

# A new atlantasellid isopod (Asellota: Aselloidea) from the flooded coastal karst of the Dominican Republic (Hispaniola): evidence for an exopod on a thoracic limb and biogeographical implications

Damià Jaume

Instituto Mediterráneo de Estudios Avanzados (CSIC-UIB), C/ Miquel Marqués 21, 07190 Esporles, Mallorca, Spain

(Accepted 22 November 2000)

## Abstract

A new representative of the thus far monotypic, Bermudan aselloid family Atlantasellidae is described from the freshwater layers of two coastal sinkholes on the south-west Dominican Republic, Hispaniola. *Atlantasellus dominicanus* sp. nov. is extraordinary among isopods in retaining a remnant of the exopod on one of its pereopods; no other isopod is known to express a schizopodous condition of thoracic limbs. The locomotory behaviour, body volvation habits, and apparent specificity of the new taxon for life on submerged decaying wood in cave waters are described. Analysis of palaeogeographic and ecological evidence supports the interpretation of the Atlantasellidae as a thalassoid lineage, contrary to previous phylogenetically supported assumptions considering them to be an ancient, freshwater lineage.

**Key words:** Crustacea, Peracarida, Atlantasellidae, biramous pereopods, regression-model evolution, Antillean biogeography

## INTRODUCTION

In 1979, Sket described an odd stygobiont aselloid isopod from the near-marine salinity reaches of an anchialine cave on Bermuda. This animal, *Atlantasellus cavernicolus*, could not be placed in either of the two recognized aselloid families (viz. Asellidae Rafinesque-Schmaltz, 1815, and Stenasellidae Dudich, 1924), and consequently received new familiar rank as the Atlantasellidae (Sket, 1979). This isopod was later found to be of considerable phylogenetic importance, when Wägele (1983) first revealed the aselloid condition of the Microcerberidae S. Karaman, 1933, with the Atlantasellidae representing a link between them and the more plesiomorphic Stenasellidae.

The monotypic condition of the Atlantasellidae, restricted to a single oceanic island that apparently has never been in contact with continental landmasses, raised interesting zoogeographic questions. On the assumption that aselloids are a primarily freshwater group (Wägele, 1983), the question arises, how did *Atlantasellus* get to be in Bermuda? Is it really a freshwater taxon secondarily adapted to the salty groundwaters of the island, as assumed by Wägele (1983, 1990), or is a direct marine origin possible (Sket, 1979; Henry, Lewis & Magniez, 1986)?

During a recent faunistic survey of the caves of the south-west Dominican Republic, Hispaniola, a tiny stygobiont isopod was caught in two cenotes located near to Laguna de Oviedo, a hypersaline coastal lagoon of 25 km<sup>2</sup> and *c.* 11 km maximum length near the town of Oviedo, inside the Jaragua National Park, Provincia de Pedernales. The zone, a highly karstified Oligocene–Miocene tabular limestone outcrop (León, 1989), is extremely rich in caves. Those along the shores of the lagoon have been reported by Trias *et al.* (1997), and their stygobiont fauna was preliminarily studied by Jaume & Wagner (1998). These caves are a few metres above sea level, and many currently have their lower reaches flooded by the waters of the nearby lagoon. Others, further inland, harbour completely fresh water. The region (< 80 m a.s.l.) was very probably covered by the sea in relatively recent times, as evidenced by the impressive series of Plio-Pleistocene marine terraces developed to the East of Cabo Rojo.

*Atlantasellus dominicanus* sp. nov., described herein, is extraordinary among isopods in expressing a proximal process that is probably homologous with the exopod on the fifth pereopod. No other isopod is known to display a biramous condition in any of the thoracic limbs. In addition, the discovery of an atlantasellid in the Antillean region, which is assumed to have no permanently emerged landmasses older than Late Eocene (see Iturralde-Vinent & MacPhee, 1999) casts

doubts on the assumption that the family is an old, primarily freshwater taxon.

The new species is the seventh stygobiont isopod known from Hispaniola, an island which is gradually revealing one of the richest crustacean stygofaunas in the world (see Stock, 1985*a,b* and Jaume & Wagner, 1998, for reports on the amphipods; or Wagner, 1994, for Hispaniolan therosbaenaceans). Other isopod taxa previously reported from the island include the freshwater cirrolanids *Anopsilana radicularis* (Notenboom, 1981) and *A. acanthura* (Notenboom, 1981) from southern Haiti (Notenboom, 1981), the janiroid *Jehaia stocki* Wagner, 1990 and the anthurid *Cyathura* (*Cyathura*) *tridentata* Wagner, 1990, both from the marine interstitial of the south-west Dominican Republic (Wagner, 1990*a,b*), the freshwater *Cyathura* (*Stygocyathura*) *motasi* Botosaneanu & Stock, 1982 from northern Haiti (Botosaneanu & Stock, 1982), and two species from the Étang Saumâtre-Lago Enriquillo-Laguna del Rincón rift valley, viz. *C. (S.) salpiscinalis* Botosaneanu & Stock, 1982 and *C. (S.) broodbakkeri* Wagner, 1990 (Botosaneanu & Stock, 1982; Wagner, 1990*b*).

## MATERIAL AND METHODS

The isopods were gathered using a hand-held plankton net attached to an extensible (to 3 m) handle. The net was used to 'shave' repeatedly along the surface of decaying submerged timber in the cave lakes, where the animals seem to concentrate. Neither baited traps nor suprabenthic fishing in the lakes produced any specimens. The net contents (mainly wood debris) were dumped immediately into a shallow tray with clean water, and left for about 10 min for the debris to sediment. Then the white isopods were visible crawling over the brown decaying wood, and could be picked up individually using soft tweezers.

Specimens were treated 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. Appendages preserved in permanent slides were mounted in lactophenol and the coverslips sealed with nail varnish. Materials are deposited in Museo Nacional de Historia Natural, Sto. Domingo, Museu de la Naturalesa de les Illes Balears, Palma de Mallorca (MNCM), and in the Crustacea collection of The Natural History Museum, London (BMNH). Location of the caves was determined with a MAGELLAN GPS Blazer12 receiver.

## SYSTEMATICS

Order Isopoda Latreille, 1817  
Suborder Asellota Latreille, 1803

Superfamily Aselloidea Rafinesque-Schmaltz, 1815  
Family Atlantasellidae Sket, 1979  
Genus *Atlantasellus* Sket, 1979

*Atlantasellus dominicanus* sp. nov.  
(Figs 1–6)

Cirolanidae: Jaume & Wagner, 1998: 39

### Material examined

DOMINICAN REPUBLIC. Prov. Pedernales, Oviedo. 'Cueva de los Bolos', UTM co-ordinates: 2466864N, 19246853E. Cenote with large (about 52 × 32 m) entrance and 29 m deep to the waterline, at 1.2 km inland from the western shore of Laguna de Oviedo; chamber of 30 × 14 m at the north-west, with the lower reaches flooded by still, completely fresh water. Remnants of an old borehole pipe in the lake. HOLOTYPE: adult female (oöstegites developed) 1.95 mm, completely dissected and mounted on 10 slides; deposited in the zoological collection of Museo Nacional de Historia Natural, Sto. Domingo. PARATYPES: four adult females (MNCM reg. no. 362) in 70% ethanol vial. Collected by author, 7 November 1999. Accompanying fauna: *Stygiomysis aemete* Wagner, 1992, *Bahadzia jaraguensis*, Jaume & Wagner, 1998, *Ottenwalderia kymbalion*, Jaume & Wagner, 1998, Cyclopidae.

'Pozimán Cadena', UTM co-ordinates: 2463326N, 19246313E. Cenote of ovoid, about 20 × 13 m entrance, 21 m deep to the waterline. Small chamber in twilight to the west, completely occupied by shallow lake. Degree of saltiness of water unknown. Collected by author, 8 November 1999. Eight adult females plus four manca (BMNH reg. nos. 2000.2260-2271) in 70% ethanol vial. Accompanying fauna: *Typhatya* sp., *Tethysbaena* sp., *Stygiomysis aemete*, *Bahadzia jaraguensis*, *Ottenwalderia kymbalion*.

### Description of adult female

Body length of seven adult females 1.81, 1.89, 1.94, 1.95, 1.95, 2.07 and 2.14 mm. Body (Figs 1a & 2a) oblong, about three times as long as wide, semi-cylindrical (Fig. 1d), completely colourless, capable of perfect volvation.

Eyes (ommatidia) absent. Body dorsal integument with numerous smooth setae distributed as in Figs 1a, d & 2a. Integument of both body and limbs covered with setulose scutellated scales.

**Fig. 1.** *Atlantasellus dominicanus* sp. nov., adult female: (a) body, dorsal (integumental ornamentation outlined only on seventh pereonite and pleotelson); (b) left antennule, ventral (= posterior); (c) left antenna, ventral; (d) postero-sagittal view of pleotelson (pleopods omitted).

Fig. 1

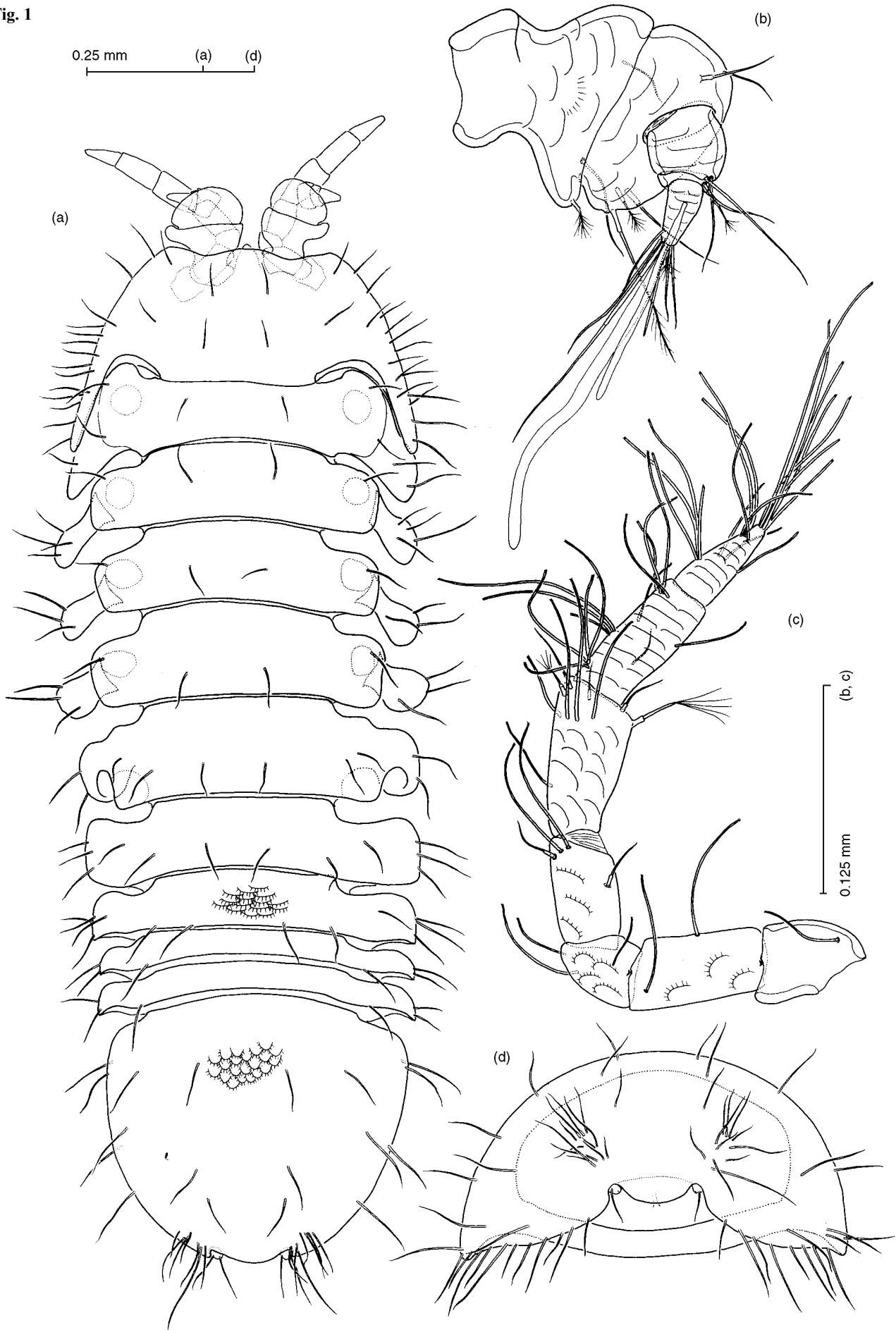
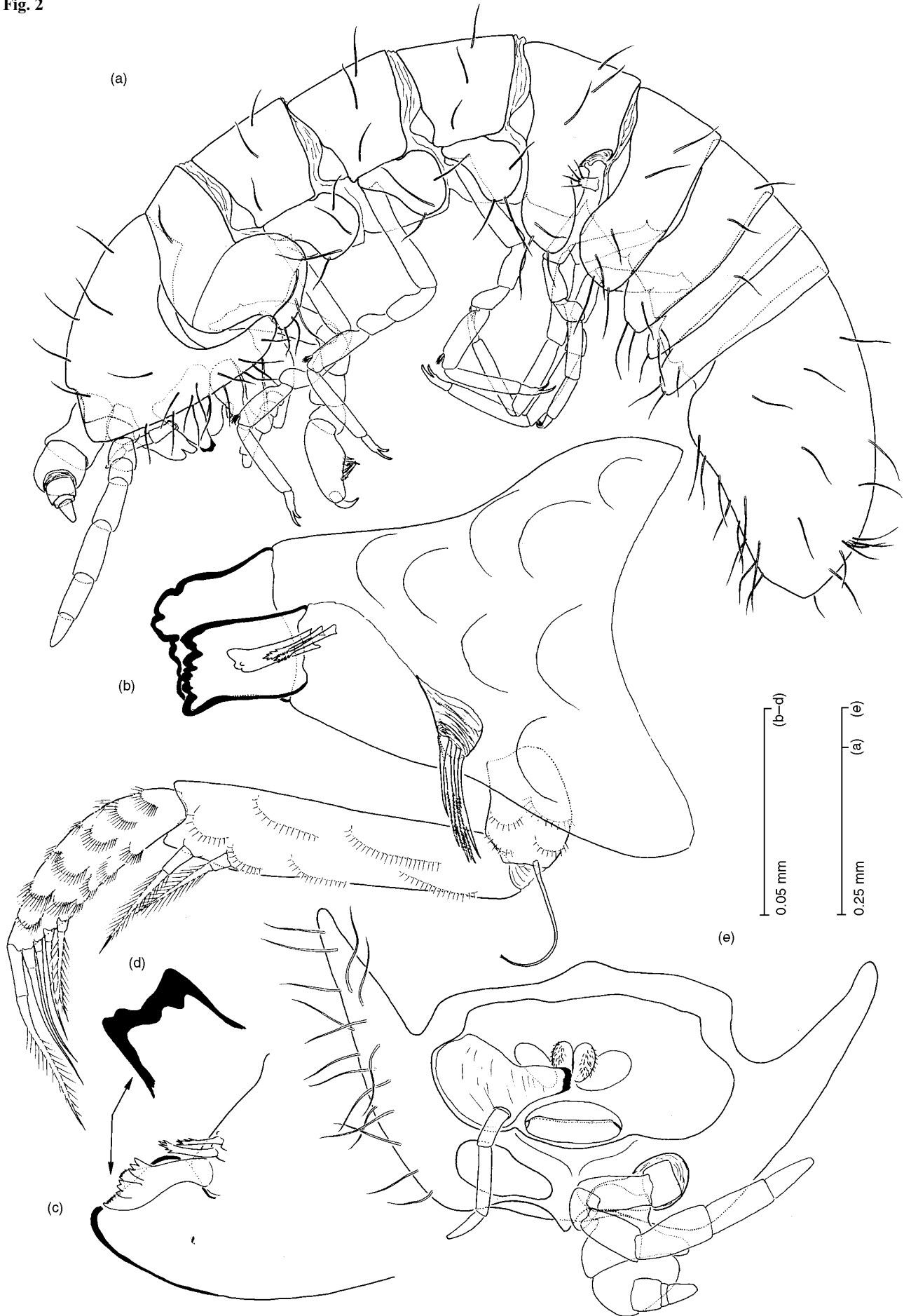


Fig. 2



Cephalothorax with slightly convex frontal margin (Fig. 1a). Anterolateral process broad, roughly triangular, with rounded tip surpassing frontal margin (Fig. 2a). Posterolateral corner produced into long, sickle-shaped, posteriorly-directed process with rounded tip; process partially overlapping first pereionite laterally. Forwardly directed, triangular ventral rostral process – representing fused frontal lamina and clypeus – separating antennule bases (Fig. 2a, e).

Pereionites (Fig. 1a) roughly rectangular, considerably wider than long; relative lengths as follows:  $1 < 2 = 3 < 4 = 5 > 6 > 7$ ; first and seventh pereionites of about similar length.

Pleonites I-II completely free, well developed, slightly shorter than preceding pereionite, with normally developed, elongated epimera with rounded tips (Figs 2a & 6b); epimera apparently posteriorly-directed with pointed tips in dorsal aspect (Fig. 1a).

Pleotelson about as long as wide, ellipsoid, with two shallow indentations subdistally where uropods insert. Distal margin between uropod insertions folded inwards, with pair of tiny setules; margin outline evenly convex in both dorsal (Fig. 1a) and posterior (Fig. 1d) aspects, slightly surpassing posterodistal corners of pleotelson in dorsal aspect (Fig. 1a). Gap between posterodistal corners representing *c.* 27% of pleotelson maximum width; corners not produced beyond uropods (Fig. 1a, d).

Labrum (Fig. 2e) rounded, with transverse apical groove giving bilobed outline from lateral aspect (Fig. 2a). Labium (Fig. 2e) bilobed, inner lobe setulose.

Antennule (Fig. 1b) short, five-segmented, about half cephalothorax length, with peduncle segments expanded, proximal cup-shaped, second wider than long, with convex distal margin. Peduncle segments contributing to closing off body completely during volvation. Flagellum shorter than peduncle, inserted subdistally on ventral (= posterior) surface of second peduncle segment. Distal flagellum segment bearing two aesthetascs, one implanted proximally at about one-third of distance along segment, other longer, implanted distally. Other antennular armature elements as figured.

Antenna (Fig. 1c) seven-segmented, slender, uniramous; third segment shortened and curved outwards; segments bearing smooth setae, each with microscopically trifold tip, distributed as figured; fifth segment with several modified setae with brush-like tip.

Left mandible (Fig. 2b) stout, with broad corpus; pars incisiva and lacinia similar, with multilobed distal edge, lacinia somewhat narrower, unmoveable; spine row consisting of club-shaped, four-cuspidate stout spine

resembling reduced lacinia, plus two similar, distally-serrate, expanded-at-base slender spines; wide gap between spine row and pars molaris; latter consisting of soft lappet crowned with five stout setae, three medial serrate, two lateral smooth. Palp triarticulate, proximal segment with zero to one slender seta with trifold tip; second segment elongate, about 4.3 times as long as wide, with one to two pectinate robust setae subdistally on anterior margin; distal segment sickle-shaped, short, *c.* 64% length of preceding segment, with four to five robust pectinate setae on distal portion of anterior margin. Right mandible (Fig. 2c, d) similar to left counterpart, but with pars incisiva with almost smooth edge (only three low, rounded cusps developed; see Fig. 2d); lacinia slender, movable, with finely serrate oblique distal margin and two tricuspidate denticles subdistally; spine row composed of only two unequal, multicuspoid spines.

Maxillule (Fig. 3a) with digitiform medial lobe bearing terminal, geniculate long pinnate seta; lateral lobe with nine stout spines, outermost three denticulate along inner margin only, rest bipectinate. Transverse row of setules on each ramus as figured.

Maxilla (Fig. 3b) trilobed, lobes of similar length. Lateral and middle lobes with two and three terminal pinnate setae, respectively; medial lobe with seven heterogeneous armature elements, corresponding to four pinnate setae, single, sparsely denticulated seta, plus two spines denticulated along outer margin only. Antero-medial surface of limb with hyaline flame-like spinules (Fig. 3d).

Maxilliped (Fig. 3c) with well-developed epipodite slightly longer than protopod. Presence of coxa unconfirmed. Protopod rectangular, somewhat longer than wide, with anterior surface bearing several clusters of hyaline, flame-like spinules (Fig. 3d). Endite subquadrate, completely incorporated into protopod, with two coupling hooks; distal margin sinuous, with seven heterogeneously ornamented spines and row of ordinary setules arranged as figured; single smooth, trifold seta proximally near to medial margin of endite on posterior surface. Palp five-segmented, four proximal segments with one, two, three, and three smooth trifold setae, respectively, on inner (= medial) margin; distal segment with four trifold smooth setae, plus stout terminal smooth seta and stout bipinnate seta subdistally.

Coxal plates (= projections of the posterior margin of coxae, as clearly shown by insertion point of basipodite) of pereiopods 1–5 ventro-laterally directed, those of pereiopods 6–7 directed dorso-laterally (Fig. 2a). Plates of pereiopods 2–4 articulated dorsally, rest completely incorporated into corresponding tergites (their homology obvious due to presence of same setae seen on coxa 1–4). Coxa 1 (Fig. 4a) wider than long, with deeply excavate anterior margin and evenly rounded posterior margin; distal margin straight; plate depressed anterodistally to accommodate posterolateral sickle-shaped process of cephalothorax; six smooth setae on plate as figured. Coxa 2 (Fig. 4d) longer than wide, with excavate anterior margin and evenly rounded posterior

◀ **Fig. 2.** *Atlantasellus dominicanus* sp. nov., adult female: (a) body, lateral; (b) left mandible, medial; (c) detail of pars incisiva, lacinia, and spine row of right mandible, medial; (d) detail of pars incisiva of former; (e) ventral view of cephalothorax showing rostral process and upper and lower lips, plus right antennule, antenna and left mandible.

Fig. 3



margin. Coxae 3 and 4 (Fig. 5a, b) subsimilar, longer than wide, ovoid, with shallowly excavate anterior margin. Coxa 5 (Fig. 5c) ovoid, strongly excavated proximally on posterior margin to accommodate pereopod 5 exopod (see Fig. 2a). Coxae 6 and 7 (Figs 5e & 6a) longer than wide, with sub-parallel anterior and posterior margins, and with slightly produced posterolateral corner; coxa 7 narrower than preceding plate. Coxae 2–7 each with three smooth setae positioned as figured.

Oöstegites on pereopods 2–4, as hypertrophied, broad overlapping membranous plates, elliptical in shape (Fig. 4d).

Pereopod 1 (Fig. 4b) strongly subchelate, with shortened ischium, merus and carpus; merus with lateral margin protruding as evenly rounded lobe. Propodus (Fig. 4c) roughly triangular, with palm angle positioned at about three-fifths of maximum distance along segment; two unequal spines on angle, proximal short, hardly denticulate; more distal long and stout, with four strong denticles proximally and pectinate frill distally along outer margin. Palm margin oblique, concave, with pair of spines similar to strong palmar spine placed about midway of margin, plus pair of smooth trifid setae located proximally and distally on margin. Posterior surface of segment with two smooth, trifid setae plus short and stout hirsute spine positioned as figured, smooth trifid seta distally on lateral margin of segment. Dactylus-unguis with two denticulate spines on medial margin and eight smooth trifid setae as figured.

Pereopods 2–7 (Figs 4d & 5d, f) subsimilar, ambulatory, composed of long, cylindrical segments, with dactylus much shorter than propodus bearing two strong claws fused to segment at base, plus short, smooth slender seta in between on posterior surface of segment (Fig. 4f); short, rounded plate-like spine subdistally on posterior surface of propodus of each pereopod, overlapping proximal portion of dactylus (Fig. 4f). Dactylus showing two transverse constrictions, one at about one-quarter and other at three-quarters of distance along segment (Fig. 4f). Pereopods 2–4 with short, shabby spine (Fig. 4d, e) subdistally on outer margin of carpus; spine absent in pereopods 5–7 (Fig. 5d, f). Pereopod 5 (Fig. 5d) retaining remnant of exopod – as short, unsegmented digitiform process crowned with four setae – proximally on basis, adjacent to coxa–basis articulation; exopod non-articulated at base, completely incorporated into basis.

Pleopods I and II wanting. Third pleopods (Fig. 6c) operculate, separate, not fused medially, uniramous, with short sympod fused to exopod; endopod wanting. Integument non-sclerotized, lacking keels, edges or any sculpture apart from ordinary setulose integumental

scales. Pleopods with truncate tip, straight inner margin, and evenly rounded outer margin; maximum width attained at *c.* 35% of distance along segment. Pleopods with short, smooth setae as figured.

Fourth pleopods (Fig. 6d) completely concealed beneath operculum within gill chamber, biramous. Sympod trapezoidal, expanded distally, about as long as wide. Exopod shorter than endopod, two-segmented. Proximal exopodal segment attached to lateral margin of sympod by means of oblique suture line; round bulge with microgranulate integument proximally on medial margin of segment. Distal exopodal segment short, subquadrate, with two short, brush-like setae distally. Lateral margin of exopod segments setulose. Endopod subrectangular, about same length as sympod and twice as long as wide, with medial margin covered with microspinules; three short brush-like setae distally on segment.

Pleopod V (Fig. 6e) somewhat reduced, consisting of simple, ovoid plate.

Uropods (Fig. 1a, d) non-articulating, reduced to tiny rounded bulges completely incorporated into pleotelson.

#### *Adult male*

Unknown.

#### *Etymology*

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

#### *Remarks*

The original description of *Atlantasellus cavernicolus* by Sket (1979), supplemented with the additional observations made by Wägele (1983) on several appendages, furnish enough data to permit recognition of the Hispaniolan taxon as a distinct, new species. *Atlantasellus dominicanus* has the posterolateral corners of the cephalothorax produced into a slender, sickle-shaped process (posterolateral corners stout, triangular in outline in *A. cavernicolus*). The anterior margin of the cephalothorax is evenly convex in dorsal aspect (margin pointed in *A. cavernicolus*). The left mandible spine row is composed of three elements (only two in *A. cavernicolus*, which lacks the distalmost, stouter, club-shaped spine present in the new species). Pereopod 5 expresses a remnant of exopod (pereopod 5 uniramous in *A. cavernicolus*). The posterolateral corners of the pleotelson are not produced beyond the uropods in dorsal aspect (corners widely surpassing uropods in *A. cavernicolus*). The gap between these posterolateral corners represents *c.* 27% of pleotelson maximum width (gap representing only about 9.5% of maximum width in *A. cavernicolus*). The distal margin of pleotelson between the uropod insertions is evenly convex in posterior view (margin

◀ **Fig. 3.** *Atlantasellus dominicanus* sp. nov., adult female: (a) stretched right maxillule, lateral; (b) right maxilla, anterior (upside down); (c) left maxilliped with disarticulated epipodite, posterior; (d) detail of flame-like hyaline spinules of maxilliped.

Fig. 4





with triangular shape in *A. cavernicolus*; see Sket, 1979: fig. 4). The third pleopods lack sclerotized ridges (ridges present in *A. cavernicolus*), and the fourth pleopods have the exopod shorter than the endopod (exopod longer than endopod in *A. cavernicolus*).

### Behaviour

The animals were observed *in vivo* in a shallow tray just after being caught in the caves. After several minutes, and once the wood debris sedimented, the tiny isopods were clearly visible crawling above the dark bottom. The animals progressed along the bottom at a uniform, slow speed, not swimming or accelerating even though I tried repeatedly to pick them up with the aid of soft tweezers. Surprisingly, the animals did not conglobate when being picked up, as might be expected if conglobation was performed as a defensive tactic in response to predators. The conglobation behaviour was observed only after the animals contacted the formaldehyde used as fixative. During conglobation, the body is flexed along the anterior and posterior margins of the fourth thoracomere, the final form resembling more a castanet than a ball; this flexure pattern is asymmetrical with the anterior portion of the body not extending far enough to cover the pleotelson completely, the uncovered portion being closed off by the modified, flattened antennules.

The apparent restriction of the species to living on submerged decaying wood only, might indicate specialized feeding habits on aquatic fungi or other micro-organisms. The study of the gut contents of several individuals revealed only an amorphous dark substance, probably wood pulp.

Even though the brood pouches of the specimens studied were apparently empty, the form of the oöstegites suggests that the eggs are carried rather than laid on the substratum, as assumed for the closely related Microcerberidae.

### On the schizopodous condition of the fifth pereopod of *Atlantasellus dominicanus*

All available specimens of the new species display a short digitiform process proximally on the outer margin of basis of pereopod 5 (Fig. 5d). This process is orientated perpendicular to the body longitudinal axis, and protrudes through the broad proximal slit present on the posterior margin of coxal plate 5 (see Fig. 2a).

The size, outline, and the presence of setae on this process gives it a very different appearance from the typical oöstegites on pereopods 2–4, although the possibility remains that it could represent a modified oöstegite that functions like a genital operculum, given the position of the papilliform female gonopore near the inner surface of coxal plate 5. Nevertheless, there is strong evidence against the derivation of the process as a modified oöstegitic condition: (1) it clearly inserts on the pereopod basis, and not on the inner surface of the coxal plate; (2) it is oriented laterally, i.e. preventing its involvement in the formation of a ventral brood pouch or as a closing mechanism for the gonopore; (3) Manca-stage specimens also display this feature. In addition, the putative exopod of *Atlantasellus* is located precisely in the position homologous to that of the exopod in most peracarid orders displaying schizopodous pereopods (i.e. thermosbaenaceans, Wagner, 1994; mictaceans, Sanders, Hessler & Garner, 1985; Bowman & Iliffe, 1985; spelaeogriphaceans, Boxshall, 1999; cumaceans, Watling, 1991; tanaidaceans, Gutu & Iliffe, 1989).

Unfortunately, no males of the new species were caught, but these would presumably allow the definitive rejection of the possibility of an oöstegitic derivation of this process. Based on the available evidence, the process, on the basis of pereopod 5 of *A. dominicanus*, is interpreted here as a remnant of the exopod, suggesting a schizopodous condition for the (fifth) pereopods in the isopod groundplan.

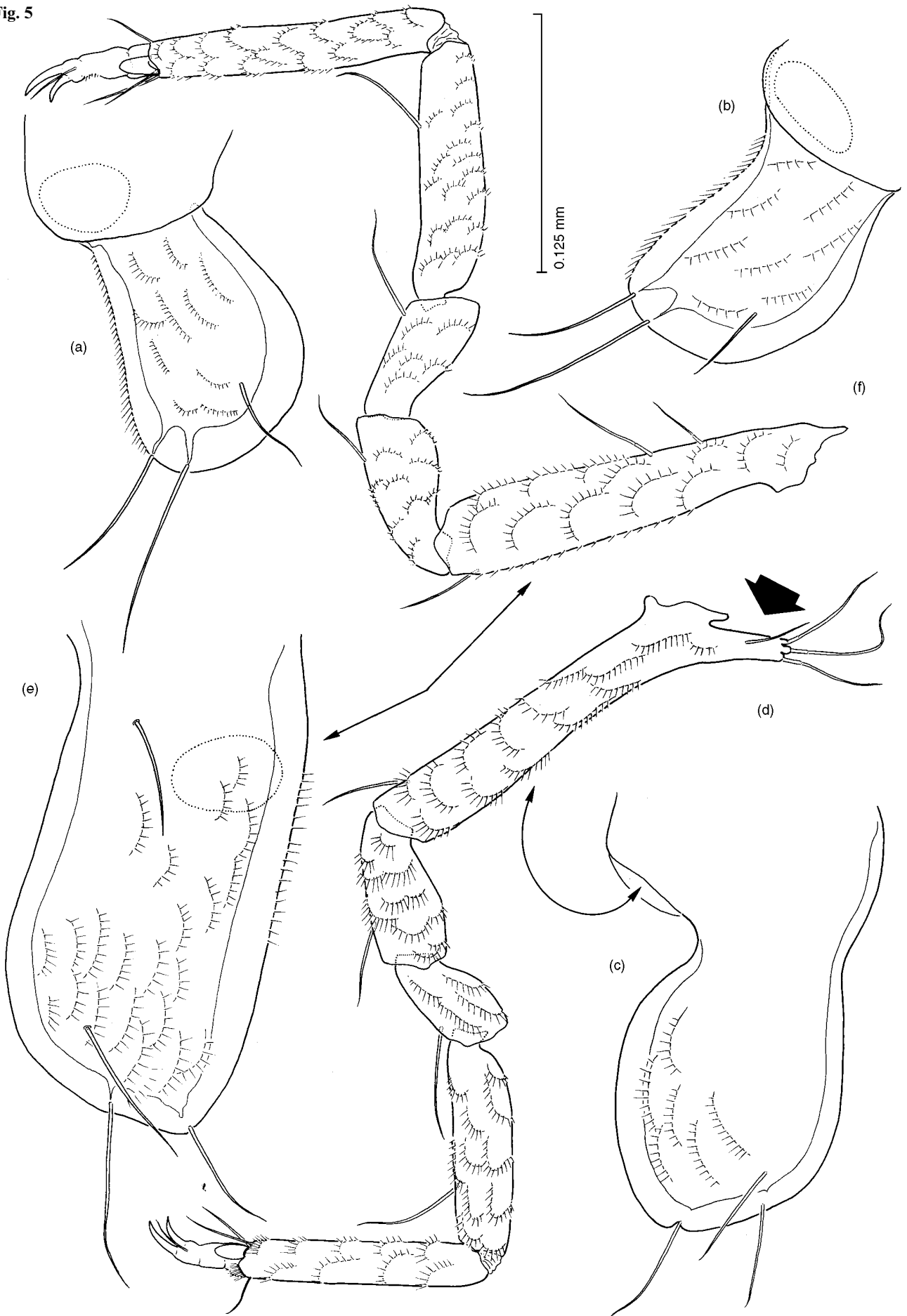
### Marine vs freshwater origin of atlantasellids

The Aselloidea is considered to be a separate, monophyletic freshwater line composed of four families within the mostly marine Asellota (Wägele, 1990). The two more primitive families, viz. Asellidae and Stenasellidae, are strictly freshwater taxa and seem convincingly to have evolved from ancestors already present in fresh waters: neither is euryhaline, nor displays distribution restricted to coastal areas or corresponding with regions flooded by epicontinental seas in the past. Their presence on almost all continental landmasses suggests an ancient (Pangaeon) origin (Wägele, 1983; Notenboom, 1991).

Even though most representatives dwell in marine coastal groundwaters, Wägele (1983, 1990; Wägele, Voelz & Vaun McArthur, 1995) arrived at a similar conclusion with respect to the more derived aselloid family, the Microcerberidae. The occurrence of the most primitive genera of microcerberids in freshwaters of Gondwanian (southern Africa) regions, combined with the presence of congeneric species of another plesiomorphic freshwater genus in North America and south-east Europe (hence implying the existence of a common ancestor before the opening of the central Atlantic), were interpreted as evidence for an ancient freshwater origin. In addition, the derived condition of the microcerberids dwelling in the coastal marine mesopsammal

◀ **Fig. 4.** *Atlantasellus dominicanus* sp. nov., adult female: (a) left coxal plate 1, lateral; (b) left first pereopod, medial; (c) detail of palm margin and nail of latter, medial; (d) left second pereopod with attached oöstegite (coxa and oöstegite, lateral; rest of pereopod, posterior); (e) detail of hirsute spine on outer margin of carpus of pereopod 2; (f) detail of distal portion of pereopod 2, posterior.

Fig. 5



(all placed in a single, monophyletic group) was regarded as supporting the hypothesis that the colonization of this habitat was a secondary event. The world-wide distribution of this marine mesopsammal clade would thus have been attained by dispersal, on the assumption that marine organisms can overcome geographic barriers much more easily than their limnic counterparts.

The intermediate phylogenetic position of the Atlantasellidae between the Stenasellidae and the more advanced Microcerberidae provided Wägele (1983, 1990) with phylogenetic arguments supporting a freshwater origin for this monotypic family as well, and consequently led him to suggest that some connection between Bermuda and older continental fragments must have existed in the past. However, such phylogenetic reasoning is not in accord with either biogeographic or ecological arguments: Bermuda has been a deep-water, submerged volcanic seamount almost since its origins (about 100 Myr BP), and there is no objective evidence of any connections with continental landmasses in the past. Subaerial conditions (i.e. the possibility for permanent fresh waters to exist) did not arise there until the early Pleistocene (see Iliffe, Hart & Manning, 1983, and references therein). In addition, no primarily freshwater lineages are known from Bermuda (Sket & Iliffe, 1980), and *Atlantasellus cavernicolous* dwells there in virtually marine water.

The discovery of a second *Atlantasellus* species in groundwaters of the Dominican Republic provides new evidence relevant to the marine/freshwater controversy on the origin of the Atlantasellidae. The Antillean (= Greater and Lesser Antilles) region has no continually emerged landmasses older than Late Eocene, which precludes the persistence *in situ* of old freshwater lineages (Iturralde-Vinent & MacPhee, 1999). The question arises of whether *Atlantasellus dominicanus* sp. nov. could have colonized southern Hispaniola from peri-Caribbean landmasses in relatively recent times. In that respect, there is convincing evidence that north-western South America was briefly connected during the Eocene-Oligocene transition with emerged landmasses now belonging to the Greater Antilles, including the Southern Hispaniolan Block harbouring *Atlantasellus* today, via the Aves Ridge (see Iturralde-Vinent & MacPhee, 1999).

Aside from the brief duration of this putative connection to the mainland (quoted to have occurred some time between 35 and 33 Myr BP), other evidence points against the possibility that Hispaniola could have been colonized by *Atlantasellus* from South America. Thus, the evidence is not conclusive as to whether the so-called

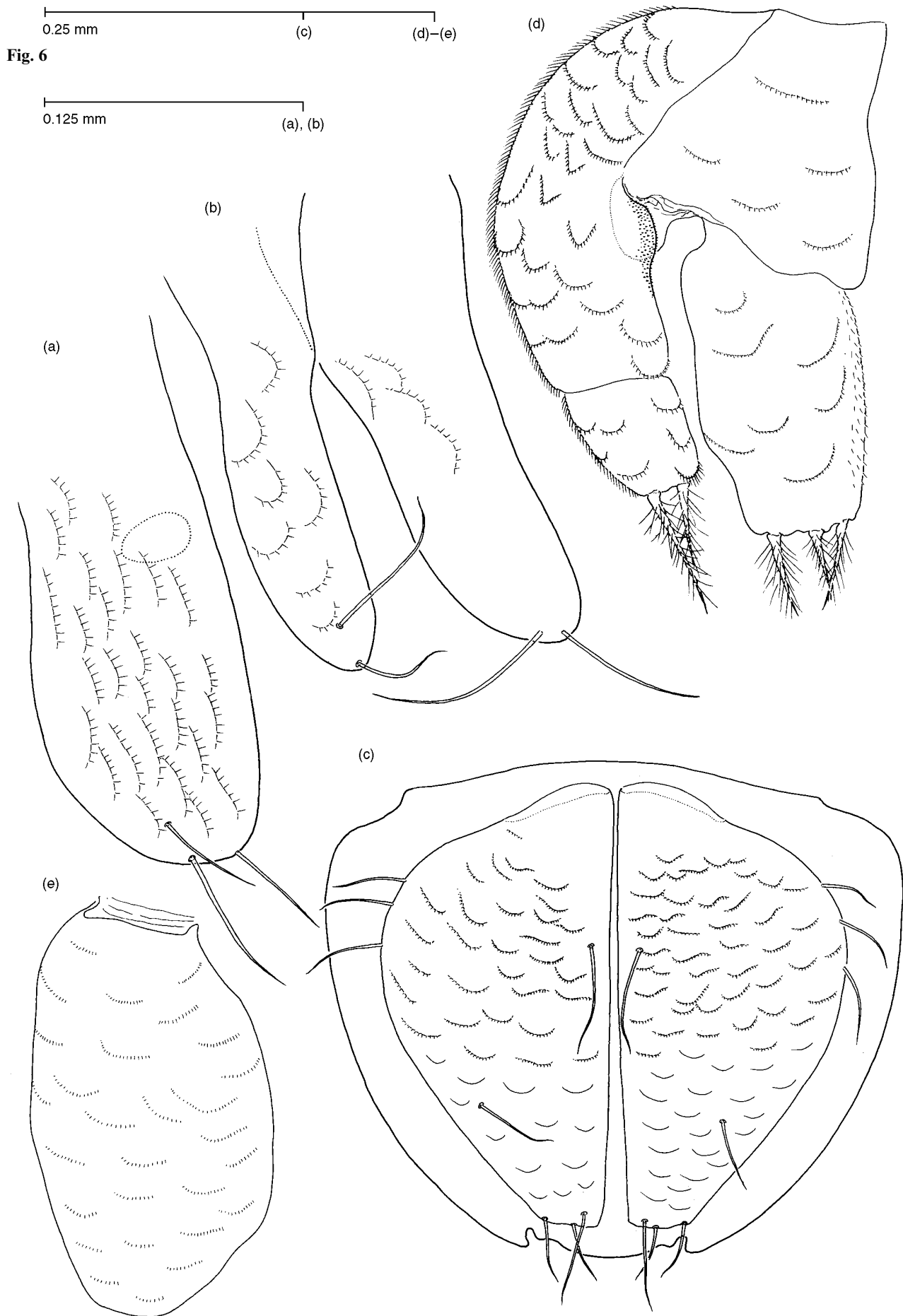
GAARlandia (Greater Antilles + Aves Ridge) landspan was a continuous landmass, or the subaerial exposure of the Aves Ridge ridgecrest created only a series of closely spaced islands stretching from northern South America to the Puerto Rico/Virgin Islands Block. In addition, the degree to which the north-western portion of South America (putatively acting as a source area for the GAARlandia terrestrial/freshwater biota) was physically separated from the rest of South America by marine barriers has not been fully clarified. Also relevant here is the apparent absence of freshwater aselloids in Central and South America south of Guatemala (Coineau, 1986; Henry *et al.*, 1986) and, more conclusively, the complete submersion of the Southern Hispaniolan Peninsula during the general subsidence phase which occurred just after the short Eocene/Early Oligocene landspan phase (see Iturralde-Vinent & MacPhee, 1999: fig. 7).

An alternative argument, already outlined by Henry *et al.* (1986), is revisited here to explain the origin of *Atlantasellus*: that this taxon is a thalassoid lineage which occupied the continental groundwaters in the way proposed by the so-called Regression-model, i.e. populations of pre-adapted, coastal marine crevicular lineages being stranded and progressively adapted to fresh groundwaters after marine regressions (Notenboom, 1991). The absence of members of the typically freshwater aselloid families Asellidae and Stenasellidae in the Antillean region, and the presence there only of Microcerberidae belonging to the coastal marine mesopsammal group (see Kensley & Schotte, 1989), could lend additional support to this view.

Both deep-sea (Sket, 1979) and shallow-water origins (Henry *et al.*, 1986) have been proposed for *Atlantasellus*, although both hypotheses are weakened since no marine relatives of this taxon are known. Assuming a derivation from a shallow water ancestor – the only marine aselloids known thus far are coastal mesopsammal microcerberids – would permit speculation on the age of the genus itself. Thus, if the synthetic Late Tertiary stratigraphic column presented by Iturralde-Vinent & MacPhee (1999: fig. 20) holds for the entire Southern Hispaniola Southern Peninsula, then it could be assumed that the area occupied by *A. dominicanus* lay in deep waters until well into the Pliocene (about 4.5 Myr BP). *Atlantasellus cavernicolous* from Bermuda could be potentially older, since the Bermudan seamount cap was in shallow waters since much earlier, about 30 Myr BP (Iliffe *et al.*, 1983). But if a coeval, vicariant origin for the two species of *Atlantasellus* is assumed, their common ancestor should not be older than Pliocene.

◀ **Fig. 5.** *Atlantasellus dominicanus* sp. nov., adult female: (a) left coxal plate 3, lateral; (b) left coxal plate 4, lateral; (c) right coxal plate 5, lateral; (d) right fifth pereopod, posterior (arrowhead pointing to exopod); (e) left coxal plate 6, lateral; (f), left pereopod 6, posterior.

**Fig. 6.** *Atlantasellus dominicanus* sp. nov., adult female: (a) left coxal plate 7, lateral; (b) left pleonites I–II, lateral; (c) third pleopods, anterior (pleotelson outlined beneath); (d) right pleopod IV, anterior; (e) right pleopod V, anterior. ▶



## Acknowledgements

This paper is a contribution to ICEX-472/95RD (Programa de Cooperación Científica con Iberoamérica, MEC), Proyecto GEF República Dominicana (PNUD/ONAPLAN), and to DIVERSITAS-IBOY project, 'EXPLORATION AND CONSERVATION OF ANCHIALINE FAUNAS'. Thanks are extended to Josep A. Alcover and Damià Ramis for their support during the cave surveys. José A. Ottenwalder (PNUD, Sto. Domingo) and members of 'Grupo Jaragua' (Oviedo, Pedernales) facilitated the fieldwork in many ways. Professor Johann W. Wägele (Rühr-Universität, Bochum), Geoff A. Boxshall (The Natural History Museum, London), and Boris Sket (University of Ljubljana) are warmly acknowledged for providing advice and literature.

## REFERENCES

- Botosaneanu, L. & Stock, J. H. (1982). Les *Cyathura* stygobies (Isopoda, Anthuridea) et surtout celles des Grandes et des Petites Antilles. *Bijdr. Dierkd.* **52**: 13–42.
- Bowman, T. E. & Iliffe, T. M. (1985). *Mictocaris halope*, a new unusual peracaridan crustacean from marine caves on Bermuda. *J. crustacean Biol.* **5**: 58–73.
- Boxshall, G. A. (1999). Ordre des Spélaeogriphacés (Spelaeogriphacea Gordon, 1957). *Mém. Inst. océanogr. (Monaco)* **19**: 35–38.
- Coineau, N. (1986). Isopoda: Microcerberidae. In *Stygofauna Mundi: a faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial)*: 473–479. Botosaneanu, L. (Ed.). Leiden: E. J. Brill.
- Dudich, E. (1924). Ueber *Protelsonia hungarica* Méhely. *Zool. Anz.* **60**: 151–155.
- Gutu, M. & Iliffe, T. M. (1989). *Apeudes orghidani*, a new species of Tanaidacea (Crustacea) from an anchialine cave on Bermuda. *Trav. Mus. Hist. nat. 'Grigore Antipa'* **30**: 161–167.
- Henry, J. P., Lewis, J. J. & Magniez, G. (1986). Isopoda: Aselloidea, Gnathostenetroidoidea, Stenetrioidea. In *Stygofauna Mundi: a faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial)*: 434–464. Botosaneanu, L. (Ed.). Leiden: E. J. Brill.
- Iliffe, T. M., Hart, C. W. & Manning, R. B. (1983). Biogeography and the caves of Bermuda. *Nature (Lond.)* **302**: 141–142.
- Iturralde-Vinent, M. A. & MacPhee, R. D. E. (1999). Paleogeography of the Caribbean Region: implications for Cenozoic biogeography. *Bull. Am. Mus. Nat. Hist.* **238**: 1–95.
- Jaume, D. & Wagner, H. P. (1998). New cave-dwelling amphipods (Lysianassidae, Hadziidae) from the Dominican Republic (Hispaniola). *Contrib. Zool.* **68**: 37–66.
- Karaman, S. (1933). *Microcerberus stygius*, der dritte Isopod aus dem Grundwasser von Skoplje, Jugoslawien. *Zool. Anz.* **102**: 165–169.
- Kensley, B. & Schotte, M. (1989). *Guide to the marine isopod crustaceans of the Caribbean*. Washington, DC: Smithsonian Institution Press.
- Latreille, P. A. (1803). Histoire Naturelle des Crustacés et des Insectes. In *Histoire naturelle, nouvelle édition, accompagnée des notes*: 5. Buffon, G. L. L. (Ed.). Paris: C. S. Sommimi.
- Latreille, P. A. (1817). Les Crustacés, les Arachnides, et les Insectes. In *Le Regne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*: 3. Cuvier, G. (Ed.). Paris.
- León, R. O. (1989). *Geología de la Sierra de Baoruco*. Santo Domingo: Museo Nacional de Historia Natural.
- Notenboom, J. (1981). Amsterdam expeditions to the West Indies Islands, report 12. Some new hypogean cirrolanid isopod crustaceans from Haiti and Mayaguana (Bahamas). *Bijdr. Dierkd.* **51**: 313–331.
- Notenboom, J. (1991). Marine regressions and the evolution of groundwater dwelling amphipods (Crustacea). *J. Biogeogr.* **18**: 437–454.
- Rafinesque-Schmaltz, C. S. (1815). *Analyse de la nature ou tableau de l'univers et des corps organisés*. Palerma.
- Sanders, H. L., Hessler, R. R. & Garner, S. P. (1985). *Hirsutia bathyalis*, a new unusual deep-sea benthic peracaridan crustacean from the tropical Atlantic. *J. crustacean Biol.* **5**: 30–57.
- Sket, B. (1979). *Atlantasellus cavernicolus* n. gen., n. sp. (Isopoda Aselloota, Atlantasellidae n. Fam.) from Bermuda. *Biol. Vestn.* **7**: 175–183.
- Sket, B. & Iliffe, T. M. (1980). Cave fauna of Bermuda. *Int. Rev. gesamten Hydrobiol.* **65**: 871–882.
- Stock, J. H. (1985a). Stygobiont amphipod crustaceans of the Hadzioid group from Haiti. *Bijdr. Dierkd.* **55**: 331–426.
- Stock, J. H. (1985b). Bogidiellidae (Amphipoda) from Haiti and some general rules on the occurrence of Crustacea Malacostraca in inland groundwaters of the West Indies. *Stylogologia* **1**: 208–223.
- Trias, M., Ottenwalder, J. A., Jaume, D. & Alcover, J. A. (1997). Una campaña en la República Dominicana. Resultados preliminares. *Endins* **21**: 63–74.
- Wägele, J. W. (1983). On the origin of the Microcerberidae (Crustacea: Isopoda). *Z. zool. Syst. Evolutionsforsch.* **21**: 249–262.
- Wägele, J. W. (1990). Aspects of the evolution and biogeography of stygobiont Isopoda (Crustacea: Peracarida). *Bijdr. Dierkd.* **60**: 145–150.
- Wägele, J. W., Voelz, N. J. & Vaun McArthur, J. (1995). Older than the Atlantic Ocean: discovery of a fresh-water *Microcerberus* (Isopoda) in North America and erection of *Coxicerberus* new genus. *J. crustacean Biol.* **15**: 733–745.
- Wagner, H. P. (1990a). *Jehaia stocki* n. g., n. sp., a new interstitial janiroid isopod from the Dominican Republic, Hispaniola (Crustacea: Isopoda: Janiroidea). *Beaufortia* **41**: 187–193.
- Wagner, H. P. (1990b). The stygobiont isopods of the genus *Cyathura* in the Dominican Republic (Crustacea: Isopoda: Anthuridae). *Bull. Zool. Mus. Univ. Amst.* **12**: 145–158.
- Wagner, H. P. (1992). *Stygiomysis aemete* n. sp., a new subterranean mysid (Crustacea, Mysidacea, Stygiomysidae) from the Dominican Republic, Hispaniola. *Bijdr. Dierkd.* **62**: 71–79.
- Wagner, H. P. (1994). A monographic review of the Thermosbaenacea (Crustacea: Peracarida). A study on their morphology, taxonomy, phylogeny and biogeography. *Zool. Verh. (Leiden)* **291**: 1–338.
- Watling, L. (1991). Revision of the cumacean family Leuconidae. *J. crustacean Biol.* **11**: 569–582.