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A REPRESENTATIVE OF THE MAINLY ABYSSAL FAMILY PARDALISCIDAE (CRUSTACEA, AMPHIPODA) IN CAVE WATERS OF THE CAICOS ISLANDS

by

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ABSTRACT

A new genus and species of Amphipoda is described from cave waters on Providenciales (Caicos Islands) as *Spelaeonicippe provo*. Another species belonging to the same new genus is known from a cave on Lanzarote (Canary Islands). The genus belongs to the Pardaliscidae, a predominantly bathyal/abyssal family. A possible evolutionary scenario for both species is discussed.

RÉSUMÉ

On décrit un genre et espèce nouveaux d'Amphipodes des eaux d'une grotte de Providenciales (Iles Caicos), sous le nom de *Spelaeonicippe provo*. Une autre espèce appartenant au même genre est connue d'une grotte de Lanzarote (Iles Canaries). Le genre appartient aux Pardaliscidae, famille connue surtout des étages bathyal et abyssal. On présente un scénario évolutif plausible pour ces deux espèces.

INTRODUCTION

During a survey of the groundwater fauna of the Bahamas and the adjoining islands in the West Indies, a sample of Amphipoda was taken in a so-called "water hole" on Providenciales, an island in the western part of the Caicos group, to the north of Haiti. The "water hole" in question is an oblique fissure in the calcareous rocks, in direct contact with the underlying water table. This particular "water hole" may be classified as a "marginal cave" (sensu Riedl & Ozretič, 1969) or anchihaline habitat (sensu Holthuis, 1973), since the high chlorinity of its waters (11.1‰) points to extensive subterranean connections with

the sea (the nearest sea coast is some 1½ km from the cave entrance). The accessible part of the water hole is in semidarkness.

The Amphipoda from this cave have been observed free-swimming ("pelagic") in the water. They are unpigmented, with a pink intestine, and devoid of eye pigment. The accompanying fauna is relatively poor, consisting of several species of Gastropoda. Dr. H. E. Coomans (Institute of Taxonomic Zoology, University of Amsterdam) has been kind enough to examine these mollusks and he informs us (in litt.) that seven species are represented. Dead shells of *Echininus nodulosus* (Pfeiffer, 1839), *Truncatella caribaeensis* (Reeve, 1842), and *Melampus (Microtralia)* sp. (possibly *M. minusculus*) were present, together with live and dead specimens of *Lyrodes* sp. Of these, *E. nodulosus* and *T. caribaeensis* are living in the marine fringe of the supralittoral of the coast; *Lyrodes* lives in pools and springs, near the sea; *Melampus* is an inhabitant of brackish waters. All are superficial species, and all indicate a certain relation to the marine environment. In addition, the cave yielded a number of terrestrial snails, all no doubt washed in from the surface, viz., *Bothriopupa* sp., *Gastrocopta* sp., and members of the family Chondropomidae. No other macro- or microfaunal elements were observed in this particular water hole, but a nearby water hole, presumably part of the same subterranean water system, harboured *Typhlatya* sp. (Decapoda Macrura) and *Sesarma* sp. (Decapoda Brachyura). *Typhlatya* is a wide-spread stygobiont element in the West Indies, probably of marine origin (cf.

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Stock, 1981), and *Sesarma* is a marine and mixohaline genus. In summary, most faunal elements in the water holes near the airport of Providenciales have distinct marine affinities.

The Amphipoda belong to a new genus, called *Spelaeonicippe*, closely related to the genus *Nicippe* Bruzelius, 1859, a member of the family Pardaliscidae. This family is well-characterized by the mandible, lacking a distinct molar process; by the very small inner and outer plates of the maxillipeds; by the short coxal plates; and by the elongate, lanceolate rami of the third uropods (Barnard, 1969).

BATHYMETRICAL DISTRIBUTION OF THE PARDALISCIDAE

The Pardaliscidae are predominantly bathyal/abyssal/hadal, pelagic Amphipoda (Bousfield, 1978), and Birstein & Vinogradov (1962: 249) consider them as "one of the basic abyssal families of gammarids". The genus *Nicippe* to which the present cave amphipods are most closely related, is not restricted to the deep sea. Most of its records are from the lower part of the continental shelf and the upper part of the continental slope (110-600 m; cf. Metzger, 1875; Sars, 1893; Chevreux, 1900; Enequist, 1949; Gurjanova, 1951; Ledoyer, 1973, 1977), with exceptional deeper ones, down to 1393 m (cf. Stephensen, 1931). According to certain authors (Barnard, 1959; Karaman & Schiecke, 1973) this genus penetrates also in waters of the upper part of the shelf, though always in the sublittoral (from 35 m down).

Although Bousfield (1978) states that the members of the Pardaliscidae are carnivorous, Enequist (1949) supposes that at least *Nicippe* might be a detritus feeder, and Wilkins & Parzefall (1974) consider diatoms the primary food source of *Spelaeonicippe buchi* (as *Nicippe*).

Only one member of the family Pardaliscidae has been found outside the open sea in cave waters: Andres (1975) described a new species, under the name of *Nicippe buchi*, from a lava tunnel (the well-known Jameos del Agua) on the island of Lanzarote in the Canarian archipelago. As will be shown in the taxonomic part of the present paper, the Canarian cave species, though closely

related to *Nicippe*, is still more close to the cave animals from Providenciales, and is therefore reckoned to the genus *Spelaeonicippe*. Certain differences in its appendages, in addition to the ocean-wide geographical gap between the caves of Providenciales and Lanzarote, justify in our opinion that the Canarian and West Indian populations are to be treated as separate species.

THE HABITAT OF SPELAEONICIPPE

Both localities from which *Spelaeonicippe* is known, Lanzarote and Providenciales, agree in at least three respects:

(1) The caves are of relatively young geological age. The Jameos del Agua on Lanzarote is part of a lava tube formed 3000-5000 years ago (Wilkins & Parzefall, 1974). The extensive karst erosion, during which caves were formed by groundwater solution, on Providenciales developed during low sea-level stages (at -100 to -120 m) of the Pleistocene (Mather, 1975), thus sometime between 10,000 and 1,000,000 years ago.

(2) The cave waters in Lanzarote and Providenciales are salty. The Lanzarote lava tube runs from the volcano la Corona to the coast where it is flooded by seawater. The blue holes and other karst features on Providenciales often extend below present sea level and are nowadays inundated by seawater, due to sea-level rises at the end of the ice ages, and — perhaps to a lesser extent — due to the general regional subsidence of the Bahamas platform.

In Lanzarote, the salinity in the cave fluctuates around 37‰ (corresponding with a chlorinity of some 20.4‰), which is slightly (0-1‰) inferior to that of the adjoining ocean (Wilkins & Parzefall, 1974, table I). The water hole on Providenciales has a chlorinity that is distinctly lower than that of the surrounding ocean, viz. about 11.1‰, but which is still very salty for inland groundwater. Apparently, fresh water mixes with salty groundwater of marine origin, a not uncommon situation in the Bahamian archipelago.

(3) *Spelaeonicippe* has been found in both the West Indian and the Canarian locality in conditions where light could penetrate and not in total darkness. As to Lanzarote, Wilkins & Par-

zefall (1974) believe that this is not accidental, since the amphipods are supposed to feed on microscopic algae developing in the cave waters. For the West Indian locality, we are less certain about this point, because the totally dark parts of the "water hole" were not explored (so no information is available about presence or absence of *Spelaeonicippe* in those parts), and no diatom growth was observed in the entrance area of the cave.

ORIGIN OF THE FAUNA IN THE MARGINAL CAVES OF LANZAROTE AND PROVIDENCIALES

It can hardly be accidental that in the Jameos del Agua on Lanzarote, in addition to *Spelaeonicippe buchi* (a species which is undoubtedly related to the sublittoral/bathyal species *Nicippe tumida* Bruzelius, 1859), two other organisms with deep-water affinities occur: *Munnidopsis polymorpha* Koelbel, 1892 (Anomura, Galatheidae) and *Mucellicephala jameensis* Hartmann-Schröder, 1974 (Polychaeta, Polynoidae).

We do not share Wilkins & Parzefall's opinion (1974: 431) that the animals in the Jameos del Agua might be wide-spread in the deeper waters of the neighbouring Atlantic. Of course, the absence of eyes and of body pigmentation of the cavernicolous forms is analogous to similar reductions found in many deep-sea animals. On the other hand, the pardaliscid cave Amphipoda of Lanzarote differ in a number of morphological characters from the nearest marine relative. Furthermore, a second species of amphipod known from the same cave, a hadziid (see Andres, 1978) has no relatives at all in deeper waters. It must be stressed that both species of cave amphipods from Lanzarote have their closest relatives in fresh and brackish groundwaters of the West Indies. This makes it more likely that they descend from marine ancestors that during some phase of the evolutionary scenario became adapted to a life in the interstia of coarse substrates (e.g. gravel). The adaptation to this kind of substrate might lie farther in the past for the exclusively benthic hadziid Gammaridae, than for the predominantly pelagic Pardaliscidae. Wilkins & Parzefall (1974: 430) have observed that *Spelaeonicippe buchi*

leaves the gravel on the cave bottom from time to time, to swim around freely, and to disappear again in the substrate after a while. The new species of *Spelaeonicippe* found in the West Indies shows a similar behaviour, but hadziid Gammaridae have never been observed swimming around freely in the water. The relatively recent origin (from marine ancestors) of the pardaliscid cave Amphipoda seems in good agreement with (1) the existence of close relatives in continental shelf and slope waters, and (2) their occurrence in geologically young caves, formed in pleistocene/holocene times.

At any rate, if *Spelaeonicippe* or blind hadziid Gammaridae are to be discovered in the open sea, we suppose they will be shallow-water, meiofaunal elements in coarse substrates. It is from such elements, and not from abyssal ones, that the cave forms presumably evolved. In agreement with this view is the fact that the temperatures in the Lanzarote cave (18.0-18.5° C) and in the Providenciales cave (23.8° C) are closely similar to shallow-water temperatures in the neighbouring ocean, and not at all to bathyal/abyssal temperatures of 10-4° C in the neighbouring ocean.

TAXONOMIC PART

Spelaeonicippe n. gen.

Family Pardaliscidae (Amphipoda). Resembling the genus *Nicippe* in the general shape of the telson, of the mouthparts, and of the large, oval propodus in the gnathopods 1 and 2. Differs from *Nicippe* in the characters enumerated in table I. Type-species: *S. provo* n. sp.

Other species: *S. buchi* (Andres, 1975) (as *Nicippe*).

Distribution: Cave waters on Providenciales (Cai-cos Islands) and Lanzarote (Canary Islands).

Derivatio nominis: From σπήλαιον (Greek, cave) and *Nicippe* (a generic name in pardaliscid Amphipoda, based on Greek mythology and named after the daughter of Pelops). Gender feminine.

Remarks: We consider in particular the non-transformed first male antenna as a diagnostic character of the new genus.

TABLE I
Salient differences between the genera *Nicippe* Bruzelius, 1859, and *Spelaeonicippe* n. gen.

<i>Nicippe</i>	<i>Spelaeonicippe</i>
1. Lateral head lobes large, acutely produced	Inconspicuous, rounded
2. A1 > A2 **)	A1 << A2
3. Segments of accessory flagellum of A1 ♂ transformed	Normal
4. Flagellum segment 1 of A1 ♂ elongated, with extra setation	Short, without special setation
5. Second and third segment of Md palp with dense setation	With sparse setation
6. Distal palp segment of Mx1 clavate (with strong distal dilatation); armature restricted to terminal margin	Not dilated; armature on terminal and medial margins
7. Outer lobe of Mx1 less wide than 2nd palp segment	Wider than 2nd palp segment
8. Outer lobe of Mx1 reaches to 75% of the length of the palp	To 33%
9. Segments 2, 3 and claw of Mxp palp slender	Plump
10. Outer lobe of Mxp setiferous	Spiniferous
11. Outer lobe of Mxp reaches to the end of the inner margin of palp segment 1	Does not reach the end
12. Merus of P5 setiferous	Spiniferous
13. Urosomite 1 with dorsal teeth	Smooth

**) Sars, 1893, pl. 145, illustrates a male of *Nicippe tumida* Bruzelius in which A1 is slightly shorter than A2, but Karaman & Schiecke (1973: 166) consider this an exceptional case.

Spelaeonicippe *provo* n. sp.

Material. — One ♀ (holotype), one ♂ (allotype), eight paratypes. Amsterdam Expeditions to the West Indian Islands, sta. 79-151. Providenciales (Caios Islands): nameless "water hole" N.W. of the airfield (estimated position 21°46'50"N 72°16'30"W); stones, silt; semi-dark; water depth over 1 m; water temperature 23.8° C; chlorinity 11,108 mg/l; 16 November 1979. Zoölogisch Museum Amsterdam coll. no. ZMA Amph. 107.495.

Description. — Body length of adult specimens 3-4 mm; body unpigmented (intestine pink); no eye pigment. Urosomites 2 and 3 with 1 or 2 minute dorsal setules; dorsum otherwise smooth. Coxal plates low. Lateral head lobes inconspicuous, rounded; no rostrum. Epimeral plates with rounded posterior corners (fig. 1a).

First antenna (fig. 1b) reaching to the end of the pedunculus of the second antenna. Pedunculus segments heavy and short. Accessory flagellum 3-segmented, almost as long as second pedunculus segment. Flagellum 17- to 18-segmented; aesthetascs on segment 1 (6 long aesthetascs), 3 and 4 (each 2 long aesthetascs), 6, 7, 8, 9 and 10 (each 1 short aesthetasc).

Second antenna (fig. 1c): gland cone short, conical. Pedunculus segments 4 and 5 elongate;

ventrally armed with a row of spinules, dorsally with groups of short setae. No calceoli. Flagellum 16- to 17-segmented.

Labrum (fig. 1d) bell-shaped.

Masticatory part of mandible asymmetrical (figs. 1e, 1f): left mandible with, right mandible without lacinia mobilis. Pars molaris reduced; cutting edge long, almost toothless; a row of 8-11 spines is present between the cutting edge and the implantation of the palp. Palp slender; segment 1 unarmed; segment 2 with 7 or 8 ventral setae; third segment narrower than the second, with 2 terminal and 2 subterminal setae only.

Labium (fig. 1g) deeply cleft, without inner lobes.

First maxilla: left (fig. 2b) and right (fig. 2a) appendages almost symmetrical. Inner lobe triangular, with 1 apical seta; outer lobe squarish, armed with 7 strong distal spines. Palp 2-segmented; distal segment ovate, not dilated distally; medial and distal margins with some 13 short spines.

Second maxilla (fig. 2c) consisting of two very slender, digitiform, lobes. Outer lobe with 3 distal setae; inner lobe with 8 or 9 medial setae.

Maxilliped (fig. 1h): inner lobe small, ovate,



Fig. 1. *Spelaonicippe provo* n. gen., n. sp., ♀ paratype: a, entire animal from the right (real size abt. 4 mm); b, first antenna (scale A); c, second antenna (A); d, labrum (B); e, right mandible (B); f, left mandible (B); g, labium (B); h, maxilliped (C). Scales see fig. 4.

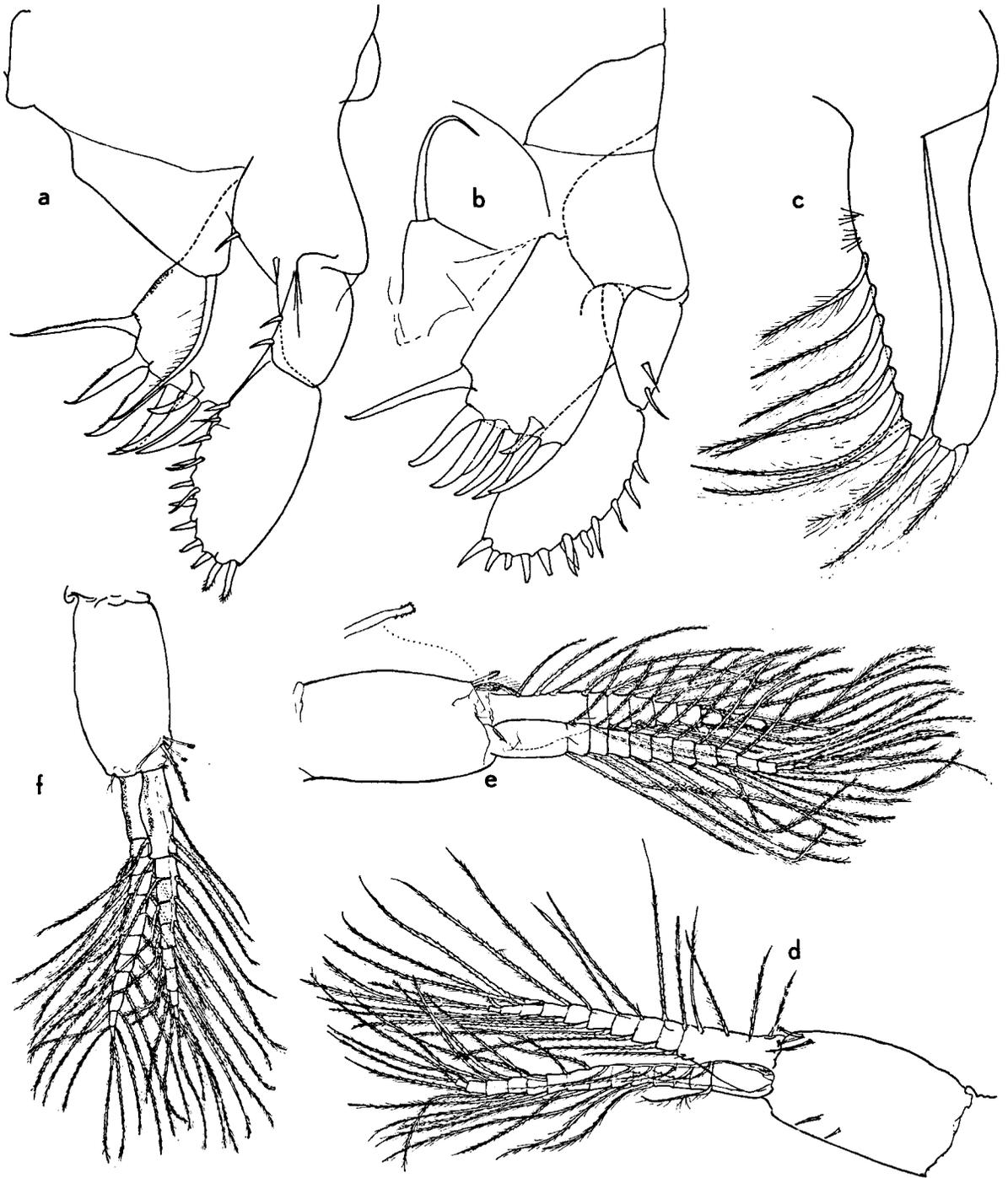


Fig. 2. *Spelaonicippe provo* n. gen., n. sp., ♀ paratype: a, right first maxilla (scale B); b, left first maxilla (B); c, second maxilla (B); d, first pleopod (A); e, second pleopod (A); f, third pleopod (A). Scales see fig. 4.

with 2 distal setae. Outer lobe very short, not reaching the distal end of the first segment of the inner margin of the palp, armed with 3 distal spines and several short medial setae. Palp segments short and robust.

First gnathopod (fig. 3a): Coxal plate with a rounded anterior projection. Carpus triangular. Propodus large, ovate. No palmar angle marked; the entire posterior edge of the propodus forms the palmar margin. This margin (fig. 3b) is densely packed with some 40 shorter setae (the proximal margin of which bears many cilia, the distal margin fewer cilia) and 5 longer setae (the proximal margin of which bears few cilia, the distal margin many). Claw long, curved; one very short setule on its outer margin.

Second gnathopod (fig. 3c) slightly larger than the first, but otherwise very similar.

Oöstegites on gnathopod 2 and pereopods 3 to 5; linear, armed with long setae. Coxal gills with an indistinct basal stalk, ovate to sausage-shaped, decreasing in size from anterior to posterior, present on gnathopod 2 and pereopods 3 to 7.

Third pereopod (fig. 3d) with modified carpus: this segment is slightly swollen and armed with numerous long, plumose setae on its posterior margin. The propodus on the contrary is practically unarmed, except for some short plumose elements on the distal end of its posterior margin. The claw is extremely elongate.

Fourth pereopod (fig. 4a) with trapezoidal coxal plate, without posterior excavation. Carpus not swollen and armed with a limited number of short plumose setae only. Propodus with numerous short plumose setae on the entire posterior margin. Claw as in the third pereopod.

Fifth pereopod (fig. 3e) slightly longer than the fourth. Basis almost linear in shape; posterodistal corner produced into a strongly overhanging lobe. Merus armed with a few short spines only. Carpus not swollen but armed with a row of long setae and some spines along its anterior margin. Anterior margin of propodus with similar armature.

Sixth pereopod (fig. 4b) much longer than the fifth. Basis less linear than in the fifth pereopod, with a very strongly produced and overhanging posterodistal lobe. Seventh pereopod (fig. 4c) as

long as the sixth; basis much wider than that of the sixth, but likewise with a strongly overhanging lobe. Both sixth and seventh pereopod armed with spines only.

Pleopods 1 to 3 (figs. 2d, e, f) similar in morphology; pleopod 3 slightly shorter than the others. All pleopods are biramous and the rami are untransformed in both sexes. Two retinacula on each pleopod; the retinacula are exceptionally long; the extreme distal part bears rake-like teeth (fig. 2e, detail).

Uropods 1 (fig. 4d) and 2 (fig. 4e) not much different in length; both with short exopodite (0.6-0.7 times as long as the endopodite).

Third uropod (fig. 4f) equiramous, both rami 1-segmented, rather wide, lanceolate to foliaceous. Outer margin of exopodite armed with 3 or 4 spines. Outer margin of endopodite with a limited number of plumose setae. Inner margin of exo- and endopodite with numerous long, plumose setae.

Telson (fig. 4g) deeply cleft; lateral margin of each slender half with 2 spines; distal part with 2 plumose (sensory) setae and 2 spines.

No secondary sexual differences have been observed in the appendages of males and females.

D i s t i n c t i o n. — *S. provo* n. sp. is very similar to *S. buchi* (Andres, 1975) from Lanzarote. The following differences exist between the two species:

- (1) Body length 3-4 mm in *S. provo* (versus 7-10 mm in *S. buchi*);
- (2) segment 1 of antenna 1 only slightly longer than wide in *S. provo* (elongate in *S. buchi*);
- (3) segment 2 of A1 about $\frac{4}{5}$ of the length of segment 1 in *S. provo* (about $\frac{1}{2}$ the length in *S. buchi*);
- (4) molar process of mandible replaced by 8 to 11 spines in *S. provo* (2 to 3 in *S. buchi*);
- (5) 2nd mandible palp segment with 7 to 8 ventral setae in *S. provo* (1 in *S. buchi*);
- (6) 2nd palp segment of maxilla 1 with at least 10 spines in *S. provo* (5 in *S. buchi*);
- (7) posterior margin of basis of gnathopods 1 and 2 with several long setae in *S. provo* (unarmed in *S. buchi*);
- (8) propodus of pereopod 4 with setae on the posterior margin in *S. provo* (spinules only in *S. buchi*);
- (9) overhanging posterodistal lobe on the basis of pereio-

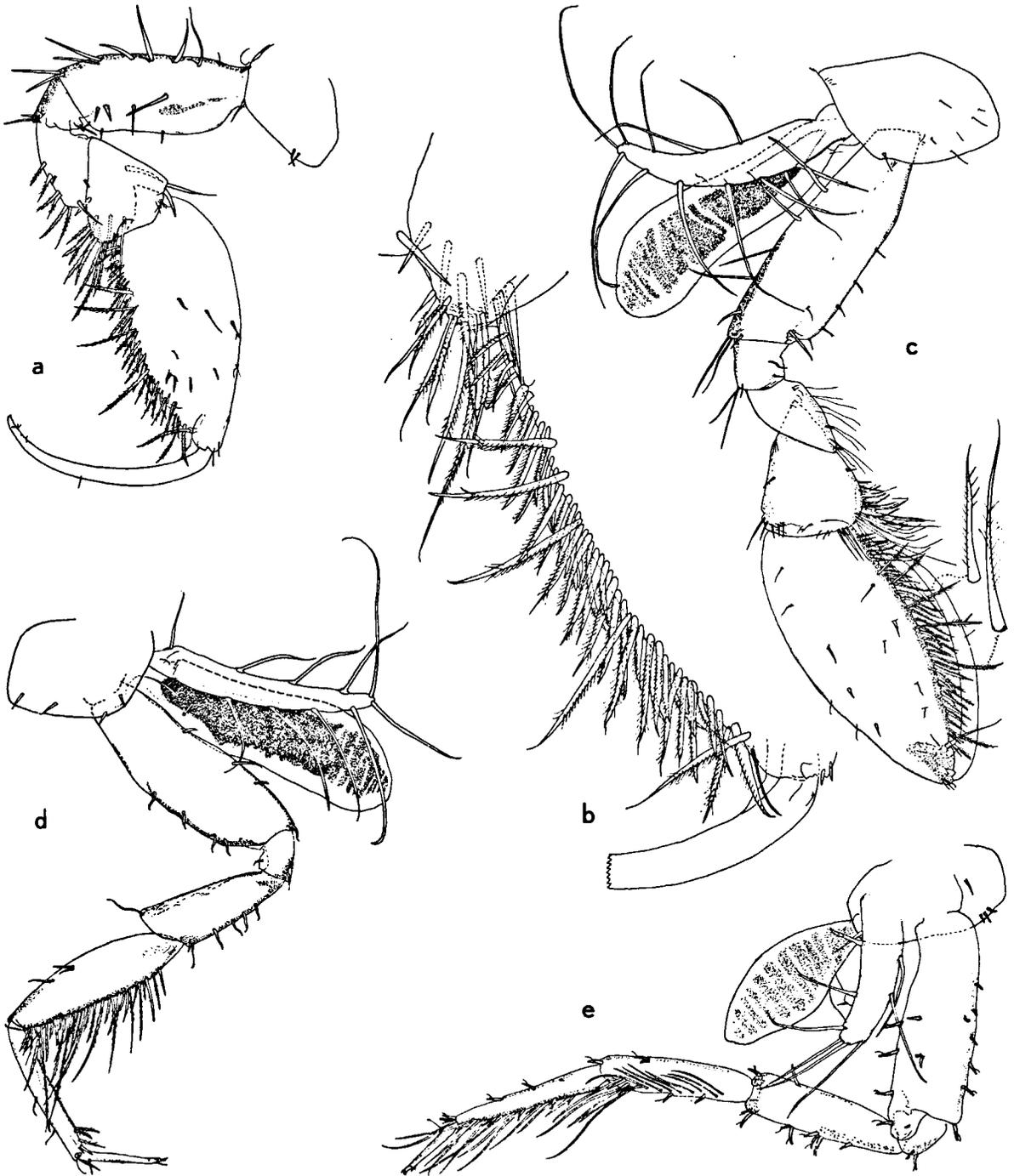


Fig. 3. *Spelaeonicippe provo* n. gen., n. sp., ♀ paratype: a, first gnathopod (scale A); b, palmar margin of propodus of first gnathopod (D); c, second gnathopod (A); d, third pereiopod (A); e, fifth pereiopod (A). Scales see fig. 4.

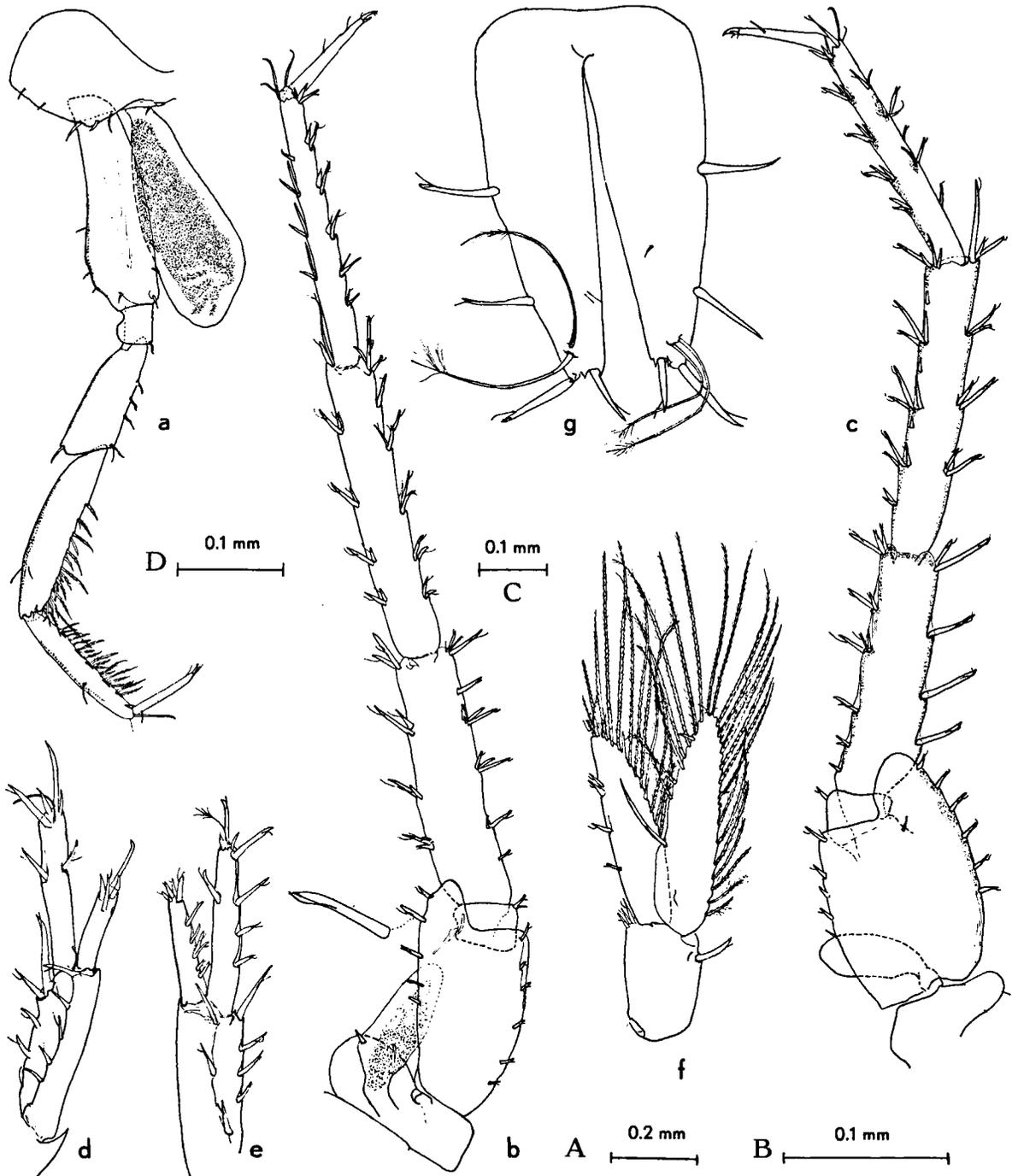


Fig. 4. *Spelaonicippe provo* n. gen., n. sp., a-f, ♀ paratype; g, ♂ allotype: a, fourth pereopod (scale A); b, sixth pereopod (A); c, seventh pereopod (A); d, first uropod (A); e, second uropod (A); f, third uropod (A); g, telson (C).

pods 5 to 7 very strongly developed in *S. provo* (moderately developed in *S. buchi*); (10) outer margin of endopodite of uropod 3 with long plumose setae in *S. provo* (with spines only in *S. buchi*); (11) telson with 2 lateral spines in *S. provo* (1 lateral spine in *S. buchi*); (12) sensory setae implanted near the tip of the telson lobes in *S. provo* (slightly over the middle in *S. buchi*).

Derivatio nominis. — The specific name, *provo*, is the popular name for the type-locality, the island of Providenciales.

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