodistal lobe developed but not extending beyond ischium. Pereiopod 6 basis (Fig. 9B) slightly longer but wider than P5 counterpart, 1.3 times as long as wide, with both posteroproximal and posterodistal lobes well developed, evenly rounded, posterodistal clearly reaching beyond ischium. Basis of pereopod 7 (Fig. 9C) of similar length to that of P5, but more ovoid (1.3 times longer than wide), with both anterior and posterior margins convex, pointed posteroproximal lobe, and wide, evenly rounded, posterodistal lobe overreaching ischium.

Epimeral plates (Fig. 5D) unarmed, with pointed posterodistal angles. Plate 1 short, subquadrate, with anterior and posterior margins straight, anterodistal angle evenly rounded. Plate 2 largest, elongate, posterior margin slightly concave, anterior margin evenly rounded. Plate 3 short, about similar length as plate 1, with straight posterior margin and evenly rounded anterior margin.

Pleopods 1-3 similar (Fig. 5E), consisting of subrectangular peduncle 2.7 times longer than wide inserted on short pedestal, up to 15-articulate outer ramus, and up to 13-articulate inner ramus. Peduncles with 2-4 club-shaped, denticulated retinacles subdistally on medial margin (Fig. 5F); lateral margin of peduncle of pleopod 1 with two (exceptionally one) short plumose setae; that of

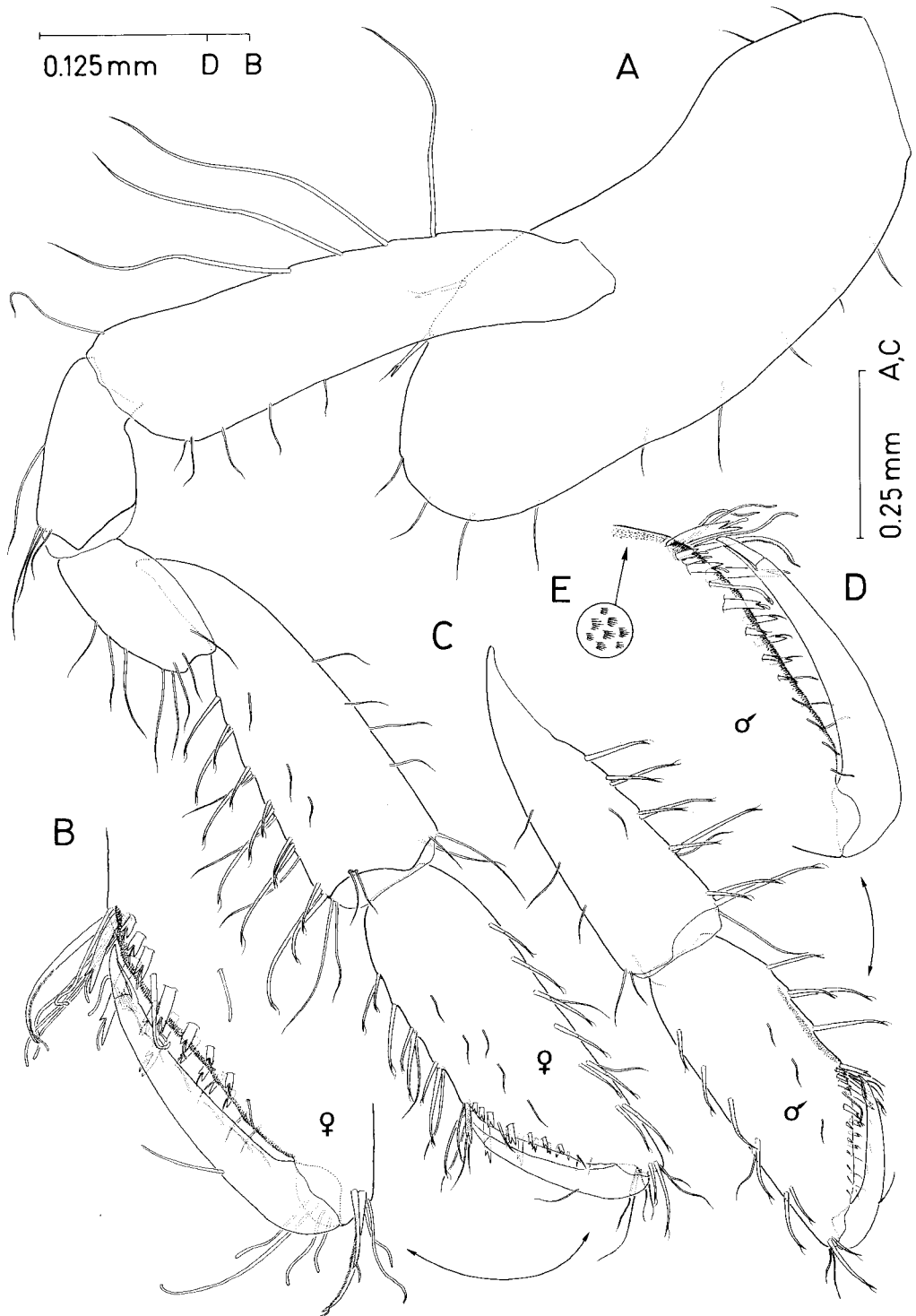


Fig. 7. *Metacrangonyx dominicanus* sp. nov., second gnathopod. A, adult female left limb, medial (armature of dactylus partially omitted; coxal gill and oöstegite omitted); B, detail of palm angle, palm margin, and dactylus of latter, medial; C, detail of carpus-dactylus of adult male right limb, medial; D, detail of palm angle, palm margin, and dactylus of latter, medial (dactylus outlined only); E, detail of clusters of spinules comprising submarginal patch of spinules on medial surface of male propodus posterior margin.

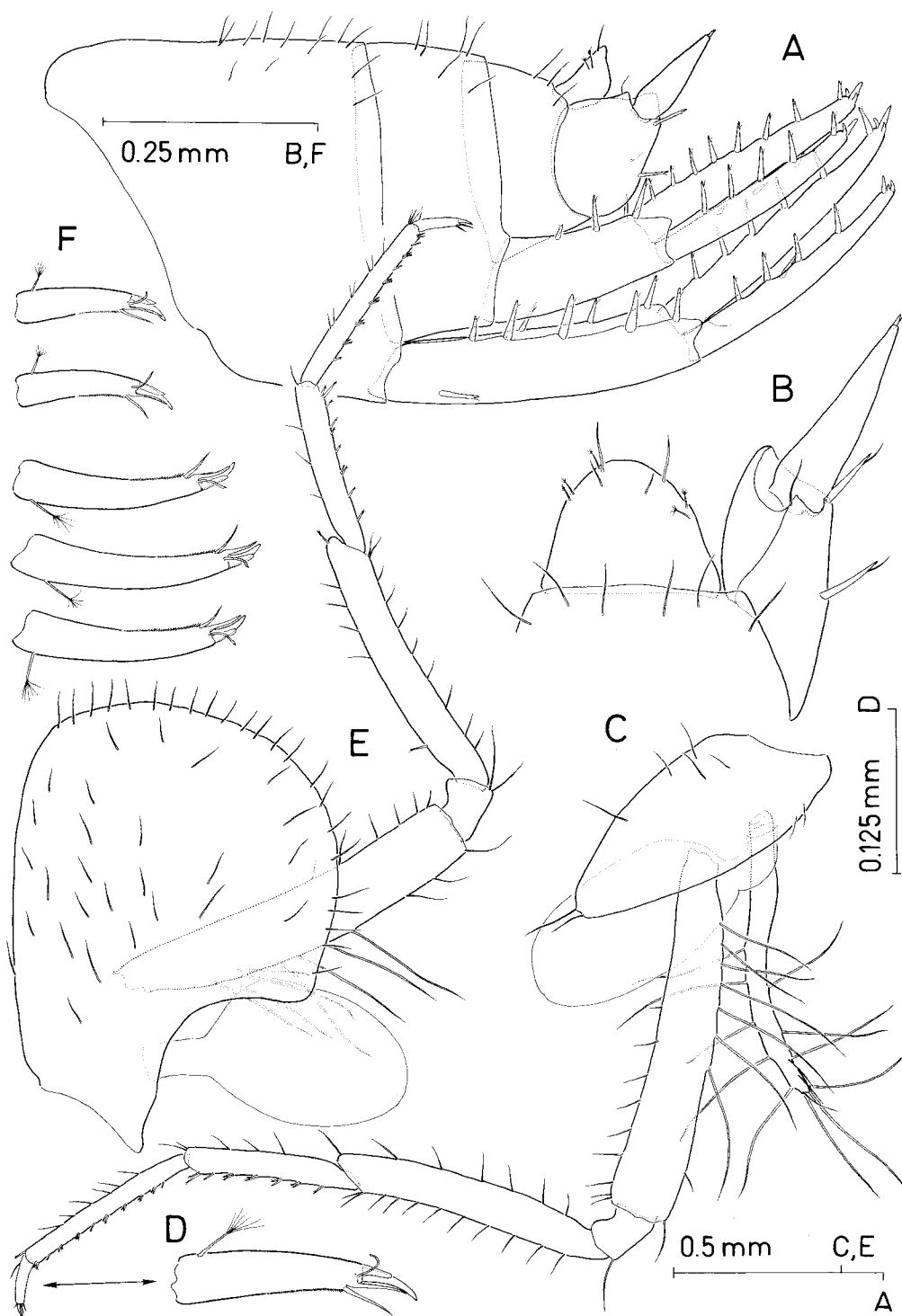


Fig. 8. *Metacrangonyx dominicanus* sp. nov., adult female. A, urosome with uropods and telson, lateral; B, right third uropod and telson, posterior (= dorsal); C, left third pereopod with attached oostegite and gill, lateral; D, detail of dactylus of latter, medial; E, right fourth pereopod with attached gill, lateral (oostegite omitted); F, relative length of, from top, dactylus of pereopod 3 to 7, medial.

pleopods 2-3 naked, although that of third pleopod exceptionally with single seta. Articles comprising both rami each with long plumose seta distally on both sides except proximal article of inner ramus, which displays proximal bifid spine and two setae along medial margin (Fig. 5G). Proximal article of outer ramus of similar length as three succeeding articles combined, with posterior surface displaying rounded bulge proximally and cluster of sparsely set setules submarginally near lateral margin (Fig. 5H, I); length of proximal article of inner ramus as 4 following articles together, with cluster of sparsely set setules submarginally on posterior surface near medial margin.

Uropods 1-2 (Fig. 8A) with peduncle compressed laterally and with lanceolate rami; outer ramus shorter than inner. Uropod 1 with peduncle elongate, longer than rami, bearing basoventral spine; row of 4-5 spines along lateral margin, and 2-3 spines along medial margin. Outer ramus with 3 to 5 spines along lateral margin, 0-1 spines on medial margin, and two spines, one of them reduced, on tip. Inner ramus with basoventral seta, 4 to 6 spines along lateral margin, 0-1 spines on medial margin, and three spines, two of them reduced, on tip. Uropod 2 shorter than preceding limb, with peduncle shorter than rami, with 2-3 spines along lateral margin and single spine on medial margin. Outer ramus with 4-5 lateral spines, 2-3 medial spines, and two spines, one reduced, on tip. Inner ramus with 6 to 8 lateral spines, unarmed medial margin, and three spines, two reduced, on tip.

Third uropod (Fig. 8A, B) short, with peduncle expanded antero-posteriorly, piriform in lateral aspect (as long as wide), and with reduced, 1-segmented outer ramus. Peduncle with two lateral spines, unarmed or with tiny seta distally on posterior (= dorsal) margin; single tiny seta on medial surface of segment. Outer ramus relatively elongate (about 87% of peduncle length), lanceolate, with single reduced spine on tip. No trace of inner ramus. Spines on uropods flagellate.

Telson (Fig. 8B) rounded, about 1.3 times wider than long, lacking spines. Ornamentation consisting of two pairs of tiny, smooth setae with brush-like tip, plus two pairs of unequal, longer setae, distalmost setae longest.

Description of male. – Body length of two specimens available 7.97 and 6.05 mm. Identical to female except for presence of narrow submarginal patch of tiny spinules on medial surface of propodus of second gnathopod, near posterior margin of segment (Fig. 7C-E). One of males with both mandibular palps 2-segmented.

Etymology. – Species name derived from its type locality, the Dominican Republic.

Remarks. – The new taxon from Hispaniola displays the typical features of metacrangonyctids (see Boutin, 1994), leaving no doubt on its placement within this family. Thus, the telson is entire and reduced, the third uropod has the inner ramus wanting and the outer ramus is 1-segmented and reduced, the mandibular palp is reduced, the lower lip inner lobes are wanting, and the third peduncle segment of the antenna 2 displays a distomedial scar.

Metacrangonyx dominicanus sp. nov. belongs in the so-called *panousei*-group of species (cf. Messouli et al., 1991; Boutin, 1994), for it displays almost all the apomorphies that characterise this cluster (Boutin et al., 1992). Only the weakly (versus strongly) sexually-dimorphic state of the second gnathopod is not shared with the rest of species of the *panousei*-group. So, the outer ramus of the third uropod has the distal end not truncate, but pointed, with the armature reduced to a single terminal spine; uropod 2 carries fewer than 9 marginal spines along the inner ramus; uropod 3 lacks the spine corresponding to the armature of the inner ramus; and there is no seta on the gland cone.

The *panousei*-group is the most widely distributed and diverse cluster of *Metacrangonyx* species, and includes most of the Moroccan taxa, namely *M. panousei* Balazzuc & Ruffo, 1953, *M. gineti* Boutin & Messouli, 1988a, the 4 species described by Messouli et al. (1991; viz. *M. goulmimensis*, *M. delamarei*, *M. ruffoi*, and *M. aroundanensis*), plus all the peripheral taxa except the Balearic species, i.e. *M. ortalii* Karaman, 1989 and *M. sinaicus* Ruffo, 1982 from the Dead Sea depression and the Sinai Peninsula, respectively, *M. ilvanus* Stoch, 1997 from Elba, and *M. repens*

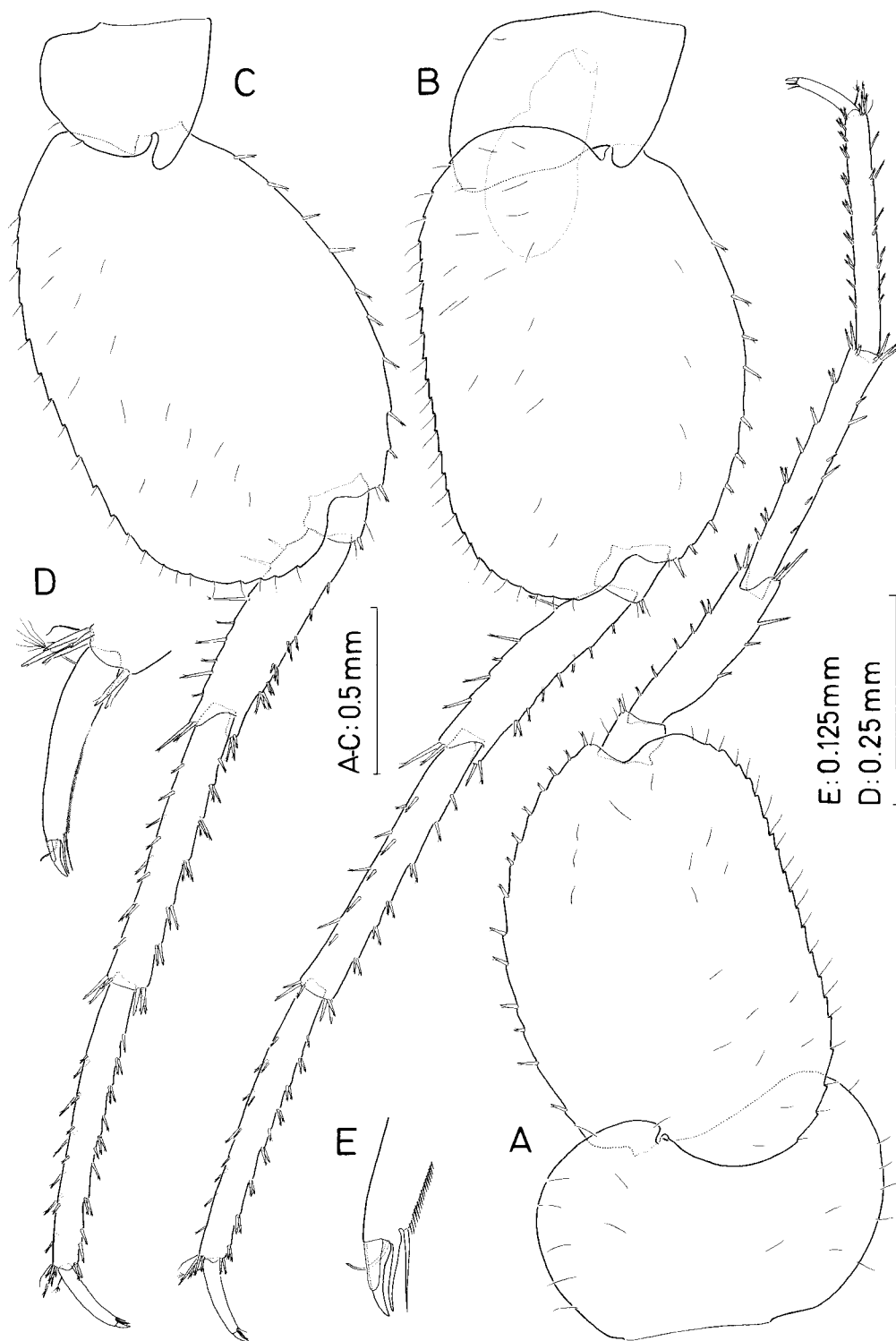


Fig. 9. *Metacrangonyx dominicanus* sp. nov., adult female. A, right pereiopod 5, lateral (coxal gill and oöstegite omitted); B, right pereiopod 6 with coxal gill, lateral; C, right pereiopod 7, lateral; D, detail of dactylus of latter, lateral; E, detail of distal part of dactylus and nail of latter, lateral.

(Stock & Rondé-Broekhuizen, 1986) from Fuerteventura (Canary Is.).

Boutin et al. (1992) recognised two sub-groups within the Moroccan members of the *panousei*-group, viz. *panousei* and *gineti*, based on the differential expression of 6 characters. As regards the non-Moroccan species, Stoch (1997) has added *M. ilvanus* to the *gineti* sub-group, and furthermore *M. repens* and *M. sinaicus* can be placed there as well. Only *M. ortalii* fails to be encased in this framework. The new species from Hispaniola falls perfectly within the *panousei* sub-group since the number of spines along the inner ramus of uropod 2 is between 4-10; the main flagellum of the antenna 1 is composed of more than 15 articles; the flagellum of antenna 2 is composed of more than 8 articles; the pereopods 5-7 basis displays a well developed posterodistal lobe; and the peduncles of the pleopods display plumose setae. This species sub-group included previously *M. panousei*, *M. delamarei*, and *M. goulmimensis*. *Metacrangonyx dominicanus* sp. nov. can be distinguished from these three species based on, among other characters, its multisegmented mandibular palp (palp unisegmented in the other species), the absence of inner ramus on the third uropod (ramus present in the other species), and by the relative length of the propodus of the female second gnathopod, which is as long as the carpus (propodus longer than carpus in the remaining species).

***Metacrangonyx samanensis* sp. nov.**
(Figs. 10-15)

Material examined. – Samaná Peninsula, northern Dominican Republic: "Cueva del Agua de Saturnino". UTM coordinates: 2128598^N 480438^E. HOLOTYPE: disarticulated adult female (oöstegites developed) 7.09 mm in ethanol 70% vial [ZMA reg. no. AMPH. 204934]. PARATYPES: five juvenile specimens in ethanol 70% vial deposited in the collection of the Museo Nacional de Historia Natural, Sto. Domingo. Collected by D. Jaume, 4 November 1999. In slightly brackish water.

Description of female. – Body (Fig. 10A) similar to *M. dominicanus*, with integument of somites and all limb segments uniformly covered with densely set microsetules, not represented in figures.

Antenna 1 (Fig. 10A) with two proximal peduncle segments elongate, second longer than first, third half length of second. First segment with three

flagellate spines along posterior margin. Main flagellum composed of more than 36 articles (flagellum broken in both first antennae of the largest specimen available). Accessory flagellum 5-segmented.

Antenna 2 (Fig. 10A) less than half length of preceding limb. Fourth and fifth peduncle segments of similar length, shorter than each of proximal segments of antennular peduncle; fourth segment with flagellate spine on medial surface. Flagellum shorter than peduncle, 11-articulate.

Upper and lower lips as in *M. dominicanus*. Left mandible (Fig. 11A) with incisor 5-cuspidate, lacinia mobilis 4-cuspidate. Spine row composed of 10 elements; row of plumose setae running parallel to spine row composed of 9 elements. Molar with 4 short plumose setae basally on distal margin; molar seta short. Mandibular palp 3-segmented, not reaching incisor, with two distal setae.

Right mandible (Fig. 11B) with 5-cuspidate incisor and multicuspidate lacinia (Fig. 11C), latter with patch of denticulate flattened spinules along lateral margin (Fig. 11D). Spine row and row of plumose setae running parallel to spine row, each composed of 7 elements. Molar seta longer and stronger than left counterpart; 9 plumose setae basally on distal margin of molar process, reduced compared to left limb counterparts.

Maxilla 1 (Fig. 12A) inner plate with 16 marginal setae. Outer plate with 11 heterogeneously serrated, distal spines. Palp of right limb (Fig. 12B) distal segment with 6 clavate spines terminally and three denticulate setae with rounded tip subdistally on posterior surface. Palp of left limb with more slender terminal spines than right counterpart, and with only two subdistal setae (Fig. 12C).

Maxilla 2 with submarginal row of setae on anterior surface of inner plate composed of 17 elements.

Maxilliped (Fig. 13A-B) differing from *M. dominicanus* in absence of patch of densely set spinules on anterodistal surface of second palp segment, lesser number of setae on fourth palp segment, and in some features of inner plate, such as presence of slender spiniform process distally on inner margin (process absent in *M. dominicanus*), and different ornamentation of three pointed spines on distomedial corner of posterior surface, that in addition are implanted closer to medial margin of

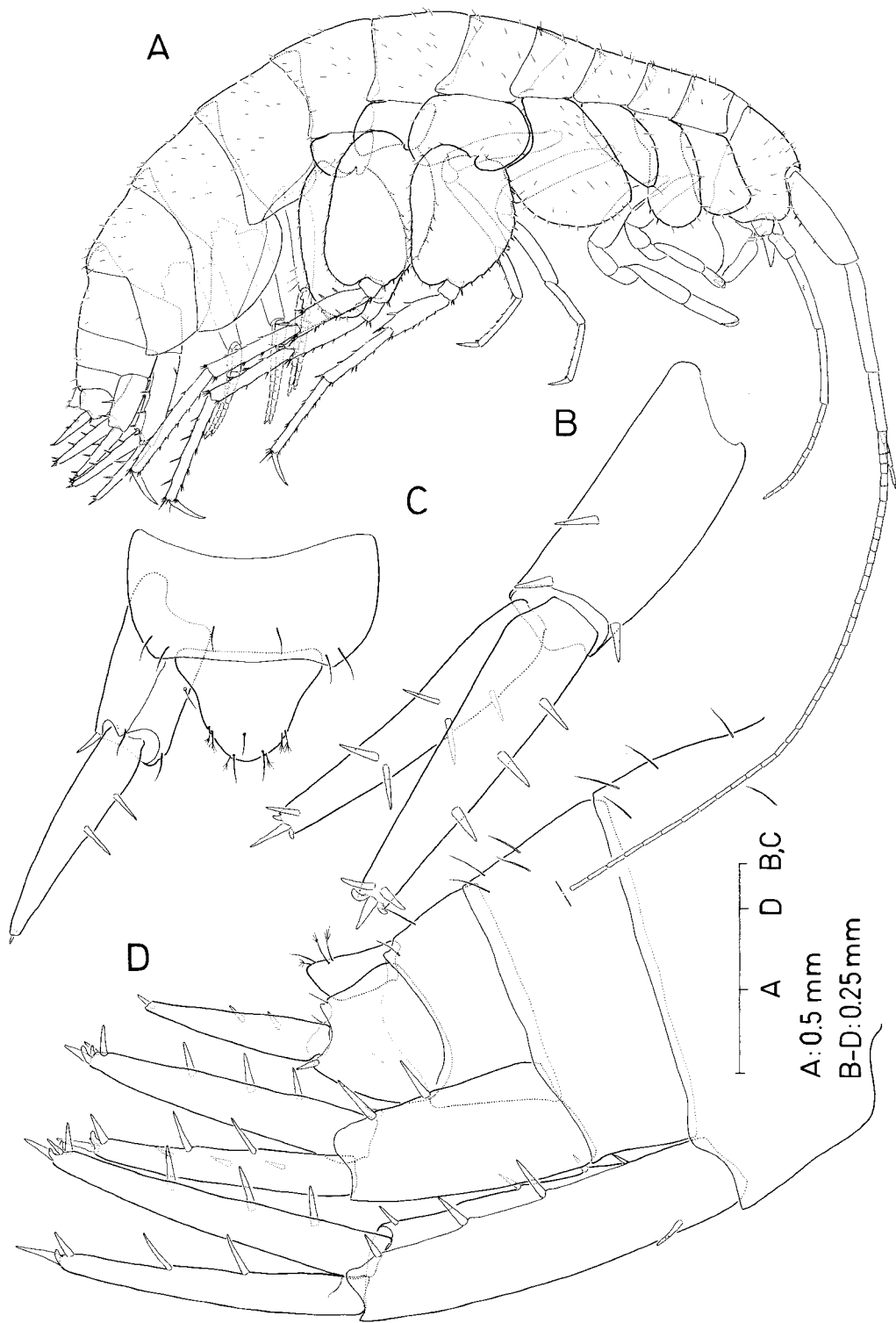


Fig. 10. *Metacrangonyx samanensis* sp. nov., adult female. A, body, lateral; B, left uropod 2, posterior; C, left third uropod and telson, posterior (= dorsal); D, urosome, lateral.

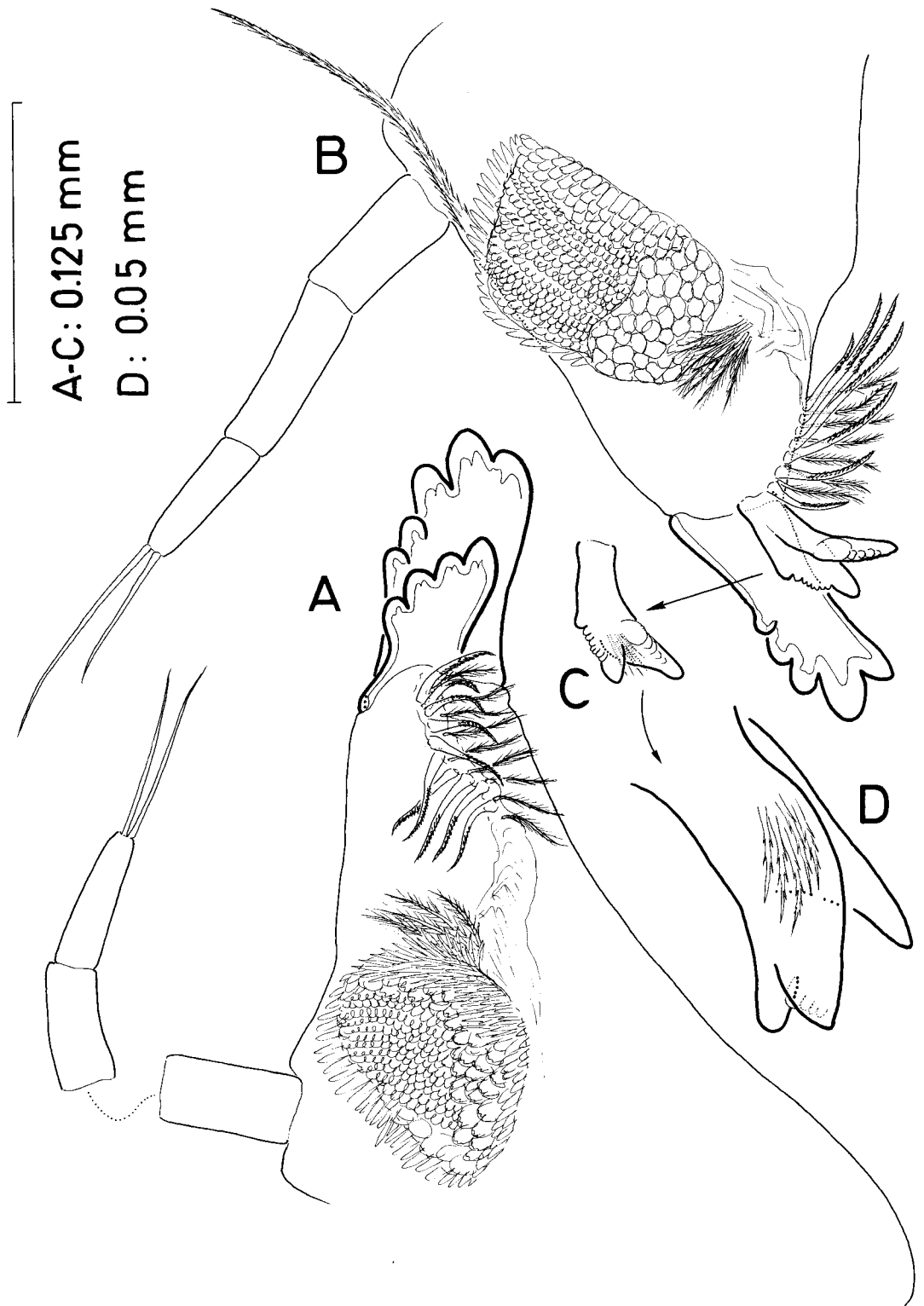


Fig. 11. *Metacrangonyx samanensis* sp. nov., adult female. A, left mandible, medial; B, right mandible, medial; C, detail of right lacinia mobilis, anteromedial; D, detail of spinules on lateral margin of latter.

plate than in *M. dominicanus*. Thus, proximal spine unipinnate, middle smooth, and distal denticulate (proximal and middle spines smooth, whereas distal bipinnate in *M. dominicanus*).

Coxal plates (Figs. 10A; 12D; 13C-D; 14A; 15A-C) similar to *M. dominicanus* except for coxal plate 1 (Fig. 14A), displaying single slender flagellate spine on posterodistal corner whereas two stout elements present in *M. dominicanus* (see Fig. 6A), and for distally-expanded coxal plate 2 (see Figs. 10A and 12D; cf. Figs. 2A and 7A). Coxal gills (Figs. 12D; 13C-D; 15A-B) and oöstegites (Figs. 12D; 15A) as in *M. dominicanus* except coxal gill on sixth pereopod, displaying well developed stalk (see Fig. 15B).

First gnathopod (Fig. 14A) differing from *M. dominicanus* in having spinules composing caespitose patch on medial surface of merus heterogeneous in size (Fig. 14B); more slender propodus (Fig. 14C; 1.96 times longer than wide, versus 1.82 times in *M. dominicanus*), which is also relatively more reduced (representing only 43.6% of carpus length, versus 47.7% in *M. dominicanus*), and stouter dactylus (compare Figs. 14D and 6H).

Second gnathopod (Fig. 12D) long and slender. Carpus elongate, about 80% of basis length, 3.9 times longer than wide; five clusters of stout flagellate setae along posterior margin. Propodus elongated, 92% of carpus length, about 3.6 times longer than wide. Posterior margin with 4 clusters of stout flagellate setae; anterior margin with 6 clusters of stout flagellate setae disposed submarginally on medial surface. Palm angle positioned at 71% of segment length, with one short, bifid flagellate stout spine on medial side and similar, but elongate, spine plus long, stout flagellate seta on lateral side (Fig. 12E, F). Palm margin oblique, with row of three stout, bifid flagellate spines plus isolated unicuspid stout flagellate spine along medial side, and three unicuspid stout flagellate spines along lateral side (see Fig. 12F). Dactylus not extending beyond palm angle, slender, with armature as in Fig. 12F.

Third and fourth pereopods (Fig. 13C-D) similar to *M. dominicanus* except for less spinose posterior (= medial) margins of both carpus and propodus. Pereopod 5 (Fig. 15A) differing from *M. dominicanus* in having propodus clearly longer

than carpus. Pereopods 6 and 7 (Fig. 15B-C) differing from *M. dominicanus* in having propodus clearly longer than carpus, P6 being longer than P7. Relative length of dactylus of pereopods 3 to 7 as in fig. 15D.

Epimeral plates and pleopods similar to *M. dominicanus*, latter with 3-0-0 plumose setae respectively on outer margin of peduncle, and 3-3-4 retinacles.

Uropods 1-2 (Fig. 10 D) differing from *M. dominicanus* in armature only. First uropod peduncle with basoventral spine, row of 4 spines along lateral margin, and three spines along medial margin. Outer ramus with three spines along lateral margin, naked medial margin, and two spines, one of them reduced, on tip. Inner ramus with basoventral seta, 4 spines along lateral margin, single terminal spine on medial margin, and three spines, two of them reduced, on tip. Uropod 2 (Fig. 10B) with peduncle bearing two spines along outer margin and single spine on inner margin. Outer ramus with three spines along each margin, and three spines, two of them reduced, on tip. Inner ramus with terminal spine on outer margin, 4 spines along inner margin, and three spines, two of them reduced, on tip.

Third uropod (Fig. 10C) peduncle with one distal spine on lateral margin and one tiny seta distally on each posterior and medial margins; single tiny seta on medial surface of segment. Outer ramus longer than peduncle, lanceolate, with two spines along inner margin and single reduced spine on tip. No trace of inner ramus.

Telson (Fig. 10C) lacking spines, roughly triangular, about 1.3 times wider than long, with slightly concave lateral margins.

Adult male. – Unknown.

Etymology. – Species name derived from its type locality, the Samaná Peninsula (northern Dominican Republic).

Remarks. – On the basis of the morphology of the third uropod, *Metacrangonyx samanensis* sp. nov. belongs to the so-called *spinicaudatus*-group (cf. Boutin, 1994). This cluster of species previously comprised only two formally described taxa, viz.

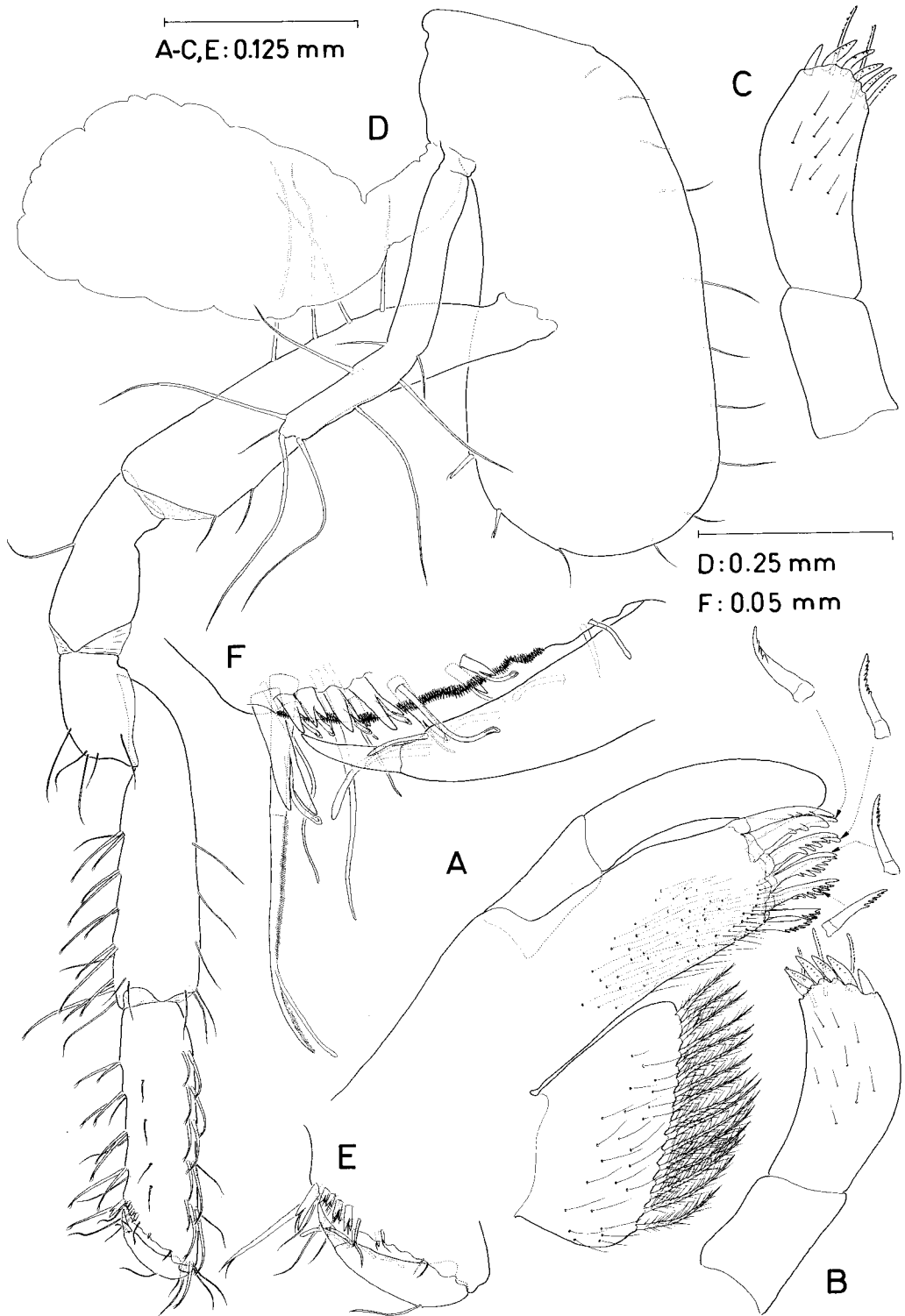


Fig. 12. *Metacrangonyx samanensis* sp. nov., adult female. A, right maxilla 1, posterior; B, detail of palp of latter, anterior; C, left maxillary palp, anterior; D, left second gnathopod with attached oostegite and coxal gill, medial; E, detail of distal margin of propodus and dactylus of latter, medial; F, same at higher magnification.

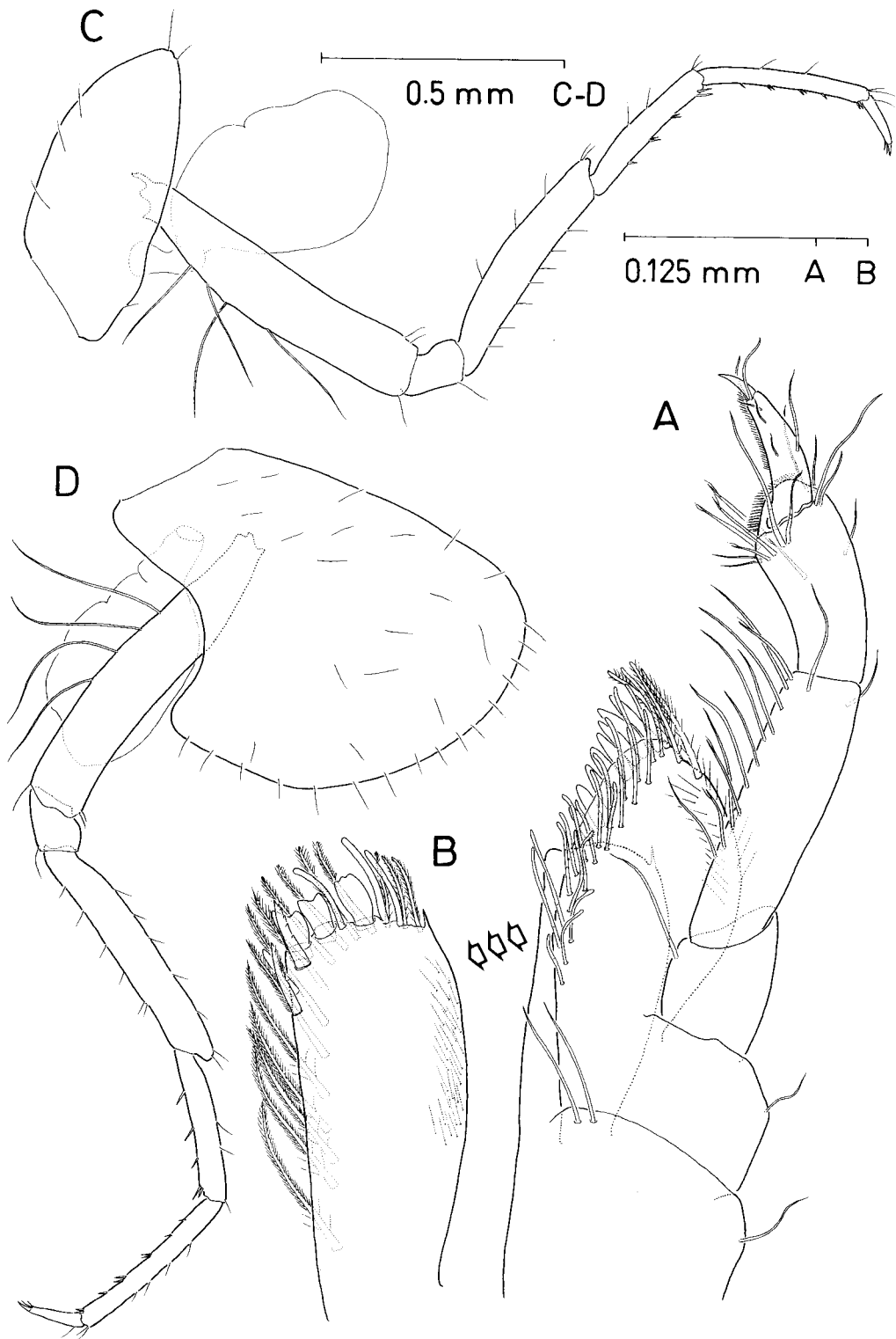


Fig. 13. *Metacrangonyx samanensis* sp. nov., adult female. A, left maxilliped, posterior; B, detail of inner plate of latter, posterior; C, right third pereiopod with coxal gill, lateral (oöstegite omitted); D, right fourth pereiopod with coxal gill, lateral (oöstegite omitted).

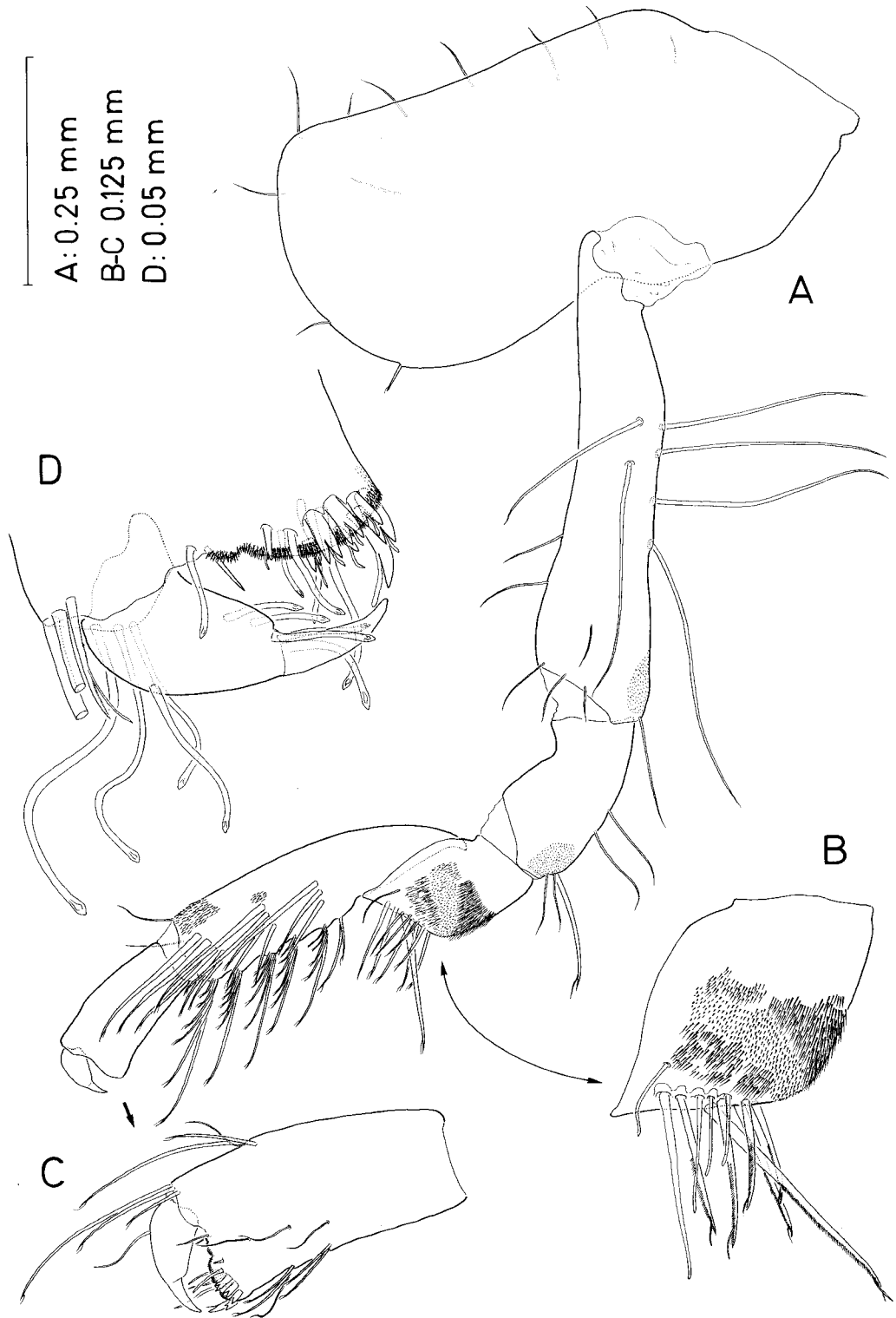


Fig. 14. *Metacrangonyx samanensis* sp. nov., adult female. A, right first gnathopod, medial (propodus-dactylus outlined only); B, detail of merus, medial; C, detail of propodus-dactylus, medial; D, detail of distal margin of propodus and dactylus, medial.

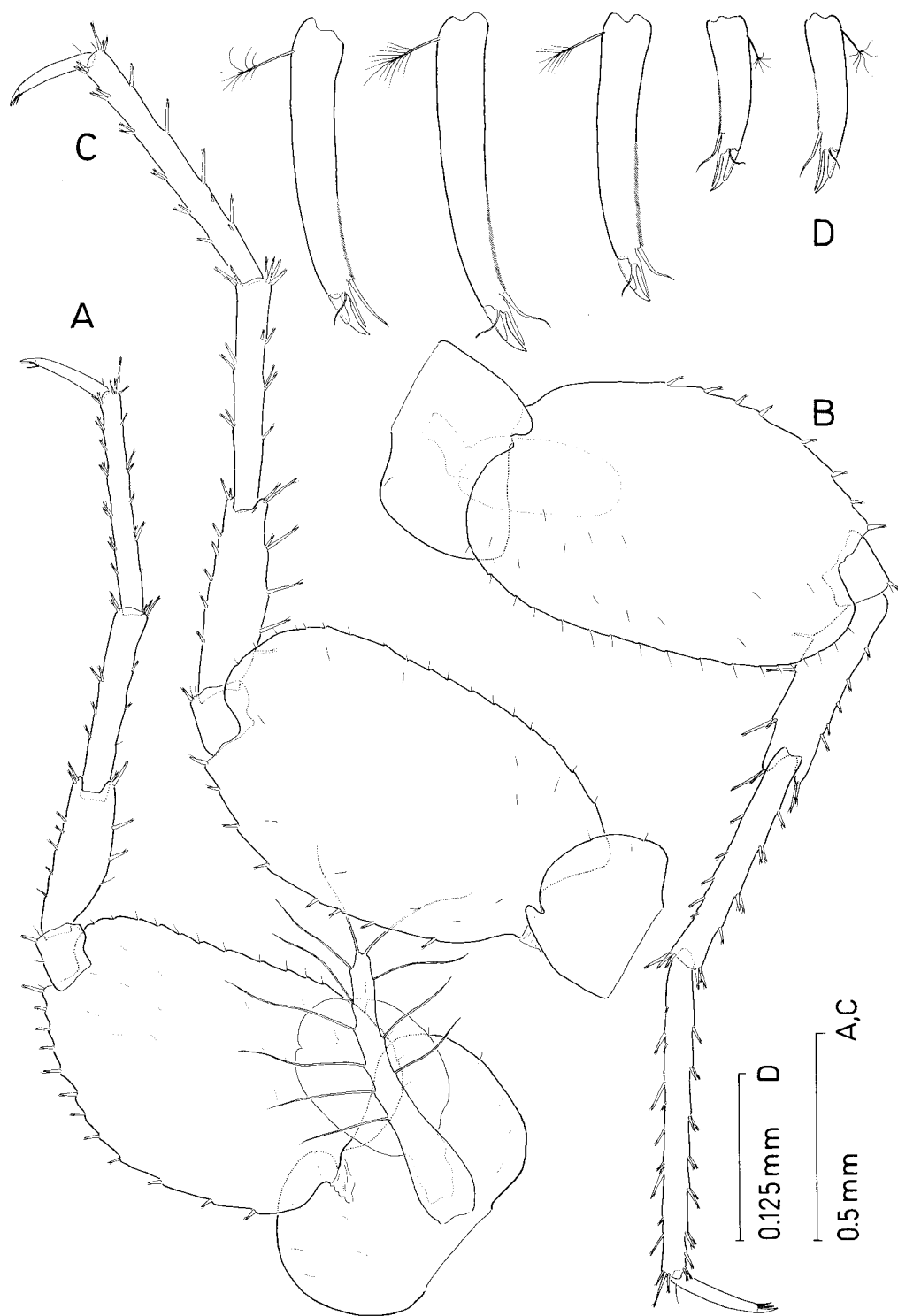


Fig. 15. *Metacrangonyx samanensis* sp. nov., adult female. A, left fifth pereiopod with attached oostegite and coxal gill, medial; B, right sixth pereiopod with attached gill, lateral; C, right seventh pereiopod, lateral; D, from right to left, dactylus of left pereiopods 3 to 7, medial.

M. spinicaudatus Karaman & Pesce, 1980 and *M. longicaudatus* Ruffo, 1954, both from Morocco, and was characterised by the peculiar third uropod, with a lanceolate outer ramus displaying a variable number of marginal spines in addition to a single apical spine. The outer ramus of the new species is lanceolate and carries (two) spines along the inner margin, in addition to a single terminal spine.

The new species can be distinguished from the other representatives of the group by its uniramous third uropod (biramous in the other species), the outer ramus displaying only two marginal spines (4 marginal spines in the other species); its longer first antennae, with the flagellum composed of more than 36 articles (main flagellum composed by less than 10 articles in the other species); its 3-segmented mandibular palp (versus 2-segmented); and by the peculiar morphology of the second gnathopod, with both the carpus and propodus long and slender, the propodus having anterior and posterior margins parallel (segments not so elongate, with propodus displaying convex margins in the other species).

Age and biogeography of the *Metacrangonyctidae*

Boutin (1994) interpreted the *Metacrangonyctidae* as a thalassoid lineage derived from marine littoral ancestors. They would have repeatedly colonized continental ground waters along the sea shores during marine regressions, in the way described by the so-called "Two-step Model" of colonization and evolution (Boutin & Coineau, 1990). After each settlement wave, the marine ancestors could either go extinct or continue to evolve independently in the sea. The very reduced capability of subterranean amphipods for dispersal would permit the correlation of areas where these animals occur with the sites of colonization of continental ground waters.

In this context, Boutin (1994) undertook a detailed taxonomic and phylogenetic analysis of the family from which he interpreted the existence of 4 apparently monophyletic lineages, namely, the *panousei*-, *remyi*-, and *spinicaudatus*-groups within

Metacrangonyx, plus the genus *Longipodacrangonyx* Boutin & Messouli, 1988. Combining zoogeographic and geological information from Morocco, he proposed approximate timings for the separation of these lineages. Thus, it was suggested that the *spinicaudatus*- and *remyi*-groups colonized continental ground waters during the Late Cretaceous Turonian regression (about 90 Myr BP). The next wave of colonizers, members of the *panousei*-group, would have established continental subterranean populations during the Late Cretaceous Senonian regression (about 70 Myr BP). The more modern colonization wave, involving *Longipodacrangonyx* species, would have penetrated continental stygohabitats during the Middle Eocene Lutetian regression (about 40 Myr BP).

Boutin (1994) also advanced possible timings for the extinction of the marine metacrangonyctids and for the origin of the family itself. Thus, the absence of *Metacrangonyctidae* from areas of Morocco flooded by the sea some time in post-Eocene epochs was interpreted as evidence that the root stock of marine metacrangonyctids disappeared a short time after the Eocene. On the other hand, the putative absence of metacrangonyctids from the other side of the Atlantic, where the continental ground waters are occupied by the closely related "weckeliid" hadziids, suggested that the *Metacrangonyctidae* were no older than the opening of the northern Atlantic ocean. The apparent absence of metacrangonyctids in areas of Morocco covered by the sea for the last time during the Jurassic transgressions would lend additional credence to this hypothesis.

The discovery of *Metacrangonyx* in continental ground waters of the Greater Antilles conflicts with the above evolutionary scenario. Firstly, it forces us to infer a much older origin of *Metacrangonyx*, from prior to the opening of the northern Atlantic. The occurrence of members of this genus on both sides of the central North Atlantic indicates that the ancestral marine littoral root stock of species had already differentiated before the completion of that vicariant event. Since there is evidence supporting the persistence of shallow-water contacts between eastern and western shores until about 110 Myr BP (Sclater et al., 1977), we propose this

age as the minimum estimate for the origin of *Metacrangonyx*. In addition, the presence of the genus in Hispaniola, the island harbouring the richest “weckeliid” amphipod assemblage in the world (see Stock, 1985), casts strong doubt on the hypothesis of the origin of the “weckeliid” hadziids as the American, vicariant sister-group of the Old World metacrangonyctids (see also Stock, 1985 for a criticism of the “weckeliid” concept).

Other problems with the evolutionary scenario proposed by Boutin (1994) now emerge. The placement of the two new Hispaniolan species into two of his species-groups obscures the presumed correspondence between species-groups and precisely dated waves of colonization of continental ground waters. Thus, the occurrence of a member of both the *spinicaudatus*-group (viz. *M. samanensis* sp. nov.) and the *panousei*-group (*M. dominicanus* sp. nov.) in the Antillean region is not in accord with the inferred age of the Moroccan members of these species-groups (90 and 70 Myr, respectively), for deep-water conditions were already established in the northern Atlantic basin 110 Myr BP and would prevent a common littoral marine stock from extending along both shores as late as 90-70 Myr BP. In addition, there is extensive geological evidence indicating that there is no permanently-emerged land in the Greater Antilles older than Middle Eocene in age (see Iturralde-Vinent & MacPhee, 1999). Accordingly, inland groundwater lineages of *Metacrangonyx* in the Greater Antilles could not be older. In fact, both Hispaniolan species occur in caves excavated in coral-reef Quaternary marine terraces placed very close to the current sea-shore, one of them even living in slightly brackish water. Both lines of evidences suggest a very recent origin of these taxa.

We infer from the discovery of the Hispaniolan species that marine populations of metacrangonyctids persisted on the western shore of the Atlantic until some time in the Quaternary, or even until the present-day. This is in contradiction to the scenario of Boutin (1994), who inferred that the extinction of the marine root stock of the Metacrangonyctidae occurred just after the Eocene. It is relevant here to report new evidence of the continuing persistence of marine populations of meta-

crangonyctids on the eastern shore of the Atlantic: the Balearic *Metacrangonyx longipes* Chevreux, 1909, a member of the *remyi*-group, that extends from near-shore brackish waters to completely fresh waters up to 200 m above sea level, was recently recorded by us in fully marine conditions (accompanying a typical marine fauna consisting of ophiuroids, holothurians, etc.) in a littoral cave (sensu Stock et al., 1986) on the southeastern coast of Mallorca (“Cova del Dimoni”, UTM coord.: 4377400^N 530050^E). This species was gathered also in the bottom layers of marine salinity of an anchialine cave adjacent to the sea-shore (viz., in the anchialine lake of “Cova de na Barxa”; UTM coord.: 4392900^N 539160^E; S: 36.4‰) forming part of a crustacean assemblage composed of both stygobiont (*Exumella mediterranea* Jaume & Boxshall, 1995, *Stygocyclopia balearica* Jaume & Boxshall, 1995, *Troglocyclopina balearica* Jaume & Boxshall, 1996, *Ginesia longicaudata* Jaume & Boxshall, 1997, *Neoechinophora xoni* Jaume, 1997) and non-stygobiont, marine species (Phoxocephalidae sp., *Chelura terebrans* Philippi, 1839, *Heteromysis* (*Gnathomysis*) sp., *Nebalia* sp., *Pseudocyclops* sp., *Euryte longicauda* Philippi, 1843, *Pterynopsyllus* sp., Oithonidae sp., Poecilostomatoida sp., etc.).

How then should we reconcile Boutin’s (1994) evolutionary scenario with the new discoveries? Assuming that the *Metacrangonyx* species-groups are really monophyletic, the only way would be to speculate that the ancestors of the two Hispaniolan species had remained in morphological stasis in the Antillean littoral marine interstitial for a long period after their respective lineages at the eastern side of the Atlantic had colonized continental ground waters, and then either became extinct or continued their independent evolution in the marine environment. The Hispaniolan species would therefore have colonized inland ground waters diachronically with respect to their own lineages in the Old World. This possible scenario is weakened by the new discovery of a Mediterranean marine population of metacrangonyctids, belonging to a taxon included in one of the two oldest species-groups of *Metacrangonyx*. The question now arises, how can the presumed absence of members of the *remyi*-group in Moroccan territories younger than Turonian in age be explained

when marine members of the same group still persist in the neighbouring western Mediterranean. It could be argued that the *remyi*-group marine root stock was never again involved in episodes of colonization of continental ground waters after the one which was coeval with the Turonian regression, persisting instead, in morphological stasis in the sea. But the inland localities of the Balearic species do not support this: they mostly correspond to middle Miocene to Quaternary outcrops and not to Cretaceous terrain, as Boutin's (1994) evolutionary scenario would suggest.

The foregoing observations suggest that it would be interesting to test the assumption of monophyly for Boutin's (1994) lineages, and to repeat the cladistic analysis incorporating the new taxa, and with more detailed analysis of homology between character states. In this context, a comparison of the two Hispaniolan species in search of synapomorphies that could demonstrate the paraphyletic condition of these lineages was inconclusive. Both taxa express apparently unique traits, such as a patch of short spinules on the medial surface of the carpus of the first gnathopod near the anterodistal corner; a bifid spine proximally on the medial margin of the inner ramus of pleopods; the pleopods display a patch of setules submarginally along the medial margin of the proximal article of the inner ramus, and another submarginally along the lateral margin of the outer ramus counterpart; moreover, the proximal article of the outer ramus displays a bulge on the posterior surface (this bulge is apparently located posterodistally on the pleopod peduncle near the insertion of the outer ramus in the rest of metacrangonyctids; see Boutin & Messouli, 1988a). All these character states are expressed also at least in *M. longipes* (D.J., pers. obs.) whereas *M. repens*, a member of the *panousei*-group from Fuerteventura (Canary Is.), shares the bifid spine on the pleopods (see Stock & Rondé-Broekhuizen, 1986).

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