

REGRESSION MODEL EVOLUTION AS EXEMPLIFIED BY THE GENUS *PSEUDONIPHARGUS* (AMPHIPODA)

by

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ABSTRACT

The genus *Pseudoniphargus* has long been considered monospecific. Its unique species, *Ps. africanus*, was supposed to occur on both sides of the Mediterranean, on the Atlantic side of the Iberian peninsula, on the Azores, and on Madeira, in localities ranging from the sea shore to more than 1000 m of altitude, and covering almost the entire natural salinity range (0-36⁰/oo).

A taxonomic revision revealed that at least nine named species and several unnamed forms (of which insufficient material is available) hide under the name *Ps. africanus*, each with a narrow ecological and geographical range.

The evolutionary scenario of the members of the genus is discussed at some length: they are presumably of marine origin, and got adapted to conditions of continental waters during various marine regressions in the Eocene and Oligocene, but notably in the Miocene.

A forma described in 1955 by S. Karaman, was raised to specific rank by G. Karaman in 1978.

In the present paper, I have revised most of the existing materials attributed to the genus, as well as a good number of newly collected samples. This resulted in a classification into nine named species, and a number of unnamed left-overs because of insufficient material. The actual names for the taxa of *Pseudoniphargus*, formerly usually recorded as *Ps. africanus*, are shown in table I.

Like in the *Gammarus* group, identification of females is much more difficult than that of males. Preferably both sexes should be available for a profitable study. Much of the "variability" recorded in the past has been based on secondary sexual differences within one species.

The evolution of *Pseudoniphargus* — the development of inhabitants of inland waters from marine ancestors — is discussed at some length. It is likely that this evolution is of the regression model type: stranding of marine populations during sea-level regressions.

The present study has been undertaken to compare the ideas previously put forward (Stock, 1977b) on regression model evolution, ideas based mainly on evidence obtained in the West Indies, with data derived from the Mediterranean area where theories on the stranding of marine populations were first developed.

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2. INTRODUCTION

Since the erection of the genus *Pseudoniphargus* by Chevreux in 1901, almost every student of it has stressed its "morphological variability" and its striking distribution, from the sea shore to caves at considerable altitudes, from the South European and North African continents to oceanic islands like the Azores and Madeira.

Up to 1955, the genus remained monotypic.

3. ACKNOWLEDGEMENTS

The author is indebted to the following persons and institutions for providing information or material:

Curators Lennart Cederholm and Hugo Andersson, Zoologiska Institutionen, Avdelningen för Systematik, Lund, Sweden (abbreviated ZIL).

Dr. E. L. Bousfield, National Museums of Canada, Museum of Natural Sciences, Ottawa, Canada.

TABLE I

Previous records of *Pseudoniphargus* in chronological order. Unless otherwise stated, all records have been published under the name of *Ps. africanus*.

Author, year, page(s)	Origin	Name in present paper († = material re-examined; * = inferred name)
Chevreaux, 1901: 211-216, figs. 1-2	Bône (= 'Annaba) (Algeria)	† <i>Ps. africanus</i>
Schellenberg, 1937: 224	Medjez-Sfâ (Algeria)	† <i>Ps. macrotelsonis</i>
	Cantabrian Mts. (Spain)	† <i>Ps. elongatus</i>
		† <i>Ps. unisexualis</i>
Schellenberg, 1939: 297-304, fig. 1, 1 map	Bône (Algeria)	† <i>Ps. africanus</i>
	Medjez-Sfâ (Algeria)	† <i>Ps. macrotelsonis</i>
	Mustapha, Algiers (Algeria)	† <i>Ps. sp.</i>
	Cantabrian Mts. (Spain)	{† <i>Ps. elongatus</i>
		{† <i>Ps. unisexualis</i>
	Split (Yugoslavia)	† <i>Ps. adriaticus</i>
	Funchal (Madeira)	† <i>Ps. sp.</i>
Schellenberg, 1943: 1	Costa da Arrábida (Portugal)	† <i>Ps. mateusorum</i>
Schellenberg, 1951: 327-328	Bonifacio (Corsica)	† <i>Ps. adriaticus</i>
Balazuc & Angelier, 1951: 309-312	Banyuls (France)	† <i>Ps. adriaticus</i>
S. Karaman, 1953: 139	Dubrovnik (Yugoslavia)	* <i>Ps. adriaticus</i>
Ruffo, 1953: 672	Philippeville (= Skikda) (Algeria)	<i>Ps. sp.</i>
Balazuc, 1954: 184-185	Banyuls (France); Bonifacio (Corsica)	† <i>Ps. adriaticus</i>
S. Karaman, 1955: 236-241, figs. 44-51 (as forma <i>adriatica</i>)	Dubrovnik, Budva (in text) or Bar (in legends)	* <i>Ps. adriaticus</i>
Dahl, 1958: 6-9, fig. 1	Faial, Pico (Azores)	† <i>Ps. brevipedunculatus</i>
Ruffo, 1960: 172-174	Menorca (Balearic Is.)	* <i>Ps. adriaticus</i>
Strinati & Coiffait, 1961: 228	Menorca (Balearic Is.)	* <i>Ps. adriaticus</i>
Sket, 1969: 148	Rupine near Sukošan (Yugoslavia)	* <i>Ps. adriaticus</i>
Margalef, 1970: 170-171, figs. 1, 2 J-L	Basque country (Spain)	{* <i>Ps. unisexualis</i>
		{ <i>Ps. sp.</i>
Mateus & Afonso, 1974: 10-11	Santa Maria (Azores)	* <i>Ps. brevipedunculatus</i>
Ginet, 1977: 174-175	Cantabrian Mts. (Spain)	† <i>Ps. elongatus</i>
Mateus & Mateus, 1978: 16-19	Costa da Arrábida (Portugal)	† <i>Ps. mateusorum</i>
	Prov. Beira (Portugal)	† <i>Ps. longispinum</i>
	Prov. Estremadura (Portugal)	<i>Ps. sp.</i>
	Madeira	<i>Ps. sp.</i>
	Azores	* <i>Ps. brevipedunculatus</i>
G. Karaman, 1978: 250-256, figs. VI-IX	Bône (= 'Annaba) (Algeria)	* <i>Ps. africanus</i>
	Oued-ed-Demane (Tunisia)	<i>Ps. sp.</i>
	Medjez-Sfâ (Algeria)	† <i>Ps. macrotelsonis</i>
	Cueva de San Adrian near Cegame (Spain)	† <i>Ps. unisexualis</i>
Do.: 241-250, figs. I-V (as <i>Ps. adriaticus</i>)	Budva (Yugoslavia)	* <i>Ps. adriaticus</i>
	Mola di Bari (Italy)	* <i>Ps. adriaticus</i>
	Isola di Montechristo (Italy)	* <i>Ps. adriaticus</i>
	Funchal (Madeira)	<i>Ps. sp.</i>
	Menorca (Balearic Is.)	* <i>Ps. adriaticus</i>
	Mustapha, Algiers (Algeria)	† <i>Ps. sp.</i>
	Prov. Santander (Spain)	† <i>Ps. elongatus</i>
	Split (Yugoslavia)	† <i>Ps. adriaticus</i>
	Dubrovnik (Yugoslavia)	* <i>Ps. adriaticus</i>
	Rupine near Sukošan (Yugoslavia)	* <i>Ps. adriaticus</i>
	Costa da Arrábida (Portugal)	† <i>Ps. mateusorum</i>
Pesce et al., 1979: 8 (as <i>Ps. sp.</i>)	Bari (Italy)	<i>Ps. sp.</i>

Mme. N. Coineau, Laboratoire Arago, Banyuls-sur-Mer, France.

Dr. J. Forest, Muséum National d'Histoire Naturelle, Laboratoire de Zoologie, Arthropodes, Paris, France (MNHN).

Prof. R. Ginet, Département de Biologie Animale et Zoologie, Université Claude-Bernard (Lyon-I), Villeurbanne, France (UL).

Dr. H.-E. Gruner, Zoologisches Museum der Humboldt Universität, Berlin, D.D.R. (ZMB).

Prof. A. Mateus, Universidade do Porto, Instituto de Zoologia "Dr. Augusto Nobre", Porto, Portugal (IZAN).

Curator G. E. Maul, Museu Municipal do Funchal, Madeira.

Mr. Jos Notenboom, Biospeleo Werkgroep, Wageningen, The Netherlands.

Dr. S. Pinkster, Zoologisch Museum, University of Amsterdam, The Netherlands (ZMA).

Furthermore, a travel grant of the University of Amsterdam (1979) is gratefully acknowledged.

The remarks made on regression model elements in transgression areas are based on unpublished observations made during an expedition to the southern Bahamas, financed by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), The Hague, and the Beijerinck-Popring Fonds, Amsterdam.

4. REGRESSION MODEL EVOLUTION (GENERALITIES)

Several authors (e.g. Bonnet, 1956; Hubault, 1938; Fryer, 1965) have emphasized the probability that populations of littoral or shallow-water animals, more in particular inhabitants of the interstia of macroporous substrates, stranded because of various marine regressions in the Mediterranean region during the Tertiary epoch. These stranded populations got gradually adapted to the conditions of more continental waters and are now distributed in land areas that were previously submerged.

Stock (1977b), studying groundwater Amphipoda of the hadziid group in the Antilles, accepted tectonic uplifts (or sea-level drops) as one of the main causes for the evolution of several groups of isopod, amphipod and thermosbaenacean Crustacea in stygobiont habitats of the various islands. For this type of evolution, through stranding of marine ancestors, Stock coined the term regression model evolution. Although this is essentially a passive model of evolution¹⁾, the regression model differs from the other passive models in that the barrier between the ancestral marine and derived limnic populations developed very slowly and gradually and may never have been 100% effective against gene flow. In other passive

models, the original distribution area of a taxon is divided, the barrier being small at the beginning, but 100% effective at a later stage (this model is particularly useful in understanding the development of populations isolated under influence of plate tectonics).

A good regression model taxon (genus, family...) must satisfy the following five conditions:

(1) In addition to the species in continental waters, marine relatives must be known.

(2) They should occur only in areas once covered by sea, but actually above the surface.

(3) They should not occur outside formerly submerged areas, since then dispersal from continental areas to areas emerging cannot be ruled out.

(4) They are lacking, or at least exceptional, in areas that show transgression (subsidence).

(5) If there is more than one inland taxon, these being developed through independent passive isolation from marine ancestors, the inland taxa tend to have cladistic relationships indicative for the passive (vicariance) model and not for the active (dispersal) model (see Rosen, 1976, fig. 20).

These five points may be adstruced as follows:

Ad 1) The marine relatives should by preference belong to the same genus as the limnic species, but they do not per se have to be ancestors of the limnic species, since the marine forms may have undergone further evolution after the isolation of the limnic taxa.

Ad 2) Several examples prove this to a surprising extent, e.g. the distribution of the Thermosbaenacea (Fryer, 1965; Stock, 1976), of *Typhlocaris* (Fryer, 1965), of the Microparasellidae (Stock, 1977a), of the hadziid Gammaridae (Stock, 1977b), and of the genus *Pseudoniphargus* (present paper).

Ad 3) This, on the other hand, implies that regression model elements have poor means of (active)

¹⁾ Passive model: parts of a population are isolated by extrinsic forces; barriers, not existing before, come to development, dividing or fragmenting the original population. This model is often called vicariance model nowadays in the New World, but I believe that the vicariance of the biogeographers of the nineteen-thirties and fourties not only "preoccupies" the name, but also had a somewhat different meaning (the homonyms are not synonyms).

Opposed to passive models are active models, according to which parts of populations actively disperse to new, previously uncolonized, areas.

dispersal. For several of them, poor dispersal means have been made plausible (Remane, 1952; Delamare Deboutteville, 1960; Stock, 1979). Usually the number (1 to 4) of eggs is low and pelagic stages are absent (*K*-strategists).

Ad 4) One of the world's largest transgression (subsidence) areas appears to be the Bahama platform (Doran, 1955; Dietz et al., 1970; Uchupi et al., 1971), which is underlain by a carbonate apron that is more than 5 km thick, maybe even 10 km. Extensive search in the Bahamas (own observations, unpublished) has shown a striking poverty in regression model elements, sharply contrasting with the abundance of such elements in regression areas like Cuba, Hispaniola and various Lesser Antilles.

Ad 5) Each isolate in a regression model situation is derived from a marine ancestor; it is even not unlikely that the same ancestral marine line has produced more than one stranding. In a dispersal model situation, a stepstone-like phylogeny is more likely.

The most striking point in regression model evolution is that seemingly continuous contact has been possible between the stranded populations and the ancestral marine ones. This point will be picked up again in the next section of the present paper.

In addition to regression model evolution in groundwater animals, very similar phenomena are known from bird populations that got isolated on mountain peaks during orogenesis (see for instance Haffer, 1974: 149).

5. EVOLUTIONARY SCENARIO AND ZOOGEOGRAPHY OF *PSEUDONIPHARGUS*

Pseudoniphargus shows, as compared to the *Gammarus* group, a number of apomorphic characters, for instance: disappearance of the eyes; reduction in size and in number of articles of the accessory flagellum of the first antenna; abbreviation of the second antenna; tendency towards elongation of the third uropod; small body size; suppression of sexual dimorphism in the gnathopods; absence of calceoli on the second antenna.

In several lines of hypogean Gammaridae (s.l.), these characters have developed independently; this can be called convergent or parallel develop-

ments. Apparently ancestral marine and polyhaline Gammarid species flocks have given rise to more than one invasion into the continental epigeal waters. Likewise, I assume that the continental hypogean waters have been populated along more than one pathway. The word "pathway" is used here in a general sense, since under that name may hide various processes: (1) active dispersal, through marine macroporous substrates (interstitia) into the hypogean habitat; or (2) passive (vicariant) development from epigeal populations isolated in groundwater accumulations during periods of drought or frost when surface waters disappeared.

The presence of a member of *Pseudoniphargus* in the Azores makes it, as Dahl (1958: 9) rightly stressed "highly probable that ... (they) ... reached the Azores by way of the sea", since the "current geological opinion seems to be in favour of their purely oceanic origin, probably as the result of submarine volcanic activity in the Miocene ...", "proof of continental connections appears not to be available". The same arguments apply to the presence of the genus on Madeira, and they seem to be supported amply by recent geological evidence (e.g. Mitchell-Thomé, 1976 and 1979).

It appears that Balazuc & Angelier, 1951, have been the first to speculate on the possibility that members of *Pseudoniphargus* originate from marine ancestors which are in the process of adaptation towards life in fresh waters. They recorded a *Pseudoniphargus* (as *Ps. africanus* but in reality *Ps. adriaticus*) from the psammon close (1½-6 m) to the sea near Banyuls at salinities from 24 to 33‰. Recent research (present paper), using the Bou-Rouch phreatic pump technique, revealed the presence of *Ps. adriaticus* in the interstitia of a coarse sand and gravel, both between the tide marks and just below low tide at full marine salinity (36‰), on the French Provence coast.

Later, both S. Karaman (1955) and his son G. Karaman (1978) advocated the view that *Pseudoniphargus* must have a marine origin.

I think it likely that ancestral *Pseudoniphargus* lived in macroporous marine substrates, such as gravel or coarse sand, and had a large distribution in the early-Tertiary Tethys Sea. Great portions of

the northern Mediterranean littoral (France, Corsica, the Balearic Isles, Yugoslavia) are inhabited by morphologically identical populations, called *Ps. adriaticus*. This is the only member of the genus known so far from marine/polyhaline waters. However, morphologically, *Ps. adriaticus* does not classify very well as an ancestral (or plesiomorph) form (see the section on cladistics). Since *Ps. adriaticus* has a fairly large salinity tolerance (Balazuc & Angelier, 1951; present paper), it is more likely one of colonization waves invading the continental waters, instead of being the ancestral form from which all continental and oceanic insular taxa evolved.

These ideas contrast sharply with those of Schellenberg (1939), who considered all populations of *Pseudoniphargus* as a single species, irrespective whether they were found in localities at the seashore, in caves at an altitude of 1000 m, or on isolated oceanic islands as Madeira. Schellenberg considered the genus to be "restricted to fresh waters", "frequently remote from the sea", and this brought him to the often-quoted statement that "*Pseudoniphargus* is not a marine immigrant, but an old freshwater element that reached its present distribution" (northern Mediterranean belt, Atlantic side of Spain and Portugal, Balearic islands, Algeria, Corsica, Madeira, the Azores),

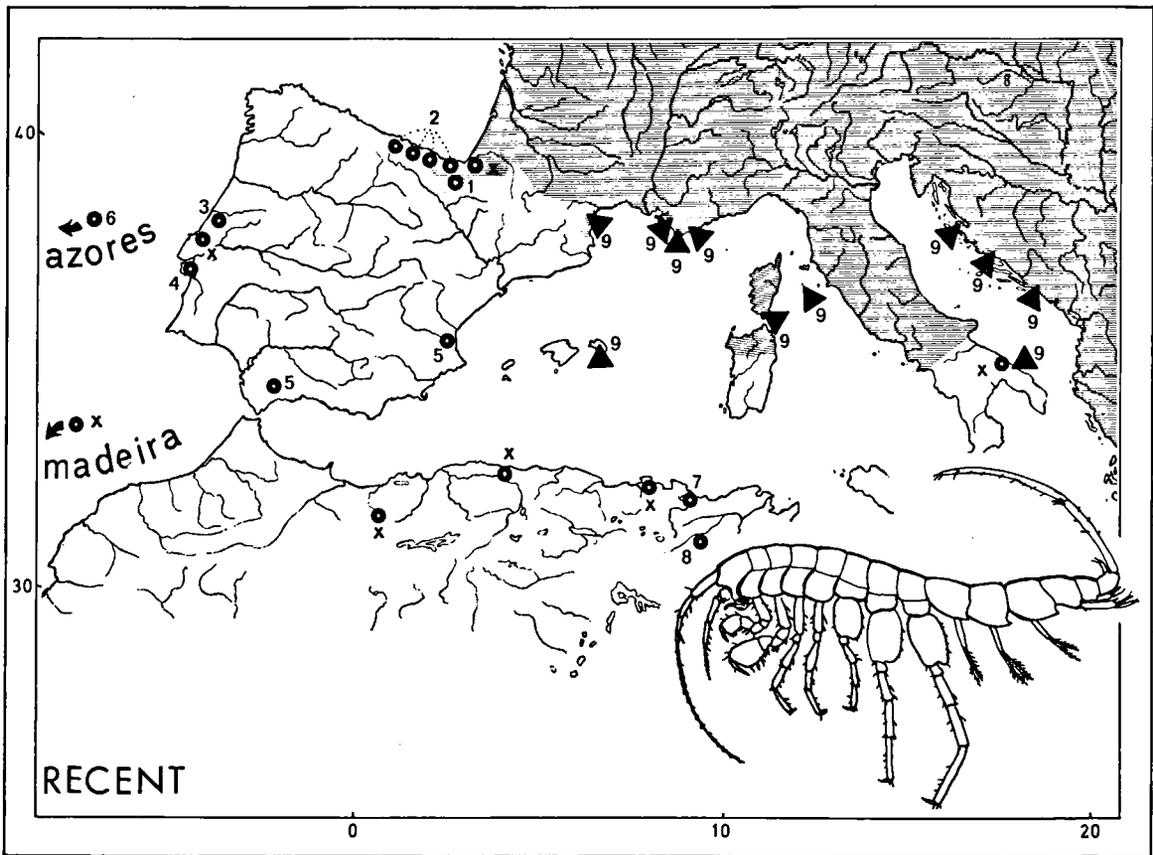


Fig. 1. Distribution of the genus *Niphargus* (hatched) and of the genus *Pseudoniphargus* (dots = taxa from continental waters; triangles = taxa from marine/polyhaline waters). Note that there is hardly any overlap between the range of *Niphargus* in Europe and that of the inland water taxa of *Pseudoniphargus*. On the other hand, the marine/polyhaline *Pseudoniphargus* does occur in *Niphargus* country.

The range of *Niphargus* is based on the publications of Ruffo (1956, 1957), Morand-Chevat (1972), and Ginot (1977); the range of *Pseudoniphargus* is based on the data presented in the present paper. 1, *Pseudoniphargus unisexualis* n. sp.; 2, *Ps. elongatus* n. sp.; 3, *Ps. longispinum* n. sp.; 4, *Ps. mateusorum* n. sp.; 5, *Ps. branchiatus* n. sp.; 6, *Ps. brevipedunculatus* n. sp.; 7, *Ps. africanus* Chevreux, 1901; 8, *Ps. macrotelsonis* n. sp.; 9, *Ps. adriaticus* Karaman, 1955. Materials that had to remain unnamed are indicated by a crosslet.

Inset bottom right: a male of *Pseudoniphargus adriaticus*.

"when these areas were still linked with each other". Schellenberg's statement (1939: 300, in translation) that "the sea, therefore, is not the bridge between the Mediterranean localities and Madeira, but the ditch" is not supported by geological evidence whatsoever, and is disproved by the discovery of an inter- and subtidal species, *Pseudoniphargus adriaticus*.

The greatest handicap for reaching zoogeographical conclusions has been the fact that almost every author up to now took it for granted that *Pseudoniphargus* was a monospecific genus. Starting with Chevreux (1901) at the creation of the genus, several authors (e.g. Schellenberg, 1939; Ruffo, 1960; Dahl, 1958) stressed the morphological "variability" and ecological plasticity, ranging from marine beaches to caves and springs in the high mountains. No one took the step of trying to split the generotype, *Ps. africanus*, into geographically, ecologically and morphologically more coherent units, with the exception of the Karamans (1955, 1978) who recognized as distinct the marine/polyhaline form and Mateus & Mateus (1978) who suggested to start a taxonomic analysis of certain populations.

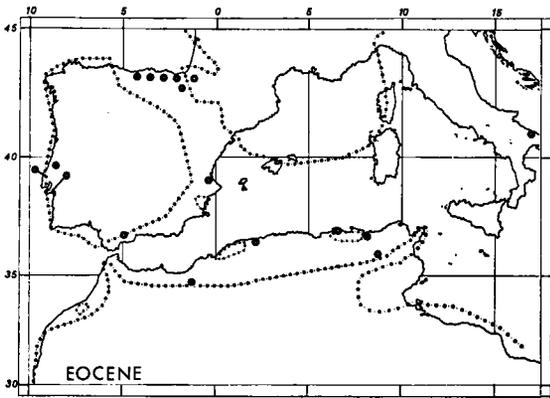
It is from (unknown) marine, interstitial ancestors, that the various brackish-water and inland populations supposedly evolved. Apparently, this evolution took place in different geological periods, by various discontinuous waves. So, the animals from the high mountains of N.W. Spain are morphologically different from those of lower altitudes, although living only 30 km remote; the same holds true for the mountain and lowland populations in Algeria. How old the various populations in continental waters are, is a matter of speculation. When we check the distribution of landmasses and sea during various geological epochs in the Tertiary period in correlation with the actual localities for nonmarine *Pseudoniphargus* (figs. 2-6), we observe some highly suggestive situations:

- (1) All localities for *Pseudoniphargus* are on dry land during the Pliocene (fig. 6).
- (2) During the early Miocene (fig. 4), the localities of the following species are located on the edge of land and sea: *Ps. africanus*, *Ps. macrotelsonis*, *Ps. sp.* from Philippeville

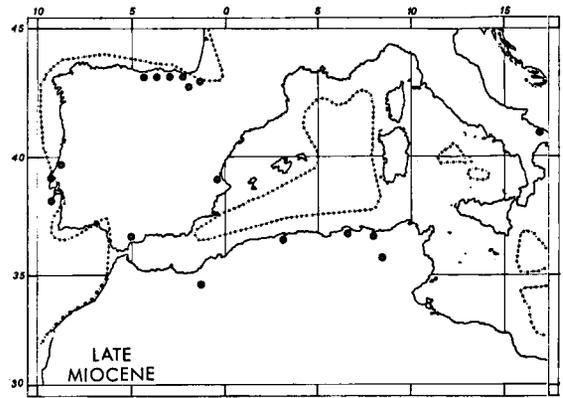
(= Skikda), Algeria and from Mustapha, Algeria, *Ps. branchiatus*, *Ps. mateusorum*, *Ps. longispinum*, and *Ps. sp.* from the province of Estremadura, Portugal.

- (3) During the Oligocene (fig. 3), most of these localities were either submerged and far off-shore (*Ps. branchiatus*, *Ps. macrotelsonis*, *Ps. sp.* from Mustapha), or on dry land (*Ps. div. sp.* from Portugal).
- (4) The Azores and Madeira are oceanic islands formed by volcanic activity, and broke through the surface of the ocean in the late Oligocene or early Miocene (Dahl, 1958; Mitchell-Thomé, 1976). Subsequently these islands underwent a considerable (several hundreds of metres) uplift (Mitchell-Thomé, 1976). It is clear that the nonmarine populations of *Pseudoniphargus* existing on these islands could only have evolved after the formation of terra firma, i.e. in the Miocene or later.
- (5) The *Pseudoniphargus* in northern Spain may be the oldest continental populations. Their localities (two well-distinguished species and one population of uncertain taxonomic position) were submerged under seawater during the Eocene (fig. 2) but emerged during the rest of the Cenozoic. It might not be accidental in this context that one of these, *Ps. unisexualis*, is the most plesiomorphic taxon actually known, and at the same time recorded from one of the greatest altitudes known for the genus (about 1000 m above sea level).

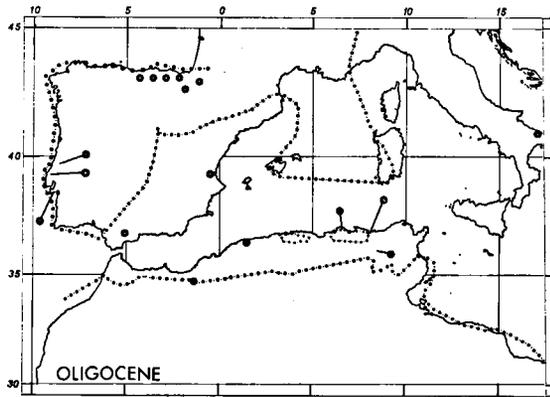
In general, these distribution patterns fit in with the findings of Hubault (1938), Bonnet (1956), Fryer (1965) and others, all in the circum-Mediterranean region, and of those of Stock (1976, 1977a, 1977b) in the Antillean region. Adaptation to continental waters appears to have taken place at different periods of marine regression in the Middle Tertiary: the actual localities of many hypogean freshwater crustaceans (the isopods *Monolistera* and *Typhlocirolana*, the prawn *Typhlocaris*, the mysids *Stygiomysis* and *Spelaeomysis*, gammarid amphipods of the hadziid group, or of the genus *Pseudoniphargus*, microparasellid isopods of the *Microcharon* group, the order Thermosbaenacea...) are all close to Tertiary Tethys shore lines. All are found in areas that were sub-



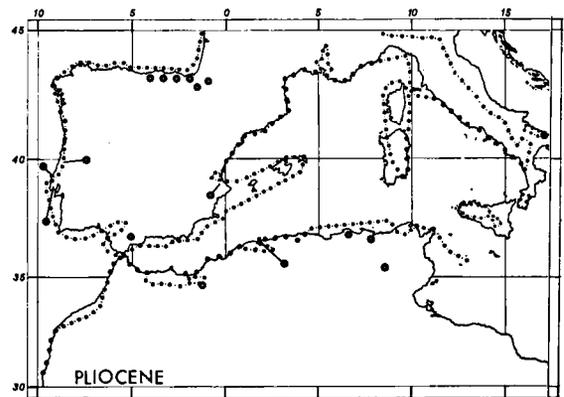
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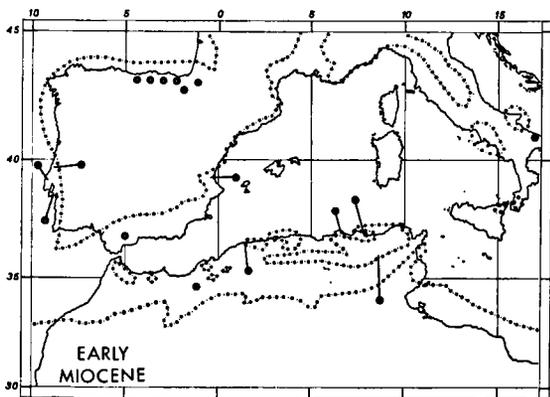
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Figs. 2-6. Approximate distribution of land and sea in four periods of the Tertiary: the Eocene (fig. 2), the Oligocene (fig. 3), the early Miocene (fig. 4), the late Miocene (fig. 5), and the Pliocene (fig. 6). The actual localities for *Pseudonipbargus* in continental waters are indicated by dots. Palaeogeographic data based on Fryer (1965), Termier & Termier (1960), and Hsü (1972).

merged beneath the sea in earlier Tertiary epochs. Since the Pliocene, all these localities are in dry land areas, and none is found outside the previously submerged areas which rules out dispersal from elsewhere. Probably the most intensive period of "stranding" of these organisms of marine origin has been the late Miocene, when the quasi-totality of the Mediterranean Sea was closed off from the Atlantic, evaporated and transformed into arid land (Hsü, 1972, and present paper fig. 5). This immense regression (the water level dropped with more than 3000 m and the erosion levels of the larger rivers, such as Rhône and Nile, were lowered by hundreds if not thousands of metres) must have caused the stranding of great numbers of formerly marine, shallow-water inhabitants.

There can be no doubt, and numerous taxonomic papers covering a wide range of animal groups testify this, that the forms from the continental waters are differentiated at least on specific (and often also on generic) level from those of marine and near-coast habitats. The question remains what caused the interruption in gene-flow between the marine and continental populations. The above-mentioned late-Miocene Mediterranean crisis might have caused such an interruption. Most of the Mediterranean basin dried up, whereas the little water that remained was in general of hypersaline nature (Hsü, 1972), presumably not suitable to support a varied crustacean life. I suppose that the great majority of the Tethyan marine ancestors of the regression elements became extinct, whereas the continental populations hiding in interstitial and groundwaters could survive. The extinction idea is corroborated by the absence in the actual Mediterranean basin of marine regression elements, such as hadziid Amphipoda, or Thermosbaenacea, whilst in the West Indies, the only other area in the world where regression faunas have been studied to some extent, marine (not necessarily ancestral) relatives have been found.

This is in agreement with the fact that the West Indian marine fauna has not suffered from a salinity/evaporation crisis like the Mediterranean. On the other hand, it is more difficult to envisage what kind of barrier has caused the evolution of the regression elements on the various West In-

dian islands. Tectonic uplifts played no doubt a more important rôle, but apart from a sharp drop in the sea surface temperature in the Miocene, and active volcanism in the late Tertiary and Recent epochs, the area seems to have been much more stable than the Mediterranean.

Another point must be stressed here, first brought up by S. Karaman (1955: 240-241). It seems significant that inland-water populations of *Pseudoniphargus* have only been found in those areas where "old" hypogean freshwater taxa are absent. Karaman mentioned this from his own experience in Yugoslavia, but I can confirm his observations from two areas, that I intensively sampled myself, viz. Mallorca (Balearic Islands) and the French Provence.

It can hardly be a coincidence that limnic or inland *Pseudoniphargus* species are known from Algeria, N.W. Spain, Portugal, Madeira and the Azores, devoid of members of ancient limnic groundwater genera. On the other hand, from France, Corsica, the Balearic Islands and Yugoslavia, where the inland waters are well-stocked with ancient forms as *Niphargus* or crangonyctids, only coastal populations of *Pseudoniphargus* are known. Fig. 1 shows the actual distribution of *Niphargus* (hatched) in Europe. The only place of overlap with limnic populations of *Pseudoniphargus* is a narrow zone in the Spanish provinces Navarra, Guipúzcoa, and Vizcaya. This overlap may be the result of dispersal of *Niphargus* along the well-known corridors on either end of the Pyrenees.

This peculiar, exclusive, distribution pattern can be explained in two different ways:

- (1) The invasion of the limnic domain by *Pseudoniphargus* is more recent than the appearance of *Niphargus*, implying that *Pseudoniphargus* could only invade those areas where the competing genera were absent, or
- (2) the older limnic populations of *Pseudoniphargus* have been expelled from their freshwater habitats by more recent migration waves of *Niphargus*.

Certain indications are in favour of the first explanation:

- (1) Several *Pseudoniphargus* taxa still prefer near-coast localities (e.g. present paper), such

localities for *Niphargus* are exceptional (Sket, 1977).

- (2) The presence of *Pseudoniphargus* on relatively young, oceanic islands (Azores, Madeira) and the absence of *Niphargus* on such islands, points to a fairly recent development of *Pseudoniphargus* from marine ancestors.
- (3) The morphology of *Pseudoniphargus* is more *Gammarus*-like, thus more similar to marine taxa, than that of *Niphargus*.

I would like to stress that the zoogeographic distribution of limnic members of the *Gammarus* group is not unlike that of *Pseudoniphargus*. Such *Gammarus* (s.l.) are likewise known from Madeira (*Sarothrogammarus madeirensis* (Dahl, 1958)), from the Azores (*S. guernei* (Chevreux, 1889)), from Algeria (*Echinogammarus simoni* (Chevreux, 1894) and others), from N.W. Spain (*Echinogammarus berilloni*-complex, vide Pinkster, 1973), and Portugal (*Ech. lusitanus* (Schellenberg, 1943) and others). Although members of the *Gammarus* group have a much larger distribution than members of the genus *Pseudoniphargus*, it might be significant that the notably euryhaline gammarids could follow, presumably at a more recent geological period, the same invasion lines as *Pseudoniphargus*. For the gammarids, a marine origin has never been doubted, and I neither doubt such an origin for *Pseudoniphargus*.

Note added at the proof-reading: Recently (December 1979), B. Sket (Bermuda biol. Stat. Newsletter, vol. 7, nr. 2/3) recorded an unnamed member of *Pseudoniphargus* from Walsingham caves, Bermuda. In the present paper, Sket's discovery could not yet be taken into account. The occurrence, on the other side of the Atlantic, forms quite a strong support for my idea that *Pseudoniphargus* invaded the inland waters from some marine stock.

6. CLADISTICS

The peculiar elongation of the third uropod, which brought Chevreux (1901) to the rather unfortunate name *Pseudoniphargus*, is not present in all taxa within the genus. A clear evolutionary line is visible from taxa with plesiomorphic to taxa with highly apomorphic third uropods²⁾. The plesiomorphic appendage is of a more or less generalized *Echinogammarus*-type, on the understanding that the exopodite has only one segment (this

condition, resulting from a reduction of the distal segment, though rare in *Echinogammarus*, is found for instance in *E. sicilianus* ssp. *monomerus* Stock, 1978). It is not sexually dimorphic, except perhaps in the setosity/spinosity; the pedunculus is short, the exopodite is not strongly elongated, straight (not upcurved), and the endopodite is short, triangular. This plesiomorphic state is encountered in *Ps. unisexualis* and in *Ps. longispinum*.

The next step is that the exopodite of the male third uropod gets elongated and upcurved, the female uropod remains in the plesiomorphic state. The exopodal spines, found in the male plesiomorphic state, are partially replaced by setules. This stage is found in *Ps. mateusorum* and *Ps. brevipedunculatus*.

Then follows a gradual elongation of the pedunculus of the male third uropod (the female third uropod still stays unchanged). This stage is encountered in *Ps. africanus*, *Ps. macrotelsonis*, and *Ps. adriaticus*.

The most apomorphic state is reached by *Ps. elongatus* and *Ps. branchiatus*, where also the female third uropod shows a distinct elongation.

Other evolutionary lines (development from a plesiomorphic into an apomorphic state) may be present in the genus. Bousfield (1977, table II) lists the plesiomorphic and apomorphic condition of various characters, including the telson (deep-cleft = plesiomorphic, shallow-cleft = apomorphic), the shape of the basis of P5 to P7 (with strong posterodistal lobe = plesiomorphic, without lobe = apomorphic), the presence (plesiomorphic) or absence (apomorphic) of a basofacial spine on uropod 1.

Table II summarizes the distribution of plesiomorphic and apomorphic conditions in the genus *Pseudoniphargus*.

Note that the only marine form known, *Ps. adriaticus*, is certainly not the most plesiomorphic one in this line.

Fig. 7 (left) shows a phylogenetic solution involving the nine taxa of *Pseudoniphargus* and the six characters discussed above (cf. table II). It is clear that character state 4a occurred twice independently in the cladogram, character state 5a four times, and character state 6a twice.

²⁾ A similar development can be observed in *Niphargus*.

TABLE II

Distribution of plesiomorphic (*p*) and apomorphic (*a*) conditions in the genus *Pseudoniphargus*.

Character *	1	2	3	4	5	6
<i>longispinum</i>	<i>a</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>
<i>brevipedunculatus</i>	<i>a</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>p</i>
<i>mateusorum</i>	<i>a</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>a</i>	<i>p</i>
<i>unisexualis</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>a</i>	<i>a</i>	<i>p</i>
<i>adriaticus</i>	<i>a</i>	<i>a</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>a</i>
<i>africanus</i>	<i>a</i>	<i>a</i>	<i>p</i>	<i>a</i>	<i>p</i>	<i>p</i>
<i>elongatus</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>p</i>	<i>p</i>	<i>p</i>
<i>branchiatus</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>p</i>	<i>a</i>	<i>p</i>
<i>macrotelsonis</i>	<i>a</i>	<i>a</i>	<i>p</i>	<i>a</i>	<i>a</i>	<i>a</i>

* Character 1 — *p*: uropod 3 ♂ unmodified and similar to uropod 3 ♀.

a: uropod 3 ♂ transformed.

Character 2 — *p*: only the exopodite of uropod 3 ♂ modified (= elongated).

a: both exopodite and pedunculus of uropod 3 ♂ modified (= elongated).

Character 3 — *p*: uropod 3 ♀ unmodified.

a: uropod 3 ♀ modified (= elongated).

Character 4 — *p*: P7 with posterodistal lobe.

a: P7 without posterodistal lobe.

Character 5 — *p*: telson deep-cleft.

a: telson shallow-cleft.

Character 6 — *p*: uropod 1 with basofacial spine.

a: uropod 1 without basofacial spine.

It is possible to construct a number of alternative possibilities for this nine species/six character problem, but always conflicting situations occur. This is a strong indication that certain character states showed a parallel development in the genus. I do believe that the development of the third uropod, from a "normal" gammarid type into an elongated appendage is an adaptation line from bottom-dwelling to interstitial habits. The way this specialized elongation is achieved is unique for certain members of the family Gammaridae (s.l.) and for this reason, I attach greater value to the characters 1 to 3, based on uropodal morphology, than to characters 4 to 6. In part, the latter character states are based on the loss of a certain morphological structure (loss of basofacial spine of the first uropod, loss of the posterodistal lobe on the seventh pereopod), and it can easily be accepted that such losses occurred more than once. Character 4 (lobe on P7) is moreover sex-linked (only present in males of certain species), and is rather unlikely therefore to express cladistic relations.

As to the cleavage of the telson (character 5), I agree with Bousfield (1977) that an entirely cleft telson represents a plesiomorphic condition, but in the case of the genus *Pseudoniphargus*, the telson is entire with a deeper or less deep terminal notch, and the depth of the notch may well be of not too great cladistic value.

Based on these considerations, the characters 4 to 6 have been omitted in the phenogram presented in fig. 7 (right). This phenogram shows a more consistent picture.

7. PLACE OF *PSEUDONIPHARGUS* AT FAMILY LEVEL

The genus *Pseudoniphargus* is one of those genera that does not fit into Bousfield's (1977) elaborate attempt to subdivide the large group of the Gammaridae into a number of superfamilies, family groups and subfamily groups, almost as numerous as there are genera.

He treats *Pseudoniphargus* in two lines on p. 304 of his account, but his treatment is obscured (as more often in the same paper) by several slips of the pen. Firstly, the genus is attributed to "Monod, 1925" (instead of Chevreux, 1901). Secondly, the type-species is called "*Gammarus africanus* Chevreux, 1901", although Chevreux never described such a combination. In the third place "several subspp., Mediterranean, brackish water" were attributed to the genus. However, the greater part of the published records are from outside the Mediterranean basin (Azores, Madeira, coast of Portugal, Cantabrian mountains in N.W. Spain), some are from brackish waters but others are marine or from fresh waters. No subspecies had been described so far (nor species other than the type-species).

The allocation of *Pseudoniphargus* in the superfamily Niphargoidea, as advocated by Bousfield, is conflicting with the diagnosis of that superfamily (Bousfield, 1977: 303). In contrast with the so-called Niphargoidea, *Pseudoniphargus* has strong inner lobes on the lower lip, strongly dissimilar gnathopods without sexual dimorphism, narrow oostegites armed with long setae, a basofacial spine on the first uropod, and lacks a 2nd exopodite segment on the 3rd uropod.

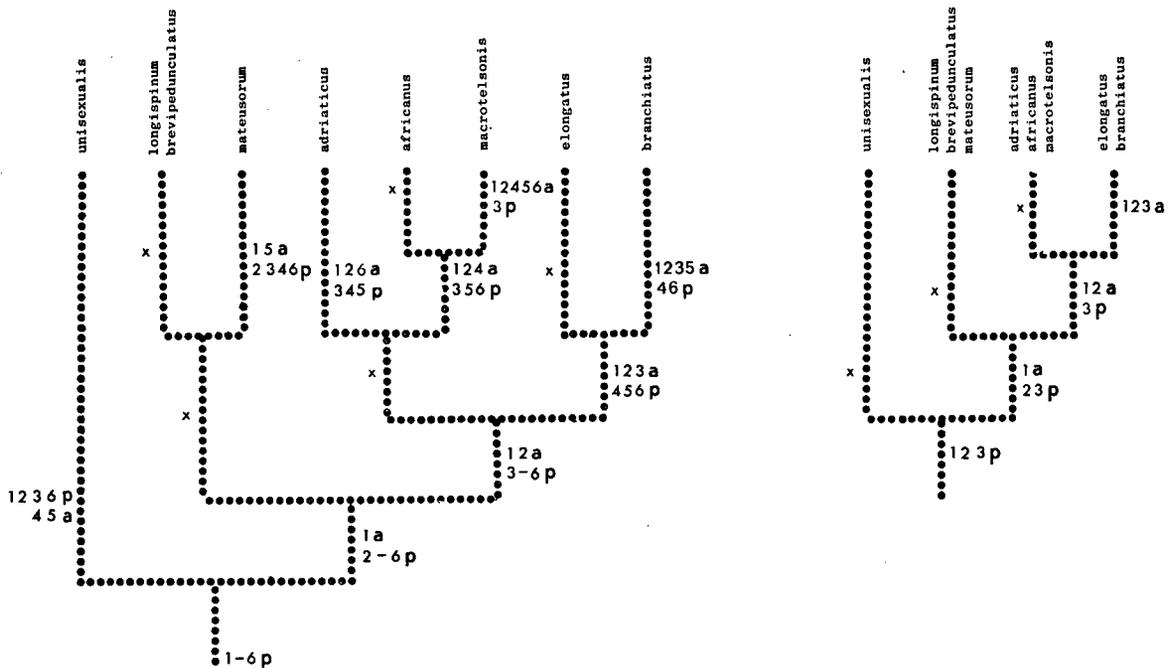


Fig. 7. Two possible phenograms for the 9 species of the genus *Pseudoniphargus*. The left one is one of the possibilities based on a 6-character analysis. In this or similar phenograms, we have to assume that the apomorphic state of character 5 evolved four times independently, the apomorphic state of characters 4 and 6 each twice. This is a strong indication that the apomorphic state of characters 4 to 6 must be considered a parallel evolution. The right phenogram is based on characters 1 to 3 only and offers a more consistent picture. Abbreviations: p = plesiomorph; a = apomorph; 1 to 6 = characters 1 to 6 of table II; x = no change in character state.

The absence of sexual dimorphism in gnathopods 1 and 2 and in antenna 2 of *Pseudoniphargus*, as well as its "normal" (not elongated) 2nd peduncle segment of antenna 1, and wide antennal sinus, are not fitting in Bousfield's diagnosis of the Melitoidea.

Also with the Gammaroidea (in Bousfield's sense) a number of differences exist (telson undivided, uropod 3 not natatory, lower lip with well-developed inner lobes, only 7 teeth on the outer plate of maxilla 1, etc...).

From Bousfield's Crangonyctoidea, *Pseudoniphargus* differs in having a larger antennal sinus, showing a very weak sexual dimorphism in having strong inner lobes on the lower lip and narrow oöstegites, in the absence of calceoli, in the presence of a basofacial spine on uropod 1....

Bousfield combines *Pseudoniphargus* with the North American genus *Allocrangonyx* in "Family group 2" of the Niphargoidea. I fail to see any

fundamental agreement between the two genera.

Barnard (1976) and Barnard & Karaman (in press) propose to reduce the number of family groups or families considerably, and place the genus *Pseudoniphargus* in the Melitoidea. Since, as I have shown above, Bousfield's diagnosis of this superfamily does not fit in completely with the characters of *Pseudoniphargus* (especially the gnathopods of this genus are more gammaroid than melitoid), I feel not able right now to follow Barnard & Karaman's allocation. Like me, Barnard & Karaman question the supposed close relationship of *Pseudoniphargus* and *Allocrangonyx*.

Like I have said before at other occasions, the subdivision of the Gammaridae (s.l.) is still in a flux, and as long as no sound system is developed, I prefer to stick to the good old Gammaridae. I consider *Pseudoniphargus* to be derived from the *Gammarus* group, having obtained a number of apomorphic characters as a result of adaptations to hypogean conditions.

8. TAXONOMY

8.1. Genus *Pseudoniphargus* Chevreux, 1901

Diagnosis. — Gammaridae (s.l.). Blind, depigmented. Body elongate. Antennal sinus shallow. Pedunculi of A1 and A2 not elongated. A1 \gg A2. Cudgel-shaped aesthetes present on distal flagellum segments of A1 (δ , ♀), absent on A2. Accessory flagellum short, 2-segmented.

Upper lip entire; lower lip wing-shaped, inner lobes prominent. Mandible palp 3-segmented, well-developed. First maxilla: outer lobe with 7 spines, inner lobe with 2 setae, palp 2-segmented with 8 distal elements. Second maxilla: outer lobe wide, with 2 distal groups of setae; no oblique rows of setae; inner lobe with terminal setae only. Maxilliped: inner lobe feebly developed, with a low number of distal setae only; outer lobe and palp well developed. Gnathopods without sexual dimorphism. Propodus P2 $>$ propodus P1. Palmar angle armed with bifid (P1) or setule-tipped (P2) spines. No mid-palmar spines. Coxal gills with well-demarcated basal stalk; on P2-P6. Coxal plates rather small; 4th plate without strong posterior excavation. Oöstegites linear, with 5-12 setae. P3 and P4 little setose, equal. P5 as long as P4. P6 and especially P7 elongate. Posterodistal corner of P5-P7 produced to overhanging, sometimes sexually dimorphic. Pleopods biramous, well developed; with two pine-tree-shaped retinacula. First uropod well developed, 2nd much smaller; basofacial spine present or absent. Third uropod with long, 1-segmented exopodite and parviramus-type endopodite; non-natatory. In the most plesiomorphic state, the pedunculus is short, and the exopodite is not elongated; in more apomorphic states, the exopodite, and later also the pedunculus, get elongated, first in males but in the most apomorphic species also in females.

Telson entire, with distal spines and a pair of sensory setules on either side, distally notched.

Distribution. — Groundwaters of interstitia, springs, wells, caves. Northern shores of Adriatic, N.W. shores of Mediterranean, Algeria, Spain, Portugal, Madeira, Azores. Marine to limnic.

Type species. — *Pseudoniphargus africanus* Chevreux, 1901.

Other species. — *Pseudoniphargus macro-telsonis* n. sp., *Ps. adriaticus* S. Karaman, 1955, *Ps. unisexualis* n. sp., *Ps. longispinum* n. sp., *Ps. matorum* n. sp., *Ps. brevipedunculatus* n. sp., *Ps. elongatus* n. sp., *Ps. branchiatus* n. sp., and four unnamed forms called *Pseudoniphargus* sp. 1 and 2 (near *Ps. africanus*), *Pseudoniphargus* sp. 3 (near *Ps. brevipedunculatus*), and *Pseudoniphargus* sp. 4 (near *Ps. elongatus*).

8.2. KEY TO THE SPECIES

- 1a) Pedunculus of third uropod δ strongly elongated 5
- b) Pedunculus of third uropod δ short 2
- 2a) Telson with a deep, V-shaped distal notch. Posterior margin of basis of P7 with numerous (15-20) setules *Ps. brevipedunculatus* n. sp. (Faial, Azores)
- b) Telson with shallow distal notch. Setules on posterior margin of basis of P7 less numerous (less than 12) 3
- 3a) Propodus of gnathopod 2 globular, about as long as wide. Basis of P7 almost rectangular, posterior margin straight. [Male 3rd uropod not differentiated] *Ps. unisexualis* n. sp. (prov. Guipúzcoa, Spain)
- b) Propodus of gnathopod 2 not globular, longer than wide. Basis of P7 oval or trapezoidal 4
- 4a) Palm of 2nd gnathopod very oblique, slightly longer than the posterior propodal margin. Basis of P5 to P7 strongly tapering, trapezoidal. Pedunculus segments 4 and 5 of A2 with long setae *Ps. longispinum* n. sp. (prov. Beira, Portugal)
- b) Palm of gnathopod 2 very little oblique, shorter than the posterior propodal margin. Basis of P5 to P7 ovoid. Pedunculus segments 4 and 5 of A2 with short setae *Ps. matorum* n. sp. (near Setubal, Portugal)
- 5a) Pedunculus and exopodite of third uropod of the adult ♀ elongated. Pereiopods 5 to 7 and A1 flagellum very slender 6
- b) Third uropod ♀ not elongated. Pereiopods 5 to 7 and A1 flagellum "normal" 7
- 6a) Basal stalk of coxal gills 2 to 3 times as long as wide. Posterodistal corner of P7 not overhanging. Aesthetes of A1 long. Telson cleft wide, U-shaped *Ps. branchiatus* n. sp. (S. E. Spain)
- b) Basal stalk of coxal gills about as long as wide. Posterodistal corner of P7 overhanging. Aesthetes of A1 short. Telson cleft narrow, V-shaped. *Ps. elongatus* n. sp. (Cantabrian mountains, N.W. Spain)
- 7a) Posterodistal corner of basis of P5 to P7 (δ) overhanging. Posterior corner of epimeres 2 and 3 rounded *Ps. adriaticus* Karaman, 1955 (Mediterranean, coastal)
- b) Posterodistal corner of basis of P5 to P7 (δ) not over-

hanging. Posterior corner of epimeres 2 and 3 pointed

- 8a) Distal telson spines about as long as the telson. Uropod 3 with basofacial spine . *Ps. africanus* Chevreux, 1901 (Bône, Algeria)
- b) Distal telson spines shorter than the telson. Uropod 3 without basofacial spine . *Ps. macrotelsonis* n. sp. (Kef Djemel, Algeria)

8.3. DESCRIPTIONS OF THE SPECIES

***Pseudoniphargus africanus* Chevreux, 1901.**

Figs. 8-11.

Chevreux, 1901: 211-216, figs. 1-2.

G. Karaman, 1978: 250-256, figs. VI-IX.

Material examined. — Many samples from wells in Bône (= 'Annaba), Algeria, including Chevreux's type-material (Feb. 1899, many specimens, MNHN coll. no. Am. 1198; Nov. 1901, 3 ♂♂, 8 ♀♀, MNHN coll. no. Am. 1200; 1910, 35 specimens, MNHN coll. no. Am. 1202; May 1924, many specimens, MNHN coll. no. Am. 1199; 15 Jan. 1943, 34 specimens, MNHN coll. no. Am. 1203; without date, 100+ specimens, MNHN coll. no. Am. 1201; without date, 1 ♂, ZMB coll. no. 23950).

Descriptive notes, supplementing Chevreux's description. — Maximum length of male (without antennae and third uropod) 7 mm, of female 5 to 6 mm. The lateral head lobes (fig. 8a) are rounded, the antennal sinus is rather deep. Preserved specimens show no eye pigment. First antenna (fig. 8b) correctly described by Chevreux. Accessory flagellum shorter than first flagellum segment (fig. 8c). Aesthetes (fig. 8d) present on the distal segments (from segment 7 onward); the terminal aesthete is about $\frac{3}{4}$ of the length of the segment; the penultimate and antepenultimate aesthetes are 40-50% of the length of the corresponding segment (fig. 8e).

The second antenna (fig. 8f) is not very slender; the gland cone is low, rounded; the flagellum is 6-segmented.

The upper lip (fig. 8g) is of the normal gammarid type. The lower lip (fig. 8k) has well-developed inner lobes.

The mandible palp (fig. 8h) is of the gammarid type. Chevreux's figure (2A) is erroneous. Segment 3 has 1 A-seta, 1 B-seta, no C-setae, a row of some 9 D-setae of decreasing length, and 3 E-setae.

The first maxilla (fig. 8i) has 7 strong spines on the outer lobe, 2 setae on the inner lobe, and 4 spines + 4 setae on the palp.

The second maxilla (fig. 8j) has a wide outer lobe, armed with 2 groups of setae.

The maxilliped (fig. 9a) differs from Chevreux's figure in having a row of spines (not setae) on the medial margin of the outer lobe.

The first gnathopod (fig. 9b) differs from Chevreux's figure in having 2 groups (of 1 and 4 setae, respectively) of elements on the posterior margin of the propodus. The palmar angle is marked by 5 bicuspidate spines; the anterior cusp of the spines is larger than the posterior cusp (fig. 9b).

The second gnathopod (fig. 9c) has 3 palmar angle spines; mid-palmar spine absent (fig. 9d). The posterior margin of the propodus bears 4-5 groups of setae.

The third pereopod (fig. 9e) has an elongate coxal plate. Its setation is rather limited.

The coxal plate of pereopod 4 (fig. 10b) has a weakly concave posterior margin but no strong incurvation. Otherwise P4 resembles P3.

The fifth pereopod (fig. 10c) is short and heavy. The basis has a strongly developed posterior lobe; the posterior margin of the basis bears some 7 distinct notches with a setule. The distal segments bear few setae. There is hardly any sexual dimorphism in the shape of the basis (fig. 11a).

The sixth pereopod is shorter than the seventh. The basis of the female is a trifle wider than that of the male (figs. 11b, c).

The seventh pereopod (fig. 10d) has a distinct posterior lobe on the basis; this lobe is slightly produced in distal direction (♂) or not produced (♀, fig. 11d). The distinctly notched posterior margin of the basis bears some 10 setules. The terminal claw (fig. 10e) is rather slender.

Oöstegites (fig. 10a) linear, armed with some 10 long setae. Coxal gills on P2 to P6, oval, with short basal stalk (figs. 9c, e).

Epimeres not sexually dimorphic; posteroinferior corner produced into a small tooth (fig. 10f), posterior margin just above this tooth concave; lower margin with 1 spine; posterior margin with 1 or 2 vague notches, each carrying a setule.

Pleopods with 2 pine-tree-shaped retinacula (fig. 11e).

Uropod 1 with small basofacial spine (figs. 10g,

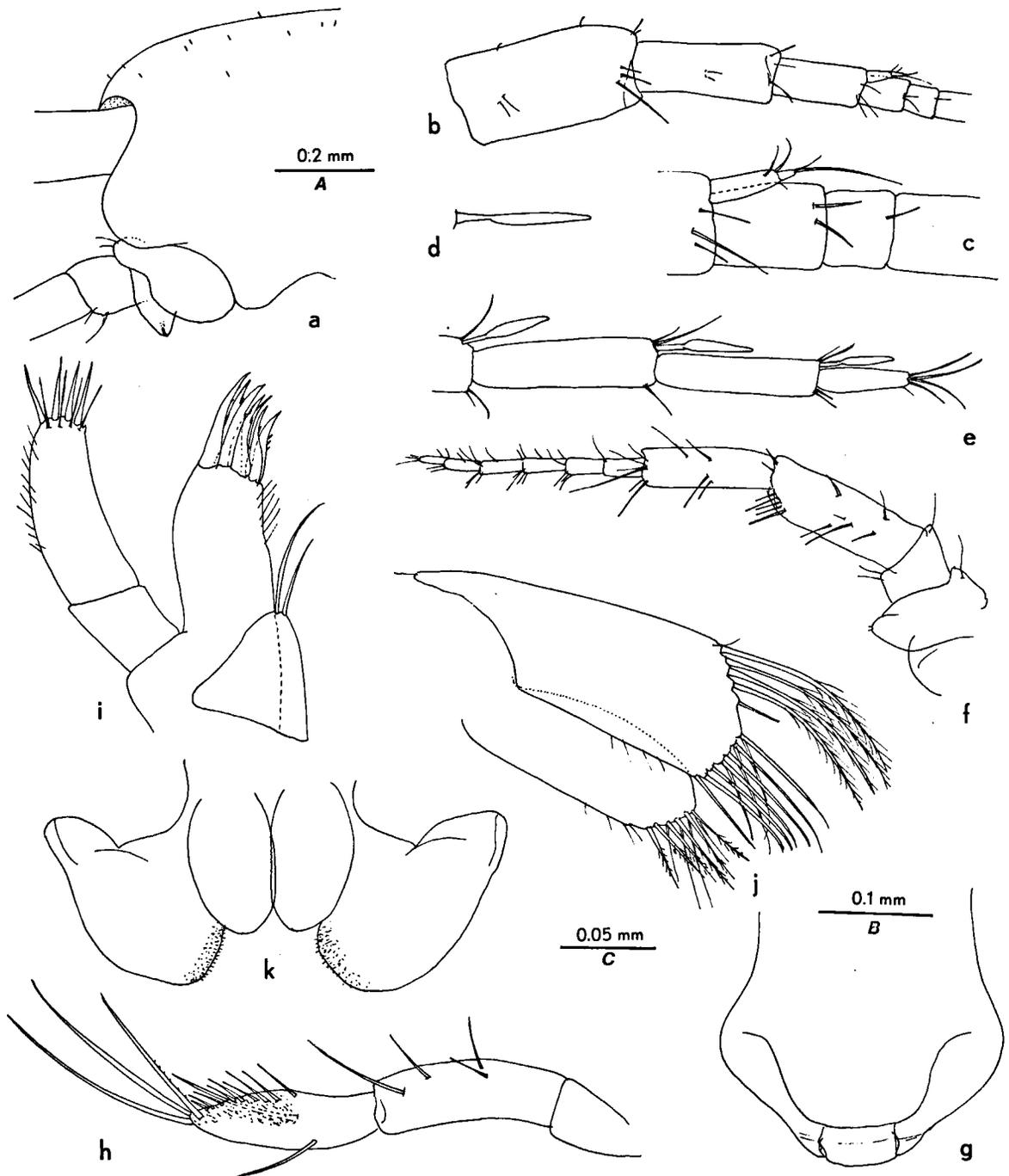


Fig. 8. *Pseudoniphargus africanus* Chevreux, 1901 (syntypes from Bône, Algeria): a, head of female, from the left (scale A); b, basal portion of first antenna, ♂ (A); c, accessory flagellum of first antenna, ♂ (B); d, aesthete of first antenna, ♂ (C); e, distal flagellum segments of first antenna, ♀ (B); f, second antenna, ♂ (A); g, upper lip, ♂ (B); h, mandible palp, ♂ (B); i, first maxilla, ♂ (C); j, second maxilla, ♂ (C); k, lower lip, ♂ (B).



Fig. 9. *Pseudoniphargus africanus* Chevreux, 1901 (syntypes from Bône, Algeria): a, maxilliped, ♂ (scale B); b, distal part of first gnathopod, ♂ (B); c, second gnathopod, ♂ (A); d, palmar margin of second gnathopod, ♂ (B); e, third pereopod, ♂ (A).

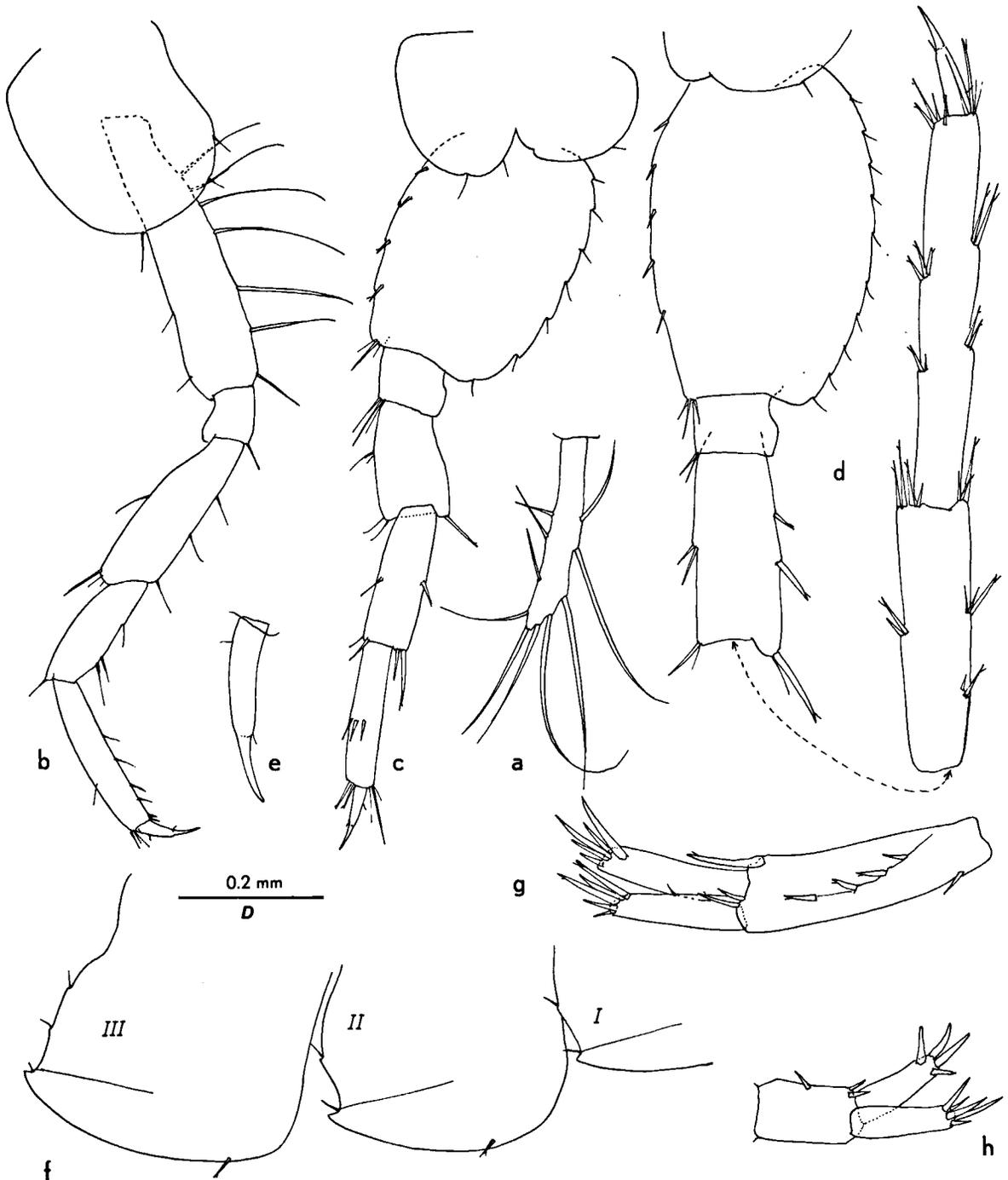


Fig. 10. *Pseudoniphargus africanus* Chevreux, 1901 (syntypes from Bône, Algeria): a, oöstegite of second gnathopod, ♀ (scale A); b, fourth pereopod, ♂ (A); c, fifth pereopod, ♂ (A); d, seventh pereopod, ♂ (A); e, claw of seventh pereopod, ♂ (D); f, epimeres I-III, ♂, from the left (A); g, first uropod, ♂ (A); h, second uropod, ♂ (A).

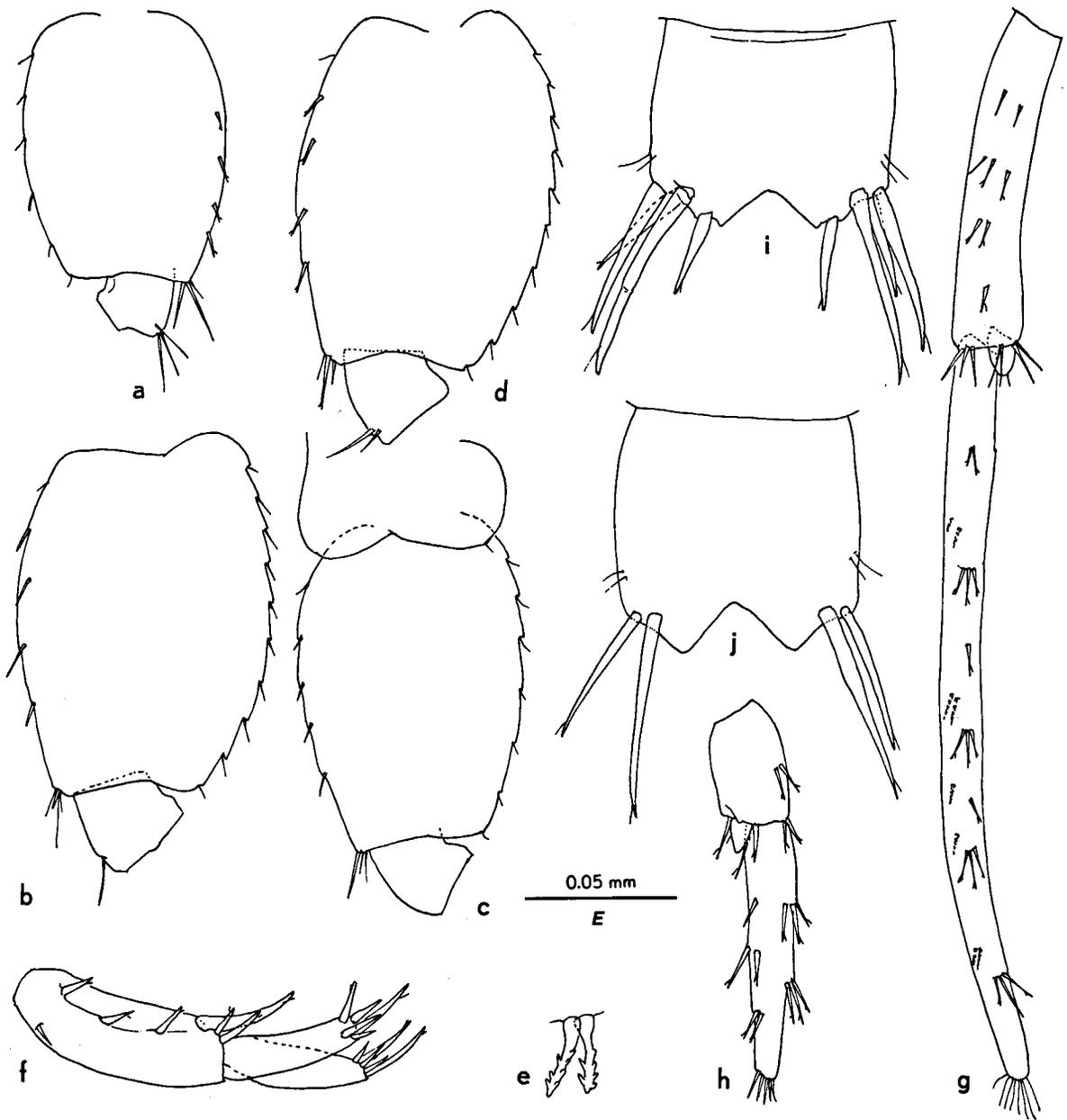


Fig. 11. *Pseudoniphargus africanus* Chevreux, 1901 (syntypes from Bône, Algeria): a, basis of fifth pereiopod, ♀ (scale A); b, basis of sixth pereiopod, ♀ (A); c, basis of sixth pereiopod, ♂ (A); d, basis of seventh pereiopod, ♀ (A); e, retinacula of third pleopod, ♂ (E); f, first uropod, ♀ (A); g, third uropod, ♂ (A); h, third uropod, ♀ (A); i, telson, ♀ (B); j, telson, ♂ (B).

11f). Contrary to Chevreux's figure, the dorso-distal spine on the pedunculus is long (almost half as long as the ramus).

Uropod 2 (fig. 10h) with short pedunculus and short rami.

Uropod 3 with strong sexual dimorphism. In the adult male (fig. 11g) the pedunculus is elongated; the unarticulated outer ramus is $2\frac{1}{4}$ times as long as the pedunculus, slightly upcurved (*Niphargus*-like); the inner ramus is a rounded lobe, armed with 1 setule. The length of both pedunculus and exopodite increase with age in males; so, their ratio stays more or less the same. In the female, the third uropod (fig. 11h) is never elongated; it resembles the type found in certain *Chaetogammarus* species. The armature of the pedunculus and the 1-segmented exopodite consists of spines only.

The telson (figs. 11i, j) is as long as wide and has a varying number (2 to 4 on each side) of distal spines; the longest of these spines may attain the same length as the telson itself. The median notch is V-shaped; its deepest point reaches to, or depasses, the implantation of the spines. There are 2 lateral sensory setules, implanted at a short distance of the distal spines.

Remarks. — The above redescription is based on Chevreux's syntypes. The species is only known with certainty from wells in the surroundings of Bône (= 'Annaba), Algeria. All other North African samples I have examined, belong to morphologically distinct forms. I hesitate, therefore, to accept G. Karaman's (1978: 254) identification from Oued-ed-Demane³), Tunisia, alt. 450 m.

³) It is not sure which locality is meant by this name. I have been unable to trace a locality with exactly the same spelling, however both Wadi ad Dmaïne (in the El Kef region, 36°08'N 09°07'E) and an unnamed oued (= dry river) near Ed (or Ad) Dmaïne (Tamera region, 37°03'N 09°00'E) come near enough in spelling to be considered as possible candidates. Neither of these two localities can be found in a regular atlas, but they are shown by the 1 : 100,000 topographic map of Tunisia. In view of the uncertainty as to the exact position of the locality, it has not been introduced on my maps (figs. 1-6).

***Pseudoniphargus macrotelsonis* n. sp.** Fig. 12.

Material examined. — One ♂ (holotype), thirty-two specimens of both sexes (paratypes). Algeria: subterranean spring at Kef Djemel near Medjez-Sfâ⁴) in the Beni Salah mountains (alt. about 600 m) (MNHN, cat. no. Am. 1197).

Description. — Largest male $5\frac{1}{2}$ mm long (excluding the uropods), largest female 5 mm.

Closely related to *Ps. africanus*, but with a number of apomorphic characters. The features not mentioned resemble to those of *Ps. africanus*.

The distalmost aesthete of the flagellum of the first antenna is about as long as the distal segment (fig. 12a).

The first uropod (fig. 12d) has a short distal pedunculus spine; the basofacial pedunculus spine is lacking.

The epimeres 1 to 3 (figs. 12c, d) have a very strongly produced posterior corner; the tooth on the posterior margin of the plates is more strongly developed than in *Ps. africanus*. Between the pointed corner and the tooth on the posterior margin, a rounded sinus is developed.

The telson (fig. 12e) is slightly longer than wide and bears 2 to 4 distal spines on either side; these spines are shorter than in *Ps. africanus*. The mediobasal notch is shallower, more rounded, and less V-shaped than in *Ps. africanus*.

Remarks. — This sample was already studied by Chevreux (1901: 216), who considered it "une variété locale". The differences with *Ps. africanus* are admittedly slight, but in several hundreds of specimens of *Ps. africanus* examined during this study, none shows intermediate characters. It depends on material collected in the future, hopefully from localities intermediate between Bône (on the sea coast of Algeria) and Kef Djemel (in the mountains), whether *Ps. macrotelsonis* can be maintained as an independent species, or must be considered a subspecies.

⁴) This locality is not recorded in the Times Atlas, but can be found in Andrees Handatlas, ed. 8, sheet 181. It is situated S.E. of Duvivier in the chain of the Monts de Medjerda.

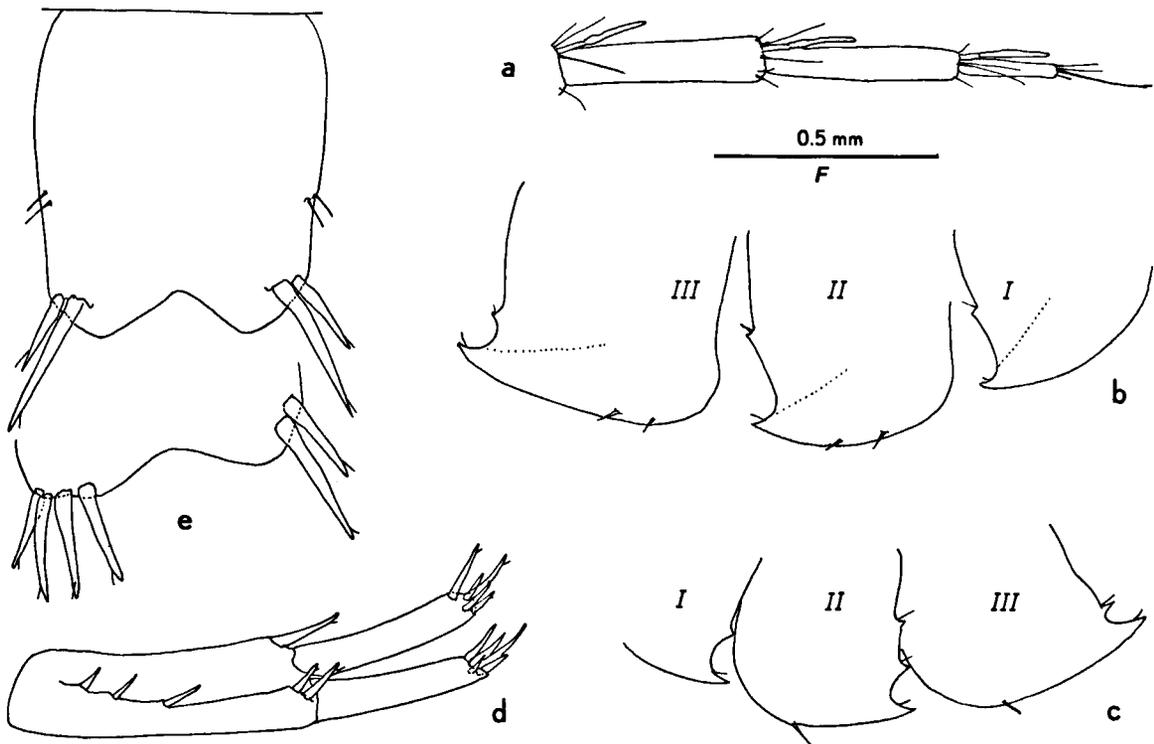


Fig. 12. *Pseudoniphargus macrotelsonis* n. sp. (paratypes from Kef Djemel, Algeria): a, distal segments of first antenna, ♂ (scale B); b, epimeres I-III, ♂, from the right (F); c, epimeres I-III, ♀, from the left (F); d, first uropod, ♂ (A); e, telson of two different males (B).

Pseudoniphargus sp. 1. Fig. 13.

Material examined. — Two ♀♀ (of which one ovigerous). Algeria: Rhar el Khal, wilaya Tlemcen, daïra Sebdo, Khemis (34°34'28"N 01°34'17"W); altitude 1150 m; 14/15 Aug. 1978. Cave, in a small stream connecting the Galerie de la Rivière with the underground brook; depth 0.2-1.0 m; stony; temp. 15° C. Biospeleo Werkgroep, sta. A 8-VIII (ZMA coll. no. Amph. 107.383).

Remarks. — In absence of males, this material is hard to classify. The two specimens differ sufficiently from *Ps. africanus* to prevent inclusion in that species. The differences pertain to the greater length of the aesthetes on A1 (fig. 13a), the more elongate shape of the basis in P5 to P7 (figs. 13b-d), the very slender claw on the posterior pereopods (fig. 13e), the shape of the epimeres (posterior margin convex instead of concave, fig. 13f), and the armature of the telson reduced to a single spine on either side (fig. 13g).

The locality (cave) where the sample was taken is described in Guldemond et al., 1979: 70.

Pseudoniphargus sp. 2.

Material examined. — One ♀. Algeria, from a well in the Mustapha suburb of Alger, leg. H. Gauthier (ZMB coll. no. 23951).

Remarks. — This is a large (length 5½ mm), no doubt adult, female specimen. It is not identical with *Ps. africanus*, because the telson has a very shallow distal notch and the third uropods are elongated (in females of *africanus* they are not elongated). The epimeres on the other hand resemble those of *Ps. africanus*. In absence of males, this specimen has not been named.

Pseudoniphargus adriaticus S. Karaman, 1955. Figs. 14-15.

Ps. africanus Chevreux forma *adriatica* S. Karaman, 1955: 236-241, figs. 44-51.

Ps. adriaticus; G. Karaman, 1978: 241-250, figs. I-V.

Material examined. — Two ♂♂, four ♀♀. France, dép. Var: Le Petit Gaou near Le Brus, steep beach (slope

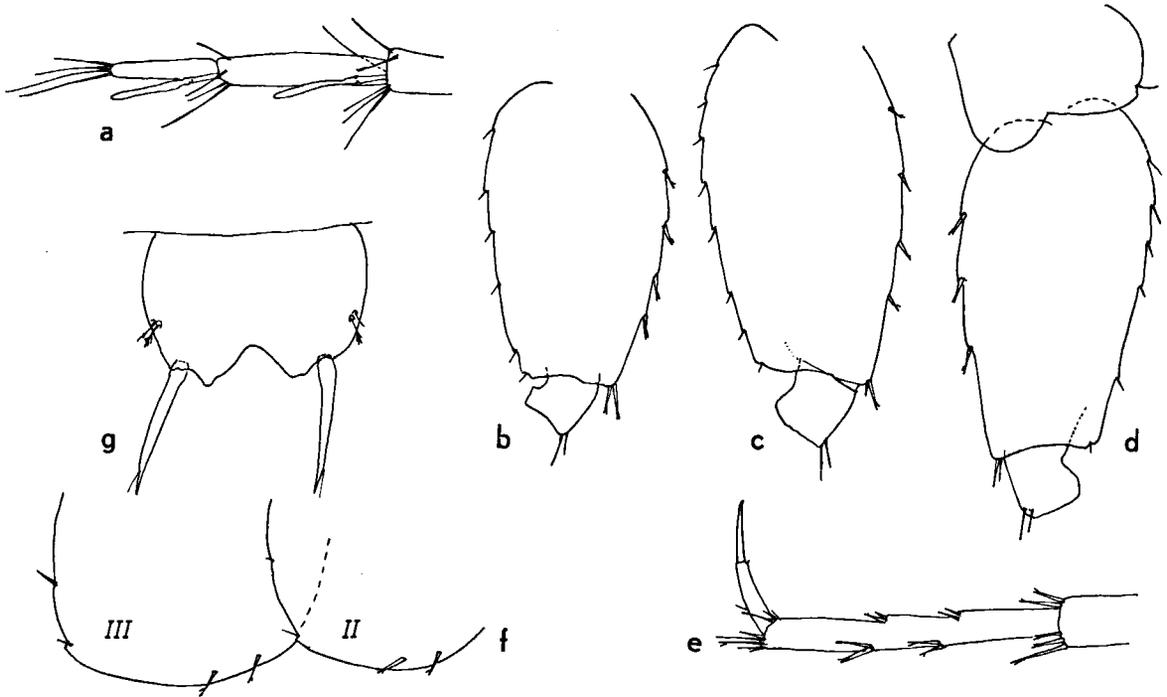


Fig. 13. *Pseudoniphargus* sp. 1 (♀ from Rhar el Khal, Algeria): a, distal segments of first antenna (scale B); b, basis of fifth pereiopod (A); c, basis of sixth pereiopod (A); d, basis of seventh pereiopod (A); e, distal segments of seventh pereiopod (A); f, epimeral plates II and III (A); g, telson (B).

25°) of coarse sand and fine gravel, just below low tide line (behind Studios meublés Le Grand Sarge); 20 Feb. 1979 (ZMA coll. no. Amph. 107.336). Leg. J. H. Stock. Accompanying fauna: Tanaidacea, *Idotea*, *Melita*, flatworms, Harpacticoida, Polychaeta.

Eleven specimens. Same locality; 15 Apr. 1979; leg. J. H. Stock (ZMA coll. no. Amph. 107.337). (Collected with biophreatic pump of type Bou-Rouch.)

Fifteen specimens. Same locality; 29 Dec. 1979; leg. J. H. Stock (ZMA coll. no. Amph. 107.382).

Three specimens. France, dép. Var; Calangue du Port d'Alon, in fine gravel, intertidal; marine; 11 Jan. 1980 (ZMA coll. no. Amph. 107.381).

Twenty-nine specimens. France, dép. Bouches-du-Rhône: Cassis, Plage du Bestouan; steep (slope 20°), coarse gravel beach, near low tide line; 16 Apr. 1979; leg. J. H. Stock (ZMA coll. no. Amph. 107.334). Accompanying fauna: *Caecum* (Gastropoda), *Neogammarus*, Annelida.

Thirty specimens. France, dép. Pyrénées-Orientales: Le Troc (Banyuls); 2 May 1950; leg. E. Angelier no. 201 (ZMB without cat. no.).

One ♂. Same locality; 25 May 1950; leg. E. Angelier (MNHN coll. no. Am. 618).

Three ♂♂, three ♀♀, one juv. France, Corse: Bonifacio, Grotte St. Barthélémy; 14 Sept. 1948; leg. P. A. Rémy (ZMB coll. no. 25469).

Three ♂♂, twenty-five ♀♀. Yugoslavia: Split, Klosterquelle; 1939; leg. F. Pax (ZMB coll. no. 25046).

Descriptive note. — A small interstitial species (adult male 4-5 mm, ovigerous female 3-4 mm, without uropods). Number of eggs small (up to 4).

First antenna (fig. 14a) with long aesthetes (longer than the distal flagellum segment, almost as long as the penultimate and antepenultimate segments).

First gnathopod (fig. 14b) differing from that in *Ps. africanus* by the shape of the palmar angle spines (fig. 14c). These are bicuspidate, but the anterior cusp is shorter than the posterior one.

The second gnathopod (fig. 14d) bears 2 or 3 groups of setae on the posterior margin of the propodus (4-5 groups in *Ps. africanus*). The palmar margin is slightly sinuous. The shape of the propodus is slightly more elongate (less globular than in *Ps. africanus*).

Pereiopods 5, 6 and 7 of the male (figs 15a, d, e, f) have a more distinctly produced posterodistal lobe on the basis and the posterior margin of the

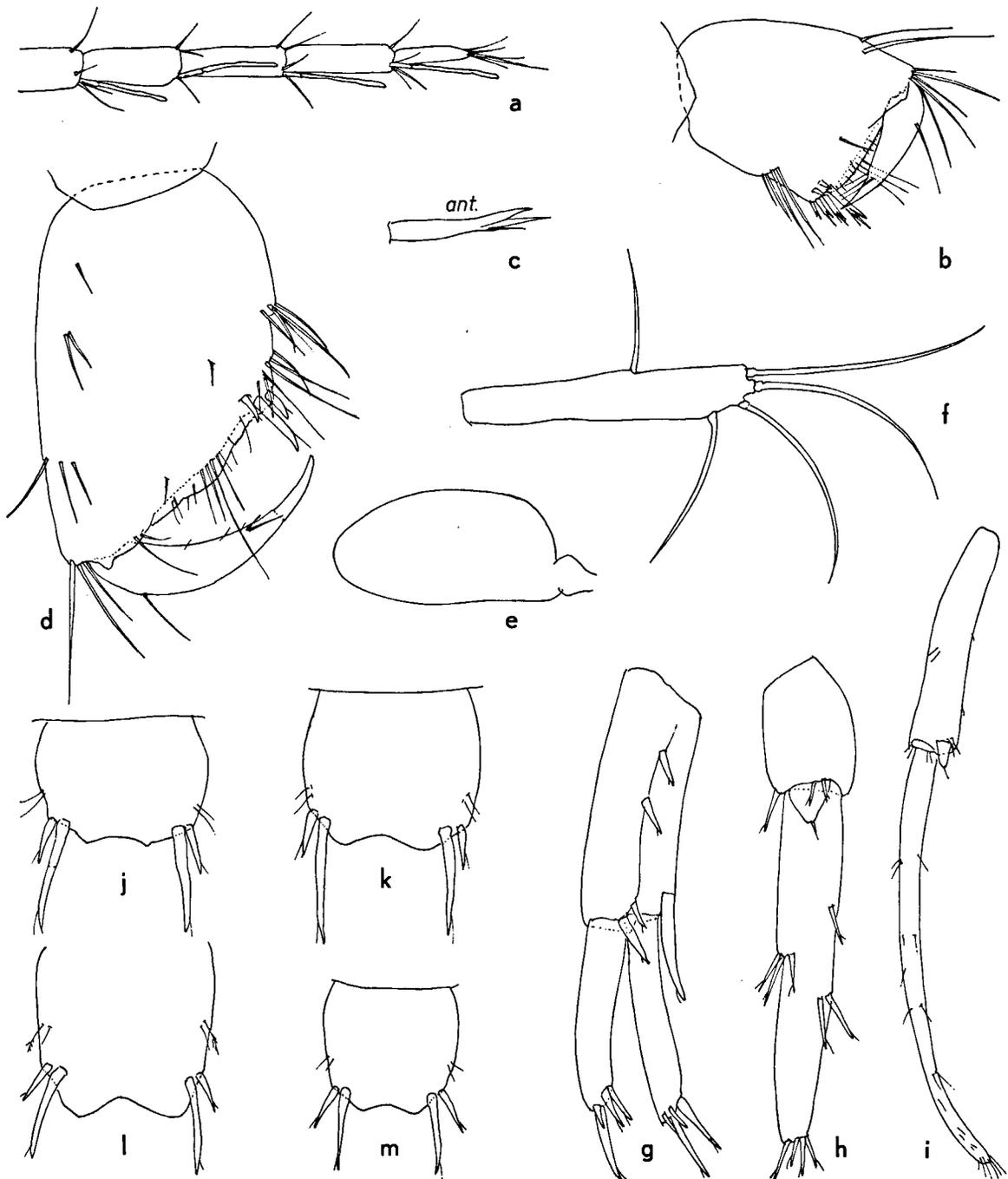


Fig. 14. *Pseudoniphargus adriaticus* Karaman, 1955 (a, c, e, g, h, i, k, m from Le Petit Gaou, France; b, d, f, j from Split, Yugoslavia; l from Le Troc, Banyuls, France): a, distal segments of first antenna, ♀ (scale B); b, distal part of first gnathopod, ♀ (B); c, palmar angle spine of first gnathopod, ♀ (ant. = anterior margin) (E); d, distal part of second gnathopod, ♀ (B); e, coxal gills of second gnathopod, ♂ (B); f, oostegite of fourth pereopod, ♀ (B); g, first uropod, ♂ (B); h, third uropod, ♀ (B); i, third uropod, ♂ (A); j, telson, ♀ (B); k, telson, ♀ (C); l, telson, ♂ (B); m, telson, ♂ (B).

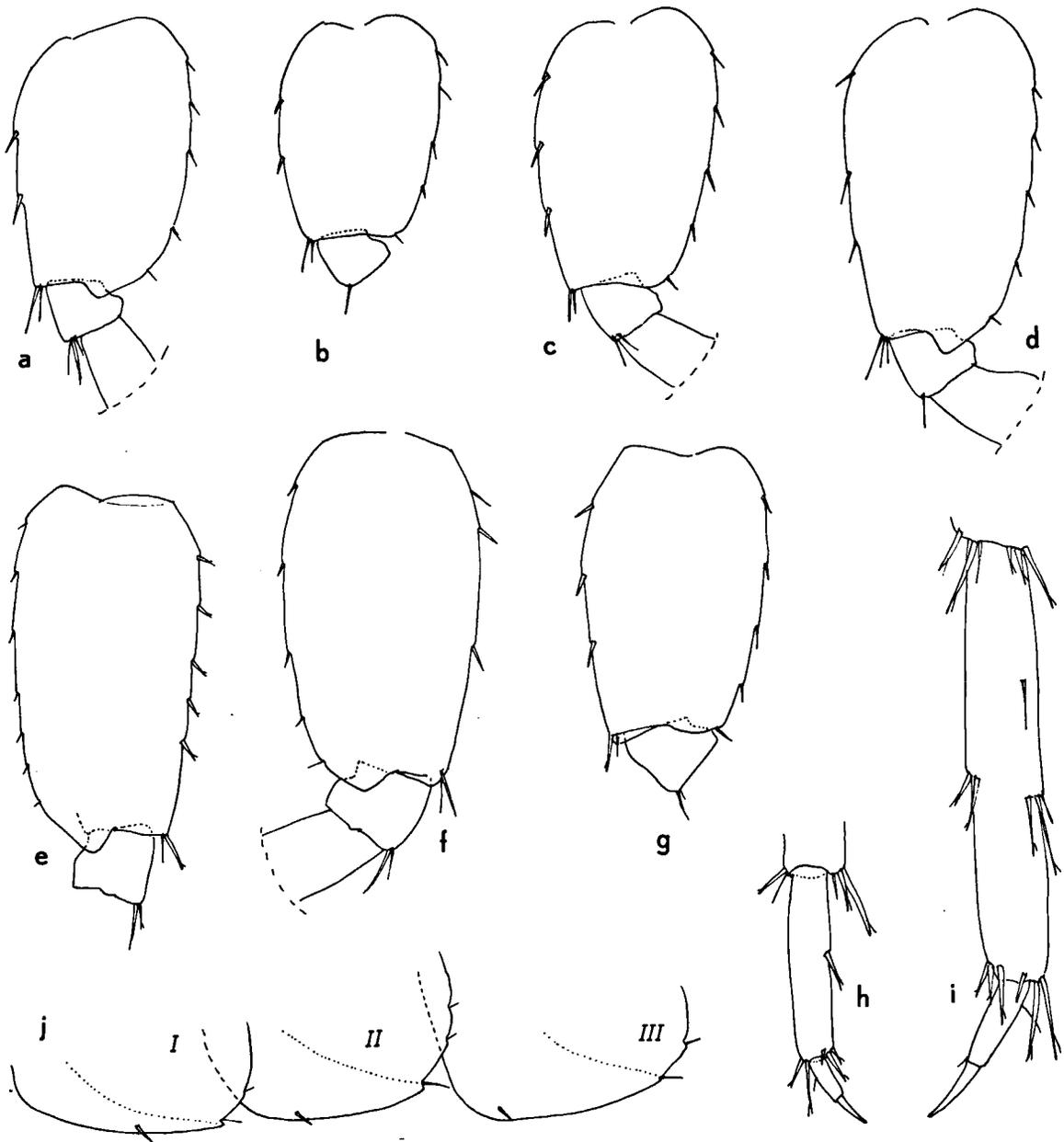


Fig. 15. *Pseudoniphargus adriaticus* Karaman, 1955 (e from Le Troc, Banyuls, France; remaining figures from Le Petit Gaou, France): a, basal part of fifth pereopod, ♂ (scale D); b, same of fifth pereopod, ♀ (D); c, same of sixth pereopod, ♀ (D); d, same of sixth pereopod, ♂ (D); e, f, same of seventh pereopod, ♂ (D); g, same of seventh pereopod, ♀ (D); h, distal segments of fifth pereopod, ♀ (B); i, same of seventh pereopod, ♀ (B); j, epimeres I-III, from the left, ♂ (D).

basis bears fewer setules than in *Ps. africanus*. In the female, the posterodistal lobe of P5 to P7 is not produced (figs. 15b, c, g).

The epimeral plates have a rounded posterior corner (fig. 15j).

The first uropod lacks a basofacial spine (fig. 14g).

The third male uropod has a modified (elongated) pedunculus and exopodite (fig. 14i). In the female, the third uropod is unmodified (fig. 14h).

The telson is slightly wider than long (figs. 14 j-m). It is distally armed with 1 long and 1 short spine on either side. The sensory setules are implanted close to the spines. The medial notch is very shallow: its deepest point does not reach the line that connects the implantation of the left and right telson spines. Remaining characters similar to those of *Ps. africanus*.

Remarks. — There are so many constant differences between typical *Ps. africanus* and the present form that I have, in agreement with G. Karaman (1978) no doubt it represents a distinct species. Specimens from remote localities, like Split, Corsica or Banyuls, are morphologically very similar.

After completion of my present revision, I received G. Karaman's redescription of *Ps. africanus* and *Ps. adriaticus* (1978; the paper is called for indistinct reasons "Revision", although no original materials are re-examined). One of the features discovered by G. Karaman to segregate *adriaticus* from *africanus* is the presence of small cuticular denticulations on the posterior margin of the second metasomite in males of the former. Since the samples on which I have based the present revision had been returned already to their respective depositaries, I have been unable to check the validity of this feature for the various taxa recorded here.

Ecology. — This is a species from marine coarse sands and gravels, from just below to just above the tide lines (the Mediterranean tides are very weak) or from anchihaline localities like the sea caves of Bonifacio (Corsica) and the "Cloister Spring" near Split, Yugoslavia.

Distribution. — Known from a large stretch of coast in the northern Mediterranean, from Banyuls (France) to Budva (Yugoslavia) and from the Balearic Islands and Corsica. Presumably, G. Karaman's record (1978: 248) from Funchal (Madeira) supports on confusion with some other species.

***Pseudoniphargus unisexualis* n. sp.** Figs. 16-17.

Material examined. — One ♂ (holotype), one ♀ (allotype), sixteen paratypes. Spain, prov. Guipúzcoa, field-no. 79-36: Cueva de San Adrian de Cegama (near the southern border of the province); completely dark; in second (= terminal) basin, left of the chapel; mud, wood debris, stones; altitude (estimated) 1000 m; 1 Aug. 1979. In a straight line, this locality is 40 km from the sea (ZMA coll. no. Amph. 107.341-343). Accompanying fauna: juveniles of *Echinogammarus* sp., Oligochaeta, Cyclopidae, Harpacticoidea.

Same locality, ("in ganz kleiner Restlache", in the remains of a very small pool); 14 Oct. 1935; leg. H. J. Stammer; one ♀ (ZMB coll. no. 24817).

Same locality ("Grössere Tropfwassertümpel", in larger dripwater pool), 14 Oct. 1935; leg. H. J. Stammer; six specimens (ZMB coll. no. 24816), and two specimens (ZMB coll. no. 24815).

Description. — Length: male 7 mm, female (ovigerous) 6.5 mm. Eggs 0.54 × 0.64 mm. Secondary sexual differences almost absent.

First antenna (fig. 16a) with 16-segmented flagellum; accessory flagellum slightly shorter than first flagellum segment. Aesthetes on all but the basal three segments of the flagellum. Aesthete on penultimate segment longer than the segment itself; on the other segments at least $\frac{3}{4}$ of the length of the segments.

Second antenna (fig. 16b) with 9-segmented flagellum.

Mandible palp (fig. 16c) with robust 2nd segment and very robust (almost trapezoidal) 3rd segment; the latter armed with 14 D-setae, 2 A-setae, 2 B-setae and 3 E-setae.

First gnathopod (fig. 16d); propodus with 3 groups of setae on posterior margin; palmar angle with 6 trifold spines (fig. 16e); spines on palmar margin also trifold.

Coxal gills with short basal stalk (fig. 16f).

Oöstegites linear (fig. 16i).

Second gnathopod: coxal plate longer than wide (fig. 16f); propodus about as long as wide, globular (fig. 16g); three palmar angle spines, of which

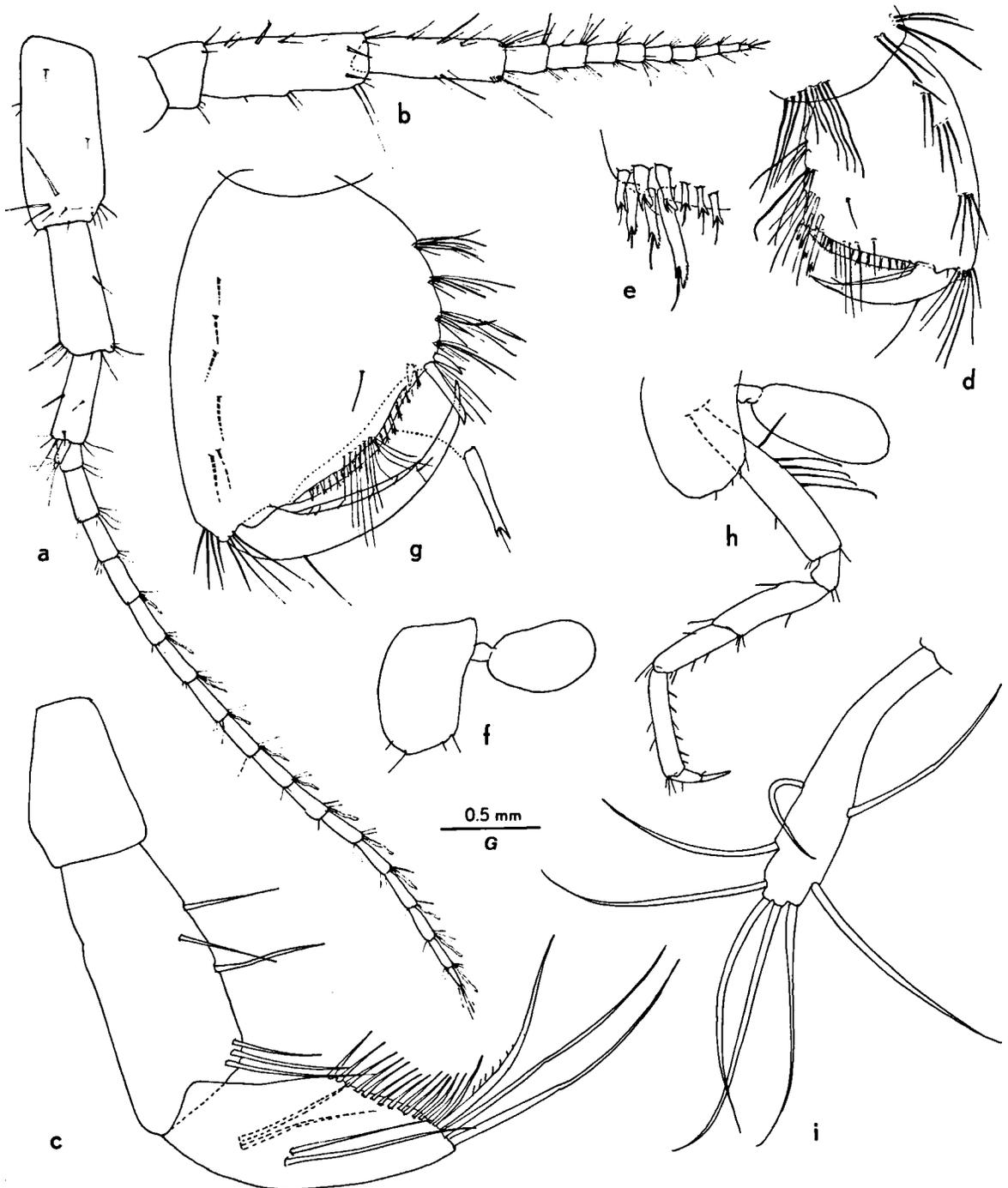


Fig. 16. *Pseudoniphargus unisexualis* n. sp. (paratypes from San Adrian de Cegama, Spain): a, first antenna, ♂ (scale F); b, second antenna, ♂ (F); c, mandible palp, ♂ (B); d, distal part of first gnathopod, ♂ (A); e, palmar angle spines of same (B); f, coxal plate and coxal gill of second gnathopod, ♂ (G); g, distal part of second gnathopod, ♂ (A); h, fourth pereopod, ♂ (G); i, oostegite of fourth pereopod, ♀ (A).

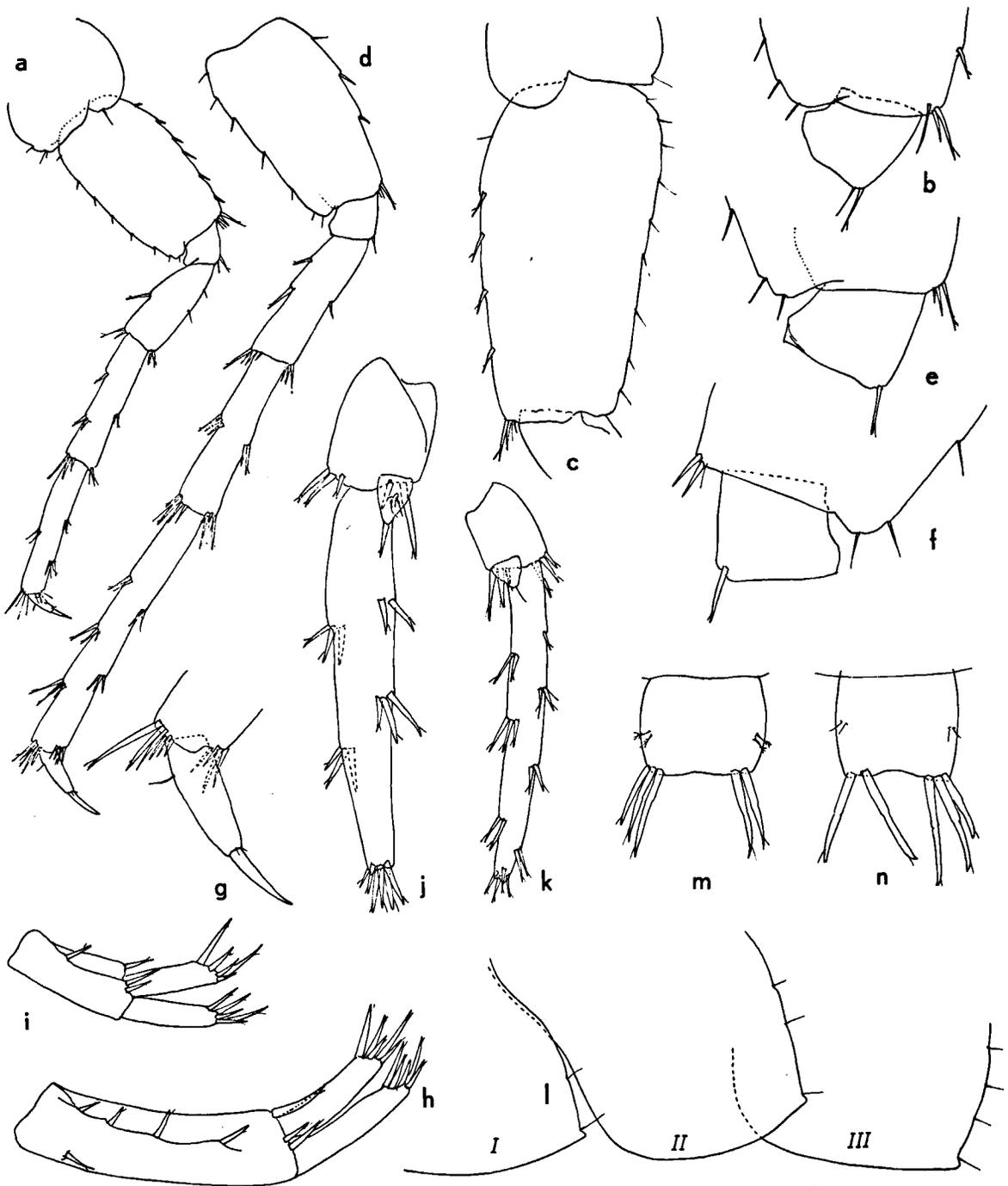


Fig. 17. *Pseudoniphargus unisexuialis* n. sp. (paratypes from San Adrian de Cegama, Spain): a, fifth pereiopod, ♂ (scale G); b, distal end of basis of fifth pereiopod, ♂ (A); c, basis of sixth pereiopod, ♂ (F); d, seventh pereiopod, ♂ (G); e, distal end of basis of seventh pereiopod, ♂ (A); f, same of seventh pereiopod, ♀ (A); g, dactylus of seventh pereiopod, ♂ (A); h, first uropod, ♂ (F); i, second uropod, ♂ (F); j, third uropod, ♀ (A); k, third uropod, ♂ (F); l, epimeres I-III, from the left, ♂ (F); m, telson, ♂ (A); n, telson, ♀ (A).

one very long; spines on palmar margin trifold; palmar margin slightly S-shaped (concave between the palmar angle spines and mid-palmar setae, convex between the mid-palmar setae and the implantation of the claw).

Third and fourth pereopods (fig. 16h) without particulars.

Fifth pereopod (fig. 17a): basis (fig. 17b) elongate, rectangular; posterior margin with 8 setules; merus rather slender.

Sixth pereopod (fig. 17c): basis very elongate, slightly tapering; posterodistal corner only slightly produced.

Seventh pereopod (fig. 17d) slender; basis very elongate, slightly tapering, posterior margin with 7 setules only, posterodistal corner only slightly produced (figs. 17e, f); claw slender (fig. 17g).

First uropod (fig. 17h) similar to that of *Ps. africanus*.

Second uropod (fig. 17i) armed with very elongate spines.

Third uropod (figs. 17j, k): basal segment (δ , ♀) hardly longer than wide; endopodite triangular. Exopodite with 3-4 (δ) or 2 (♀) lateral groups of spines, and 3 (δ) or 2 (♀) medial groups of spines. Several (4-6) distal spines.

Telson (figs. 17m, n) almost rectangular; terminal excavation very slight; left and right lobe each with 2 or 3 very long spines; a pair of sensory setae implanted near the middle of the lateral margin.

Epimeral plates (fig. 17l): posterior corners rectangular, produced into a minute tooth; ventral margin unarmed.

Remarks. — There is no secondary sexual dimorphism in the gnathopods and pereopods. The exopodite of uropod 3 in the female is slightly less slender and slightly less spinose than in the male, but the pedunculus is not sexually dimorphic. The absence of noticeable sexual dimorphism has inspired the specific name, *unisexualis*, a name reminiscent of the unisex dresses so in vogue a couple of years ago.

The two other species which have a short pedunculus in the third male uropod (*Ps. mateusorum* and *Ps. brevipedunculatus*), differ from the

present one in having strong sexual dimorphism in the exopodite of uropod 3 (elongated and up-curved in the male). Moreover, *Ps. brevipedunculatus* has a more deeply cleft telson than *Ps. unisexualis*, and the propodus of gnathopod 2 is much longer than wide. *Ps. mateusorum* differs from *Ps. unisexualis* in the overhanging posterior lobe of the basis of pereopod 7 (δ), in the more numerous setules on the posterior margin of the same segment, and in the rounded epimeral plates.

Up to now the species is only known from the type-locality, the San Adrian cave⁵), on the southern slopes of the Cantabrian mountain chain. The other *Pseudoniphargus* from the Cantabrian mountains, *Ps. elongatus*, occurs in a number of localities on the northern slopes.

Margalef (1970) records a *Pseudoniphargus* from a cave not far from San Adrian, viz. Aya-Ataún⁶). I have been unable to re-examine this sample, but Margalef's figures (especially of the P2) seem to indicate that this material belongs to the present species.

***Pseudoniphargus longispinum* n. sp. Figs. 18-19.**

Material examined. — One ♀ (holotype), one δ (paratype). Portugal, prov. Beira Litoral: Ponte de Mucela (= E. of Coimbra), in a well; 14 June 1958 (IZAN).

Three ♀ (fragmentary). Portugal, prov. Beira Litoral: Anadia (= N.W. of Coimbra); 17 March 1968 (IZAN).

Description. — Body length 4-4.5 mm. First antenna (fig. 18a) with fairly slender pedunculus; accessory flagellum about as long as the first flagellum segment. Flagellum 16-segmented. Distal-most aesthete slightly longer than distal flagellum segment, penultimate and more proximal aesthetes about 2/3 of the length of the corresponding segment (fig. 18b).

Second antenna (fig. 18c) with long setae on peduncle segment 4 and 5. Mandible palp as in *Ps. brevipedunculatus*.

First gnathopod: shape of palmar angle spines resembling that in *Ps. adriaticus*.

⁵) This locality is not shown by any usual atlas. It can be found on the Mapa Turístico, scale 1 : 200,000 (ed. Firestone Hispania), sheet T-22, on the S. slope of the Monte Aitzgorri.

⁶) Firestone Hispania, sheet T-22; situated in the Sierra de Aralar, S.S.W. of Beasain, some 13 km E.N.E. of San Adrian.

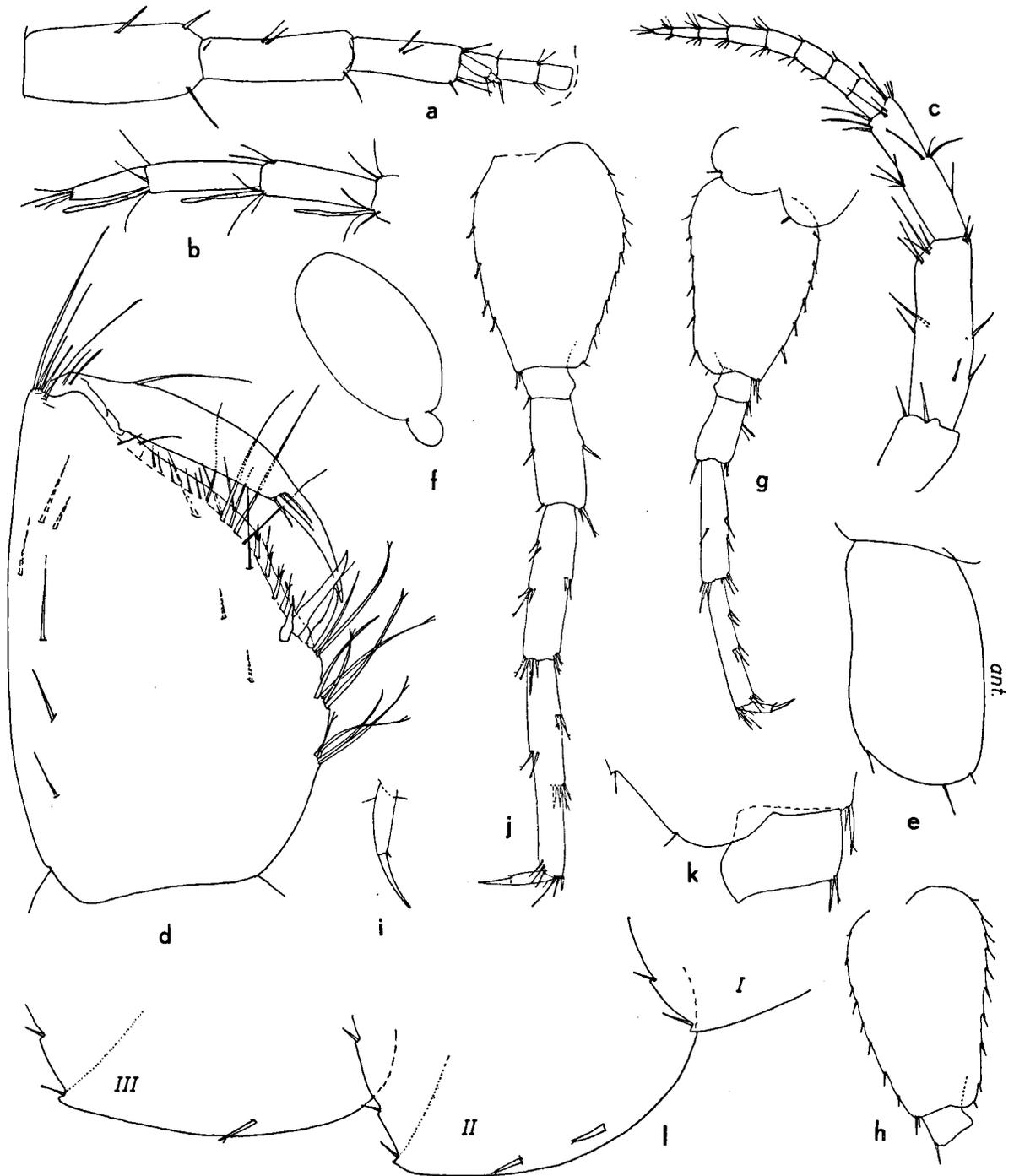


Fig. 18. *Pseudoniphargus longispinum* n. sp. (♂ from Ponte de Mucela, Portugal; ♀ from Anadia, Portugal): a, basal portion of first antenna, ♀ (scale A); b, distal segments of flagellum of first antenna, ♀ (B); c, second antenna, ♀ (A); d, distal part of second gnathopod, ♀ (B); e, second coxal plate, ♀ (ant. = anterior margin) (A); f, coxal gill of fourth pereopod, ♀ (A); g, fifth pereopod, ♀ (F); h, basis of sixth pereopod, ♀ (F); i, dactylus of fifth pereopod, ♀ (D); j, seventh pereopod, ♀ (F); k, distal margin of basis of seventh pereopod, ♂ (D); l, epimeral plates I-III, ♀ (D).

Coxal plates 1-4 elongate (fig. 18e). Coxal gills with short basal stalk (fig. 18f). Oöstegites linear, non-setose (= non-reproductive stage) in specimens examined.

Propodus of 2nd gnathopod trapezoidal with very oblique palma; length of palmar margin longer than that of the posterior propodal margin; posterior margin with 3 groups of long setae (fig. 18d).

Third and fourth pereiopods without particular characters. Basis of 5th to 7th pereiopods (figs. 18g, h, j) tapering, much wider proximally than distally; posterior margin armed with 8 to 10 widely spaced setules. Merus short. Claw slender (fig. 18i). Distal propodal setae of normal length.

The posterodistal corner of the basis of P5 to P7 is in the male more strongly overhanging than in the female (cf. fig. 18k).

The epimeral plates II and III have rectangular posterior corners armed with a small pointed tooth and a setule. Inferior margin with 1 or 2 strong spines (fig. 18l).

First uropod with very strong spines. Basofacial pedunculus spine strong, curved. Rami slender (fig. 19a).

Second uropod likewise armed with long spines (fig. 19b).

Third uropod with slight sexual dimorphism: exopodite slightly more slender in the male (fig. 19d) than in the female (fig. 19c). Exopodite armed with spines only. Pedunculus not (♀) or hardly (♂) elongate.

Telson (fig. 19e) with broad, not very deep, apical notch. Terminal spines (2 on either side) unusually long. Sensory setules placed at some distance of the insertion of the spines.

Remarks. — This form belongs to the group of species in which the pedunculus of the 3rd male uropod is not strongly elongated. The exopodite of uropod 3 in the male is not strongly elongated either, which distinguishes the present form at once from *Ps. mateusorum*, the only other species from continental Portugal. The tapering shape of the basal segment of pereiopods 5 to 7, the very oblique palma in gnathopod 2, the setosity of the second antenna, the spinosity of the first uropod, etc. form distinct additional differences.

The most closely related species may be *Ps. unisexualis* from northern Spain, which resembles

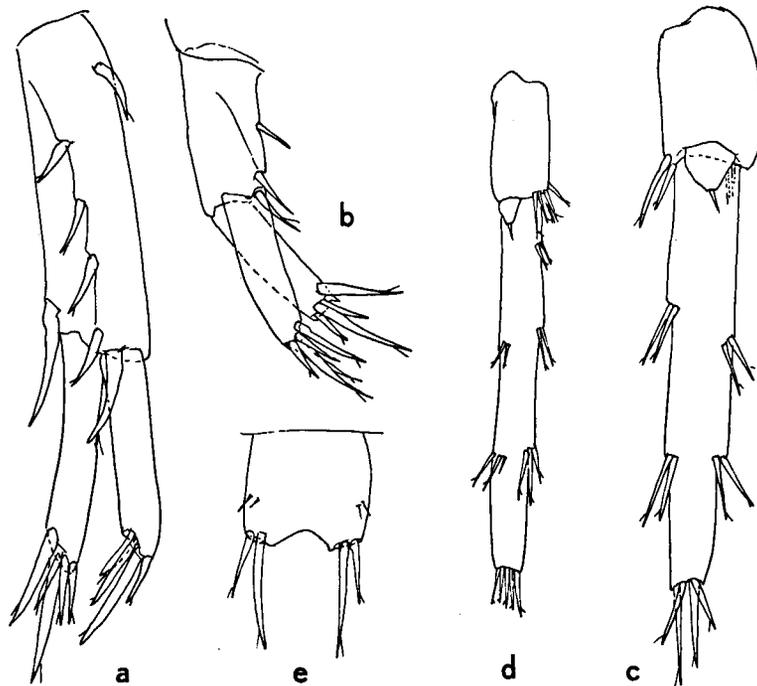


Fig. 19. *Pseudoniphargus longispinum* n. sp. (♂ from Ponte de Mucela, Portugal, ♀ from Anadia, Portugal): a, first uropod, ♀ (scale D); b, second uropod, ♀ (D); c, third uropod, ♀ (D); d, third uropod, ♂ (A); e, telson, ♀ (D).

the present taxon in the morphology of uropod 3, but differs in many other ways (depth telson notch, less strongly spinose first uropods, absence of spines on lower margin of epimeral plates, shape of the basis in P5 through P7, more globular propodus in P2, less elongate coxal plates 1-4 ...).

The proposed specific name, *longispinum*, alludes to the armature of the telson, and first and second uropods.

***Pseudoniphargus mateusorum* n. sp.** Fig. 20.

Material examined. — One ♂ (holotype), forty-seven ♀♀ and juveniles (paratypes). Portugal: Costa da Arrábida (Bight of Setubal), Lapa dos Morcegos (= bat cave); 26 June 1941; leg. A. Barros Machado (ZMB coll. no. 25248).

One ♂, same locality; 22 February 1973; leg. A. Barros, A. Mateus & E. Mateus (IZAN).

Description. — Male 4½ mm; ovigerous female (5 eggs) 4½ mm; female with oöstegites 5 mm.

First antenna: pedunculus and accessory flagellum (fig. 20a) as in *Ps. africanus*. Flagellum 15-segmented; aesthetes on segment 3 to 14; distal aesthetes (fig. 20b) as long as or slightly longer than the corresponding segment; proximal aesthetes about half as long as the segment (fig. 20a).

Second antenna (fig. 20c): pedunculus slender, little setose.

Mandible palp about as in *Ps. adriaticus*; it has 4 E-setae.

First gnathopod as in *Ps. adriaticus*.

Second gnathopod: propodus of about the same shape as in *Ps. brevipedunculatus*; 3 groups of setae on its posterior margin. Oöstegites as in *Ps. unisexualis*.

Third and fourth pereopods as in *Ps. adriaticus*.

Fifth (fig. 20d), sixth (fig. 20e) and seventh pereopods (figs. 20f, g) in the male with a strongly projecting posterodistal lobe. Basis of P6 and P7 of elongate shape; basis of P5 with some 8 setules on posterior margin, of P6 with 9, of P7 with 11. No inner spines on the basis. Dactylus of P7 very slender (fig. 20h). Shape of basis of P5-P7 in the female as in *Ps. adriaticus*.

Epimeres (fig. 20i) rounded.

First uropod (fig. 20j) with basofacial pedun-

culus spine, distal peduncular spine shorter than half the length of the slender rami.

Third uropod in the male (fig. 20k) with short pedunculus (about as long as the telson + its distal spines). Third uropod in the female (fig. 20l) with still shorter pedunculus; distal segment slightly elongated, tapering.

Telson (fig. 20m) wider than long; distally armed with 1 very long and 1 shorter spine on either side; sensory setules plumose, implanted near the insertion of the distal spines. Medial notch very wide and shallow.

Remarks. — The new species is, by the structure of the third male uropod and by other characters, closely related to *Ps. brevipedunculatus* from the Azores. For the differences between the two, see the remarks under the latter species.

Etymology. — This species is named in honour of Dr. Amílcar Mateus and Emília de Oliveira Mateus in recognition of their various contributions to the knowledge of the Portuguese amphipod fauna.

***Pseudoniphargus brevipedunculatus* n. sp.**

Figs. 21-22.

Material examined. — One ♂ (holotype), one ♀ (allotype), fifty-six paratypes. Azores: Faial, Horta, coast, poço no. 2; 2/3 Apr. 1957; Exped. P. Brinck & E. Dahl, loc. 83 (ZIL cat. no. 1).

Description. — Adult male 6½-7 mm, female 6½ mm.

The first antenna has slender pedunculus segments (fig. 21a); the flagellum is 16-segmented; the 2-segmented accessory flagellum (fig. 21c) is slender and about as long as the first flagellum segment. The aesthetes on the penultimate and antepenultimate segments are slightly longer than the corresponding flagellar segment (fig. 21b); the other aesthetes are ¾ to 4/5 of the length of the corresponding segment.

The second antenna (fig. 21d) is rather slender and setose.

The mandible palp has 7 setae on segment 2 and bears 2 A-setae on segment 3; otherwise it is as in *Ps. africanus*.

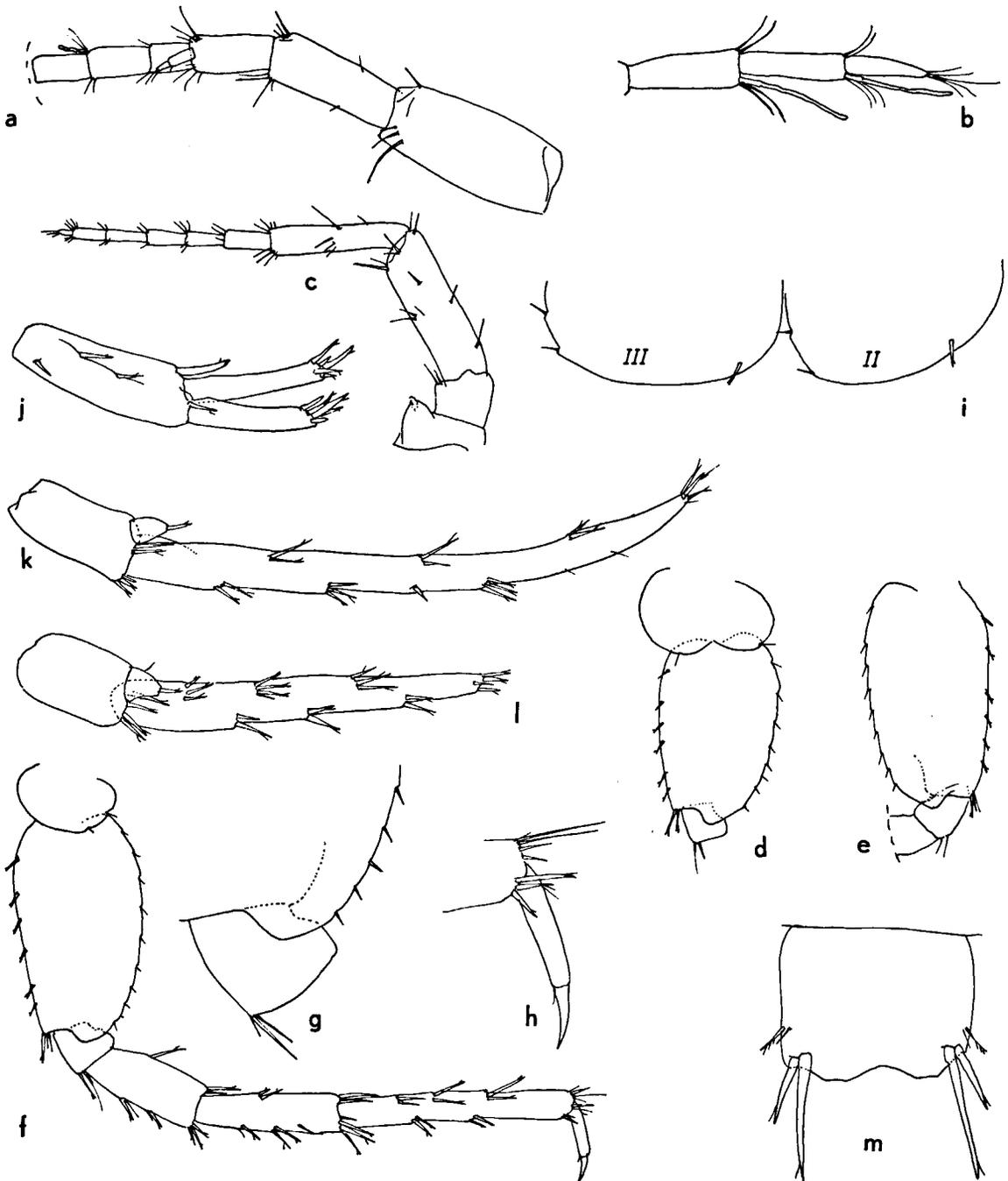


Fig. 20. *Pseudoniphargus mateusorum* n. sp. (♂, holotype and ♀, paratype, from Lapa dos Morcegos, Portugal): a, basal portion of first antenna, ♂ (scale A); b, distal segments of flagellum of first antenna, ♂ (B); c, second antenna, ♂ (A); d, basis of fifth pereiopod, ♂ (F); e, basis of sixth pereiopod, ♂ (F); f, seventh pereiopod, ♂ (F); g, posterodistal corner of basis of seventh pereiopod, ♂ (D); h, dactylus of seventh pereiopod, ♂ (D); i, epimeral plates II and III, from the right, ♂ (A); j, first uropod, ♂ (A); k, third uropod, ♂ (A); l, third uropod, ♀ (A); m, telson, ♂ (B).

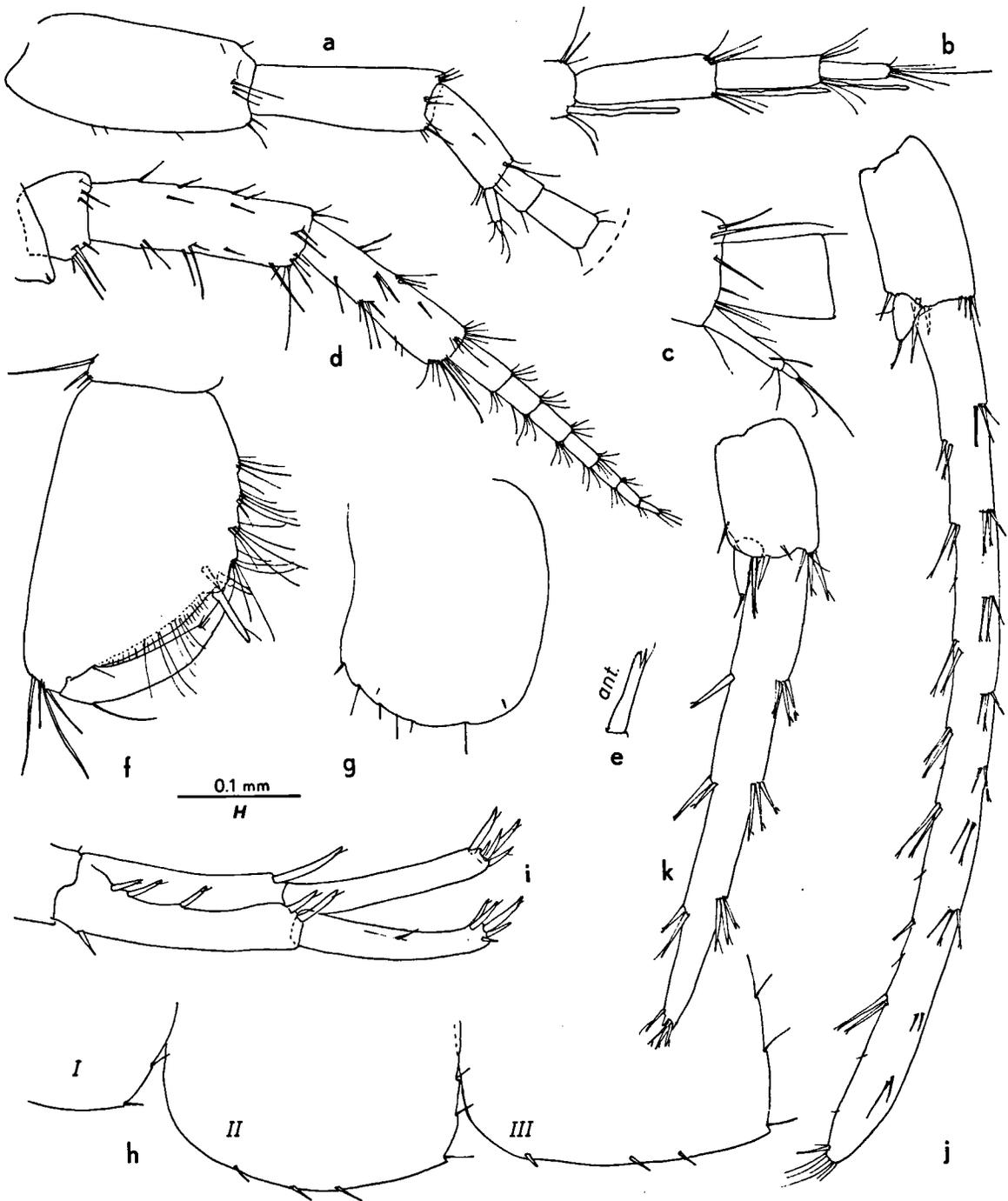


Fig. 21. *Pseudoniphargus brevipedunculatus* n. sp. (paratypes from Horta, Faial, Azores): a, basal portion of first antenna, ♂ (scale A); b, distal segments of flagellum of first antenna, ♂ (B); c, accessory flagellum, ♂ (B); d, second antenna, ♂ (A); e, palmar angle spine of palma of first gnathopod, ♂ (H) (ant. = anterior margin); f, distal part of second gnathopod, ♂ (A); g, fourth coxal plate, ♂ (A); h, epimeral plates I-III, from the left, ♂ (A); i, first uropod, ♂ (A); j, third uropod, ♂ (A); k, third uropod, ♀ (D).

The palmar angle spines of gnathopod 1 (fig. 21e) have 2 cusps of about equal length.

The second gnathopod has an elongate, trapezoidal propodus (fig. 21f); the posterior propodal margin bears 4 groups of setae; the palmar margin is regularly curved.

The coxal plates of pereopods 3 and 4 (fig. 21g) bear a few more setules than in *Ps. africanus*. The coxal gills are as in *Ps. africanus*.

The basis of the 5th to 7th pereopod has a produced posterodistal corner in the male (figs. 22a, d). In the female, this corner is only feebly produced (fig. 22g). The posterior margin of the basis is densely set with setules (up to 20 setules have been counted). Moreover, the basis of P7 bears two inner subdistal spinules.

The epimeral plate 1 is rounded; plates 2 and 3 have rectangular posterior corners; their lower margin bears 3 spines (fig. 21h).

Uropod 1 (fig. 21i) possesses a basofacial peduncle spine; the distal peduncle spine is less than half as long as the rami; rami and pedunculus slender.

Uropod 3 male (fig. 21j): pedunculus short (less than twice as long as wide); endopodite as usual; exopodite very elongated, upcurved, armed with long, slender spines; exopodite 6 times as long as the pedunculus.

Uropod 3 female (fig. 21k): pedunculus short ($1\frac{1}{2}$ times as long as wide); exopodite slightly elongate, tapering, $3\frac{1}{2}$ - $3\frac{3}{4}$ times as long as the pedunculus, armed with long slender spines.

Telson (fig. 22h) wider than long, armed with 1 shorter and 1 very long distal spine on either side; sensory setae implanted very closely to the insertion of the spines. Distal notch V-shaped, rather deep; cleft narrower than in *Ps. africanus*.

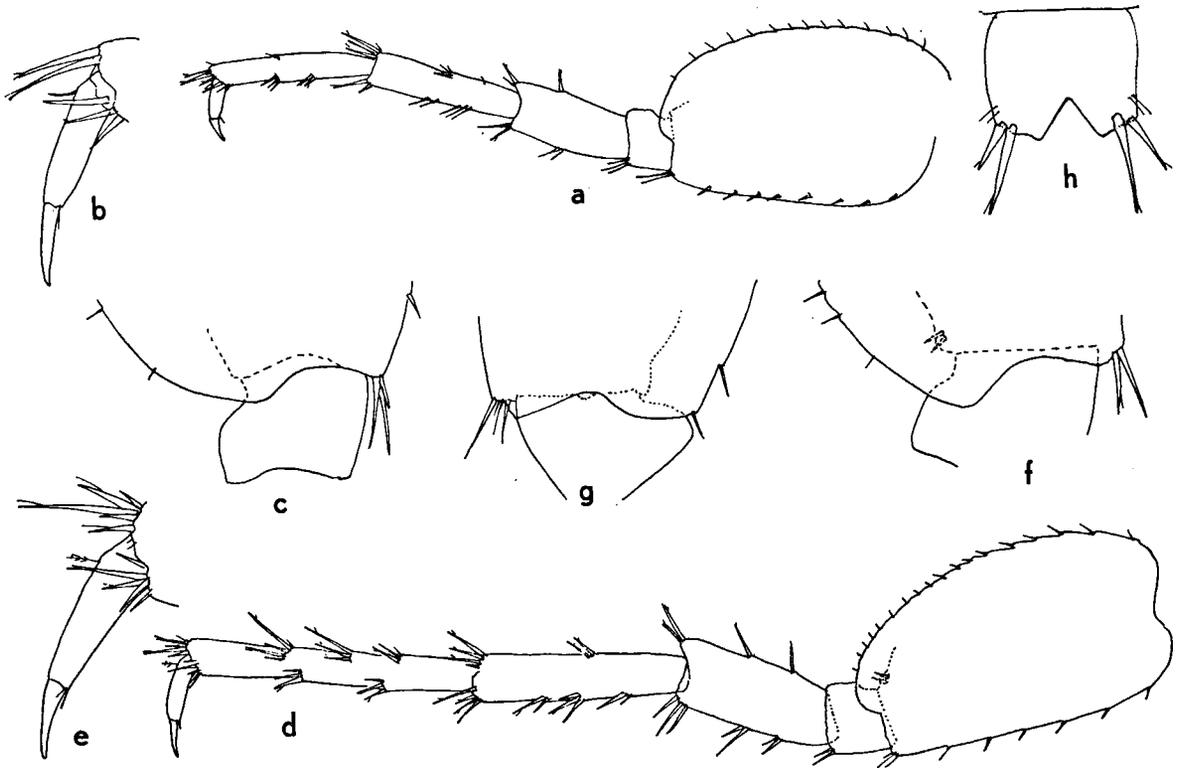


Fig. 22. *Pseudoniphargus brevipedunculatus* n. sp. (paratypes from Horta, Faial, Azores): a, fifth pereopod, ♂ (scale F); b, dactylus of fifth pereopod, ♂ (D); c, distal end of basis of fifth pereopod, ♂ (D); d, seventh pereopod, ♂ (F); e, dactylus of seventh pereopod, ♂ (D); f, distal end of basis of seventh pereopod, ♂ (D); g, same of ♀ (D); h, telson, ♀ (D).

Remarks. — The only other species in which the pedunculus of uropod 3 in the male is short, whereas the exopodite is strongly elongated, is *Ps. mateusorum* from continental Portugal. The latter species has a very shallow telson notch, more rounded epimeres, a very slender claw on the posterior pereopods, a less slender A1 pedunculus, and a less setose A2. The number of differences is rather small, but clear cut. On morphological grounds alone, *Ps. brevipedunculatus* might be considered a subspecies of *Ps. mateusorum*. Since I do not adhere to the idea of a landbridge connecting Portugal and the Azores, I prefer to consider both populations as separate species.

***Pseudoniphargus* sp. 3.**

Material examined. — One ♀. Madeira: Funchal, cistern of the Seminary; June 1933; leg. J. de Goureira Barreto (ZMB coll. no. 25082).

Remarks. — This, unfortunately single specimen of the female sex is of small size (length 3 mm). The general morphology resembles that of *Ps. brevipedunculatus* from the Azores, but in absence of males or of large females, I refrain from identifying the Madeiran material firmly.

***Pseudoniphargus elongatus* n. sp. Figs. 23-25.**

Material examined. — One ♂ (holotype), one ovigerous ♀ (allotype). Spain, prov. Santander, Ramales de la Victoria, Cueva la Cullevera; in shallow pool; 22 July 1979; leg. J. H., M. & D. Stock (ZMA coll. no. Amph. 107.333).

Five specimens, same locality; Aug. 1958; leg. Rousset & De Lorient (MNHN coll. no. Am. 617).

Three specimens, same locality; 7 Aug. 1965; leg. De Lorient (UL coll. no. Et. 36).

Four specimens, Spain, prov. Santander, Cueva la Cascada; 6 Aug. 1962; leg. De Lorient (UL coll. no. Et. 19).

Three specimens, Spain, prov. Santander, Cueva del Molino; 6 Aug. 1959; leg. De Lorient (UL coll. no. Et. 18).

Twenty-one specimens, all ♀♀, Spain, prov. Santander, Cueva de la Station de Santa Isabel; 8 Oct. 1936; leg. H. J. Stammer (ZMB coll. nos. 24812, 24813, 24814).

One ♂, one ♀, Spain, prov. Santander, Cueva de Castillo near Puente Viesgo; 6 Oct. 1935; leg. H. J. Stammer (ZMB coll. no. 24811).

Fifty-three juveniles, probably this species, Spain, prov. Guipúzcoa, Cuevas de Landarbaso, S.E. of San Sebastian, in pool; 18 Sep. 1935; leg. H. J. Stammer (ZMB coll. nos. 24809, 24808, 24810).

Description. — Large males up to 6 mm long, adult males from 4-4½ mm present in the samples; ovigerous females from 3 to 5 mm long. Number of eggs small (2 to 4).

First antenna: pedunculus (fig. 23a) only slightly more slender than in *Ps. africanus*. Accessory flagellum as long as or longer than, the first flagellum segment (fig. 23b). Flagellum 19- to 20-segmented. Distal flagellum segments exceedingly slender (fig. 23c); aesthete on penultimate segment about 80% of length of the distal segment, on the remaining segments less than half as long as the corresponding segment (fig. 23c).

Second antenna (fig. 23d) slightly more slender than in *Ps. africanus*.

Mandible palp (fig. 23e) as in *Ps. africanus*.

First gnathopod as in *Ps. adriaticus*.

Second gnathopod (figs. 23f, g): propodus of very elongate shape. Coxal gills as in *Ps. africanus* (fig. 25a).

Pereopods 3 and 4 without peculiarities; claw of P4 slender (fig. 23h).

Fifth pereopod: basis with slightly (male, fig. 23i) or not (female, fig. 24a) projecting posterodistal corner. Posterior margin of basis with some 8 (P5) to 12 (P7) setules. Basis of P6 male (fig. 23j) and P7 male (fig. 24c) distinctly projecting; in P6 female and P7 female projecting (fig. 24b). The posterior pereopods and their terminal claws, in particular in P7, very slender.

Epimeral plates rectangular to somewhat rounded (figs. 23k, l); lower margin with 1 spine.

Uropod 1 (fig. 25b) with basofacial spine. Distal peduncle spines short; rami slender.

Uropod 2 (fig. 25c) with slender rami.

Uropod 3 (male) with strongly elongate pedunculus and strongly elongate exopodite (fig. 25d). Uropod 3 (ovigerous female) with moderately elongate pedunculus and moderately elongate exopodite (fig. 25f). In smaller, non-ovigerous females, the 3rd uropod has a hardly elongated pedunculus and a slightly elongated exopodite (fig. 25e).

Telson (figs. 24d, e) with 2 to 4, not exceedingly long, distal spines; sensory setules placed at some distance from the insertion of the spines; distal notch V-shaped, medium deep.

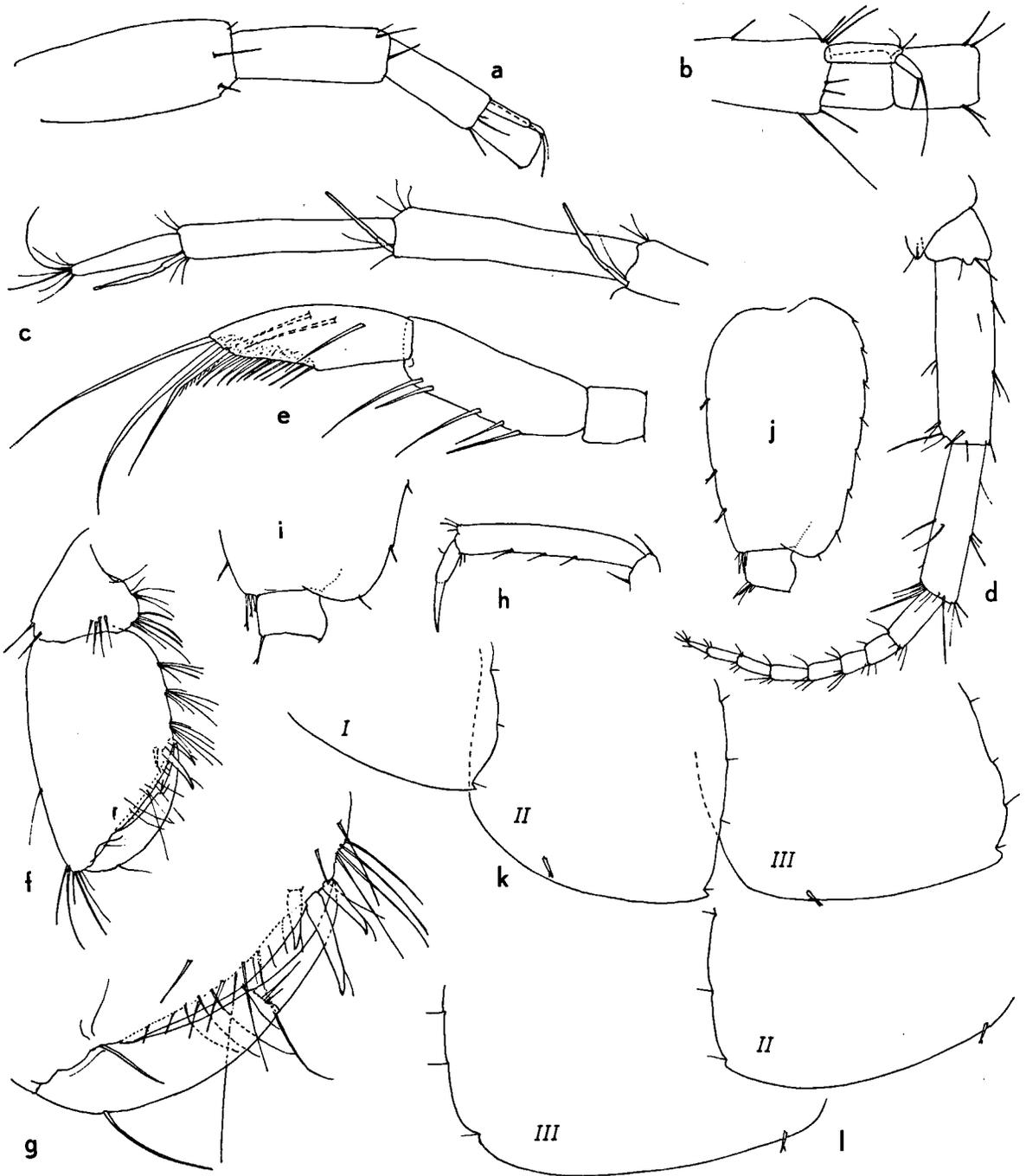


Fig. 23. *Pseudoniphargus elongatus* n. sp. (b from Santa Isabel, Spain, remaining figures from Ramales de la Victoria, Spain): a, basal portion of first antenna, ♂ (scale A); b, accessory flagellum, ♀ (B); c, distal flagellum segments of first antenna, ♂ (B); d, second antenna, ♂ (A); e, mandible palp, ♂ (B); f, distal part of second gnathopod, ♂ (A); g, palmar margin of second gnathopod, ♂ (B); h, distal part of fourth pereopod, ♂ (A); i, distal part of basis of fifth pereopod, ♂ (A); j, basis of sixth pereopod, ♀ (F); k, epimeral plates I-III, from the left, ♂ (A); l, epimeral plates II and II, from the right, ♂ (A).

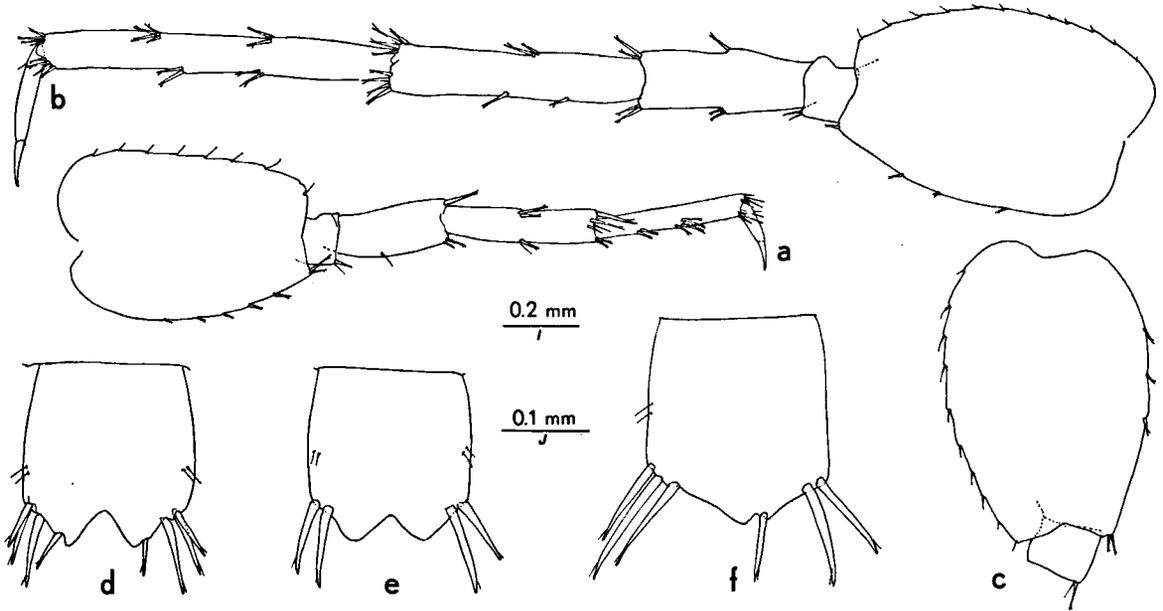


Fig. 24. *Pseudoniphargus elongatus* n. sp. (f from Cueva la Cascada, Spain, remaining figures from Ramales de la Victoria, Spain): a, fifth pereopod, ♀ (scale I); b, seventh pereopod, ♀ (I); c, basis of seventh pereopod, ♂ (I); d, telson, ♀ (J); e, telson, ♂ (J); f, anomalous telson, ♂ (J).

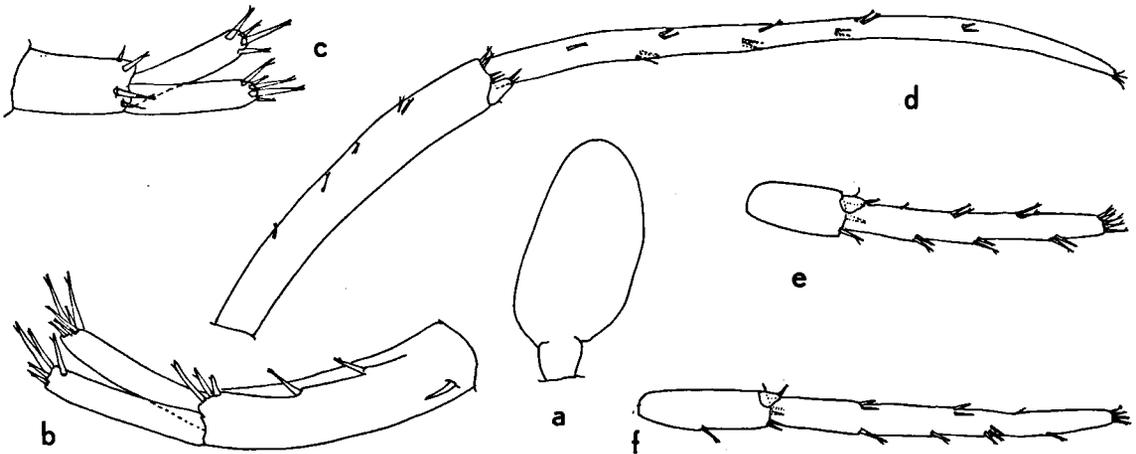


Fig. 25. *Pseudoniphargus elongatus* n. sp. (e from Cueva la Cascada, Spain, remaining figures from Ramales de la Victoria, Spain): a, coxal gill of second pereopod, ♂ (scale A); b, first uropod, ♂ (A); c, second uropod, ♂ (A); d, third uropod, ♂ (F); e, third uropod, small ♀ (F); f, third uropod, large ovigerous ♀ (F).

Remarks. — From the most eastern locality (in the province Guipúzcoa) only juveniles are known. Adults from this province are necessary to ascertain their taxonomic status.

A male from the Cueva la Cascada has an anomalous telson (fig. 24f), asymmetrical and with a distal projection instead of with a distal notch.

This species is characterized by the fact that also the pedunculus of the female third uropod is elongated; this elongation is less strong than in the male, but nevertheless clear in comparison with *Ps. africanus* (in *Ps. africanus* the pedunculus is $1\frac{1}{2}$ times as long as wide, in *Ps. elongatus* 4 times). The proposed specific name alludes to the elongation found in the 3rd uropod, but also in the pereopods 5 to 7, and in the A1 flagellum.

***Pseudoniphargus* sp. 4.**

Material examined. — Six juveniles. Spain, prov. Navarra, near French border, Cueva de las Brujas (= W. of Zugarramurdi); in pool, entirely dark; 19 July 1979; leg. J. H., M. & D. Stock (ZMA coll. no. Amph. 107.335).

Remarks. — It is not possible to identify these juvenile specimens with certainty. They could well be *Ps. elongatus*, but being recorded at the far eastern end of the range of that species makes me cautious.

The locality, the Las Brujas caves, is shown on sheet T-23 of the Firestone Hispania map, scale 1 : 200,000 (see footnote 5).

***Pseudoniphargus branchiatus* n. sp. Figs. 26-28.**

Material examined. — One ovigerous ♀ (holotype). Spain, prov. Valencia, mouth of river Jugar at Cullera (= S. of Valencia), about 500 m from the sea; reeds, stones; temp. 26.4° C, chlorinity 1400 mg/l; 9 Sep. 1970; leg. J. H. Stock & S. Pinkster (ZMA coll. no. Amph. 106.154).

Two ♂♂, seven ♀♀ (of which five ovigerous), paratypes. Spain, prov. Malaga, cave system of Hundidero-Gato near Benaolan (36°44'N 05°14'W); altitude of cave entrance 423 m. In dripstone basin ("gours") in the large room; loamy gravel; temp. 14.0° C; 31 July 1978; leg. Biospeleo Werkgroep, sta. S 4-XI (ZMA coll. no. Amph. 107.384).

Description. — Ovigerous females: length $4\frac{1}{2}$ - $5\frac{1}{2}$ mm (without uropods); males: 4 mm. First antenna with rather slender pedunculus (fig. 26a, c); accessory flagellum longer than first

flagellum segment (fig. 26b); flagellum 17-segmented; distal flagellum segments not exceedingly slender; distal aesthete slightly longer than distal flagellum segment; penultimate and antepenultimate aesthetes more than half as long as the corresponding segment (figs. 26d, e).

Second antenna resembling that of *Ps. unisexualis*; flagellum rather short, 5- to 7-segmented (fig. 26f).

Mandible palp as in *Ps. africanus*.

First gnathopod: 6 palmar angle spines; smaller ones bicuspidate with terminal setule (fig. 26g); larger ones bifid, posterior cusp the longest (fig. 26g).

Second gnathopod: propodus rather elongate; posterior margin with 3 groups of setae (fig. 26i); coxal plate elongate; basal stalk of coxal gill about 3 times as long as wide (fig. 26h).

Oöstegites linear, armed with 7 setae (fig. 26h).

Coxal plates 3 and 4 elongate; stalk of coxal gill elongate (figs. 28a, b). Remaining part of pereopods 3 and 4 (fig. 26j) as in *Ps. africanus*, but with 5 to 6 spinules on the propodal sole.

Pereopod 5 (fig. 27a): basis rather elongate (fig. 28c), posterior margin armed with 6 setules; propodus with long spines. Stalk of coxal gills elongate.

Pereopod 6 (figs. 27b, c): basis with 10 setules on posterior margin. Posterodistal corner of basis of P5 to P7 (♂, ♀) not overhanging (figs. 27d, e). The distal spines on the propodus of P5 to P7 are about as long as the claw in the female holotype (fig. 27c), shorter in the paratypes (fig. 27d). Dactylus of P7 rather slender (fig. 28d).

Epimeral plates with a small tooth at the posterior corner. Lower margin of plate II with 2 spines; of plate III with 4 spines (fig. 27f).

Uropod 1 (fig. 28e) rather slender; basofacial spine present; distal peduncle spine less than half as long as the rami.

Uropod 2 (fig. 28f): pedunculus and rami with several short marginal spines.

Uropod 3 of the female (figs. 28h, i): pedunculus over twice as long as wide; exopodite elongate, about 10 times as long as wide. Uropod 3 of the male (fig. 28g): both pedunculus and exopodite curved and very elongate.

Telson (figs. 28j-l) with a shallow, rounded

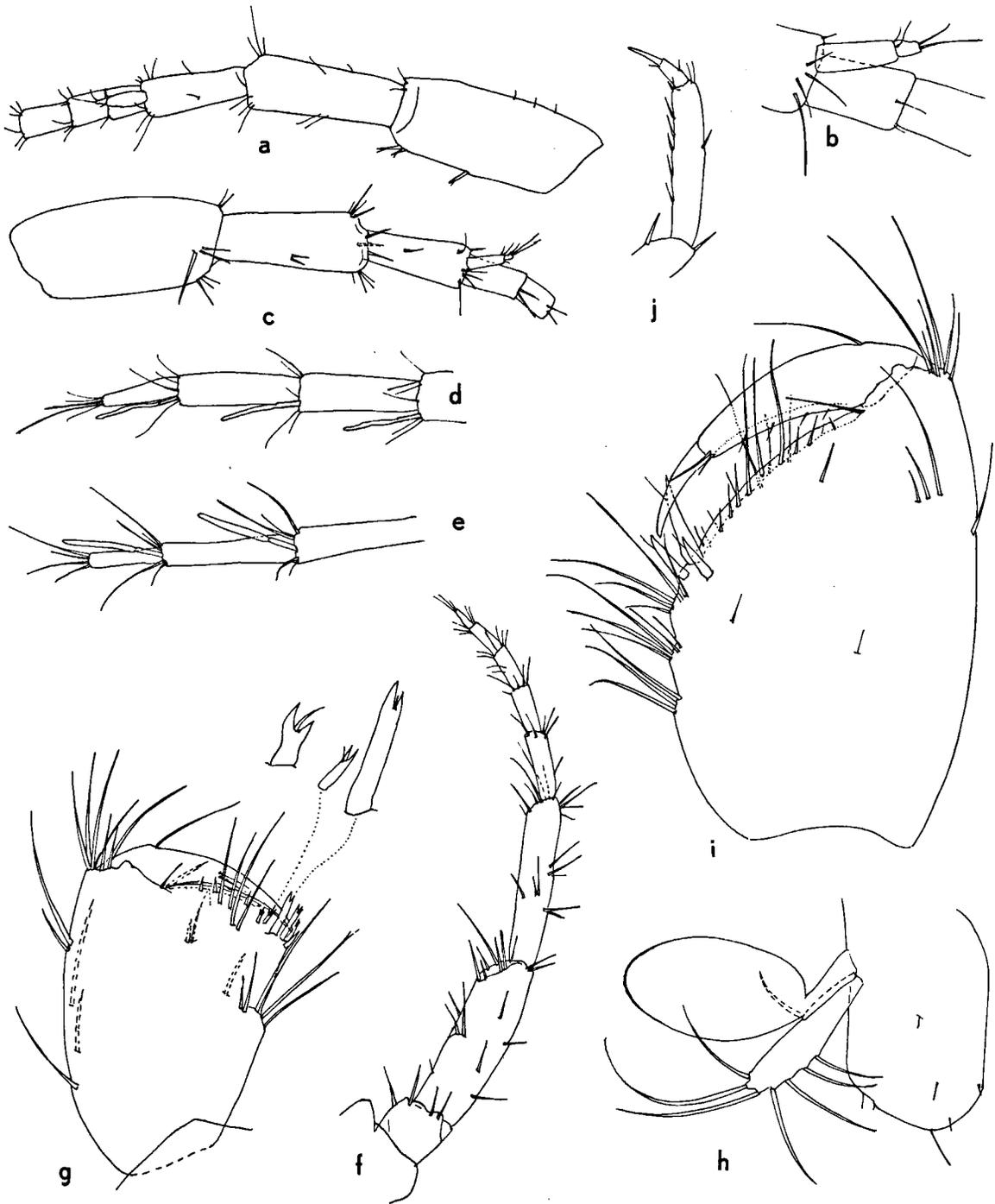


Fig. 26. *Pseudoniphargus branchiatus* n. sp. (a, b, d, h, i from Cullera, Spain; c, e, f, g, j from Benaolan, Spain): a, basal portion of first antenna, ♀ (scale A); b, accessory flagellum, ♀ (B); c, basal portion of first antenna, ♂ (A); d, distal flagellum segments of first antenna, ♀ (B); e, same of ♂ (B); f, second antenna, ♂ (A); g, distal part of first gnathopod, ♂ (B); h, coxal plate, oostegite and coxal gill of second gnathopod, ♀ (A); i, distal part of second gnathopod, ♀ (B); j, distal part of fourth pereopod, ♂ (A).

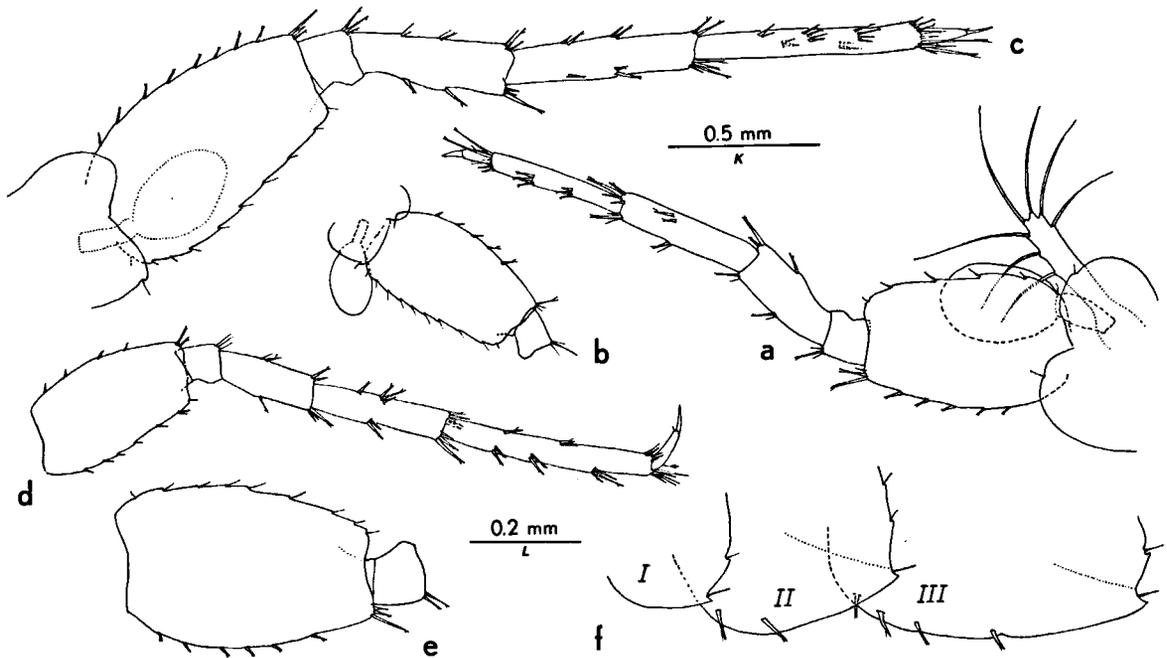


Fig. 27. *Pseudoniphargus branchiatus* n. sp. (a, c, e, f from Cullera, Spain; b, d from Benaojan, Spain): a, fifth pereopod, ♀ (scale I); b, basis of sixth pereopod, ♂ (K); c, sixth pereopod, ♀ (I); d, seventh pereopod, ♂ (K); e, basis of seventh pereopod, ♀ (I); f, epimeral plates I-III, from the left, ♀ (L).

distal notch; each laterodistal corner with 3 to 5 spines, some of which are almost as long as the telson.

Remarks. — The only other species of *Pseudoniphargus* having an elongate exopodite of uropod 3 in the female sex is *Ps. elongatus*. From the latter *Ps. branchiatus* differs in the morphology of the telson (with a wide, rounded distal notch), in the less slender A1 flagellum segments, in the lack of an overhanging posterodistal lobe on the basis of P5 to P7, in longer aesthetes on A1, etc.

The main morphological character in which the new species differs from all others so far described in *Pseudoniphargus*, is the elongation of the stalk of all coxal gills. In all other species this stalk is about as long as wide, in *Ps. branchiatus* it is 2 to 3 times as long as wide. The proposed specific name alludes to the shape of the coxal gills.

At the type-locality, the species apparently has been found in hyporheic conditions of the riverbed. The other locality, the Hundidero-Gato cave system, is described by Anonymous (1974: 29 et seq.).

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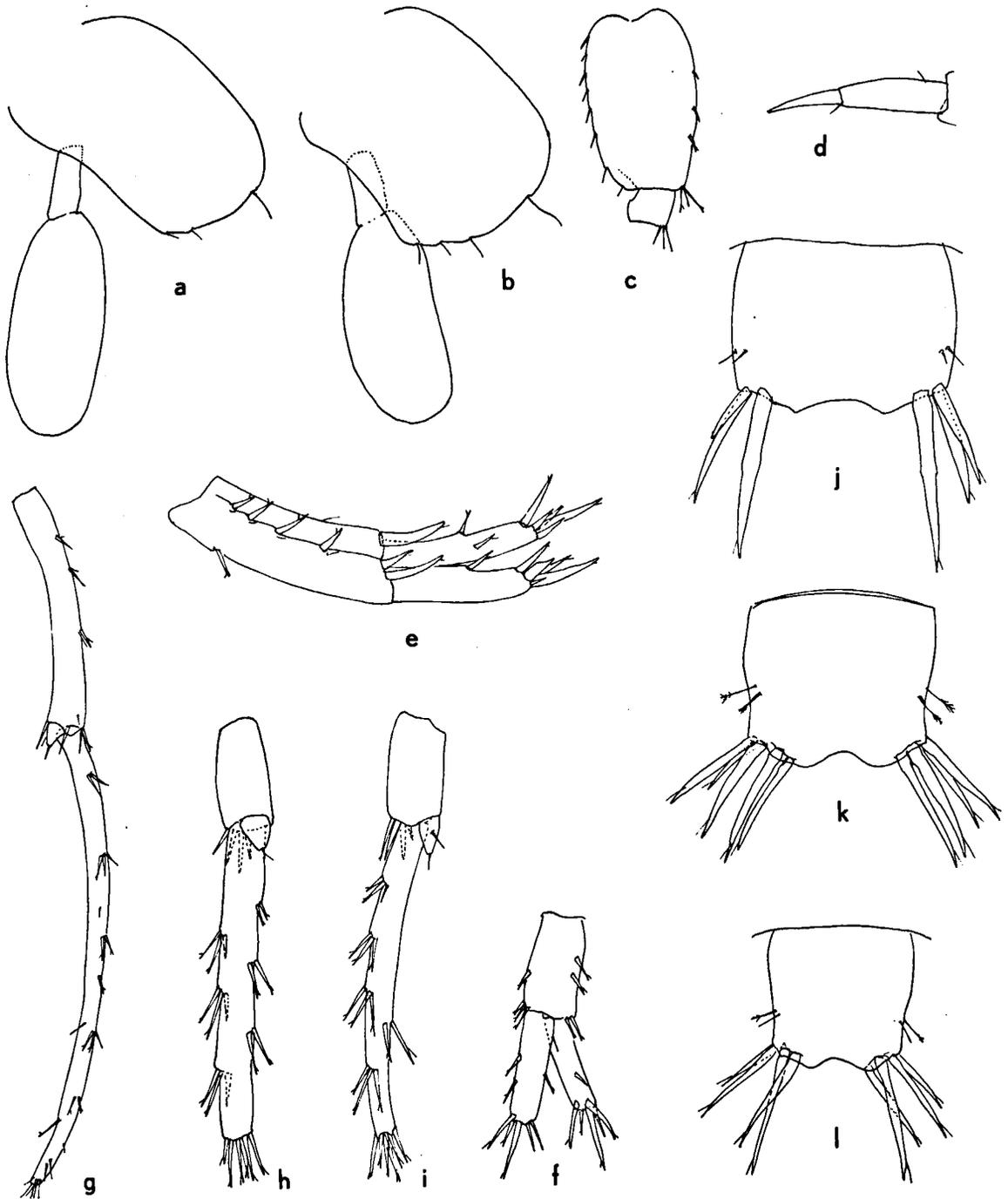


Fig. 28. *Pseudoniphargus branchiatus* n. sp. (a, b, d, e, f, h, i, j from Cullera, Spain; c, g, k, l from Benaolan, Spain): a, coxal plate and coxal gill of third pereiopod, ♀ (scale A); b, same of fourth pereiopod, ♀ (A); c, basis of fifth pereiopod, ♂ (F); d, dactylus of seventh pereiopod, ♀ (D); e, first uropod, ♀ (A); f, second uropod, ♀ (A); g, third uropod, ♂ (F); h, i, third uropod, ♀ (A); j, telson, ♀ (B); k, telson, ♀ (D); l, telson, ♂ (D).

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