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Part A

*Mechanisms, patterns and deep history*
Ingolfiellidea (Crustacea, Malacostraca, Amphipoda): a phylogenetic and biogeographic analysis.

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Abstract

The suborder Ingolfiellidea currently consists of 39 named species. An historical overview is presented and phylogenetic and biogeographic analyses are made. The result of the phylogenetic analysis suggests the definition of two new genera within an African freshwater group, namely Paraleleupia n. gen. and Proleleupia n. gen. Re-examination of the Italian relict species, Metaingolfiella mirabilis, with the aid of SEM techniques reveals a half-fusion of the head region with the first pereionite. The issue of the function of the 'eyelobe' is addressed and an explanation presented after examining with SEM such lobes in different species. Furthermore, additional descriptions are given based on the type-material of Metaingolfiella mirabilis, Trogloleleupia eggerti, Trogloleleupia leleupi, Ingolfiella littoralis, I. tabularis, I. margaritae, I. quadridentata, and I. abyssi. An attempt to relate the geographic distribution and ecological characteristics to the phylogeny of the Ingolfiellidea results in a paleogeographic scenario that points to a freshwater subterranean origin for the group that dates from at least Triassic times.

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Introduction

The ingolfiellidean amphipods are not abundant in regards to the number of species. To date, some 39 species are recognized, a remarkably low number considering the wide-ranging ecological conditions in
which they occur. It is also a low number when compared to other family groups of amphipods with partly overlapping habitat requirements such as bogidiellids, with 110 species (Koenemann & Holsinger, 1999) and crangonyctids (250 species, pers. comm. Koenemann).

The first species of Ingolfiellidae were reported by Hansen in 1903. He classified them in a new suborder, a rank they have continued to hold in most publications (Bousfield & Shih, 1994; Ruffo & Vigna Taglianti, 1989; Martin & Davis, 2001) despite several objections over the years (Dahl, 1977; Bowman & Abele, 1982; Barnard & Karaman, 1983). It is a challenge to compare this small group of crustaceans to other larger well-defined groups and try to find comparable habitat preferences and overlapping biogeographic distribution patterns. From consideration of the literature a picture emerges of the uniqueness of ingolfiellids within the entire crustacean world with regard to their incredibly diverse habitat tolerances. No other small taxon of crustaceans is found in the soft mud of the deep sea floor, as well as in high mountain freshwater river beds, or in subterranean fresh, brackish and marine interstitial waters of continental ground waters and continental shelves (Fig. 1, map).

The study of the first species of Ingolfiella marked this habitat diversity. Hansen (1903) described two species, Ingolfiella abyssi, from 3521 m. deep sea bottom out of a trawl of 1 litre of mud in the Davis Strait, east of Greenland, and I. littoralis, from coral sands on the shores of Thailand. Several years later another species, I. acherontis (S. Karaman, 1933), was described from a ground water well in Skopje, Macedonia. The material of I. acherontis has been lost and only a few incomplete drawings remain. S. Karaman apparently was not aware of the work by Hansen, 1903. Therefore he described Balcanella acherontis n. gen. n. sp. in a new family Balcanellidae.

After the Second World War expeditions focused more on environments that were difficult to access, and the majority of species of ingolfiellids were collected in the last half of the twentieth century. A large species was found in cave-waters from Congo, later ranked in a separate genus: Trogloleleupia leleupi (Ruffo, 1951). Compared to the 2.5 mm specimens for previous taxa this African cave lake species stood out at 14.5 mm maximum length.

Then more species were discovered in Macedonia: Ingolfiella petkovskii S. Karaman, 1957, and I. macedonica S. Karaman, 1959. S. Karaman characterized their rarity when he stated that he had searched through several thousand samples from ground water and wells. He concluded that Ingolfiella is either very rare or lives in inaccessible biotopes (S. Karaman, 1959).

Meanwhile, another species was found in South America in a new habitat, the coastal groundwater in a coarse shingle beach. In the description of I. ruffoi Siewing, 1958, Siewing posed a dilemma particularly relevant to the work underlying this publication. He asked whether the large African cave form was ancestral to the smaller marine and freshwater forms, or if it was the other way around.

Another type of habitat was added to the list with the collection of 20 specimens of I. britannica Spooner, 1960, from the shell gravel at the sea bottom at 46 meter depth off the south coast of England. Spooner remarked on the true deep subsurface occurrence of these ingolfiellids in contrast with other small malacostracans that more typically inhabit only the first few centimeters of these gravels.

Euryhaline tolerance was revealed within one species with the discovery of I. mannii Noodt, 1961, taken from both brackish and fresh groundwater in Chile. In addition, I. mannii was found not only at sea level, but also at 800 m. Later I. uspallatae Noodt, 1965 was described from Argentina in the riverbanks of a floodplain at 2000 m in the Andes mountains.

In Europe at this time, two freshwater species were reported from the interstices of river alluvia of southern France: I. catalanensis Coineau, 1963 and I. thibaudi Coineau, 1968. This marked the discovery of more species where special subsurface habitats were sampled in a conscious effort to uncover new taxa. A large 2.3 cm ingolfiellid was found in a well in Namibia, first described as Leleupiella eggerti, Ruffo, 1964, later renamed by Ruffo (1974a) as Trogloleleupia eggerti.

From the Indian Ocean I. xarifae Ruffo, 1966 and I. kapuri Coineau & Rao, 1973 were reported from the Maldives in shallow coral sands, and from the Andaman and Nicobar Islands in intertidal muddy shell debris, respectively.

A second deep-sea species, I. atlantisi Mills, 1967, was collected at more than 4700 m depth in the North American Basin of the Atlantic Ocean. This species probably occupies the same habitat as I. abyssi and was found amidst typical abyssal fauna elements, presumably residing "...in the flocculent and relatively oxidized upper centimeters or two on the surface of the deep sea ooze." (Mills, 1967).

Back in Europe, an environment equally difficult to access as the deep sea was tapped, namely the ‘fossil water’ of a 50 m deep well in Italy. Here the aberrant Metaingolfiella mirabilis Ruffo, 1969
Fig. 1. World map of distribution of Ingrolfiellidea. Black dots = marine localities. Open stars = brackish water conditions. Open circles = fresh water localities.
was described, for which a new family was necessary, the Metaingolfiellidae. Later efforts to recapture this rare species were never successful (pers. comm. Ruffo). Not surprisingly, the area south and east of Yugoslavia has yielded more specimens of *I. petkovskii* and the new species *I. vandeli* Bou, 1970. They were reported from wells and river sediments on the Greek mainland and the large islands of the Peloponnesus and Euboea.

Another discovery occurred in the littoral sands of Table Bay, Cape Town: *I. berrisfordi* Ruffo, 1974. From the same environment, but a little deeper at 8 m below surface in the Gulf of Naples, Italy, Schiecke (1976) described *I. ischitana*. Stock named 6 species from islands off the coast of Venezuela. These species are: *I. (Gevgeliella) putealis* Stock, 1976, in a slightly brackish well on Bonaire (Dutch Antilles); *I. (Gevgeliella) fontinalis* Stock, 1977, from a spring on Bonaire; *I. (Gevgeliella) tabularis* Stock, 1977, from marine sands situated below a cave entrance on Bonaire (also recorded on Curacao); *I. (Hansenliella?) quadridentata* Stock, 1979, from coarse coral sand of a submarine flat, Curacao; *I. (Trianguliella?) grandispina* Stock, 1979, pumped from brackish ground water in gravel at a cave entrance; *I. (Gevgeliella) margaritae* Stock, 1979, from a capped freshwater well used for drinking water on Isla de Margarita (Venezuela). These southern Caribbean species were sampled either by diving in shallow coastal water, or pumped up from beach interstitia and oligohaline water reservoirs more inland. In addition, animals occurred in wells and small cave chambers with brackish water or water with frequently and strongly fluctuating salinities.

Stock utilized subgeneric names, but the splitting of the genus *Ingolfiella* into smaller units had already begun with that earlier discovery of *Ingolfiella* (*Balcanella*) *acheronitis* Karaman, 1933. Nevertheless, Karaman’s original effort did not prove very useful due to subsequent workers’ lack of male or female specimens in cases where both sexes were needed to make critical distinctions. Consequently, new species were difficult to incorporate into the existing system.

Ruffo (1985) described another large ingolfiellid from Namibia’s freshwater reservoirs, *Stygobarnardia caprellinoides*. The most striking aspect of this animal was the resemblance of the form of the cephalon to that of the Italian *Metaingolfiella*. In *Metaingolfiella* the fusion of the first segment (perionite) with the cephalon was described as fully complete (although we have discovered after SEM investigation that this appears not to be the case), while in *Stygobarnardia* the head form with a typically small cephalon could be interpreted as in a partial stage of the fusion.

One of the larger Canary Islands facing the coast of West Africa, Fuerteventura, yielded *Ingolfiella similis* Rondé-Broekhuizen & Stock, 1987, from an oligohaline freshwater well. *Ingolfiella fuscina* Dojiri & Sieg, 1987, was found in the Gulf of Mexico and off the coast of South Carolina in box core and grab samples ranging in depth from 17 – 151 m. This was the first time a species from the bottom of the sea was reported over a large area. On Bermuda, *I. longipes* Stock, Sket & Illiffe, 1987 was collected in a brackish water cave pool. More large ingolfiellids came from Namibia: *Trogloleleupia dracospiritus* Griffiths, 1989 and *T. gobabis* Griffiths, 1989, were found in cave lakes, 350 km apart from each other.

The Southwest Pacific yielded no ingolfiellids until Lowry & Poore (1989) described *I. australiana* and *I. bassiana* from the Bass Strait at, respectively, 85 m depth in sandy shell, and 121 m at another locality in the strait. A cave on a small offshore island of Sardinia, Italy, brought to light *I. cottarelli* Ruffo & Vigna-Taglianti, 1989 from a freshwater pool. The most recent of the large, cave dwelling, African ingolfiellids is *Trogloleleupia nudicarpus* Griffiths, 1991 from subterranean waters in western Namibia. It was found crawling on stones in shallow water in a small pool 60 m below ground surface.

*I. canariensis* Vonk & Sánchez, 1991, was collected with a Bou-Rouch bioporeptic pump on several beaches along the north coast of Tenerife, Canary Islands, and in bottom debris of an anchialine cave on El Hierro, another island in the geologically younger part of the Canary group. From the island of Madeira, some 700 km to the north, *I. unguiculata* Stock, 1992 occurs in the coarse sand bottom of an anchialine lagoon. In Slovenia, *I. beatriceis* Ruffo & Vonk, 2001 was described from a single specimen caught in a feeble flowing cave stream with a hand net.

Of course, more species will be discovered, and we must wait to see how far the ecological tolerance and biogeographical spread of this group of amphipods can be stretched. Already there are reports of discoveries in fresh- and brackish water of Japan (Shokita, 1992) and in marine sediments of the Prince William Sound, Alaska, and the Virgin Islands, Caribbean (Cadien, pers. comm.) that are yet to be confirmed.
From the above it is clear that almost all previous work on the Ingolfiellidea has concentrated on alpha-taxonomy. To remedy this situation we undertook the following:

a. Performed a cladistic analysis of phylogenetic relationships within the Ingolfiellidea based on a comprehensive character matrix.
b. Restudied of type material of *Metaingolfiella mirabilis*, *Trogloleleupia eggerti*, *T. leleupi*, *Ingolfiella abyssi*, *I. littoralis*, *I. tabularis*, *I. quadridentata*, and *I. margaritae* to add more details to former descriptions.
c. Compared the cephalic lobes of *Ingolfiella putealis* and *I. ischitana*, using SEM photography, to lend insight into the structural and functional role this structure plays.
d. Re-examined the type material of *Metaingolfiella mirabilis* to determine the degree of fusion between the head and the first pereionite.
e. Performed a biogeographic analysis with the results of the cladistic analysis and explored palaeobiogeographic patterns and the timing of evolutionary events in the deep history of ingolfiellideans.

Methods and material

We employed 43 characters to analyze patterns of relationships throughout the Ingolfiellidea. Some 30 characters are multistate, while 13 features are binary. Following here is a list of the characters employed and an explanation of the several alternative states we have used in constructing a matrix (Table I). Given the 'reduced', worm-like body plan of these animals our 43 characters essentially covered all aspects of the recognizable anatomy, so there has been no undo emphasis of one aspect of morphology over another. The characters we used are as follows.

**Character descriptions**

1. Ocular (cephalic) lobes
   state 0 = developed
   state 1 = reduced
   state 2 = absent
   In one of the out-group taxa chosen, *Mictocaris halope*, this character is termed the eyestalk. Its location is not between antenna 1 and antenna 2 on the front margin of the cephalon, as in the Ingolfiellidea, but is rather located a little higher, flanking the peduncle of antenna 1. Still we consider this possible remnant of a stalk in *Mictocaris* as an homologous feature with the typical ingolfiellidean cephalic lobe, simply because no other function can be ascribed with certainty to this lobe at the moment. Lowry and Poore (1989) observed that three peracaridan orders have representatives with eyestalks or remnants of stalks, i.e. the mysidaceans, the spelaeogriphaceans, and the mictaceans. However, they conclude that the typical position of the reduced stalks, which are often in the form of scales or pointed lobes, lies at the base of the first antenna and at the rostrum. This is different from that seen in the Ingolfiellidea, where, as noted, the lobes reside between the first and second antennae. Therefore, they do not regard these features as homologous and thus not of subordinal importance.
   However, spelaeogriphaceans and mictaceans do not have the lateral compressed head of ingolfiellideans (and of most amphipods) and the position of the lobes could easily have shifted ventrally when that would be the case. We have made SEM photographs of two ingolfiellid species, *Ingolfiella ischitana* (Fig. 2a) and *I. putealis* (Fig. 3a,b), in which the difference between the developed state of the lobe in the former (Fig. 2, b-e) and the reduced state (Fig. 3, a-c, e, f) in the latter is clearly visible. In both cases, there is a neat fit of this lobe between the bases of the first and second antennae, and this suggests that the original function (eye-stalk) has been replaced by a new function. The lobes close off the otherwise open space between the antennae to mud particles. Thus the appressed lobes and the rostrum form a tight seal around the protruding antennal peduncles, preventing fine granular material from fouling the head region.

2. Antenna 1, flagellum
| Character Matrix | (1-43) | Characters used in a parsimony analysis in PAUP 4.0 b10 (Altivec). Multiple scores in one cell refer to multiple states present in one character. |
state 0 = longer than basal peduncular segment
state 1 = medium length, more than half of basal peduncular segment
state 2 = short, less than half of basal peduncular segment

The low number of segments (4) on the antennal flagellum is a consistent character throughout the Ingolfiellidae and as such not informative towards distinguishing between species or species groups within the family. However, the length of the flagellum as a whole does vary in a few cases, and the differences were scored. Out-groups have more segments, as is common in most peracaridans, and thus bear a relatively long antennal flagellum (state 0). Absolute measurements of the flagellum depend on the size of the individual. With a ratio character like this it is often difficult to divide continuous distributions into integral states. Still an effort is made to distinguish between longer and shorter antennae as our goal was to score as much character differentiation as possible.

3. Antenna 1, accessory flagellum
state 0 = four segments
state 1 = three segments
state 2 = two segments

The accessory flagellum is positioned on the inner side of the flagellum (Fig. 3d, 5k, 7c) and could be called the “inner” flagellum, if we want to keep the terminology that would be comparable to early, fossil finds of diverse crustaceans. The positional homology is important here for in Mictocaris the outer flagellum has eight segments and the inner has four segments. We might ask if the accessory flagellum in amphipods is comparable to the outer or inner flagellum of Mictocaris?

“The primitive biramous origin is retained in the form of a small accessory flagellum that arises from the end of the peduncle,” (Lincoln, 1979, p.16). In Mictocaris, the eight-segmented “outer” flagellum bears the aesthetascs, which would suggest the four-segmented “inner” flagellum, which lacks aesthetascs, is equivalent to the accessory flagella in amphipods, also lacking aesthetascs.

4. Mandibular palp
state 0 = present
state 1 = vestigial
state 2 = absent

The mandibular palp is lacking in the Ingolfiellidea. This implies that the palp is not necessary towards either securing and moving larger food particles to the mouth and the molars, or in cleaning and grooming, as is typically the case for the larger palps seen in malacostracan crustaceans. Fine food particles make up the diet in this line of reasoning. One genus in the Ingolfiellidae, Stygobarnardia Ruffo 1985, possesses a rudiment of the mandibular palp and is scored as vestigial (1).

This reduction and/or complete loss of a mandibular palp occurred in many groups of crustaceans (Richter and Scholtz, 2001) and shows a great variability within families and genera of Amphipoda. For instance, a mandibular palp may be present or absent within the Amphithoidae and Hadziidae, or it may vary in length as in Metacrangonyx. Even so, this phylogenetically uninformative character is retained here to emphasize the special situation in Stygobarnardia and to be available for use with possible finds of new taxa.

5. Molar process size
state 0 = well-developed lobe
state 1 = vestigial peg or spine
All Ingolfiellidea share the reduced state (Figs. 5c, 6l, n, arrows). In combination with the absence of mandibular palps, this feature perhaps points to a lack of need for structures to chew up large particles of food.

6. Maxilla 1, inner lobe setae (Figs. 5a, 6j, m)
state 0 = numerous
state 1 = four or more
state 2 = three
state 3 = two
Fig. 2. Ingolfiella ischitana, paratype. SEM photographs of: a, habitus; b – c, lateral view of a well developed cephalic frontal margin lobe; d – e, lobe seen from outside and inside (removal of first antenna), cuticular "hinge" visible (e, right arrow).
Fig. 3. *Ingolfiella putealis*, paratype. SEM photographs of: a – c, e,f, views from different angles on a small cephalic lobe. Photo c reflects best the possible ‘closing off’ function of the lobe, a similar fit is made by the tiny rostrum (d).
state 4 = one
state 5 = none

This character is constant within those taxa wherein populations were used for species descriptions, thus it seems significant at least for differentiation of species. This feature is often mentioned only in the ‘remarks’ section of species descriptions as one that differs between species. The condition in which the lobe is fringed with numerous hairs seems to point to an original state. Decidedly more generalized forms, such as Euphausiacea, have many setae on the inner lobe of the maxillule (Maas & Waloszek, 2001)

7. Maxilla 1 outer lobe, inner seta (Figs. 5a, 6j, m)
   state 0 = simple
   state 1 = bifid
   state 2 = dentate

   When comparing the tips of the robust apical setae on the distal margin of the outer lobe of maxilla 1, clear differences were noticed between several species. In most species the inner seta stands apart from the others and is implanted on the lateral/submarginal, inner side of the plate. Often it is clearly dentate with a little comb, at other times it is simple.

8. Maxilla 1 outer lobe, outer setae (Figs. 5a, 6j, m)
   state 0 = simple
   state 1 = bifid
   state 2 = dentate

   “Simple” setae are smooth, spiniform setae without hooks. In case more states are present, a multistate score is used (0/1 or 0/1/2). Comparison with the out-group Mictocaris halope seems to indicate that an earlier condition might have resembled an undifferentiated tuft of soft setae (Bowman & Iliffe, 1985)

9. Maxilla 1, outer lobe, setae orientation
   state 0 = continuous row
   state 1 = 7 + additional inner seta
   state 2 = 7
   state 3 = 6 + additional inner seta
   state 4 = 6 (Fig. 5a)
   state 5 = 5

   The setae on the distal margin of the outer plate of the maxilla 1 can differ in number. The additional seta often sits a little sideways on the inner margin of the lobe. We have no preconceived notion as to what might be the derived situation. We suspect, however, that the most reduced situation (5 setae) reflects the derived state here.

10. Maxilla 1, palp size
    state 0 = larger than outer lobe
    state 1 = subequal to outer lobe
    state 2 = smaller than outer lobe

    The need for elaborate handling of larger food items may require a long palp (0) as opposed to a short palp (2). Assumption of the interstitial mode of life, generally supposed to be a secondary habitat choice in the evolution of Amphipoda, may have induced the loss of importance for a maxillular palp.

11. Maxilla 1, palp setae
    state 0 = four setae or more
    state 1 = three (Fig. 6j, m)
    state 2 = two
    state 3 = one
    state 4 = absent

    The number of palp setae is a constant feature in those cases where larger numbers of individual specimens of a species were studied by us. Therefore, it is a useful diagnostic character. A decrease in the number of these setae is noted for what is seen in the out-group taxa.
12. Maxilla 2, setae number outer lobe
state 0 = large complex limb with many setae
state 1 = five setae, or more
state 2 = four setae (Fig. 6k)
state 3 = three setae
state 4 = two setae
The maxilla 2 is a greatly reduced limb with little, aside from setal number, to distinguish variation.

13. Maxilliped basis
state 0 = free and separate
state 1 = fused base proximally
Free and separate bases of the maxilliped suggests a condition close to the plesiomorph situation, e.g., (0) where the maxillipeds are a pair of thoracic walking limbs. The basis is free and separate in mictaceans and in *Metaingolfiella* (Ruffo, 1968, fig II, 3)

14. Maxilliped lobes
state 0 = with basal lobe only
state 1 = with basal and ischiial lobes
Ischiial lobes on the maxilliped are lacking in Ingolfiellidae and in Mictacea (0). Other members of the out-groups we employed, the bogidiellids and the pseudoingolfiellids, do have ischiial lobes (1). So this character adds no information to in-group polarization of character states. It merely shows the convergent development of pseudoingolfiellids as compared to Ingolfiellidae.

15. Maxilliped, medial palp setation
state 0 = numerous
state 1 = 1 or 2 per segment
Only *Metaingolfiella* and the other members of the out-group share the primitive state wherein the setation displays the 'numerous' condition (0). The Ingolfiellidae all share the derived condition of a reduction to 1 or 2 setae per palp segment (1).

16. Maxilliped, lateral propodal setae
state 0 = present
state 1 = absent
The presence of this row of setae is recorded in only a few instances.

17. Maxilliped, dactyl claw
state 0 = absent
state 1 = single setae
state 2 = robust spine
state 3 = spine with flanking setae
state 4 = falcate (Fig. 5e)
There is considerable variety in the form and number of setae on the apex of the maxilliped palp. No apparent difference in function can be ascribed to forms with one or more spines at the apex. One might be tempted to speculate that blunt and strong spines may assist in heavy food particle holding. However, without functional studies of live material such speculations are of only anecdotal interest.

18. Second thoracic segment (= first pereionite)
state 0 = free
state 1 = fused to cephalon
The situation in the family *Metaingolfiellidae* is different from that seen in all other species in the Ingolfiellidae and in the chosen members of the out-groups. Although the half-fusion of the cephalon is an autapomorphy and thus phylogenetically uninformative in this analysis, this character cannot be ignored and deserves a place in the matrix to emphasise its peculiarity. Another type of partial fusion of the cephalon and first pereionite can be observed in *Caprogrammarus gurjanovae* Kudrjaschov &
Vassilenko, 1966 (in Takeuchi & Ishimaru, 1991). This particular member of the suborder Caprellidea also exhibits a partial fusion of the cephalon and first pereionite but on the ventral side of the segment, while in Metaingolfiella the fusion starts from the dorsal side (Figs. 4a-e). However, the position of the suture is similar in the two genera, and corresponds with the position of first gnathopods, which are shifted anteriorly from their more typical location more posteriorly.

19. Pereional segments
state 0 = deeper than long
state 1 = subrectangular
state 2 = elongate
This character serves to capture the overall body habitus (Fig. 2a). This may be an important feature in regard to the habitat requirements. Life in finer sand interstices calls for a "worm-like" appearance.

20. Coxal plates
state 0 = not developed, or weakly so
state 1 = robust
Part of the out-group, but not Mictocaris, exhibits the robust development of the coxal plates (1) more typical of amphipods as a whole. It is a unique character of the Ingolfiellidea that the coxal plates are rudimentary (0). For the Ingolfiellidea as such it is an uninformative state. Coxal plates may have arisen separately on different occasions. For instance, they are present in both amphipods and isopods but form in this case one of the few specific characters common to both groups (Siewing, 1963: p.96)

21. Lenticular organs
state 0 = absent
state 1 = incipient
state 2 = well developed
This is a feature encountered, within Ingolfiellidea, only in species of the African trogloleleupians. The lenticular organs are distinctive, semi-transparent, "windows" of cuticle on the side of the segments of the pereion and pleon (Griffiths, 1989). Their function is unknown. They resemble in some respects the foramen ovale, a similar transparent area of cuticle on the heads of the syncarid genus Allanaspides — another meiofaunal crustacean. In Pseudoingolfiella there is mention of "hyaline spots" but in a different location. Noodt (1959, p. 203) remarks on Pseudoingolfiella chilensis: "todos los segmentos toracicos libres poseen entre la insercion de las extremidades un punto circular hialino bien delimitado de funcion desconocida".

22. Gnathopods
state 0 = simple limb
state 1 = subchelate
state 2 = carpo-subchelate
Since all ingolfiellideans have the carpo-subchelate state (2) this character gives no information of generic or specific relationships within the suborder. The feature is not unique either because, as is remarked by Lowry & Poore (1989), it is also seen in relatively unrelated groups such as the the Pardaliscidae, Aoridae, Corophiidae, Leucothoidae, and the Hyperiidea. Ischyroceridae have also carpochelate second gnathopods (Lowry & Springthorpe, 2001) Nevertheless, this feature is scored here because the out-group does show states 0 and 1.

23. Gnathopod 1, dactyl
state 0 = no gnathopod
state 1 = simple
state 2 = serrate
state 3 = blade-like
state 4 = spines
The simple state is reflected in a smooth posterior margin of the dactylus. This is encountered in Metaingolfiella and Stygobarnardia but also in Ingolfiella littoralis (Fig. 6a). The serrate state (Fig. 7a) is exemplified by I. abyssi. Blade-like forms are observed in two species of Trogloleleupia and in
Fig. 4. Metaingolfiella mirabilis, paratype. SEM photographs of: a – e, views from different angles on the partially fused head region (arrows); f, cephalic lobe; g, ramus of third pleopod; h, dactylus of first gnathopod (tip form artefactually distorted). Ceph = cephalic segments (cephalon and first thoracic somite with maxilliped attached). Segm 1 = first body segment with first pereiopod attached.
Ingolfiella britannica. Here the spines on the posterior margin are broad and flattened or, another way of interpreting, the serrated margin has become more widely interspaced. An intermediate form of this is shown in Fig. 5h, on the gnathopod 2 of Trogloleleupia leleupi. When the serrations are broad in contrast to the space between, these would be interpreted as blades. The fourth state, spines, is scored for species with clearly distinguishable rounded spines protruding from the margin.

24. Gnathopod 2 carpus, palmar angle spines
state 0 = unspecialized
state 1 = with elongate spine, not angulate
state 2 = pedicillate
state 3 = protruding angulate process, with spine

The palmar angle spines are often used in amphipod taxonomy as an important character in helping determining differences between species within one genus. These spines are often quite robust and placed at the end of where the tip of the dactylus reaches the inner margin of the propodus/carpus. In some cases the palm makes an angle here as in Trogloleleupia leleupi (state 3, angulate, Fig. 5h). When this seta is placed on a small distinct pedestal we call this pedicillate (state 2, not illustrated). In the case of a straight palmar margin line and a relatively long seta this is scored elongate (state 1, Fig. 6b), and in the unspecialized state (0) the spine is relatively short (Fig. 7b) or not present.

25. Gnathopod 2, carpal saw
state 0 = absent
state 1 = serrate (Fig. 6b)
state 2 = dulled (Fig. 5h)
state 3 = setose brush
state 4 = finely serrate

We found this feature to be very consistent in a sizeable population example in at least one population of Ingolfiella canariensis. We examined more than 50 individuals collected from beach interstitia on the Canary Islands, and all specimens exhibited the serrate state (1) (Vonk & Sánchez, 1991).

26. Gnathopod 2, distal propodus form
state 0 = unmodified
state 1 = tooth-like
state 2 = finger-like
state 3 = blade-like

The propodus in Ingolfiella is typically smaller than the carpus and is positioned at a place where normally the dactylus is attached, i.e., just distal to the sub-flexure. This article displays a spur-like process at its distal end that varies in form from pointed, to blunt, to blade-like, to unmodified. The propodus in Ingolfiella littoralis shows the unmodified state (Fig. 6b, arrow), Trogloleleupia leleupi has the finger-like condition (Fig. 5h, arrow) and Ingolfiella abyssi the tooth-like (Fig. 7b, arrow).

27. Gnathopod 2, dactyl teeth
0 = absent
1 = 3 teeth (Fig. 6b)
2 = 3 blades (Fig. 5h)
3 = 4 teeth
4 = 4 blades (Fig. 7b)

We observed differences in the form of the teeth lining the inner margin of the dactyl of the gnathopods. These thorn-like structures probably help in securing prey and/or mates, or to strengthen the grip when the claspers are used to pull the animal forward. In some species, these teeth are broad and formed into blades. In other species, these structures are more rounded and form tooth-like outgrowths of the cuticle. The number of the structures varies and is also incorporated as a character state.

28. Gnathopod 2, dactyl tip
0 = simple (thin moderate)
Fig. 5. *Trogloeleupia eggerti*, male 2.6 mm: a, maxilla 1, left side (scale B); b, maxilla 2 (B); c, left mandible (A); d, right mandible (A); e, apex of maxilliped (B); f, female 2.3 mm, pleopod 1 (B). g, *T. leleupi* male, 8.5 mm: gnathopod 2 (B); h, male 12 mm, gnathopod 2 (B); i, pleopod 1 (B); j, female 7 mm, pleopod 1 (B); k, male 12 mm, antenna 1 with accessory flagellum and aesthetasc (B); l, specimen of unknown sex, from a broken pleon, urosome with exceptionally long uropod 3; m, female, 7 mm, aberrant gnathopod 2 dactylus with 2 teeth instead of 3 (C); mp = molar peg; il = inner lobe; ol = outer lobe, pas = palmar angle seta.
1 = simple and thick  
2 = long and thin  
3 = long and thick  

The tip of the dactyl could be perceived as a combination of a proximal "dactylar" part and the distal "lingular" part, although a suture is not easily observed. Some species, like *Ingolfiella canariensis* and *I. similis*, have a visible division (Fig. 7b); other species do not. The length and thickness of this tip is variable and can be scored.

29. Gnathopod 2, size  
0 = subequal to P3  
1 = larger  
2 = smaller  

The second gnathopod is a powerful tool for an ingolfiellid. It is more robust than the first gnathopod, which has a carpus that is often less broad and more pointed (Figs. 7a, b; 8a, b). The size of the second gnathopod relative to the third pereiopod is measured by summing the lengths of the five podomeres of both appendages.

30. Gnathopod 2, palm  
0 = transverse  
1 = oblique  

The form of the carpus is either robustly triangular with a short palmar margin, "transversely" cut when seen from the side, as in *I. littoralis* (Fig. 6b), or elongate with a faint sloping, oblique palmar side as in *I. abyssi* (Fig. 7b).

31. Pereiopods 3 and 4, claw  
0 = absent  
1 = simple  
2 = dentate or bifid  

Spiny structures on the termini of the third and fourth pereiopod may be used for better grip. Most species in *Ingolfiella* have the dentate or bifid state (Fig. 7d), and only a few possess a simple spine. All species in *Trogloleleupia*, the large African cave species, have the simple state.

32. Pereiopods 3 to 7, dactyl form  
0 = similar  
1 = dissimilar  

A common feature in gammaridean amphipods involves the different positioning of the third and fourth pereiopod in relation to other pereiopods, e.g., the fifth, the sixth, and the seventh. Pereiopods 1 to 4 form an 'embryological unit' (Dahl, 1977), or, as we would interpret, a functional/morphological unit. However, the form of the dactylus also can differ between those of P3 and P4 on one hand, and those of P5-P7 on the other. For instance in *I. littoralis* the forms of the dactylus on P3 and P4 (Fig. 6c, d) are dissimilar (state 1) from P5 (Fig. 6e).

33. Pereiopods 5-7, dactyl  
0 = with claw  
1 = without claw  

The dactylus has a separate claw in for instance *Ingolfiella abyssi* (Fig. 7. d-g). Other species, like *I. littoralis* (Fig. 6e) lack such a claw.

34. Pereiopods 3-7, dactyl ends or termini  
0 = not produced  
1 = with spur (Fig. 6c)  
2 = with seta (Fig. 7d)  

This character involves an added bit of decoration to the distal aspect of the dactyli. The spur is a robust spike-like process and is opposed to a more flexible setose extension.
35. Pleopods 1 - 3, female
0 = present
1 = absent
There is a trend in ingolfiellids toward reducing the pleopods to a minimum number. The absence of all the pleopods would be the ultimate condition in this regard. The problem with assessing this feature adequately is that we do not always have sufficient samples of both sexes for some species of ingolfiellids. In males, the first pleopods always seem to be present.

36. Pleopod form
0 = biramous
1 = uniramous, narrow (Fig. 5i)
2 = uniramous, short fin
3 = uniramous, long fin (Fig. 5f)
Reductions of various sorts can be observed throughout the family Ingolfiellidae. Truly interstitial life of a certain mode might induce short appendages on the rear, or pleonal, end of a wriggling body that moves in a worm-like fashion. In this vein, the oceanic mud dwelling species and the terrestrial cave pool species would tend to have longer pleopods than the beach and riverine taxa that occupy open interstitial spaces between sand grains.

37. Uropod 1, rami
0 = free
1 = fused at peduncle
In Metaingolfiella, the aberrant species from a deep well in Italy, the rami are fused at the peduncle (1) In all other species in this analysis, the rami are free (0). This character provides no information to the phylogeny but is maintained to stress the peculiar situation in Metaingolfiella.

38. Uropod 1 and 2, size comparison
0 = uropods 1 and 2 not present
1 = subequal
2 = u2 larger than u1
3 = u1 larger than u2
This character measures the size of the first and second uropods relative to each other. No clear pattern emerges and although we consider these types of characters susceptible to allometric change, there is no alternative in dealing with these appendages. Age and molt stage might perhaps influence the relative size of the rami, but it is impossible to effectively take this into account. Our reasoning to include this feature here is that if there is a clear pattern, then we take the risk that it is due to coincidence; and if there is no pattern, then nothing is lost.

39. Uropod 1 and 2, total length
0 = no such uropods present
1 = long
2 = short
See comments vis-à-vis character 38.

40. Uropod 1, inner versus outer ramus length
0 = equal length
1 = outer ramus more than half of inner ramus length
2 = outer ramus less than half of inner ramus length
The variation in length of both rami of uropod 1 is not readily explained. No obvious function can be ascribed to this difference. It is possible that the outer ramus, which is in line with the underside of the body, should be longer to protect the inner ramus and the urosome from damage or to interact actively with other appendages (as was observed by Spooner, 1961, in grooming).

41. Uropod 3
0 = biramous
Fig. 6. *Ingolfiella littoralis*, holotype: a, gnathopod 1 (scale D); b, gnathopod 2 (D); c, pereiopod 3 (D); d, pereiopod 4 (D); e, pereiopod 5 (D); f, uropod 2 (D); g, *I. tabularis*, female 2.1 mm, mandible (A); h, male 1.9 mm, mandible (A); i, female 2.1 mm, mandible (A); j, maxilla 1 (A); k, male 1.9 mm, maxilla 2 (A); l, *I. quadridentata*, female, paratype, mandible (A); m, maxilla 1 (A); n, *I. margaritae*, male holotype, mandible (A); mp = molar peg; il = inner lobe; ol = outer lobe, pas = palmar angle seta; da = dactylius; cs = cup shaped spine.
This character involves in *Pseudoingolfiella*, a member of the out-group but with a uniramous third uropod (1) and emphasises the most interesting role of such intermediate taxa.

42. Uropod 3 fusion

0 = right and left unfused
1 = fused peduncle

Only in *Metaingolfiella* are the peduncles fused to each other. The tendency towards fusing of elements in this species is three-fold now, given also the fusions already noted in the head and the rami of uropod 1. Tendency in this species seems to be towards fusion of adjacent elements into large units.

43. Telson form (Fig. 51)

0 = well developed
1 = medium, fleshy
2 = short, flat
3 = short, fleshy
4 = short, bifurcate

A sturdy, well-developed telson is considered plesiomorphic with reference to the Amphipoda (Barnard & Karaman, 1983).

The following characters were also examined. They were not used in our final cladistic analysis, however, because there were too many question marks concerning them in the matrix. They all involve sexual differentiation, and because of the rarity of most ingolfiellideans it is not always possible to have adequate sample sizes that contain both sexes. We list them here, nevertheless, because at some point in the future, with better collections, it may become feasible to assess these features in a phylogenetic context across all species.

a. Gnathopod 2 male, reverse element on carpus

0 = absent
1 = present

At the end of the palmar margin, in the region of the large palmar setae delimiting the palm, an outgrowth of irregular cuticular tissue often appears in older males (Fig. 6h)

b. Uropod 2 male, baso-facial spine

0 = absent
1 = present

In some species, a conspicuous, often somewhat hooked, spine is present on the basal part of the peduncle in the male. In other species, this is absent, no intermediate situation has been reported.

c. Ööstegites

0 = present
1 = absent

Out of twenty species in *Ingolfiella*, only ten could be scored with ööstegites or brood plates.

**Cladistic analysis**

Using PAUP 4.0 b10 (Altivec) we analysed the character matrix (Table I) that we entered into MacClade 4. An heuristic search with unordered and unweighted characters resulted in 4 trees with a tree length of 261 steps. We chose one tree (Fig. 8) upon which to optimize the obtained character transformations. The other three trees differed only slightly in out-group topology or character optimization in that the *Ingolfiella* clade had a different grouping within the brackish water species arrangement (Fig. 8, insert). However, these trees could have equally well served the purpose.

The analysis used Mictacea and selected gammaridean amphipods as out-groups. The suitability of *Mictocaris halope* as an out-group taxon arises from its comparable habitat requirements.
Fig. 7. Ingolfiella abyssi, holotype: a, gnathopod 1 (scale D); b, gnathopod 2 (D); c, antenna 1 (D); d, pereiopod 3 (D); e, pereiopod 5 (D); f, pereiopod 6 (D); g, pereiopod 7 (D); h, pleopod 1 (D); i, pleopod 2 (D); j, pleopod 3 (D); k, uropod 1, (D); da = dactylus; pas = palmar angle seta.
- marine caves on Bermuda - and also a similarity in form and position of oöstegites that are of "gammaridean amphipod type" (Just & Poore, 1988). In addition, the lobe on the frontal margin of the cephalon is comparable to the equally enigmatic lobes in Ingolfiellidae. Mictocaris also possesses reduced pleopods. The plesiomorphic state of cephalic and thoracic appendages serve as a basis for polarizing supposedly homologous features in the other taxa included in the analysis.

The gammaridean amphipods Bogidiella Hertzog, 1933, and Pseudingolfiella Noodt, 1965, have closer affinities to ingolfiellideans than Mictocaris. Bogidiella has reduced pleopods and a strictly stygobiont life cycle, with most representatives living in fresh water but also a few in the brackish and marine environment. Their body plan is certainly less reduced, and thus holds potentially more plesiomorphies, than that of the ingolfiellideans. The overall habitus of Pseudingolfiella earned this genus its name. Pseudingolfiella has much reduced pleopods, as in Ingolfiellidae. Two species are known: Pseudingolfiella chilensis (Noodt, 1959) and Pseudingolfiella soyeri Coineau, 1977. We used both of them in the out-group as bridging forms between Ingolfiellidea and Mictocaris, and as stand-ins for the gammaridean amphipods.

We have considered using as out-groups the other two remaining, exclusively marine, suborders in the Amphipoda: Caprellidea and Hyperidea. However, many characters in our matrix would have been left unscored. The adaptations found in caprellids and hyperids, which relate to their very different way of living, made them an unlikely choice for comparison. Caprellids cling to sea weeds and lower metazoans in the sublittoral zone, and they have a strongly modified pleon. Hyperids are pelagic with a highly modified head region.

**Results**

The cladogram (Fig. 8) reveals a far from random array of species. The out-group, Mictocaris, Bogidiella and the two species of Pseudingolfiella, remained apart from the in-group whether or not we enforced an out-group constraint in PAUP. We have placed capital letters to focus attention on the most interesting branches of the cladogram. These branches display good apomorphies, i.e., with high consistency indexes. For instance, the lack of an ischi al lobe (character 14) on the maxillipeds in Mictocaris halope results in a strong emphasis by the program on the presence of this lobe in Bogidiella and Pseudingolfiella. This example is also illustrative of how such changes must be interpreted in a relative way. The mictaceans are not necessarily a close sister group to the bogidiellids and pseudingolfiellids (node A). We lack in fact countless numbers of species relevant to amphipod history that never made it through to the present, and we undoubtedly lack many deep groundwater forms that could enlighten us on the origins and early evolution of the group. We merely wish to say, before we go on to interpret character state changes, that given these taxa and these particular characters, and provided one watches out for specific assumptions, then the particular phylogenetic patterns we obtained seem to prevail.

At the base of the ingolfiellidean clade, we note Metaingolfiella, characterized by the uniquely partially fused second thoracic segment into the head, and the fusion of elements in uropod 1 rami and uropod 3 peduncles. (This last feature is interesting in regard to the caudal furca/rami situation in other crustaceans, Schram & Koenemann, in lit.). Nevertheless, these autapomorphies are associated with many plesiomorphic features that insures this species remains at the base of the ingolfiellidean clade.

Stygobarnardia (node B) regains a vestigial mandibular palp in this scenario. It was lost in the transition from the out-group to the in-group (node A). While such character reversals appear to pose problems for diagnosing taxa, they can perhaps best be understood in terms of paedomorphic shifts of developmental timing of events.

The "trogloleleupians" emerge as paraphyletic. The members of a small clade (node C), made up of T. eggerti, T. dracospiritus and T. leleupi, share weakly developed lenticular organs, while the other two "trogloleleupian" species are set off by having either strongly developed lenticular organs, or a differently implanted palmar angle seta. Two new genera are necessary to recognize their isolated locations on the tree.

Ingolfiella is retained as a distinct genus despite its wide habitat and biogeographic spread. The shortening of the uropod 1 stands out as an apomorphy. This character state is stable throughout the genus, no alternating of states is encountered. Other changes defining the Ingolfiella node are the
Fig. 8. Tree number 1 (rooted by using user-specified outgroup): Tree length = 261, Consistency index, (CI) = 0.3511, Homoplasy index (HI) = 0.6489, CI excluding uninformative characters = 0.3436, HI excluding uninformative characters = 0.6564, Retention index (RI) = 0.5550, Rescaled consistency index (RC) = 0.1949. Capitals (A- G) on several nodes represent groups (see text). Species of Ingolfiella without a symbol for subgeneric classification entered the literature after 1989. Insert: alternative topology within the brackish water clade.
transitions from blades to spines on the margin of the dactylus in gnathopod 2, and the diminishing number of crenelations on the palmar margin (although reversals to the absent state are seen, scattered throughout the Ingolfiella clade).

A coastal Mediterranean clade (Fig. 8, node D) is separated on the basis of losing one seta on the inner lobe of maxilla 1. These setae are sparse relative to what is common in gammaridean amphipods. Reverting from four to three setae would seem to reduce the power of that limb for handling food particles.

The transition to the brackish water grade (Fig. 8, between nodes E and F) is defined by a single character state shift: the size of gnathopod 2 going from smaller than the length of pereiopod 3, to subequal to this length.

Finally, a marine clade can be recognized (node F) on the basis of gaining one tooth/spine on the dactylar margin of gnathopod 2, but reversals are possible further up in the clade. Furthermore, a process on the tip of the propod reverts to an unmodified state on this node but is reversed again in the Australian species, the South-African, the Atlantic Ocean, and a Caribbean species.

We have omitted from our analysis four species: *Ingolfiella abyssi*, *I. atlantisi*, *I. littoralis* and *I. kapuri*. The many unscoreable character states for these species clouded the initial analyses that we ran. When we removed one species after the other from the heuristic searches, the number of trees became fewer and the branching pattern of the remaining taxa began to stabilize. We would hope that some day additional material of these taxa will become available that will allow more characters to be scored for these species. Furthermore, it is our desire that by laying out the characters and their alternative possible states in the detail that we have, that future describers of ingolfiellidean species will become more focussed on what descriptors they should seek to elicit from the study of their specimensthna has been the case up to this point.

Systematics

Of course, one can diagnose any taxon without benefit of a rigorous cladistic phylogenetic analysis. However, ideally, the taxonomy of a group should reflect the phylogeny. In consequence, now having performed for the first time a cladistic analysis of the entire suborder Ingolfiellidea, we can go back and present taxonomic diagnoses that emerge naturally from the phylogeny. We provide the supraspecific taxa of the suborder below with such diagnoses (diagnostic apomorphies). For a world catalogue and bibliography of the Ingolfiellidea we refer to the Appendix

**Taxonomic diagnoses derived from cladistic analysis**

Suborder Ingolfiellidea Hansen, 1903

*Diagnosis.* - Mandible palp rudimentary or absent, molar process vestigial peg or spine; maxilla 1 outer lobe outer setae generally dentate; maxilliped with only proximal part of basis fused; pereiopod segments subrectangular to elongate (not deeper than long); gnathopods carpo-subchelate; gnathopod 2 palmar angle setae variable (seldom simple), dactyl tip elongate (usually thinner than thick); uropod 2 generally larger than uropod 1 or subequal.

*Remarks.* - Of these characters, the features concerning the mandible and the carpo-subchelate nature of the gnathopods are robust, with consistency indexes of 1. Hansen (1903) utilized two of these features to erect his superorder, and we can now see from our analysis that in fact these are robust features. However, these exclude the plesiomorphic features one could use. Thus, we have some additional arguments to supply towards justifying Ingolfiellidea as a natural taxon, e.g., vis-a-vis the arguments of Lowry & Poore (1989) and Dahl (1977). The state of the maxilla 1 outer lobe outer setae and the dactyl tip of the second gnathopod are also useful in diagnosing this suborder (cl’s = 0.4 or higher). However, the other features, while helping to define the clade on in our analysis, nevertheless, are rather homoplasic characters. For instance, the palmar angle setae of the second gnathopod is quite variable displaying elongate, pedicillate, angulate forms and these are diagnostic only in so far as they are seldom simple (see character discussion). The relative sizes of the uropod 1 to uropod 2 are even more homoplasic.
Family Metaingolfiellidae Ruffo, 1969
Metaingolfiella Ruffo, 1969

*Type species.* Metaingolfiella mirabilis (by monotypy)

*Diagnosis.* Ocular lobes developed; maxilla 1 with single inner lobe seta, 4 or more palp setae; maxilliped lateral propodal setae present; second thoracic segment partially fused to cephalon; gnathopod 2 carpal saw as setose brush; uropod 1 rami fused to peduncle; uropod 3 fused peduncles.

*Remarks.* The most effective characters (ci = 1) towards defining this monotypic family are the partial fusion of the second thoracic segment to the head and the two features involving the uropods. In contrast, the other characters mentioned here display some degree of homoplasy.

Family Ingolfiellidae Hansen, 1903

*Diagnosis.* Antennule flagellum moderate in size, i.e., more than half the length of the basal peduncular segment, accessory flagellum typically of 3 segments; maxilla 1 outer lobe spines generally 6 in number, palp most often subequal to outer lobe; maxilliped medial palp setation with only 1 or 2 setae per segment; pleopods more often than not as short fins; telson short and fleshy; uropod 1 typically with outer ramus less than half the inner ramus.

*Remarks.* Of these features, only one, that of the medial palp setation, is robust (ci = 1). In addition, the size of the antennular flagellum and the number of outer lobe spines on the maxilla 1 have an acceptable consistency index (ci ≥ 0.5). All the other features mentioned above are rather homoplasic (ci < 0.5).

Genus Stygobarnardia Ruffo, 1985

*Type species.* Stygobarnardia caprellinoides Ruffo, 1985 (by monotypy)

*Diagnosis.* Mandible palp vestigial; maxilla 1 outer lobe outer setae typically bifid; gnathopod 2 carpal saw typically serrate; dactyl ends on pereiopods 3 to 7 produced as a seta; uropod 1 and uropod 2 subequal.

*Remarks.* Of these features, only the state of the mandibular palp is a unique feature for this genus. The other features noted above also appear amongst various species of the genus Ingolfiella.

Genus Trogloleleupia Ruffo, 1974

*Type species.* Trogloleleupia nudicarpus Griffiths, 1991.

*Diagnosis.* Maxilla 1 palp with 4 or more setae; lenticular organs at least incipiently developed; gnathopod 1 dactyl serrate; telson medium in size and fleshy.

*Remarks.* Of these features, the state of the lenticular organs is critical. In Trogloleleupia eggerti and T. leleupi they are only incipiently developed, but in T. dracospiritus they are well developed. This is the most important diagnostic feature of the characters above, although well-developed organs also occur in Paraleleupia gobabis. It is noteworthy to mention that in T. dracospiritus we also see the unique appearance of a short and bifurcate telson, although in our analysis (Fig. 8) T. dracospiritus is more closely related to T. leleupi than to T. eggerti. A former definition of the genus Trogloleleupia by Ruffo (1964) was based on T. leleupi and T. eggerti and mentions their large body length, presence of lenticular organs on thoracic segments 3-10, long pereiopods and uropods, pedicle of the second uropod with numerous rows of setae, and dimorphic first pleopods.

Proleleupia new genus

*Type species.* Trogloleleupia nudicarpus Griffiths, 1991.

*Diagnosis.* Maxilla 1 inner lobe setae 3 in number, palp larger than the outer lobe; gnathopod 1 dactyl with inner margin spines blade-like; gnathopod 2 carpal saw absent.
Remarks.- A separate genus, *Proleleupia*, for what was known as *Trogloleleupia nudicarpus* Griffiths, 1991 is required by our cladistic analysis, wherein the formerly large-bodied genus *Trogloleleupia* Ruffo, 1974 emerged as a paraphyletic taxon. The core species of the trogloleleupian group, containing the type species for *Trogloleleupia, T. leleupi* (Ruffo, 1951), is part of a fairly distinct clade, but two of the five species formerly placed in the genus *Trogloleleupia* in fact sort separately from this core species group. In addition, *Proleleupia nudicarpus* is the only trogloleleupian that lacks lenticular organs, a negative feature to be sure, but nonetheless one that separates it from all the other large-bodied trogloleleupians.

**Paraleleupia** new genus

*Type species.- Trogloleleupia gobabis* Griffiths, 1989

*Diagnosis.* - Pereonal segments sub-rectangular, lenticular organs well developed; gnathopod 2 dactyl teeth developed as 4 blades, dactyl tip simple; pleopods as long fins; uropod 1 and uropod 2 subequal.

*Remarks.* - A separate genus, *Paraleleupia*, for what was known as *Trogloleleupia gobabis* Griffiths, 1989 is required by our cladistic analysis, wherein, as mentioned earlier the large-bodied genus *Trogloleleupia* Ruffo, 1963 emerged as a paraphyletic taxon. Its well-developed lenticular organs clearly characterize *Paraleleupia gobabis*, a feature shared only by *T. dracospritus*. In addition, the simple dactyl tip on the second gnathopod is a feature seen also in *T. eggeri* but no place else amongst all the ingolfiellideans. By erecting separate genera for *Proleleupia nudicarpus* and *Paraleleupia gobabis* we effectively set up an hypothesis of taxonomic relationships in this part of the tree. We can test this hypothesis either with discovery of future 'trogloleleupians', or accumulation of sequence data, or further insight into gross features of morphology.

**Ingolfiella** Hansen, 1903.

*Type species.- Ingolfiella abyssi* Hansen, 1903.

*Diagnosis.* - Gnathopod 1 dactyl either as a simple spine or serrate, gnathopod 2 palmar angle seta not pedicillate, carpal saw typically serrate; dactyl ends on pereiopods 3 through 7 typically produced as a spur; uropods 1 and 2 short.

*Remarks.* - The nature of the short uropods and the lack of a pedicillate palmar angle seta on gnathopod 2 stand out as very diagnostic for the species within the ingolfiellideans. These characters are quite stable throughout the genus: no alternate states concerning the uropods are encountered, and diverse variants of the palmar angle seta can be seen except the pedicillate form. In addition, species of *Ingolfiella* generally have a serrate carpal saw on gnathopod 2, exceptions being *I. cottarelli*, in which it is uniquely finely serrate, and *I. beatricis, I. macedonica, I. xarifae, I. fuscina, and I. grandispina*, in which it is absent.

The genus *Ingolfiella* is retained here as a single, undivided taxon, even though it is world wide in distribution and can be found in localities ranging from fresh groundwater, through diverse brackish, to deep-water ocean habitats. Given this wide distribution and variety of habitats it is instructive to examine several points on the cladogram for *Ingolfiella* with further comment as to character state changes.

A coastal Mediterranean clade (Fig. 8, Node D) is separated on the basis of loss of one seta on the outer lobe of the maxilla 2. These setae are reduced relative to what is common in gammariidean amphipods. Reverting from 4 setae to 3 setae would seem to reduce the ability of this limb to handle food particles. This may appear as a "subtle" feature, nevertheless the members of this clade exhibit a relatively high degree of geographic proximity.

The change over point from freshwater to brackish habitats (Fig. 8, Node E) is also defined by a single character state transition: the size of gnathopod 2 shifts from being smaller than the length of pereiopod 3 to being subequal to the latter. It again is difficult to conceive of any purported selective advantage of such a feature. Nevertheless, this node marks a distinct habitat shift within the genus. Another critical habitat shift occurs into pure marine waters (Fig. 8, Node F) and corresponds with changes in aspects of the second gnathopod. At this point we note an alteration of ornament on the dactylyar margin of gnathopod 2, going from 3 blade-like processes to 3-4 teeth. Furthermore, we also note increasing variability on the distal propodus of gnathopod 2. Most freshwater *Ingolfiella* display
blade-like distal propodi. Within brackish habitats we also see a finger-like form appearing. In the marine realm, an unmodified propodus reappears, a structural form characteristic of taxa typically outside the genus.

What surprises us about the above points is that while the habitat or geographic shifts are rather striking, the anatomical changes at these points are subtle in the extreme.

Past authors (S. Karaman 1959, Stock 1976b, Ruffo 1970, and Ruffo & Vigna Taglianti 1989), have made arguments to subdivide the genus *Ingolfiella* into either more genera, or at least subgenera (see bibliography). As can be seen in Fig. 8, these subgenera have little value in light of the cladistic analysis here. Nevertheless, we do see clades appearing within the genus. We have already noted the Mediterranean clade of the *I. beatricis* species group, characterized by a single feature. Another such clade is the *I. macedonica* species group (Fig. 8, Node G). This clade is characterized by two good features: 1) the claws of pereiopods 3 to 4 are simple in form, and 2) pereiopods 3 to 7 dactyls lack any decoration such as spurs or setae. These are good features at that point in the tree. If characters nicely delineating discrete clades would justify the erection of subgenera in a cladistic context, one might be tempted to look upon the so-called *I. macedonica* species group as a good one. We might even be tempted to say this species group is even more robust than that of *I. beatricis* species group discussed above, which only has a single, rather subtle diagnostic feature. However, the *I. beatricis* group is geographically continuous, while the members of the so-called *I. macedonica* species group are hardly so: *I. macedonica* is found in northwestern Greece, *I. manni* was collected from northern Chile and *I. uspallatae* comes from the high Andean passes of western Argentina. How do we bridge the gap from the Balkans to South America?

Thus, at this time we see no justification for establishing subgenera, or breaking up *Ingolfiella* into separate genera. The shifting morphological changes noted amongst the optimized characters on the cladogram are too subtle and homoplastic, and discrete clades are too few and far between. We remain confident, however, that as more taxa are added to the genus the cladogram will acquire some additional structure. Then at that time, the issue of what to do with such a wide ranging, both geographically and ecologically, genus as *Ingolfiella* currently represents can be revisited.

**Additional descriptions**

Re-examination of type and other material in light of the cladistic analysis allows additions and revisions to be made to existing species descriptions.

*Metaingolfiella mirabilis* Ruffo, 1969  
Fig. 4a-h  
**Material examined.**- collection of the Natural History Museum Verona.  
Additional redescription: cephalon fused over about half the lateral lower side with the first pereionite.

*Trogloleleupia eggerti* (Ruffo, 1964)  
Fig. 5a-d  
**Material examined.**- collection of the Natural History Museum Verona.  
The allotype (female) designated by Ruffo was restudied and some more sexual dimorphism is reported. Not only is the form of the first pleopod different - elongate in males and triangular in females - as mentioned by Ruffo, but also the female lacks a hooked spine on the base of the peduncle of the first uropod and the claviform process on the peduncle of the second uropod. Another noteworthy difference is the lack of the palmar corner process in the second gnathopod, but this occurs in other ingolfiellids too.  
**Additional description:**  
Maxillae 1, (Fig 6a) palp two-segmented with 4 setae on distal segment. Outer lobe with 6 serrated and combed robust setae. Inner lobe with 5 setae almost evenly distributed along its margin.  
Maxilla 2 (Fig 6b), with both lobes having 5 setae, some plumed.  
Mandible (Fig 6c, d). Left side with pointed pars molaris and 3 hooked and serrate spines at the base of the masticatory teeth. Right side with two such curved hooks.
Maxilliped (Fig. 5e). Palp with 3 spines apically and 1 spinule on a small pedestal submarginally on the propodal segment.

Pleopod 1 (Fig. 5f). Triangular fin with a slightly serrated hind corner margin and 3 tiny spinules on the lower margin.

*Trogloleleupia leleupi* Ruffo, 1951

*Material examined.* - British Museum, Lusaka Boreholes, Zimbabwe, 9 specimen; Zoological Institute and Museum, University of Hamburg, 15 specimens, Kivu, Distric de Kindu, Territoir e de Kasongo, Grotte de Mwana-Kussu, Congo, 24-X-1954

In the descriptions of Ruffo (1951) and Ingle (1961) no special emphasis was placed on the form of the first pleopod. These pleopods have in most ingolfiellids a different form in males and females. However, in the many specimens of *Trogloleleupia* (44 + from Belgian Congo and 9 from Lusaka, Zimbabwe), no distinction could be made between the sexes. We checked the pleopods for such differences. Indeed, some of the smaller specimens carry the digitiform first pleopods with two setules on the apex typical of males, while the larger specimens have the more spatulate crenelated type as in pleopod 2 and 3.

Additional description:
Antenna 1 (Fig. 5k) with a 4 segmented flagellum, bearing an aesthetasc on each segment. Accessory flagellum 3 segmented.

Gnathopod 2 (Fig. 5g, h) differs in aspect with increasing size. The 8 mm male (6e) has a hyaline lobe aligning the margin right under the palmar process but this is not seen in a 12 mm specimen (Fig. 5h), with a sculptured palmar process. The crenelations are more numerous on the palmar margin.

Pleopod 1 (Fig. 5i, j) is long and slender in the male, having two setae on the apex. The female form is somewhat triangular and lightly serrate on the hind margin.

Uropod 3 (Fig. 5l) in one instance quite long, with five slender setae on its apex.

*Ingolfiella littoralis* Hansen 1903

*Material examined.* - Holotype specimen, Zoological Museum of Copenhagen (ZMUC-CRU-7088)

Additional description:
Gnathopod 1 (Fig. 6a), margin of palm smooth, without structures or serrations
Gnathopod 2 (Fig. 6b), margin of palm serrated.

Pereiopod 3, 4 (Fig. 6c, d), claws tapering to a forked end
Pereiopod 5 (Fig. 6e), claw thick, undifferentiated.

Uropod 2 (Fig. 3g), with three oblique rows of setules on the inner side of the peduncle and a small group of setules on the inner side of the inner ramus.

*Ingolfiella tabularis* Stock 1977

*Material examined.* - Zoological Museum of Amsterdam, paratypes, cat. nr. 106.107

Additional description:
Mandible (Fig. 6g, h, i), with cup shaped spine on left mandible.

Maxilla 1 (Fig. 6j), with 6 combed and serrate setae of irregular length on outer lobe. Inner lobe with 1 seta, palp with 3 setae on apex.

Maxilla 2 (Fig. 6k), fitted with sparse setae on both lobes.

*Ingolfiella margaritae* Stock 1979

*Material examined.* - Zoological Museum of Amsterdam, holotype cat. nr. 106.443 - 444

Additional description:
Mandible (Fig. 6n), with apparently broken off molar process. Left or right side could not be discerned. Three curved spines just below pars incisiva.

*Ingolfiella quadridentata* Stock 1979
Material examined. - Zoological Museum of Amsterdam, paratypes cat. nr. 106.445 - 446

Additional description:
Mandible (Fig. 6l) with pointed molar process. Three very small spinules below the pars incisiva
Maxilla 1 (Fig. 6m) has an outer lobe with 6 robust spines, bifid or serrate. Inner lobe with 1 seta, palp with 3 on apex.

Ingolfiella abyssi Hansen 1903

Material examined. - Museum of Copenhagen ZMUC-CRU-5030

Additional description:
Antenna 1 (Fig. 7c), with 4-segmented flagellum, bearing aesthetasc s on the second and fourth segment.
Accessory flagellum 3-segmented.
Gnathopod 1 and 2 (Fig. 7a, b), with 4 incisions on the inner margin of the dactylus, forming 4 blades.
Gnathopod 2 claw with a clear articulation between dactylus and unguis.
Pereiopods 3 – 7 (Fig. 7d-g), with bifid claws in p3 and p4 (8d) and straight in p5-7 (8e, f, g)
Pleopods 1 – 3 (Fig. 7h-j), with more or less triangular form.
Uropod 1 (Fig. 7k), with 3 spiniform processes (instead of 4 in the original description) on inner ramus.
Outer ramus with a breach on two-thirds of its length, dividing the ramus in two articles.

Biogeographic analysis

An accepted approach to elucidating patterns of historic biogeography would typically begin with either a Brooks Parsimony, or COMPONENT Analysis. This would require that the distribution information (Fig. 9) be converted into a supplementary matrix, which would then be subjected to further analysis. Though effective and widely accepted, these methods pose some conceptual disadvantages. The biogeographic analysis is performed on top of the results of a previous cladistic analysis. This imposes a number of new equally parsimonious trees on top of the supposedly equally parsimonious trees from the base analysis. In effect, one accumulates uncertainty on top of uncertainty.

There are, of course, ways to handle all these alternative trees, but there is an additional conceptual problem to this approach. This treats the biogeographic history as if it were a completely separate and subsequent set of events in the evolution of a group when in fact the spatial and distributional components are an integrated part of a taxon’s biology. One possible solution to this could be to attach a step matrix to the primary analysis that would code for all possible biogeographic movements within the recorded range of the group in question (Berge, 2000). The biogeography could then be integrated into the base analysis. This is worthy of further exploration within the Amphipoda, but must be the subject of a separate study.

A conceptually simpler approach, however, is suggested by the data at hand. The biogeographic history of the separate clades (Fig. 8, nodes A-G) can be projected onto paleomaps (see Ebach & Humphries, 2002). This is a process of straightforward inspection. But where to begin? Since our cladogram clearly points to an early development of the large fresh water African and Mediterranean cave species it leads us to look for a paleomap, in this case Triassic, that would combine both areas and show a continuous land mass with those areas present at some particular point in earth history. Actual fossil evidence for the existence of the Amphipoda does not go beyond approximately 40 million years ago (Coleman and Myers, 2000), when epigean as well as hypogean forms where trapped in amber resin. These cenozoic fossils closely resemble the living forms of today, and therefore would seem to point to a much older amphipod origin perhaps one more in line with other groups within the Peracarida such as the isopods, tanaids, cumaceans and spelaeogriphaceans. Fossils of these latter groups date back to the Carboniferous (Schram, 1981).

Why is it that no Paleozoic or Mesozoic fossils are found among the Amphipoda? The reason is probably twofold. Either no recognizable form existed, i.e., somehow the amphipods arose from relatively recent ancestors, or the amphipods living in the Mesozoic (or earlier) occurred in habitats
Fig. 9. Cladogram with Recent geographic character states projected on its branches.
Fig. 10. Cladogram with paleogeographic character states projected on its branches. Tr. = Triassic; EJ = early Jurassic; LJ = Late Jurassic; LK = Late Cretaceous.
that were quite unsuitable for fossilization. These latter ancestors could be deep sea, interstitial, and/or cave inhabitants. We assume that the colonization of the marine interstitial by small benthic crustaceans was an ancient event. A trend can be seen in the evolution of worm-like bodies in amphipods, which invaded older areas in ancient times and are present today in areas that have been emergent at least since the late Cretaceous. This stands in contrast to forms with rounder bodies, which resemble more their benthic relatives (Vonk, 1990; Coineau, 2000).

The present day ingolfiellideans that occupy underground waters far inland on the continents are the large cave lake inhabitants of Africa below the Equator. Their counterpart, in body length and micro-environmental requirements, is the one species of Metaingolfiella, known from a well in Italy. Returning to our original question of where to begin and project a common history on a paleomap, it seems justifiable to search for to a time where the African and Mediterranean freshwater forms could have had contact. The map from the Early Triassic (Scotese, 1977) reflects such a situation. The Pangaea and Gondwana geography of the Triassic can be fitted to the branches of those taxa that group together low in the clade of the ingolfiellideans (Fig. 10, Fig. 11A).

"Above" these stem taxa on the tree, we encounter species of Ingolfiella found today in groundwater habitats along the North Mediterranean coasts. As above, if we seek a period after the Triassic, we find in the Early Jurassic a time when the central Atlantic Ocean and western Mediterranean Sea was forming from the older West Tethys Ocean. We can plot the taxa that are found nowadays in the northern Mediterranean near-coastal areas onto the northern coast of the West Tethys Ocean in the Early Jurassic geography (Fig. 11B). There are exceptions, like Ingolfiella macedonica and especially I. ischitana that occur in this same geographic area but appear higher in the cladogram (Fig. 10).

In a similar manner, we find that the grade on the cladogram that represents the freshwater and brackish species from the present day Atlantic Islands and Caribbean area are easily projected paleogeographically onto the northern coast of Late Jurassic Gondwana (Fig. 12A).

The extremely high sea levels of the late Cretaceous and further opening of the Atlantic Ocean (Haq et al., 1987) could have seen an evolution and dispersal of marine benthic and infaunal elements linked with the expansion of coastlines and deep waterways. From the Cretaceous onward the spread of ingolfiellids over the earth might have taken place at a faster pace (Fig. 12B) into the North Atlantic and out over the unfolding Indo-Pacific.

Discussion

Our justification for interpreting paleomaps and looking for continuous landmasses that may have held vast underground bodies of freshwater through long periods of geological time, is congruent with the results of our analysis in which the species inhabiting the African Pre-Cambrian shield are primitive forms. Such ideas have been formulated earlier (Ruffo, 1951; Leleup, 1955, Siewing, 1963), but Dahl (1977) remarks that a reduction of pleopods is unusual in species living in larger bodies of subterranean waters and thus he maintained that this feature must have been inherited from interstitial ancestors without fully developed pleopods. Therefore it is unlikely, according to Dahl, that these cave forms could have been ancestral to the smaller interstitial types. However, a detailed description of Leleup (1955) on the ecology of Trogloleleupia leleupi, a large cave-inhabiting ingolfiellidean from Congo, reveals that this species does not employ a free swimming behavior but rather moves across the bottom on its side. This suggests the true bottom dwelling nature of ingolfiellideans. Further speculations on whether small interstitial forms with reduced pleopods transformed back into larger cave forms with, secondarily derived, functionally active pleopods cannot be investigated any further without fossil forms.

A number of alternative evolutionary scenarios concerning ingolfiellidean origins now present themselves. First, a marine ancestor could have invaded the fresh-water underground environment in the Early Triassic, or even Late Paleozoic, with concomitant anatomical reductive adaptations taking place. In some cases, a "rebuilding" of reduced features (pleopods, third uropods) might have occurred especially when the infestation of the interstitial environment (with its confined spaces) was followed by radiation into cave-lake systems and underground rivers. Second, limno-stygobionts, as the large African inland species represent could have evolved into cave forms from surface water limnic
Fig. 11. Early parts of the phylogenetic tree projected on different epochs of geological history. A, three rectangles on the map of the Early Triassic represent roughly the distribution of the depicted taxa. B, The dark grey area on the map of the early Jurassic represents the area adjacent to the Recent mediterranean distribution of the earliest evolved species of the *Ingolfiella* clade (see Fig. 8). Notice this distribution is continuous and restrained to a limited area (maps modified after Scotese, 1997).
Fig. 12. A. The intermediate taxa of the Ingolfiella clade, the fresh and brackish water species of the Caribbean, the Mediterranean, and South America. The dark grey area represents the species distribution projected on a map of the Late Jurassic with their nowadays occurrence. B. the most derived taxa of Ingolfiella containing marine species with a scattered distribution virtually worldwide, projected on a map of the Late Cretaceous (maps modified after Scotese, 1997).
ancestors. This phenomenon has been extensively studied in recent times by Culver et al. (1995) in the case of *Gammarus minus*. In the case of ingolfiellids, however, this route is unlikely because no epigean relatives are known to exist. Third, the peracarids may have been interstitial and/or groundwater forms in origin. This possibility has been little considered. In its favor, however, is the fact that the most primitive gammaroids (crangonyctids, bogidiellids) occupy such habitats. The spelaeogrphaceans also occur in caves, and Spears (pers. comm.) believes molecular evidence supports a common origin of spelaeogrphaceans and amphipods. In addition, the most primitive isopods, the phreatoicids, occupy allied habitats (Wilson, 1998).

In contrast, much has been written as to how preadapted marine benthic crustaceans could passively or actively invade the insular and continental ground water. Recent overviews (with numerous references to authors who have published on this subject) are presented by Holsinger, 2000; Coineau, 2000; Stock, 1993; Humphreys, 1999; Botosaneanu, 2001.

In summary, by plotting the grades of taxa found in our cladogram onto a succession of paleographic maps we can perceive shifting patterns that suggest a possible scenario of ingolfiellidean evolution. From an origin in the tropic cave and ground waters of Triassic Pangaea, the early progenitors of the genus *Ingolfiella* appear to have dispersed eastward along the sub-tropical and temperate shores of the Western Thetys Ocean in the Early Jurassic. Dispersal in the westward direction along the northern and western coasts of Gondwana happened in the Late Jurassic. As the Atlantic continued to open through the Cretaceous, species of *Ingolfiella* found themselves isolated on the proto-Atlantic and Caribbean islands. One can envision that some members of the group rode the spreading seafloor down as the Atlantic deep was created. Afterward further dispersal into the deep Tethys and south Atlantic allowed the ingolfiellids to reach the far reaches of the Indo-Pacific and southern Ocean in the Cenozoic.

Finally, the cladogram we obtained (Fig. 8) suggests, as we pointed out above, that the African and Italian cave species may have given rise to smaller interstitial freshwater species and these have evolved further via brackish forms into marine interstitial and deep-sea species. A way to test this working hypothesis would be to sample for large cave Ingolfiellidea in the eastern parts of South America. The presence of large freshwater cave ingolfiellideans would lend credit to the idea that a freshwater continuum underground in Pangea existed before the break-up of the African and South American landmasses in the Early Cretaceous. In a far inland cave in southwestern Brazil (Gruta do Lago Azul), a large bogidiellid belonging to a newly erected genus, *Megagidiella*, was found recently (Koenemann & Holsinger, 1999). The size of this species is exceptional in relation to the widely distributed smaller sized bogidiellids. This situation is more or less comparable to what is seen in ingolfiellideans, i.e., large cave species far inland that are rare and found in places with 'relict' faunas, as opposed to the small species from the species-rich interstitial habitats closer to the sea. The strictly stygobiont freshwater isopod family Stenasellidae has a distribution that points to a Cretaceous origin. Consequently, the occurrence of this family on the northeastern South American Venezuela-Guiana Shield (Magniez, 1981) strengthens the proposition that ancient bodies of freshwater gave rise to 'relict' species that can be found on the fragments of Gondwana.

We predict that future research on early origins of stygobiont crustaceans that concentrates on sampling cave environments deep in the heart lands of old cratons in the tropical and temperate climate zones, will yield new taxa with ancient origins that will further elucidate patterns of evolution reaching back to the Triassic or even earlier.

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References


Appendix

**World catalogue and bibliography of the Ingolfiellidea**

Ingolfiellidea Hansen, 1903

1927 Ingolfiellidea Reibisch, in: Kukenthal W. Handbuch der Zoologie, Bd. III, 1: 802-803, fig. 858.

*Diagnostic features.* Mandibular palp vestigial or absent, molar process vestigial or reduced to a peg or spine; maxilliped bases fused proximally; gnathopods carpo-subchelate.  
In addition, these also generally prevail: maxilla 1 outer lobe outer setae dentate; pereion segments elongate; coxal plates weakly developed; gnathopod 2 palmar angle setae pedicillate, and dactyl tip long and thick; uropod 2 longer than uropod 1.  
*Remarks.* Although some authorities have maintained that the two ingolfiellidan families are little more than special gammaroideans, we believe that the Ingolfiellidea constitute a definable sister taxon to the rest of the Amphipoda.

Metaingolfiellidae Ruffo, 1969


*Diagnostic features.* See the diagnosis of the genus.  
*Remarks.* While possessing all the hard and soft apomorphies of the suborder, the high number of autapomorphies insures a clearly distinct position for this taxon.

*Metaingolfiella* Ruffo, 1969


*Diagnostic features.* Second thoracic segment fused to cephalon; gnathopod 2 carpal saw as a setose brush; uropod 1 rami fused to peduncles; uropod 3 rami fused at peduncles.  
*Remarks.* Only a single genus and species has been recognized so far.

*Metaingolfiella mirabilis* Ruffo, 1969


*Diagnostic features.* Accessory flagellum 2 segments; mandibular palp absent, molar process as a peg or spine; maxilla 1 inner lobe with 1 seta, outer lobe inner setae dentate, outer lobe outer setae dentate, 7 outer lobe spines; maxilla 2 with 5 or more setae; maxilliped lateral propodal setae absent, pereional segments elongate; gnathopods carpo-subchelate; gnathopod 1 dactyl simple; gnathopod 2 palmar angle seta pedicillate, dactyl teeth absent, dactyl tip long and thick, gnathopod subequal to pereiopod 3, pereiopods 3-4 claws simple; pereiopods 3-7 with dactyls similar, not produced; pereiopods 5-7 dactyls with claws; uropod 1 rami equal in
length; uropods 1 and 2 long, 2 longer than 1; uropod 3 uniramous; uropod 3 left and right peduncles fused; telson medium and fleshy.

**Distribution.** - 40° 19' 38"N, 15° 30' 55"E, southern Italy.

**Habitat.** - freshwater well

**Depth range.** - well opening 41.65 m (level of water table 50.25 m below this).

**Size.** - male, 13.5 mm; female, 15.5-18.7 mm.

Ingolfiellidae Hansen, 1903


**Diagnostic features.** - Antennular flagellum more than half (but less than the total of) the length of the basal peduncular segment; maxilliped medial setation on the palp reduced to only 1 or 2 per segment.

In addition, antennular accessory flagellum with 3 segments; maxilla 1 with 6 spines on the outer lobe and palp subequal to the outer lobe; maxilliped dactyl claw as a spine with flanking setae; pleopods as short fins; telson short and fleshy; uropod 1 outer ramus less than half the inner ramus.

Stygobarnardia Ruffo, 1985

1989 Stygobarnardia, - Griffiths, Cimbebasia 11: 59, 61. [key]

**Diagnostic features.** - Mandibular palp vestigial.

**Remarks.** - Little about this genus is distinctive, aside from the vestigial mandibular palp, to mark it from other ingolfiellids, and its lack of lenticular organs to mark it from many (but not all) of the other large bodied cave-dwelling species of central Africa.

Stygobarnardia caprellinoides Ruffo, 1985

1989 Stygobarnardia caprellinoides, - Griffiths, Cimbebasia 11: 61

**Diagnostic features.** - Ocular lobes absent; antennular flagellum medium in size, accessory flagellum with 3 segments; maxilla 1 inner lobe with 4 or more setae, outer lobe inner setae dentate, outer lobe outer setae bifid, outer lobe with 6 spines, palp subequal to outer lobe, palp with 3 setae; maxilla 2 with 5 or more setae; maxilliped dactyl claw as a spine with flanking setae; pereiopod segments elongate; gnathopod 1 dactyl simple; gnathopod 2 palmar angle seta pedicillate, with 7 serrate teeth on the carpal saw, distal propodus unmodified, dactyl teeth absent, dactyl tip long and thick, gnathopod subequal to pereiopod 3, palm oblique; pereiopods 3-4 with claws simple; pereiopods 3-7 dactyl ends produced as seta; pleopods as short fins; uropod outer ramus less than the inner ramus; uropod 1 and 2 subequal and long; telson short and fleshy.

**Distribution.** - Wag'n Bietjie farm, near Tsumeb (19° 13.5' S., 17° 40.5' E.), Manheim farm, 6 miles away, Namibia.
Habitat.- freshwater wells

Size. - male, 10-12 mm; female, 15 mm.

Remarks. - 6 specimens from Tsumeb, 1 from Manheim from Barnard (1966). This species is found at the Wag’n Bietjie farm with *Trogloleleupia eggerti*.

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*Trogloleleupia* Ruffo, 1963

1959 *Leleupiella* Karaman, Bioloski Glasnik 12: 78. (non *Leleupiella* Jeannel, 1952 [Coleoptera]).
1989 *Trogloleleupia*, - Griffiths, Cimbebasia 11: 59, 61 [key].

Diagnostic features. - Ocular lobes absent; accessory flagellum 3 segments; mandibular palp absent; maxilla 1 palp subequal to outer lobe; gnathopod 1 dactyl blade-like; gnathopod 2 palm oblique, generally smaller than the pereiopod 3, dactyl with 3 or 4 teeth, and dactyl tip long and thin; pereiopods 3-4 claws simple; uropods 1 and 2 long.

Remarks. - It appears under our current understanding of the phylogenetic relationships of the 5 known species that this genus is paraphyletic. Its main diagnostic feature according to Griffiths (1989) is the development of the lenticular organs, but these find different expression amongst the various species. Furthermore, of the features provided here, the relative size of gnathopod 2 and the 3 teeth on the dactyl are shared with primitive members of *Ingolfiella*. Furthermore, each species of this genus seem to be characterized by many apomorphies, though generally of low consistency.

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*Trogloleleupia* dracopiritus Griffiths, 1989

1989 *Trogloleleupia* *dracopiritus* Griffiths, Cimbebasia 11: 62-65, figs. 3-4.

Diagnostic features. - Ocular lobes absent; antennular flagellum medium; maxilla 1 inner lobe with 2 setae, outer lobe inner setae dentate, outer lobe outer setae dentate, outer lobe with 5 spines, palp with 4 or more setae; maxilla 2 with 4 or more setae; maxilliped dactyl as spine with flanking setae; pereion segments deeper than long; gnathopod dactyl serrate; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle seta angulate, carpal saw absent, distal propodus tooth-like, dactyl with 3 teeth, dactyl tip long and thin, subequal to pereiopod 3, palmar angle setae angulate, carpal saw absent, dactyl with 3 teeth; pereion segments deeper than long; lenticular organs well developed; pleopods are short fins; uropod 2 longer than uropod 1; uropod 1 outer ramus more than half the inner ramus; telson short and bifurcate.

Distribution. - ~19° 32.7' S., 18° E., Dragons Breath Cave, west of Grootfontein, Namibia.

Habitat. - silt-covered rocks in pools up to 40m in depth

Size. - 10-16 mm.

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*Trogloleleupia* eggerti (Ruffo, 1964)


Diagnostic features. - Antennular flagellum (short) less than half basal peduncular segment; maxilla 1 inner lobe with 4 or more setae, outer lobe inner setae dentate, outer lobe outer setae bifid and dentate, outer lobe with 6 spines, palp with 4 or more setae; maxilla 2 with 5
or more setae; maxilliped dactyl claw falcate; lenticular organs incipiently developed; pereion segments subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle seta pedicillate, carpal saw with 9 peg-like structures, distal propodus unmodified, dactyl with 4 teeth, dactyl tip simple; pleopods as short fins; uropod 2 longer than uropod 1; uropod 1 outer ramus shorter than inner ramus; telson of medium size and fleshy.

**Distribution.** - 19° 13.5' S., 17° 40.5' E., Wag'n Bietjie farm, near Tsumeb, Namibia.

**Habitat.** - freshwater wells

**Size.** - male, 22.5 mm.; female, 23 mm.

**Remarks.** - This species is found in association with *Stygobarnardia*. This is the only place where two species of ingolfiellids are found sympatrically.

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**Trogloleleupia leleupi** (Ruffo, 1951)


**Diagnostic features.** - Antennular flagellum various (medium to short); maxilla 1 inner lobe with 4 or more setae, outer lobe inner setae simple, outer lobe outer setae dentate, outer lobe with 5 spines, palp subequal to outer lobe, palp with 4 or more setae; maxilla 2 with 3 setae; maxilliped dactyl claw as spine with flanking setae; pereion segments elongate; lenticular organs incipiently developed; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle spine angulate, carpal saw with 9 peg-like structures, distal aspect of propodus tooth-like, dactyl with 3 blades; dactyl tip long and thin, gnathopod 2 subequal to pereiopod 3; pleopods as long fins; uropod 1 outer ramus less than the inner ramus; uropod 1 and 2 subequal and long; telson of medium size and fleshy.

**Distribution.** - (-11° 9' S., 27° 5.5' E.) Kakontwe Cave (7 km. from Jadotville), (4° 16' S., 26° 19' E.) Mwana Kussu Cave, near Kasongo, Congo; borehole, (15° 26' S., 28° 20' E.) Lusaka, Zambia.

**Habitat.** - cave pools, groundwater well.

**Depth range.** - borehole @ 121-127 ft.

**Size.** - 8.5-20 mm.

**Remarks.** - No evident dimorphism noted by both Ruffo and Ingle.

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**Paraleleupia gobabis** (Griffiths, 1989)

2002 *Paraleleupia gobabis*, Vonk & Schram

**Diagnostic features.** - Antennular flagellum medium in length; maxilla 1 inner lobe with 2 setae, outer lobe inner setae dentate, outer lobe outer setae dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 3 setae; maxilla 2 with 4 setae; maxilliped dactyl claw as a spine with flanking setae; lenticular organs well developed; gnathopod dactyl blade-like; gnathopod 2 palmar angle seta pedicillate, carpal saw with 9 peg-like structures, distal aspect of propodus unmodified, dactyl with 4 blades, dactyl tip simple, gnathopod 2 smaller than
pereiopod 3; pereion segments subrectangular; pleopods as long fins; uropod 1 and 2 subequal and long, uropod 1 outer ramus more than half the inner ramus; telson short and fleshy.

Distribution. -22° 34' S., 17° E., Arnhem Cave, west of Windhoek, Namibia.

Habitat. - cave pool

Depth range. - 103 m. below ground (pool is 260 m. from entrance).

Size. - 14-20 mm.

Remarks. - Total of 21 specimens collected, none of them sexed because of a lack of dimorphism. It would appear that this species is actually more closely related to members of the genus Ingolfiella than it is to the other species of Trogloleleupia.

Proleleupia nudicarpus (Griffiths, 1991)


2002 Proleleupia nudicarpus, Vonk & Schram.

Diagnostic features. - Antennular flagellum various (medium to short); maxilla 1 with 3 setae on inner lobe, outer lobe inner setae dentate, outer lobe outer setae dentate, outer lobe with 6 spines, palp with 3 setae and longer than the outer lobe; maxilla 2 with 5 or more setae; maxilliped dactyl claw as a spine with flanking setae; pereion segments elongate; lenticular organs absent; gnathopod 1 dactyl blade-like; gnathopod 2 with palmar angle setae angulate, carpal absent, distal aspect of propodus unmodified, dactyl with 3 teeth, dactyl tip long and thin, gnathopod 2 shorter than pereiopod 3; pereiopods 3-4 claws simple; pleopods as short fins; uropod 2 longer than uropod 1, both relatively long; uropod 1 outer ramus lesser than the inner ramus; telson short and fleshy.

Distribution. - Wondergat Cave, Twyfelfontein, Namibia.

Habitat. - cave pool

Depth range. - 60 m. below ground

Size. - 8-11 mm.

Remarks. - 13 specimens collected in a small pool about 10 cm. deep. The diagnostic features here display a high degree of homoplasry with conditions seen in all ingolfiellids.

Ingolfiella Hansen, 1903

1903 Ingolfiella Hansen, J. Linn. Soc. (Zool.), London. 29: 118.

1959 Hanseniella, Karaman, Bioloski Glasnik 12: 78

1959 Gevgeliella, Karaman, Bioloski Glasnik 12: 78


1976 Ingolfiella (Hanseniella), - Stock, Stud. Fauna Curacao. 50: 60, [definition & key].

1976 Ingolfiella (Trianguliella), Stock, Stud. Fauna Curacao. 50: 60, [definition & key].

1976 Ingolfiella (Gevgeliella), Stock, Stud. Fauna Curacao. 50: 60, [definition & key].

1976 Ingolfiella (Balcanella), - Stock, Stud. Fauna Curacao. 50: 60, [definition & key].


**Diagnostic features.**- Mandibular palp absent; uropods 1 and 2 short. In addition, several homoplastic features typically prevail such as: maxilliped dactyl claw with a single seta; gnathopod 2 carpal saw with 7 teeth, dactyl as a spine; pereiopods 3-7 dactyls often produced with a spur. However, these features exhibit much variability throughout the genus.

**Remarks.**- Much effort has been put into trying to establish subgenera in the genus. This grew out of Karaman's efforts to actually break the genus *Ingolfiella* into separate genera. Many have contributed to comparison among types, but the major efforts to establish these with keys and comparative discussions were Stock (1976) and Ruffo & Vigna Taglianti (1989). However, with the possible exception of *Balcanella*, these subgenera are either paraphyletic, like *Antilleela* and *Tyrrhenidiella* or polyphyletic such as *Tethydiella*, *Hanseniella*, and *Gevgeliella*.

*Ingolfiella abyssi* Hansen, 1903


**Diagnostic features.**- Ocular lobe developed; antennular flagellum medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 2 setae, [outer lobe outer setae dentate, outer lobe with 5 setae, palp longer than outer lobe, palp with 4 setae]; maxilla [with 4 setae]; maxilliped dactyl claw [as robust spine]; gnathopod 1 dactyl simple; gnathopod 2 [palmar angle spine simple, carpal saw serrate, dactyl teeth absent, dactyl tip long and thin, palm transverse]; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls similar and not produced; pereiopods 5-7 dactyls with claws; pleopods 1-3 of female present; uropod 1 outer ramus more than 1/2 inner ramus.

**Distribution.**- 59° 12' N, 51° 05' W, Davis Strait, southwest from the southern tip of Greenland.

**Habitat.**- mud bottom

**Depth range.**- 1870 fathoms, 3422 m.

**Size.**- male, 2.5 mm.

**Remarks.**- Only a single specimen is known, collected from station 38 of the Ingolf Expedition.

*Ingolfiella acherontis* (Karaman, 1933)

1959 *Ingolfiella acherontis*, - Karaman, Biologski Glasnik. 12: 74, figs. 35-44.
Diagnostic features. - Ocular lobe developed; antennular flagellum medium, accessory flagellum as 3 segments; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle seta simple, carpal saw absent, distal aspect of propodus unmodified, dactyl with 3 teeth, dactyl tip long and thin, palm transverse; pereiopods 5-7 dactyls with claws; pleopods as long fins.

Distribution. - 42° N., 21° 27.5' E., Skopje, Macedonia.

Habitat. - ground water

Depth range. - ~2.50m.

Size. - male, 2.5 mm.

Remarks. - Poorly described species. Material lost in second world war.

Ingolfiella atlantisi Mills, 1967


Diagnostic features:

Distribution. - 33° 56.8' N, 65° 47' W

Habitat. - mud bottom

Depth range. - 4892-4743 m.

Size. - male, 2.1 mm. male(?).

Remarks. - Collected on the Gay Head-Bermuda transect in the North American Basin. Dojiri & Sieg suggest that the single specimen is a female.

Ingolfiella australiana Lowry & Poore, 1989


Diagnostic features. - Ocular lobe well developed; antenna 1 flagellum long and larger than basal peduncular segments, accessory flagellum of 3 segments; mandible palp present; maxilla 1 inner lobe with 3 setae, outer lobe inner setae dentate, outer lobe outer setae bifid, outer lobe inner setae dentate, outer lobe with 6 spines, palp with 3 setae, palp longer than the outer lobe; maxilla 2 with 5 or more setae; maxillipeds dactyl claw absent; pereiopods segments subrectangular to elongate; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle seta elongate, carpal saw serrate (with 7 teeth), distal aspect of propodus blade-like, subequal to pereiopod 3, distal propodus blade-like, dactyl with 3 teeth and tip long and thin, palm oblique; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls produced with spurs, dactyls dissimilar; pereiopods 5-7 dactyls without claws; pleopods as long fins; uropod 2 larger than uropod 1, uropod 1 outer ramus less than the inner ramus; telson short and fleshy.

Distribution. - 40° 26.7' S, 143° 41.4' E, 34 km SW of King Isl., Bass Strait

Habitat. - sandy shell bottom

Depth range. - 85 m.

Size. - male, 2.3 mm; female, 2.2 mm.

Ingolfiella bassiana Lowry & Poore, 1989

**Diagnostic features.** - Ocular lobes developed; antennula flagellum medium, accessory flagellum with 2 segments; maxilla 1 inner lobe with 3 setae, outer lobe inner setae dentate, outer lobe outer setae dentate and bifid, outer lobe with 6 spines, palp with 3 setae, palp longer than the outer lobe; maxillipede lateral propodal setae present, dactyl claw falcate; pereion abdominal segments subrectangular; gnathopod 1 dactyl as a spine; gnathopod 2 subequal to pereiopod 3, palmar angle seta simple, carpal saw serrate, distal aspect of propodus blade-like, dactyl with 3 teeth, dactyl tip long and thick, palm oblique; pereiopods 3-4 claw dentate or bifid, pereiopods 3-7 dactyls dissimilar; pereiopods 5-7 dactyls without claws; pleopods as long fins; uropod 2 larger than uropod 1, uropod 1 outer ramus less than the inner ramus; telson short and fleshy.

**Distribution.** - 39° 02.4' S, 142° 37.8' E, Bass Strait.

**Habitat.** - Shelly sand

**Depth range.** - 121 m.

**Size.** - male, 1.7-1.9 mm.; female, 1.1-1.8 mm.

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**Ingolfiella beatricis** Ruffo & Vonk, 2001


**Diagnostic features.** - Ocular lobes developed; antennular flagellum medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 2 setae, outer lobe inner setae dentate, outer lobe outer setae bifid, outer lobe with 5 spines; palp subequal to outer lobe, palp with 2 setae; maxilla 2 with 3 setae; maxilliped claw falcate; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle seta simple, carpal saw absent, distal aspect of propodus blade-like, dactyl with 4 teeth, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws dentate to bifid; pereiopods 3-7 dactyls similar and produced with spurs; pereiopods 5-7 dactyls with claws; pleopods 1-3 on females present; pleopods as short fins; uropod 1 shorter than uropod 2, both short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.

**Distribution.** - 45° 59' 51" N., 14° 16' 15" E., Pajsarjeva Jama Cave, Pajsar, Vrhnika, Slovenia.

**Habitat.** - Stream in a cave

**Size.** - 2.0 mm.

Remarks: single specimen, probably a female, and interesting because it is an essentially alpine region.

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**Ingolfiella berrisfordi** Ruffo, 1974


**Diagnostic features.** - Optic lobes developed, antennular flagellum long and larger than basal peduncular segments, accessory flagellum with 2 segments; maxilla 1 palp bearing 4 or more setae, inner lobe with 2 setae, outer lobe with 5 spines and outer setae bifid, outer lobe inner setae dentate, palp longer than the outer lobe; maxilla 2 with 3 or 4 setae; maxillipede claw falcate; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle seta...
elongate, carpal saw serrate, distal propodus blade-like, dactyl with 3 teeth, palm oblique; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls dissimilar; pereiopods 5-7 dactyls without claws but produced as setae; pleopods in males as short fins; uropod 2 larger than uropod 1, uropod 1 outer ramus less than the inner ramus; telson short and fleshy.

_Distribution._ Blaauwberg Beach, Table Bay, Cape Town, South Africa.

_Habitat._ interstitial in sand

_Depth range._ sea level

_Size._ 1.61 mm.

**Ingolfiella britannica** Spooner, 1960


_Diagnostic features._ Ocular lobes developed; antenna 1 flagellum medium and larger than 1/2 basal peduncular segments, accessory flagellum of 3 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae dentate, outer lobe outer setae dentate, outer lobe with 6 spines, palp longer than outer lobe, palp with 4 or more setae; maxilla 2 with 5 or more setae; maxilliped claw as a spine with flanking setae; pereiond segments subrectangular; gnathopod 1 dactyl blade-like; gnathopod 2 larger than pereiopod 3, palmar angle seta elongate, carpal saw serrate, distal aspect of propodus unmodified, palm transverse, dactyl armed with 4 teeth, dactyl tip long and thin; pereiopods 3-4 claws simple, 3-7 dactyls dissimilar with ends produced as setae, 5-7 with claws; uropod 1 outer ramus less than half the inner ramus; uropod 2 longer than uropod 1; telson short and fleshy.

_Distribution._ 50° 11.4 ' N., 4° 16.6 ' W., 1 mile (1.7 km.) northwest of Eddystone Rock

_Habitat._ shell gravel

_Depth range._- 25 fathoms.

_Size._- male: 1.71 mm.

**Ingolfiella canariensis** Vonk & Sánchez, 1991

1991 _Ingolfiella canariensis_ Vonk & Sánchez, Hydrobiol. 223: 293-297, figs. 1-5.

_Diagnostic features._ Ocular lobes developed; antenna 1 flagellum medium and larger than 1/2 basal peduncular segment, accessory flagellum with 3 segments; maxilla 1 inner lobe with 2-3 setae, outer lobe inner setae dentate, outer lobe outer setae bifid, outer lobe with 6 spines, palp longer than the outer lobe and with 2 setae; maxilla 2 with 5 or more setae; maxilliped dactyl claw falcate; pereiond segments subrectangular; gnathopod 1 dactyl as a spine; gnathopod 2 subequa l to pereiopod 3, palmar angle seta elongate, carpal saw serrate, distal aspect of propodus unmodified, dactyl with 4 blade-like teeth, dactyl long and thin, palm transverse to oblique; pereiopods 3-4 claws dentate to bifid, pereiopods 3-7 dactyls dissimilar and distal ends produced as setae; pereiopods 5-7 dactyls with claws; female pleopods present and pleopods narrow; uropod 1 shorter than uropod 2, outer ramus more than 1/2 inner ramus; uropods 1 & 2 short; telson medium in length and fleshy.

_Distribution._- diverse beaches along the north coast of Tenerife between Punta Hidalgo (28° 32.7 ' N., 16° 20' W.) and Punta de Teno (28° 21' N., 16° 61' W.); (-27° 45' N., 18° W.) Tamaduste Harbor & J amaeos del Puerto, El Hierro; Canary Islands.

_Habitat._- beach sand; anchialine cave debris bottom
**Depth range.** - sea level.

**Size.** - 1.8 mm.

**Remarks.** - see Vonk & Sanchez (1991) for details of 10 beach localities on Tenerife, and 2 localities on El Hierro.

**Ingolfiella catalanensis** Coineau, 1963


**Diagnostic features.** - Optic lobes absent; antennular flagellum medium in size, accessory flagellum 3 segments; maxilla 1 inner lobe with 2 setae, outer lobe inner setae simple, outer lobe outer setae bifid and dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 2 setae; maxilla 2 with 3 setae; maxilliped dactyl claw as a single seta; pereonal segments elongate; gnathopod dactyl 1 with spines; gnathopod 2 smaller than pereiopod 3, palmar angle seta elongate, carpal saw serrate, distal aspect of propodus finger-like, dactyl with 3 teeth, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws dentate or bifid, pereiopods 3-7 dactyls similar, ends produced as setae, pereiopods 5-7 dactyls with claws; pleopods of male as short fins; uropod 1 & 2 subequal and short; uropod 1 outer ramus shorter than inner ramus; telson medium and fleshy.

**Distribution.** - 42° 34' N., 3° E., Tech valley, Pyrénées-Orientales, France; 40° N., 0° 01' E., Camino Donacion, Castellón, Spain.

**Habitat.** - well water.

**Depth range.** - 6 m.

**Size.** - male: 2.1 mm.

**Remarks.** - The French specimens came from a well 7 km from the sea, while the Spanish specimen was within 2.1 km of the Mediterranean.

**Ingolfiella cottarelli** Ruffo & Vigna Taglianti, 1989


**Diagnostic features.** - Ocular lobes absent; antennular flagellum medium, accessory flagellum with 3 segments; maxilla 1 inner lobe with 2 setae, outer lobe inner setae dentate, outer lobe outer setae dentate and bifid, outer lobe with 6 spines, palp subequal to outer lobe, palp with 3 setae; maxilla 2 with 4 setae; maxilliped dactyl claw as single seta; pereonal segments deeper than long; gnathopod dactyl with spines; gnathopod 2 smaller than pereiopod 3, palmar angle seta simple, carpal saw finely serrate, distal aspect of propodus unmodified, dactyl with 3 teeth, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws simple; pereiopods 3-7 dactyls similar, ends produced as spurs; pereiopods 5-7 with claws; pleopods 1-3 of female absent; pleopods as short fins; uropod 1 shorter than uropod 2, both uropods short; uropod 1 outer ramus more than 1/2 the inner ramus; telson short and fleshy.

**Distribution.** - 40° 54' 52" N., 2° 42' 31" E., Grotta del Papa, Tavolara Isl., northeastern Sardinia, Italy.

**Habitat.** - freshwater, cave pool

**Depth range.** - sea level.

**Size.** - Male: 2.3-2.5 mm.; female: 2.5-2.7 mm.

**Remarks.** - Used as a basis to develop a further sub-generic classification of *Ingolfiella.*
Ingolfiella fontinalis Stock, 1977

1977 Ingolfiella (Gevgeliella) fontinalis, - Stock, Bijdr. Dierk. 49: 86, fig. 5f.
1992 Ingolfiella (Antilleella) fontinalis, - Stock, Bocagiana 159: 5.

Diagnostic features. - Ocular lobes reduced; antenna 1 medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae simple, outer lobe outer setae dentate, outer lobe with 6 spines, palp larger than outer lobe, palp with 3 setae; maxilla 2 with 3-4 setae; maxilliped dactyl claw as a spine with flanking setae; pereiopods subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle setae angulate, carpal saw serrate, distal aspect of propodus finger-like, dactyl teeth as 3 blades, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls dissimilar, ends produced as spurs; pereiopods 5-7 dactyls with claws; pleopods 1-3 of female present; pleopods as long fins; uropod 1 shorter than uropod 2, both uropods short; uropod 1 outer ramus less than 1/2 the inner ramus; telson short and fleshy.

Distribution. - 12° 14' 34" N, 68° 17' 54" W, Bonaire.

Habitat. - Sand and calcareous gravel in a fast flowing spring issuing from the Fontein Cave.

Depth range. -
Size. - 2.0-2.5 mm.
Remarks. -

Ingolfiella fuscina Dojiri & Sieg, 1987


Diagnostic features. - Ocular lobe reduced; antenna 1 flagellum medium, accessory flagellum as 3 segments; maxilla 1 palp with 3 setae, outer lobe inner setae dentate, outer lobe outer setae bifid, outer lobe with 6 spines, palp longer than the outer lobe, palp with 3 setae; maxilla 2 with 5 or more setae; maxilliped dactyl claw falcate; pereiopods segments deeper than long; gnathopod 1 dactyl claw falcate; gnathopod 2 larger than pereiopod 3, palmar angle setae angulate, carpal saw absent, distal propodus finger- to blade-like, distal part of propodus unmodified, dactyl with 4 teeth, distal end long and thin, palm oblique to transverse; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls dissimilar, with ends produced as setae; pereiopods 5-7 dactyls with claws; pleopods 1-3 of females present; uropods 1 and 2 subequal and short; uropod 1 outer ramus more than 1/2 inner ramus; telson short and fleshy.

Distribution. - 32° 54' 06" N, 79° 11' 58" W, and 32° 29' 06" N, 78° 49' 18" W, off S. Carolina; 28° 42' 00" N, 84° 20' 01" W, off Crystal River, 29° 55' 59" N, 86° 06' 29" W, off Panama City, 29° 36' 00" N, 80° 10' 59" W, and 29° 40' 00" N, 83° 15' 28" W, off Tampa Bay, Florida.

Habitat. - Mud bottoms

Depth range. - 17-151 m.
Size. - male, 1.25-1.33 mm; female, 1.43-1.8 mm.
Remarks. - 5 males, 29 females

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**Ingolfiella grandispina** Stock, 1979

1979 *Ingolfiella (Trianguliella?) grandispina* Stock, Bijdr. Dierk. 49: 89-92, figs. 9-11.

**Diagnostic features.** - Ocular lobes developed; antenna 1 flagellum medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 4 or more setae, outer lobe inner setae dentate, outer lobe outer setae bifid, outer lobe with 6 spines, palp subequal to outer lobe and bearing 4 or more setae, palp longer than the outer lobe; maxilla 2 with 4 setae; maxilliped dactyl claw falcate; pereiopodal segments.; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle setae elongate, carpal saw absent, distal propodus blade-like, dactyl with 3 blades, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls dissimilar with ends produced as spurs and setae; pereiopods 5-7 with claws; pleopods 1-3 of female present; pleopods of male as short fins; uropod 2 larger than uropod 1, uropod 1 outer ramus less than the inner ramus; uropods 1 and 2 short; telson short and fleshy.

**Distribution.** - 12°08' 20" N., 68°59' 05" W. near entry to Blauw Baai Cave, Curacao.

**Habitat.** - Anchialine sand and gravel, during marine prevailing season.

**Depth range.** - Sea level.

**Size.** - Female, 2.28 mm.

**Remarks.** - Single specimen

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**Ingolfiella ischitana** Schiecke, 1976


**Diagnostic features.** - Ocular lobes developed; antenna 1 flagellum medium, accessory flagellum as 3 segments; maxilla inner lobe with 2 setae, outer lobe inner setae simple, outer lobe outer setae dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 3 setae; maxilla 2 with 4 setae; maxilliped dactyl claw with single seta; pereiopodal segments subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle setae angulate, carpal saw serrate, distal propodus finger-like, dactyl with 3 teeth, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls dissimilar, dactyl ends not produced; pereiopods 5-7 dactyls without claws; pleopods 1-3 of females present; pleopods as short fins; uropod 1 and 2 subequal and short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.

**Distribution.** - 40°44' N., 13°58' E., Ischia, Italy.

**Habitat.** - Coarse sand

**Depth range.** - 6-30 m.

**Size.** - Male, 1.7 mm; female, 1.8 mm.

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**Ingolfiella kapuri** Coineau & Rao, 1973

**Diagnostic features.** Ocular lobes developed; antennular flagellum medium, accessory flagellum as 3 segments; maxilla 1 ?; maxilla ?; maxilliped ?; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle setae angulate, carpal saw serrate, distal propodus blade-like, dactyl with 4 teeth, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyl dissimilar, ends not produced; pereiopods 5-6 dactyls with claws; pleopods 1-3 of female present; pleopods as short fins; uropods 1 and 2 subequal and short; uropod 1 outer ramus more than 1/2 inner ramus; telson short and fleshy.

**Distribution.** Andaman and Nicobar Islands.

**Habitat.** Marine, muddy shell debris in the intertidal

**Depth range.** 5-30 cm. below the surface

**Size.** 1.11-1.27 mm.

**Remarks.** 5 specimens known. However, the listed material on p. 79 comes from a total of 9 localities from which the authors collected specimens.

*Ingolfiella littoralis* Hansen, 1903


**Diagnostic features.** Ocular lobes developed, antennular flagellum short, accessory flagellum as 4 segments; maxilla 1 ?; maxilla ?; maxilliped ?; gnathopod 1 dactyl simple; gnathopod 2 palmar angle spine elongate, carpal saw serrate, distal propodus unmodified, dactyl with 3 teeth, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyl dissimilar and not produced; pereiopods 5-7 dactyls without claws; pleopods 1-3 of females present; pleopods as short fins; uropod 1 less than uropod 2, both short; uropod 1 outer ramus less than 1/2 inner ramus; telson short and fleshy.

**Distribution.** 13° 8.5' N., 100° 49' E., Koh Chang Island, Gulf of Thailand.

**Habitat.** Coral sand.

**Depth range.** 2 m.

**Size.** 1.5 mm.

**Remarks.** Known from a single specimen. Although this species frequently figures in the literature as a point of comparison with other species, it is not in fact very well described. So much so, we did not include it in our phylogenetic analysis because there were simply too many question marks for our character set. We suspect it would emerge rather high in the clade of marine species.

*Ingolfiella longipes* Stock, Sket, & Iliffe, 1987

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**Diagnostic features.** - Ocular lobes developed; antenna 1 flagellum medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae simple, outer lobe outer setae dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 2 setae; maxilla 2 with 3 or 5 setae; maxilliped dactyl claw as single seta; pereiopods subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle seta elongate, carpal saw serrate, distal part of propodus unmodified, dactyl with 4 teeth, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls dissimilar, dactyl ends not produced; pereiopods 5-7 dactyl with claws; pleopods of female present, pleopods as short fins; uropod 1 & 2 subequal and short; uropod 1 outer ramus more than half the inner ramus; telson short and fleshy.

**Distribution.** - Walsingham Sink Cave, Bermuda.

**Habitat.** - brackish pool from cave

**Depth range.** - 1 m. (?)

**Size.** - female, 1.6 mm.

**Remarks.** - single specimen. Salinity at the collection site ranges from ~ 17% at the surface of the pool to 32% at 1 m depth. It is assumed that the ingolfiellid was collected from the sediment at the bottom of the pool (not clear from text).

This species lacks any distinguishing autapomorphic features, except those that it shares with its sister clade (and these of low consistency as well). Either this species is truly primitive with regard to the members of the sister clade, or it is simply too poorly known to adequately characterize it. We suspect the latter.

*Ingolfiella macedonica* Karaman, 1959


**Diagnostic features.** - Ocular lobes absent; antenna 1 accessory flagellum as 3 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae simple, outer lobe outer setae dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 3 setae; maxilla 2 with 3-4 setae; maxilliped dactyl claw as robust spine; pereiopods subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle seta simple, carpal saw absent, distal propodus tooth-like, dactyl teeth as 4 blades, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws simple; pereiopods 3-7 dactyls not produced, dactyl ends not produced; pereiopods 5-7 with claws; pleopods 1-3 on female present; uropods 1 and 2 short; uropod 1 outer ramus more than 1/2 the length of inner ramus.

**Distribution.** - ~42° N., 21° 42.2' E., near the Pcinja River, 25 km. east of Skopje, Macedonia.

**Habitat.** - ground water

**Size.** - 2.2 mm.
Ingolfiella manni Noodt, 1961

1965 Ingolfiella manni, - Noodt, Crustaceana. 9: 19, fig. 2, table 1.  

Diagnostic features.- Ocular lobes absent; antenna 1 medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 3 setae, outer lobe inner setae dentate, outer lobe outer setae dentate, outer lobe with 5 spines, palp smaller than outer lobe, palp with 3 setae; maxilla 2 with 4 setae; maxilliped dactyl claws robust spine; pereiopod segments subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle seta angulate, carpal saw serrate, distal aspect of propodus blade-like, dactyl with 3 teeth, dactyl tip simple and thick, palm transverse; pereiopods 3-4 claws simple; pereiopods 3-7 dactyls similar and not produced; pereiopods 5-7 with claws; pleopods 1-3 of female present; pleopods as short fins; uropod 1 subequal to uropod 2, both short; uropod 1 outer ramus more than 1/2 inner ramus; telson short and fleshy.

Distribution.- (-25° S, 70° 29' W.) Paposo, (-25° 22.5' S, 70° 32' W.) Taltal, province of Antofagasta, northern Chile; (-31° 36' S, 71° 9.5' W.) Illapel, central Chile.  
Habitat.- Brackish and limnic ground water

Depth range.- Altitude 800 m, 1000 m from sea.

Size.- Males: 1.35 mm., female: 1.55 mm..  
Remarks.- ~ 120 specimens known.

Ingolfiella margaritae Stock, 1979

1979 Ingolfiella (Gevgeliella) margaritae Stock, Bijdr. Dierk.. 49: 86-89, figs. 6-8.  
1992 Ingolfiella (Antilleella) margaritae, - Stock, Bocagiana. 159: 5.

Diagnostic features.- Ocular lobes absent; antenna 1 medium, accessory flagellum as 3 segments; maxilla 1s ?; maxilla 2; maxilliped dactyl claw as robust spine; pereiopod segments gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle seta elongate, carpal saw serrate, distal propodus finger-like, dactyl teeth as 3 blades, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls similar and produced as spurs; pereiopods 5-7 dactyl with claws; pleopods of female ?; pleopods as short-fins; uropod 1 and 2 subequal and short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.  
Distribution.- 11° 05' 53'' N, 63° 51' 35'' W., Isla de Margarita, Venezuela.  
Habitat.- Freshwater well

Depth range.- 4 m. in a well 9 m. deep

Size.- Male, 2.07 mm.  
Remarks.- Single specimen

Ingolfiella petkovskii Karaman, 1957

1957 Ingolfiella petkovskii Karaman, Folia Balcanica 1(7), 4 pp..  
Diagnostic features. - Ocular lobes absent; antenna 1 medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 3 setae, outer lobe inner setae dentate, outer lobe outer setae dentate, outer lobe with 6 spines, palp larger than outer lobe, palp with 2 setae; maxilla 2 with 4 setae; maxilliped dactyl claw as robust spine; pereion abdominal segments elongate; gnathopod 1 dactyl serrate; gnathopod 2 larger than pereiopod 3, palmar angle seta simple, carpal saw serrate, distal aspect of propodus blade-like, dactyl teeth as 3 blades, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws dentate, pereiopods dactyls similar, dactyls distally produced with spurs; pereiopods 5-7 with claws; pleopods as short fins; uropod 1 shorter than uropod 2, both short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.

Distribution. - near Gjevgjelija, Macedonia; 42° 9.5' N., 26°34.8' E., along the Tundzha River, near Elkhovo, Bulgaria; 38° 54.5' N., 23° 2.5' E., Euboea, Greece.

Habitat. - ground water

Depth range. - ~50 m (in Macedonia).

Size. - < 2.0 mm.
Diagnostic features.- Ocular lobes developed; antenna 1 flagellum medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae dentate, outer lobe outer setae bifid and dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 3 setae; maxillae ?, maxilliped dactyl claws as robust spine; pereiopods 2-4, palmar angle setae elongate, carpal saw serrate, distal aspect of propodus unmodified, dactyl with 4 teeth, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws dentate or bifid, pereiopods 3-7 dactyls dissimilar with ends produced as spurs; pereiopods 5-7 dactyls with claws; pleopods 1-3 on females present; pleopods as short fins; uropods 1 shorter than uropod 2, both short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.

Distribution.- 12° 07' 42" N., 68° 58' 18" W., 500 m. west of Piscadera, Curacao.

Habitat.- coarse coral sand

Depth range.- 4 m. (from top 30 cm. of sand).

Size.- female: 1.26-1.58 mm.

Remarks.- females only collected

**Ingolfiella ruffoi** Siewing, 1958


**Diagnostic features.**- Ocular lobes developed; antenna 1 flagellum medium, accessory flagellum with 2 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae dentate, outer lobe outer setae dentate, outer lobe with 5 spines, palp longer than the outer lobe and with 2 setae; maxilla 2 with 3 setae; maxilliped dactyl claw as single seta; pereiopods subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 larger than pereiopod 3, palmar angle seta elongate, carpal saw ?, distal propodus unmodified, dactyl with 4 teeth, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws dentate; pereiopods 3-7 dactyl ends with claws; pereiopods 5-7 dactyls with claws; pleopods 1-3 on females present; pleopods as long fins; uropods 1 and 2 subequal and short; uropod 1 outer ramus less than half the inner ramus; telson short and fleshy.

**Distribution.**- ~ 16° 32.4' S., 71° 21.6' W., southern Peruvian coast, 40 km. north of Ilo.

**Habitat.**- ground water (with true marine salinity)

**Depth range.**- intertidal

**Size.**- 1.12-1.52 mm.


**Diagnostic features.**- Ocular lobes absent, antenna 1 flagellum medium, accessory lobe as 3 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae simple, outer lobe outer setae dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 2 setae; maxilla...
2 with 3-4 setae; maxilliped lateral propodal setae present, dactyl claw with single seta; pereiopod segments subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle seta elongate, carpal saw serrate, distal aspect of propodus blade-like, dactyl teeth as 3 blades, dactyl tip long and thick, palm transverse; pereiopods 3-4 claws dentate of bifid; pereiopods 3-7 dactyls similar and distally produced with setae; pereiopods 5-7 dactyls with claws; pleopods 1-3 on female present; pleopods as long fins; uropod 1 shorter than uropod 2, both short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.

**Distribution.** - 28° 30' N., 13° 51' W., Las Playas, Fuerteventura, Canary Islands.

**Habitat.** - Slightly brackish well (300 m distance to sea).

**Size.** - 2.22 mm.

**Remarks.** - A single specimen known.

**Ingolfiella tabularis** Stock, 1977

1979 *Ingolfiella (Gevgeliella) tabularis* Stock, Bijdr. Dierk. 49: 85-86, figs. 2-4, st.

**Diagnostic features.** - Ocular lobes absent, antenna 1 flagellum medium, accessory lobe as 3 segments; maxilla 1 inner lobe with 3 setae, outer lobe inner setae dentate, outer lobe outer setae bifid and dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 3 setae; maxilla 2 with 3-4 setae; maxilliped dactyl claw falcate; pereiopods 3-4 claws dentate of bifid; gnathopod 1 dactyl serrate; gnathopod 2 palmar angle seta elongate, carpal saw serrate, distal aspect of propodus blade-like, dactyl teeth as 3 blades, dactyl tip long and thin, palm transverse; pereiopods 3-7 dactyls similar and produced as spurs; pereiopods 5-7 dactyls with claws; pleopods 1-3 present in female; pleopods as long fins; uropod shorter than uropod 2, both short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.

**Distribution.** - 12° 22' 19" N., 69° 06' 49" W., near Boca Tabla Cave, and 12° 13' 12" N., 68° 59' 58" W., Sjingoet Cave, Curaçao; 12° 32' 26" N., 69° 57' 01" W. Andicuri Cave, Aruba.

**Habitat.** - Marine beach sand below entry to the Boca Tabla Cave; anchialine lake in Sjingoet Cave; wave washed marine beach.

**Depth range.** - In caves at 0-3 m.; ~ sea level for beaches (Sta. 78/305)

**Size.** - Male: 1.9 mm; female: 1.5 mm.

**Remarks.** - 3 male, 6 female, + 35 specimens of both sexes. This species appears to occur in both freshwater and marginal marine habitats.

**Ingolfiella thibaudi** Coineau, 1968


**Diagnostic features.** - Ocular lobes absent, antenna 1 flagellum medium, accessory lobe as 3 segments; maxilla 1 inner lobe with 3 setae, outer lobe inner setae simple, outer lobe outer setae simple, bifid or dentate, outer lobe with 6 spines, palp subequal to outer lobe and with 2
setae; maxilla 2 with 3 setae; maxilliped lateral propodal setae present, dactyl claw as robust spine; pereionites segments 2; gnathopod 1 dactyl as spine; gnathopod 2 palmar angle seta elongate, carpal saw serrate, distal aspect of propodus finger-like, dactyl with 3 teeth, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws simple; pereiopods 3-7 dactyli similar and not produced distally; pereiopods 5-7 with claws; pleopods 1-3 of females absent; pleopods as short fins; uropod 1 and 2 subequal and short; uropod 1 outer ramus shorter than inner ramus; telson medium and fleshy.

**Distribution.** -44° 7.5' N., 4° 5.3' E., St. Hilaire-de-Brethmans (valley of the Gardon d’Alès) Gard; ~ 44° 26.5' N., 4° 7' E., St. Alban-sous-Sampzon (valley Chassezac), Ardèche; ~ 44° 27.5' N., 4° 19.5' E. near Ruoms, along the Ardèche River, France.

**Habitat.** - groundwater wells

**Size.** - 2.0-2.29 mm.

**Remarks.** - 3 females, 1 male, + 3 additional individuals

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**Ingolfiella unguiculata** Stock, 1992


**Diagnostic features.** - Ocular lobes reduced; antenna 1 flagellum medium, accessory flagellum 2 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae simple, outer lobe outer setae simple, bifid and dentate, outer lobe with 5 spines, palp larger than outer lobe, palp with 3 setae; maxilla 2 with 4 setae; maxilliped dactyl claw as robust spine; pereionites segments subrectangular; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle spine elongate, carpal saw serrate, distal paces of propodus finger-like, dactyl with either 3 teeth or 3 blades, dactyl tip long and thin, palm transverse; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyli dissimilar, produced as spurs; pereiopods 5-7 dactyli with claws; uropod 1 shorter than uropod 2, both short; uropod 1 outer ramus shorter than inner ramus; telson medium and fleshy.

**Distribution.** - ~44° 7.5' N., 4° 5.3' E., St. Hilaire-de-Brethmans (valley of the Gardon d’Alès) Gard; ~ 44° 26.5' N., 4° 7' E., St. Alban-sous-Sampzon (valley Chassezac), Ardèche; ~ 44° 27.5' N., 4° 19.5' E. near Ruoms, along the Ardèche River, France.

**Habitat.** - anchialine lagoon, in coarse sand

**Depth range.** - sea level.

**Size.** - 1.08-1.74 mm.

**Remarks.** - 32 specimens collected

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**Ingolfiella uspallatae** Noodt, 1965

1965 *Ingolfiella uspallatae* Noodt, Crustaceana. 9: 25-27, figs. 3-19.


**Diagnostic features.** - Ocular lobe absent; antenna 1 flagellum longer than peduncular segment, accessory flagellum as 3 segments; maxilla 1 inner lobe with 1 seta, outer lobe inner setae simple, outer lobe outer setae bifid and dentate, outer lobe with 5 spines, palp smaller than outer lobe, palp with 1 seta; maxilla 2 with 3 setae; maxilliped dactyl claw as a spine with flanking setae; pereionites segments 2; gnathopod 1 dactyls serrate; gnathopod 2 palmar angle seta elongate, carpal saw serrate, distal aspect of propodus blade-like, dactyl with 3 teeth, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws simple; pereiopods 3-7 dactyli similar and not produced; pereiopod 5-7 dactyli with claws; pleopods 1-3 on females present; pleopods as short fins; uropod 1 shorter than uropod 2, both short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.

**Distribution.** - ~32° 41.3' S., 69° 22' W., Uspallata Pass, province of Medoza, Argentina.

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Habitat.- ground water
Depth range.- at 2000 m in Andes.
Size.- female: 2.5 mm.
Remarks.- single specimen known

**Ingolfiella vandeli** Bou, 1970


**Diagnostic features.**- Ocular lobes absent, antennular flagellum medium, accessory flagellum as 3 segments; maxilla 1 inner lobe with 2 setae, outer lobe inner setae dentate, outer lobe outer setae dentate, outer lobe with 6 spines, palp subequal to outer lobe, palp with 2 setae; maxilla ?, maxilliped dactyl claw as robust spine; pereion abdominal segments ?; gnathopod 1 dactyl with spines; gnathopod 2 palmar angle seta elongate, carpal saw serrate, distal aspect of propodus blade-like, dactyl with 3 teeth, dactyl long and thin, palm oblique; pereiopods 3-4 claws dentate, pereiopods 3-7 dactyls similar with ends produced as spurs; pereiopods 5-7 dactyls with claws; pleopods 1-3 of female present; pleopods as short fins; uropod 1 and 2 subequal and short; uropod 1 outer ramus shorter than inner ramus; telson short and fleshy.

**Distribution.**- Along the rivers (37° 44' N., 21° 51' E.) Ladon (37° 39' N., 21° 41' E.) and Alpheios [Peleponnisos], and (38° 23.5' N., 21° 34.5' E.) Evinos [Sterea], Greece.

**Habitat.**- Fluvial deposits

**Size.**- male: 1.5-1.7 mm; female: 1.43-1.87 mm.

**Remarks.**- 6 males, 17 females.

**Ingolfiella xarifae** Ruffo, 1966


**Diagnostic features.**- Ocular lobes developed; antenna 1 flagellum medium, accessory flagellum as 3 segments; maxilla 1 ?; maxilla ?; maxilliped ?; pereion abdominal segments ?; gnathopod 1 dactyl serrate; gnathopod 2 subequal to pereiopod 3, palmar angle seta elongate, carpal saw absent, distal part of propodus unmodified, dactyl with 4 teeth, dactyl tip long and thin, palm oblique; pereiopods 3-4 claws dentate or bifid; pereiopods 3-7 dactyls dissimilar and produced with spurs, pereiopods 5-7 dactyls with claws; pleopods 1-3 on female present; pleopods as short fins; uropod 1 shorter than uropod 2, both short; uropod 1 outer ramus more than 1/2 inner ramus; uropod 2 longer than uropod 1; telson medium in length and fleshy.

**Distribution.**- 4° 18' N., 73° 00' E., Rasdhu Atoll, Maldives.

**Habitat.**- Marine, out of coral sand (Favites)

**Depth range.**- ~ sea level.

**Size.**- 1.2 mm.

**Ingolfiella sp. A**
1999 *Ingolfiella* sp., personal communication from Don Cadien, Mar. Biol. Lab – JWPCP, California, USA.

**Distribution.** Prince William Sound, Alaska.

**Habitat.** Marine

**Depth range.** ~ subtidal.

**Remarks.** Collected as part of the clean-up after the Exxon Valdez oil spill, the specimen(s) are under legal lock and key at Dames & Moore, Inc. and unavailable for study.

*Ingolfiella* sp. B

1999 *Ingolfiella* sp., personal communication from Don Cadien, Mar. Biol. Lab – JWPCP, California, USA.

**Distribution.** British Virgin Islands.

**Habitat.** Coarse coral sand

**Depth range.** 12 m.

*Ingolfiella* sp. C


**Distribution.** Okinawa and Iriomote (Ryuku Islands, Japan).

**Habitat.** Fresh and brackish waters.

**Remarks.** Single specimen, now lost.

Bibliography


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THE GROUNDWATER AMPHIPOD *Bogidiella turcica* n. sp. AND OTHER BOGIDIELLIDS (MALACOSTRACA, AMPHIPODA) IN SOUTHWEST TURKEY

BY

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ABSTRACT

*Bogidiella turcica* n. sp. and the male of *Bogidiella minotaurus* Ruffo & Schiecke, 1976 are described from, respectively, a brackish littoral submarine spring and the interstitial of a river mouth in Turkey. *Bogidiella longiflagellum* S. Karaman, 1959 was found in 13 inland wells and riverbeds in the region between Izmir and Antalya (Anatolia). Morphological variation within and between three populations of *B. longiflagellum* from distant localities has been measured by comparing 8 specimens per station.

RÉSUMÉ

*Bogidiella turcica* sp. nov. et le mâle de *Bogidiella minotaurus* Ruffo & Schiecke, 1976 sont décrits de, respectivement, une source littorale sous-marine saumâtre et de l’interstitiel de l’embouchure d’une rivière en Turquie. *Bogidiella longiflagellum* S. Karaman, 1959 a été trouvé en 13 puits et lits de rivière de l’intérieur, entre Izmir et Antalya (Anatolie). La variation morphologique dans et entre 3 populations de *B. longiflagellum* a été mesurée par comparaison de 8 spécimens par station.

INTRODUCTION

In the spring of 1987 the Dutch biospeleological group “Speleo Nederland” and the Turkish speleological society “M.A.D.” sampled some 100 groundwater localities in southwestern Turkey. This was done along the Aegean and

*) Netherlands Biospeleological Explorations in Turkey, 6.
Mediterranean shores and in the mountainous interior (Taurus Mountains). The most suitable places for collecting groundwater fauna along the coast and on the coastal plains of Anatolia are ancient, shallow wells, the underflow of permanent rivers, and the fresh or oligohaline interstitial waters in beds of intermittent rivers cutting marine beaches. This region has already been sampled by an earlier expedition of the Zoological Institute of the University of Rome in 1970-71, and they mentioned the presence of the genus *Bogidiella* Hertzog, 1936 (cf. Ruffo & Vigna Taglianti, 1987).

The Dutch expedition also reported bogidiellids. *Bogidiella longiflagellum* S. Karaman, 1959 occurred in most instances: 13 times out of 15 stations. This species has a large distribution range, viz., South Yugoslavia, Greece, and Anatolia so far.

The new species *Bogidiella turcica* appeared in a coastal locality with upwelling brackish water. All three specimens lack their seventh pereiopod and were damaged in some other respects, too. A description is made here, combining parts of two specimens. Sex could not be determined.

*Bogidiella minotaurus* Ruffo & Schiecke, 1976 had been described from the Greek island of Crete. It was collected from the interstitial of a marine beach with coarse sand, and only females could be identified. Karaman (1979: 21) re-examined the material and reported males, but defining and portraying them only by some details in modified spines on the rami of the second uropod.

The specimens of *B. minotaurus* from Turkey were brought to the surface with a Bou-Rouch pump at the mouth of the river Göynük, near Kemer (map, fig. 7) at sea level but in purely fresh water. Over a hundred specimens were collected from which 4 males could be identified. The males are usually longer than the females, have larger gnathopods, and possess a 3-segmented accessory flagellum on the first antenna, as opposed to the females with a 2-segmented accessory flagellum. Males lack, however, modified spines on the second uropod. Surprisingly, male juveniles could not be recognized.

The objectives of this study are: (a) To document morphological variation within and between 3 populations of *Bogidiella longiflagellum*. (b) To redescribe the male of *B. minotaurus*, now found outside the island of Crete in a nearcoast locality near Kemer, Anatolia. (c) To describe a new species, *B. turcica*.

**MATERIAL**

See table I.

See table I.
### TABLE I

List of all stations that yielded *Bogidiella* with data on conductivity (Cl microSiemens/cm) and chlorine content of the water (Cl⁻ mg/l) and accompanying fauna

<table>
<thead>
<tr>
<th>Station</th>
<th>Cl μS cm⁻¹</th>
<th>Cl⁻ mg/l</th>
<th>Specimens</th>
<th>Bogidiellids</th>
<th>Accompanying stygofauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>87-5/6</td>
<td>835</td>
<td>116</td>
<td>2</td>
<td><em>B. longiflagellum</em></td>
<td><em>Asellus aquaticus</em> (Linnaeus, 1758),</td>
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<td></td>
<td></td>
<td><em>Microcharon anatolicus</em> Pesc &amp; Galassi, 1990,</td>
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<td></td>
<td><em>Niphargus sp.</em></td>
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<tr>
<td>87-5/5</td>
<td>540</td>
<td>45</td>
<td>8</td>
<td><em>B. longiflagellum</em></td>
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<tr>
<td>87-5/8</td>
<td>505</td>
<td>44</td>
<td>3</td>
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<td><em>Niphargus sp.</em></td>
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<td>87-5/11</td>
<td>605</td>
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<td>333</td>
<td>16</td>
<td>43</td>
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<td><em>Asellus aquaticus</em>, <em>Jaera nordmanni aff. massiliensis</em> Lemercier, 1960,</td>
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<td><em>Microcharon ullaes</em>, <em>Microparasellus sp.</em>, <em>Niphargus sp.</em>, <em>Turcolana smyrneae</em></td>
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<td><em>Botosaneanus &amp; Notenboom, 1989</em></td>
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<tr>
<td>87-5/33</td>
<td>390</td>
<td>36</td>
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<td><em>B. longiflagellum</em></td>
<td><em>Microcharon ullaes</em>, <em>Microparasellus sp.</em>, <em>Niphargus sp.</em>, <em>Turcolana smyrneae</em></td>
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<td><em>Botosaneanus &amp; Notenboom, 1989</em></td>
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<td>Station</td>
<td>Cl ( \mu S ) cm(^{-1})</td>
<td>Cl(^-) mg/l</td>
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<td><em>Microparassellus</em> sp., <em>Niphargus</em> sp.</td>
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<td><em>Proasellus</em> sp.</td>
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<td><em>Turiolana adaliae</em></td>
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<td>Botosaneanu &amp; Notenboom, 1989</td>
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<td><em>Niphargus</em> sp.</td>
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</table>

**Family BOGIIDIELLIDAE** Hertzog, 1936

*Bogidiella* Hertzog, 1933

*Bogidiella longiflagellum* S. Karaman, 1959

Material. — Sta. 87-5/6, Vilâyet İzmir, in a pit dug at a sandy beach along the coast 1 km SW of Sigâcik, UTM coordinates MC7928, sea level: 2 specimens.

Sta. 87-5/5, Vilâyet İzmir, about 1 km E of mosque of Sigâcik, 10 m W of road to Seferihisar, UTM coordinates MC8227, alt. 10 m: 8 specimens.

Sta. 87-5/8, Vilâyet İzmir, about 900 m SW of mosque of Seferihisar, 200 m W of the road to Tepecik, 50 m S of dry riverbed, UTM coordinates MC8526, alt. 20 m: 3 specimens.

Sta. 87-5/11, Vilâyet İzmir, about 400 m N of Haritacilar, about 300 m from the coast, UTM coordinates MC8423, sea level: 22 specimens.

Sta. 87-5/18, Vilâyet Müğla, Bou-Rouch pump in Kamis Çay river near crossing with road 330 to Milas, 900 m W of Yatagan, UTM coordinates NB9834, alt. 400 m, temp. 18.8°C: 43 specimens.

Sta. 87-5/33, Vilâyet İzmir, Bou-Rouch pump in Derebagaz river, 6.5 km upstream of Gümüşsu, UTM coordinates NC0619, alt. 10 m, temp. 17.3°C: about 170 specimens.

Sta. 87-5/51a, b, Vilâyet Burdur, Insuyu magarası cave, 8.5 km SE of Burdur, about 900 m E of the road to Antalya, UTM coordinates TG6773, alt. 1160 m, temp. 13.2°C: about 100 specimens.

Sta. 87-5/54, Vilâyet Burdur, well 0.7 km SW of Incir Han, about 6 km WNW of Buçak, UTM coordinates TG8153, alt. 750 m, temp. 12.0°C: 4 specimens.

Sta. 87-6/1, Vilâyet Antalya, Bou-Rouch pump in Karpuzçay river, 5.5 km E of Kisi lot, UTM coordinates UF7665, alt. 20 m, temp. 18.3°C: about 100 specimens.

Sta. 87-6/5, Vilâyet Antalya, well just E of dust road to Tülkiler, about 500 m W of crossing with road to Barage Oymapınar, about 11.5 km NE of Manavgat, UTM coordinates UF6786, alt. about 50 m, temp. 15.5°C: 1 specimen.

Sta. 87-6/15, Vilâyet Antalya, well 50 m W of road from Manavgat to Oymapınar, 10 km NE of Manavgat, along temporary river, UTM coordinates UF6780, alt. 40 m, temp. 20.0°C: 2 specimens.

Sta. 87-6/22, Vilâyet Antalya, fixed pump in garden just S of local road to Belbidi, about 6 km N of Kemer, 20 m from the sea, UTM coordinates TF8061, sea level, temp. 17.8°C: 10 specimens.
**BOGIDIELLA TURCICA NOV. IN SW TURKEY**

**Bogidiella turcica** n. sp. (figs. 1-3)

Material. — 1 holotype, 1.2 mm, sex unknown, 2 paratypes, Sta. 87-5/36 (ZMA Amph. nr. 204350) Vilâyet Mugla, Bou-Rouch pump in littoral submarine brackish springs, 2 km S of Güvercencilik, 12 km S of Gülük, N of the road Milas-Bodrum, UTM coordinates NB5110, sea level, temp. 18.5°C, Cl- 7.1 g/l.

Description. — Body length of the three specimens varying from 1.2 to 1.9 mm.

First antenna (fig. 1d) relatively short; flagellum consists of 7 segments; accessory flagellum 2-segmented, overreaches the third flagellum segment. Aesthetascs on third, fifth, sixth, and apically on seventh flagellum segment. They have a short basal stalk and a long, transparent sensorial part.

Second antenna (fig. 1b) shorter than first antenna; flagellum 5-segmented; small aesthetascs on third and last segment.

Mandible (fig. 1c, f) not symmetrical. Left mandible with pointed incisor (fig. 1c) and 3-toothed lacinia; spine row consisting of 2 finely serrate spines and 3 smaller, smooth spines; molar with subapical 2-segmented spiniform process (molar seta). Palp 3-segmented; segment 1 short, unarmed; segment 2 with 1 small, subapical seta; segment 3 with 4 apical setae and short, irregular setae along the outer margin. Right mandible (fig. 1f) with blunt incisor and 4 or 5-toothed lacinia; spine row of two spines; molar without spiniform process.

Upper lip (fig. 1g) with small tufts of hairs on both sides of anterior margin.

Lower lip (fig. 2c) with rounded mandibular lobe and small tufts of hairs on inner margin of outer lobe.

Maxilla 1 (fig. 2a, b) with 2-segmented palp with 3 apical setae; outer lobe with 7 spines of which 2 bear a denticle on inner margin in right maxilla but which are smooth in left maxilla; inner lobe with 1 seta on the left maxilla and 2 on the right maxilla.

Maxilla 2 (fig. 1e) with 8 setae on outer lobe and 7 on inner lobe.

Maxillipede (fig. 2d) with short inner and outer lobe; inner lobe with 2 thick apical spines; outer lobe with 3 apical spines, 2 apical setae and 1 lateral seta; palp carpal segment with 4 marginal setae; propodal segment with 4 distal setae and a row of fine setae laterally; claw with lateral row of fine setae and 1 terminal and 1 subterminal seta.

Gnathopod 1 (fig. 2f). Coxa (fig. 2i) subrectangular, no setules; basis with 1 seta on posterior margin; merus with 1 seta and many setules forming a dense patch; carpus with posterior projection covered with setules and 3 longer setae; propodus with curved palmar margin ornamented with row of tiny denticles; palmar edge armed with 3 stout setae and 6 smaller setules, irregularly placed.
Fig. 1. *Bogidiella turcica* n. sp., holotype, 1.2 mm. a, habitus (scale A); b, second antenna (B); c, left mandible (C); d, first antenna (B); e, second maxilla (C); f, right mandible (C); g, upper lip (C).
Fig. 2. Bogidiella turcica n. sp., a-f, i, holotype, 1.2 mm. a, left first maxilla (scale B); b, right first maxilla (B); c, lower lip (B); d, maxillipede (B); e, second gnathopod (A); f, first gnathopod (A); g, paratype, 1.2 mm, third pereiopod (?); h, paratype, 1.9 mm, fourth pereiopod (A); i, coxal plates of gnathopods 1 and 2, and pereiopods 3 and 4 (A); j, coxal plates of pereiopods 5 to 7 (A).
along the posterior rim; claw with 1 tooth on inner margin, no clear division between dactylus and unguis.

Gnathopod 2 (fig. 2e). Coxa (fig. 2i) subrectangular with rounded anteroventral corner and 1 spinule at posteroventral corner; basis with 1 setule on posterior margin and 1 setule on anterior margin; ischium with 1 setule and a slightly barbed posterior margin; merus with 1 setule; carpus with fine, short setae on posterior margin and 5 longer setae; propodus with curved palmar edge irregularly ornamented with rows of fine denticles, on palmar corner 2 thick setae and 2 setules, another 3 setules along the distal side; claw with 1 tooth on inner margin, no division between dactylus and unguis.

Pereiopod 3 (fig. 2g). Coxa (fig. 2i) with 1 spine on posteroventral corner; carpus and propodus with 2 setae on posterior margin.

Pereiopod 4 (fig. 2h). Coxa (fig. 2i) with 1 spine on anteroventral corner and 1 spine on posteroventral corner; carpus and propodus with 2 setae on posterior margin.

Pereiopod 5 (fig. 3a) short and robust. Coxa (fig. 2j) of triangular shape with 1 seta, midventrally. Distal margins of ischium, merus, carpus and propodus armed with strong setae; dactylus short.

Pereiopod 6 (fig. 3b) more slender than P5. Coxa (fig. 2j) small and subtriangular, no setae; propodus with 2 spines on anterior margin; dactylus slender, unguis small.

Pereiopod 7 lacking on all three specimens (broken off). Coxa (fig. 2j) triangular with anterior notch and anterior setule.

Epimeral plates (fig. 1a) with almost rectangular posteroventral corner; posterodistal angle of each plate with setule in small notch.

Pleopods 1-3 (fig. 3c, d, e) biramous. Exopod 3-segmented with 2 brushed setae per segment; exopod consists of 1 segment only; subdistrally the peduncle bears 2 coupling hooks.

Uropod 1 (fig. 3f) without basoventral spine on peduncle; rami of equal length, inner ramus with 2 distal setae and 2 implanted on the dorsolateral margin, outer ramus with only 1 dorsolateral spine.

Uropod 2 (fig. 3i) with inner ramus shorter than outer ramus; with 2 apical setae and 1 dorsolateral seta; outer ramus with 1 long distal seta with slightly deformed tip and 3 shorter distolateral setae (U2 shown not from holotype but from (larger) paratype).

Uropod 3 (fig. 3h) with endopod and exopod of equal length. They are slender with both 2 apical setae and 1 lateral seta; peduncle with 2 distal setae.

Telson (fig. 3g) rounded, with 2 long spines on each distal corner and 2 plumose setules on lateral margin.
Fig. 3. Bogidiella turcica n. sp., a-h, holotype, 1.2 mm. a, fifth pereiopod (scale A); b, sixth pereiopod (A); c, first pleopod (A); d, second pleopod (A); e, third pleopod (A); f, first uropod (B); g, telson (B); h, third uropod (B); i, paratype, 1.2 mm, second uropod (B).

Gills were observed on pereiopods 4, 5, and 6 (fig. 1a) but no oöstegites or genital papillae could be discerned.

Etymology. — The epithet turcica refers to Turkey, the state; it is an adjective agreeing in gender with the (feminine) generic name.

A remarkable resemblance in some characters, but not in others, is found with the Caribbean species *Bogidiella* (*Actogidiella*) *cultrifera* Stock, 1981 of the interstitial of marine sandy beaches from Tortola Island: the position, form, and number of the spines on the palmar edge of the propodus of the second gnathopod are almost identical to those of *B. turcica*, as is the curved and ornamented palm. To a lesser extent, also in the first gnathopod. Another curious fit is the short first antenna with, however, 6 instead of 7 flagellar segments but with the long aesthetasc lacking in the same position, e.g., segment 3, counting from the tip.

**Bogidiella minotaurus** Ruffo & Schiecke, 1976 (figs. 4-6)

Material. — More than 100 specimens, at least 4 males and the rest females, Sta. 87-6/18, (ZMA Amph. nr. 204351), Vilâyet Antalya, Bou-Rouch pump at mouth of Göynük river, 9 km of Kemer, UTM coordinates TF8261, sea level, temp. 23.0°C, Cl~ 0.016 g/l.

Description of male. — Body length varying from 2.7 to 3.2 mm.

Antenna 1 (fig. 4c) with 10-segmented flagellum, aesthetasc on flagellar segments 3-8; accessory flagellum 3-segmented.

Antenna 2 (fig. 4d) with 4-segmented flagellum, no aesthetasc.

Mandibles (fig. 4b, c, h). Right incisor (fig. 4b) with a scalpel-shaped lacinia mobilis consisting of two separate processes, finely serrate along one margin; spine row with 3 spines; molar conspicuous, densely covered with setules. Left mandible (fig. 4e) with pronged incisor; spine row with 1 thick and 2 thin spines; molar with 1 seta protruding laterally. Palp (fig. 4h) 3-segmented; first segment without armament, second segment with 1 distolateral seta, third segment with 4 distal setae of almost equal length.

Upper lip (fig. 4i) with oblique lateral margins, no observable epistome.

Lower lip (fig. 4g) with rounded mandibular lobes and a small ridge on inner margin.

Maxilla 1 (fig. 4j). Inner lobe with 3 setae on distal margin; outer lobe with 7 spines, finely serrate along distal end of inner margin; palp 2-segmented, distally with 2 setae and 1 distolateral seta.

Maxilla 2 (fig. 4k) with 9 and 6 setae on lobes.

Maxillipede (fig. 4f). Inner plate with 2 cup-shaped spines and 2 small setae on distal margin; outer plate with 3 distal robust spines and 7 small teeth on
Fig. 4. *Bogidiella minotaurus* Ruffo & Schiecke, 1976. a, male, 2.4 mm, habitus (scale A); b, female 2.5 mm, right mandible (B); c, male, 2.8 mm, first antenna (A); d, second antenna (A); e, female, 2.5 mm, left mandible (B); f, male, 2.1 mm, maxillipede (B); g, male, 2.8 mm, lower lip (C); h, mandible palp (C); i, upper lip (C); j, male, 2.7 mm, first maxilla (B); k, male, 2.1 mm, second maxilla (B).
inner margin on left palp and 4 of such teeth on right palp; carpal segment with 7 setae on inner margin; propodal segment robust with 5 long setae and on distal margin a row of fine setules; dactyl irregularly covered with setules, unguis clearly separated.

Gnathopod 1 (fig. 5a). Coxae nearly rectangular; basis with 2 proximal setae; ischium unarmed; merus with 1 seta; carpus with long distal projection, covered with dense bush of setules and 5 setae; propodus with 5 setae along lower palm edge grouped in 3 and 2, and 7 spinules in a regular row along palmar edge opposing the claw; claw with 2 teeth on inner margin, no division between dactylus and unguis.

Gnathopod 2 (fig. 5b), coxa widening from anterior end to posterior end; basis with 1 seta on posterior margin; ischium and merus unarmed; carpus with a partly setose patch of setules along posterior margin and 3 at anteroventral corner; propodus with fine setules at posterior margin ranging from basal end to palmar corner, palmar corner with 2 thick setae and 2 slim ones, along palmar edge 5 short setae present; claw with 2 teeth on inner margin, no visible division between dactylus and unguis.

Pereiopod 3 (fig. 5c). Coxae (fig. 4a) almost rectangular, without spinules; basis with 3 short setae on posterior margin; propodus with 2 short setae on posterior margin and 2 longer posterodistal setae.

Pereiopod 4 (fig. 5d). Coxae rectangular with rounded anterior corners and 2 setules on ventral margin; basis with 3 lateral spines on anterior margin and 1 anterodistally, on posterior margin 2 setules; no lateral setules on propodus but 2 setae distally; claw with small but distinct unguis.

Pereiopod 5 (fig. 5e) short, not very robust. Coxae anterolobate with 2 setules on margin and 1 setule on posterior margin; basis with 1 medial setule on anterior margin and 1 anterodistal setule, posterior margin with 2 lateral setules and 1 distal setule; claw small.

Pereiopod 6 (fig. 5f). Coxae small, slightly lobate with equal lobes, 1 posterior setule; basis with paired setules, 1 medial on anterior margin, 2 on posterior basis; claw slender.

Pereiopod 7 (fig. 5g) long and very robust compared to P6. Coxae small and slightly posterolobate; basis with 4 setules on posterior margin; propodus with 6 short setules in a regular row; claw long and slender, small unguis.

Pleopod 1-3 (fig. 6a, b, c, d) biramous. Exopod 3-segmented with 2 brushed setae per segment; exopod consists of 1 segment only and bears a long brushed seta; subdistally the peduncle bears 2 coupling hooks. Peduncle of pleopod 2 with a spinous process distally (fig. 6c).
Fig. 5. *Bogidiella minotaurus* Ruffo & Schiecke, 1976. a, male, 2.7 mm, first gnathopod (scale B); b, second gnathopod (B); c, male, 2.8 mm, third pereiopod (A); d, fourth pereiopod (A); e, fifth pereiopod (A); f, sixth pereiopod (A); g, seventh pereiopod (A).
Fig. 6. *Bogidiella minotaurus* Ruffo & Schiecke, 1976. a, male, 2.8 mm, first pleopod (scale A); b, second pleopod (A); c, do (B); d, third pleopod (A); e, male, 3.2 mm, third uropod (C); f, male, 2.8 mm, first uropod (C); g, second uropod (C); h, telson (C); i, female, 2.7 mm, accessory flagellum of first antenna (B); j, female, position of gills and oostegites (A).
Uropod 1 (fig. 6f) with 1 medioventral spine on peduncle; exopod a little shorter than endopodite, both with 1 long distal seta and 2 short setae, exopod also with 1 seta subdistally.

Uropod 2 (fig. 6g) with exopod shorter than endopodite, both with 1 long distal seta and 2 short setae.

Uropod 3 (fig. 6e) with rami of equal length. Exopod with 2 groups of 3 setae on lateral margin and 6 distal shorter and longer setae; endopodite with 2 groups of 1 long seta and 1 very short setule on lateral margin and 4 distal setae.

Telson (fig. 6h) small and with slightly concave notch in posterior margin. Armed with 4 setae.

Gills in male could only be seen with certainty on P5 and P6.

Females (fig. 6j) with gills from P3-P6 and oöstegites from P2-P5. The oval spot (only in females) in the basis of the pereiopods (Hertzog’s Organ) was observed on P3-P6. Accessory flagellum in all females 2-segmented.

VARIABILITY

In order to get an impression of morphological variability within and between 3 populations of Bogidiella longiflagellum of considerable geographic distance from each other (see map, fig. 7), 24 individuals were scored on 5 characters

![Map of Southwestern Turkey (Anatolia)](image_url)

Fig. 7. Map of Southwestern Turkey (Anatolia).
### Table II
See text for explanation

#### A. B. *longiflagellum* S. Karaman, 1959 from Burdur, Sta. 87-5/51

<table>
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<th>Sex Length</th>
<th>Female 2.8 mm</th>
<th>Female 3.0 mm</th>
<th>Female 4.0 mm</th>
<th>Female 2.5 mm</th>
<th>Female 3.1 mm</th>
<th>Male 2.5 mm</th>
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#### B. *longiflagellum* of Kamis river, Yatagan, Sta. 87-5/18

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<th>Sex Length</th>
<th>Female 2.7 mm</th>
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<th>Female 2.8 mm</th>
<th>Female 2.5 mm</th>
<th>Female 2.9 mm</th>
<th>Female 2.2 mm</th>
<th>Male 1.6 mm</th>
<th>Male 2.3 mm</th>
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<tr>
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<tr>
<td>Number of setae on inner lobe first mx</td>
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<tr>
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<tr>
<td>Number of spines on palmar corner of gnathopod 1</td>
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C. B. longiflagellum of Gümüssu, Sta. 87-5/33

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<tr>
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<td>2</td>
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<td>Number of setae on basis of gnath. 1/2</td>
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<td>2/2</td>
<td>2/2</td>
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</tr>
<tr>
<td>Number of spines on palmar corner of gnathopod 1</td>
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<td>3</td>
<td>3</td>
<td>3</td>
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(Table IIa-c). These characters are sometimes used in diagnostic descriptions and we feel that in case populations are large enough to allow for comparisons between specimens, this is recommended. As is often the case with groundwater amphipods and isopods, they are randomly sampled and seldom in large numbers. However, there is always variability worthwhile describing, as is shown in the following table. Figures in bold face are deviations from the normal.

The total number of males (6 out of 24 specimens) does not allow for conclusions on sex-related differences. In general, it seems that number of segments, spines, and setae increases with overall length of the animal as can be expected. However, a clear relation with body length cannot be found.

The number of segments of the accessory flagellum varies from 2 to 3. This is especially so in the Gümüssu population, where males and females can have 2 segments; 3 segments is the normal situation.

The number of spines on the outer lobe of the first maxilla varies from 6 to 7. Again, most variation is observed in the Gümüssu population.

The number of setae on the inner lobe of the first maxilla varies from 2 to 3. Here, the Burdur population has, in 4 individuals, 3 setae instead of 2 in the other individuals and in the other populations.
The number of setae on the basis of the first and second gnathopod has a stable character state of 2 on each gnathopod, but still, there is one exception in a female from Burdur with 3 setae.

The number of spines on the palmar corner of the first gnathopod, an important diagnostic character, varies in the Yatagan population. In two instances males and females have 2 spines instead of 3.

The overall conclusion from this simple comparison is that variation is not very large but that caution is needed in using the characters compared for diagnostic purposes. For example, if *B. longiflagellum* had been described for the first time from the Gümüşsu population and only a few specimens had been involved, one could easily have ended up with 2 accessory flagellum segments and 6 spines on the outer lobe of the first maxilla for the dissected specimen instead of the more frequent 3 segments and 7 spines in the larger population.

**GEOGRAPHY**

The salinity crisis during Messinian times must have had its effect on the distribution of populations nowadays recognized as different species. The eastern Mediterranean was divided some 6 My ago in several smaller basins and the isolation barrier between populations of *Bogidiella* now found on Crete, Rhodes, Cyprus, and in Anatolia may have been less obvious: assuming the ancestral populations were there. There was a continuous land mass in the eastern Mediterranean connecting the aforementioned regions (Gvirtzman & Buchbinder, 1977) with groundwater flows that may have allowed for large areas of distribution, as is now seen in *Bogidiella longiflagellum* across broad ranges of Anatolia.

It is interesting to note that a species such as *B. longiflagellum* is widely distributed in Anatolia while other species like *B. turcica* and *B. minotaurus* apparently are confined to small pockets in near coast localities. Can there be thalassoid lineages constantly invading coastal groundwaters next to old (Pangaea) freshwater clades? This is an idea that can, in part, already be construed from the papers of Stock (1977, 1983) and that was restated by Por (1986) in explaining bogidiellid occurrence in the Middle East.

No mention was made, however, of the then already known *Bogidiella* sp. (Spooner, 1959), a purely marine species from gravel in shallow depths in the British Channel. With regard to this sighting, we expect future reports of marine bogidiellids in the eastern Mediterranean as well. This might place the strange character distribution (similarities in gnathopod and antennal features between Caribbean and Turkish species) in another perspective.
ACKNOWLEDGEMENTS

Simona Seveso worked on this project under a grant (ICP94NL3041/43) of the ERASMUS network for student mobility. We thank Jan Stock, when he was still there to hint us on overlooked publications, Stefan Könemann for his help in finding literature, and Fred Schram for critical remarks on the text.

REFERENCES


— —, 1983. Discovery of a bogidiellid amphipod crustacean in inland waters of the East Indian archipelago: Bogidiella (Medigiella) sarawacensis n. sp. Crustaceana, 44: 198-204.

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THE NIPHARGUS KOCHIANUS-GROUP
(CRUSTACEA, AMPHIPODA) IN THE AQUITANIAN BASIN,
SOUTH-WESTERN FRANCE, AND A SUPPOSED CASE OF
INTROGRESSIVE HYBRIDIZATION

BY

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SUMMARY

Three members of the Niphargus kochianus-group — Niphargus kochianus kochianus Bate, 1859,
Niphargus pachypus Schellenberg, 1933 and a possible hybrid: Niphargus k. kochianus × Niphargus
pachypus — are treated. Their distribution pattern in the northern part of the Aquitanian Basin
(France) is shown on maps and an attempt is made to integrate geological history and distribu-
tional data. The possibility of introgressive hybridization is suggested. In order to identify the
hybrid, tables on inter- and intraspecific variability, intrapopulational variability and mor-
phometric differences are provided.

The male of N. pachypus, unknown before, is shortly described.

RÉSUMÉ

Sont pris en considération trois membres du groupe d'espèces Niphargus kochianus, à savoir N.
kochianus kochianus Bate, 1859, N. pachypus Schellenberg, 1933, et un éventuel hybride: N. k.
kochianus × N. pachypus. Des cartes de distribution sont données pour la partie septentrionale
du Bassin d'Aquitaine et un essai est fait d'intégrer histoire géologique et données sur la
distribution. On suggère la possibilité d'une hybridation introgressive. Dans le but d'identifier
l'hybride, on présente sous forme de tableaux des données sur la variabilité inter- et intraspécifi-
que, sur celle à l'intérieur des populations, et sur les différences morphométriques.

Le mâle de N. pachypus, auparavant inconnu, est décrit.

INTRODUCTION

Study of the niphargids of the Aquitanian Basin is part of a project aiming at
study of the origin of the stygobiont malacostracan fauna of the Iberian Penin-
sula, Canary Islands and southern France. This paper concentrates on the
distribution and taxonomy of the Niphargus kochianus-group.

Publications concerning the kochianus-group are strewn with passages
describing difficulties in species delimitation. Stock & Gledhill (1977), in their
comprehensive article about the group in north-western Europe, reported on
"intermediates" between the kochianus-group and the Niphargus skopljensis-group.

Cărăuşu et al. (1955) described some 'formae' of N.kochianus from phreatic waters of different localities in Rumania and discussed specimens deviating from the nominal form. Schellenberg (1933) made remarks about the variability of maxilla 1 armature of populations from widely separated localities.

These observations called for an extensive sampling program in order to find a spatial pattern of morphological variability, since earlier observations on members of the kochianus-group were based on material from few localities, often separated by large distances.

In the course of this study an area was sampled comprising the French departments Charente-Maritime, Charente, Gironde, Dordogne, Lot-et-Garonne, Gers, and Lot. Sampled were 125 man-made wells, 17 caves, 3 springs and 29 hyporheic habitats of running waters, including main rivers such as Dordogne, Isle, Charente, Lot, Gers, and Dronne.

In 25 samples members of the kochianus-group were found. The 25 stations are wells (21), caves (2) and springs (2).

Although members of the kochianus-group are widely distributed through the sampled area, the numbers in which they are caught remain small in comparison to those of two other Niphargus species, belonging to the aguilex-tauri-group and the stygius-puteanus-group (Straskraba, 1972): Niphargus ladmiraulti Chevreux, 1901 and Niphargus longicaudatus plateaui Chevreux, 1901, respectively.

In a narrow zone, roughly between the rivers Dordogne and Lot, a deviant form of N. pachypus was found. It is here described as a possible hybrid, having a combination of characters resembling those of bordering species.

**TAXONOMIC PART**

*Material and methods*

The following instruments were used for sampling: in wells a Cvetkov-net (mesh 300 μmm); in caves and surface springs a handnet (mesh 300 μmm) and a small sieve; in hyporheic habitats a Bou-Rouch biophreatical pump. In the field several parameters were measured; conductivity (μS/cm) and temperature were recorded directly with a WTW-LF-91 Field-meter, chlororinity with an Aquamerk 1106 kit.

Fifty-eight specimens were dissected and mounted on slides to study phenotypic variability. All specimens are kept in the Zoölogisch Museum Amsterdam (ZMA). A detailed description of stations not mentioned in this paper is given in a separate checklist which may be obtained from the author.
**Niphargus kochianus kochianus** Bate, 1859

Material examined.—
Sta. 85-505, Dép. Dordogne, La Baurie, well, conductivity 657 μS/cm, Lambert III coordinates 491.11, 3325.48, alt. 120 m; 12 Sept. 1985, 3 specimens (ZMA coll. no. Amph. 108.405).


Sta. 85-260, Dép. Charente, Cognac, well, chlorinity 38 mg/l, conductivity 743 μS/cm, Lambert II coordinates 398.76, 2075.73, alt. 3 m; 4 Oct. 1985, 7 specimens (ZMA coll. no. Amph. 108.407).

Sta. 85-640, Dép. Dordogne, Festal, well, chlorinity 38 mg/l, conductivity 697 μS/cm, Lambert II coordinates 453.42, 2023.64, alt. 56 m; 11 Oct. 1985, 3 specimens (ZMA coll. no. Amph. 108.408).


Sta. 85-551, Dép. Gers, 9 km W of Fleurance, well, chlorinity 400 mg/l, conductivity 2520 μS/cm, Lambert II coordinates 457.10, 1853.85, alt. 130 m; 21 Sept. 1985, 5 specimens (ZMA coll.no. Amph. 108.412).


Sta. 85-520, as previous station, handnet in subterranean river, chlorinity 17 mg/l, conductivity 644 μS/cm; 15 Sept. 1985, 2 specimens (ZMA coll. no. Amph. 108.414).

Sta. 85-524, Dép. Lot, 30 km NW of Cahors, well, chlorinity 12 mg/l, conductivity 599 μS/cm, Lambert II coordinates 516.05, 1965.92, alt. 160 m; 16 Sept. 1985, 1 specimen (ZMA coll. no. Amph. 108.415).

Sta. 85-546, Dép. Lot-et-Garonne, Cuq, well, chlorinity 60 mg/l, conductivity 830 μS/cm, Lambert II coordinates 468.27, 1899.63, alt. 150 m; 20 Sept. 1985, 71 specimens (ZMA coll. no. Amph. 108.416).

Sta. 85-548, Dép. Gers, Lectoure & Castelnau, 5 km NE of Fleurance, well, chlorinity 33 mg/l, conductivity 915 μS/cm, Lambert II coordinates 468.62, 1877.26, alt. 175 m; 20 Sept. 1985, 1 specimen (ZMA coll. no. Amph. 108.417).


Sta. 85-561, Dép. Lot-et-Garonne, 11 km SSE of Marmande, well, chlorinity 78 mg/l, conductivity 945 μS/cm, Lambert II coordinates 436.55, 1941.62, alt. 40 m; 22 Sept. 1985, 1 specimen (ZMA coll. no. Amph. 108.419).

Sta. 85-562, Dép. Lot-et-Garonne, Gontaud-de-Nogaret, well, chlorinity 21 mg/l, conductivity 817 μS/cm, Lambert III coordinates 437.92, 3242.13, alt. 35 m; 22 Sept. 1985, 1 specimen (ZMA coll. no. Amph. 108.420).

Sta. 85-587, Dép. Dordogne, Velines, well, chlorinity 38 mg/l, conductivity 623 μS/cm, Lambert III coordinates 424.91,3288.07, alt. 100 m; 27 Sept. 1985, 2 specimens (ZMA coll. no. Amph. 108.421).
Fig. 1. *Niphargus k. kochianus* × *Niphargus pachypus*, ♀, 4.8 mm.

Sta. 85-678, Dép. Lot, Concares, well, chlorinity 8 mg/l, conductivity 526 µmS/cm, Lambert II coordinates 525.18, 1962.13, alt. 180 m; 23 Oct. 1985, 4 specimens (ZMA coll. no. Amph. 108.422).

Remarks.—

The female of *N. pachypus* has been described by Schellenberg (1933) and later by Stock & Gledhill (1977). We have found the unknown male in a well near Fleurance (Sta. 85-551).

The male (4.1 mm) resembles the female and can be identified with certainty only by its genital papillae. The gnathopods in both sexes have short setae on the anterior margin of the propodus and the females have shorter palmar angle spines than the females of *N. pachypus* found in the Netherlands.

*Niphargus k. kochianus* × *Niphargus pachypus* (figs. 1-3, 6-11, 14-31)

Material examined.—

Sta. 85-512, Dép. Dordogne, St. Martial de Nabirat, well, chlorinity 10 mg/l, conductivity 582 µmS/cm, Lambert II coordinates 512.11, 1970.45, alt. 120 m; 13 Sept. 1985, 41 specimens (ZMA coll. no. Amph. 108.423).

Figs. 2, 3, 6-11, *Niphargus kochianus* × *Niphargus pachypus*; 2, ♂, 3.5 mm, pereopod 7; 3, ♂, 3.8 mm, pereopod 7; 4, *N.k. kochianus*, ♀, 5 mm, pereopod 7; 5, *N.pachypus*, ♂, 4.5 mm, pereopod 7; 6-11, maxilla 1 outer lobe, animals varying from 2.8 mm to 5 mm bodylength; 12, *N. pachypus*, ♀, 4.5 mm, maxilla 1 outer lobe; 13, *N.k. kochianus*, ♂, 4 mm, maxilla 1 outer lobe.
Figs. 14-23, *Niphargus k. kochianus* × *Niphargus pachypus*, Q, 5 mm; 14, pereopod 7; 15, pereopod 6; 16, pereopod 5; 17, maxilliped; 18, pereopod 4; 19, pereopod 3; 20, uropod 3; 21, telson; 22, uropod 2; 23 uropod 1.

Sta. 85-568, Dép. Dordogne, Razac, well, chlorinity 32 mg/l, conductivity 806 μS/cm, Lambert II coordinates 450.27, 1967.15, alt. 100 m; 24 Sept. 1985, 3 specimens (ZMA coll.no. Amph. 108.426).


Figs. 24-29, Niphargus k. kochianus × Niphargus pachypus, Q, 5 mm; 24, lower lip; 25, left mandible; 26, pleopod 1; 27, upper lip; 28, right mandible; 29, epimeral plates 1-3.
Largest male 4.2 mm, largest female 5 mm. Live colour bright white.

Morphology (fig. 1) very similar to that of *N. pachypus* with the following exceptions:

Outer lobe of maxilla 1 with spines having more than one medial denticle. Only the most medial spine has one medial denticle or none (figs. 6-11).

Pereopods (figs. 2, 5, 14-16, 18, 19) slightly less robust than in *N. pachypus* (fig. 5, Table 3) and subchelate.

Gnathopod 1 (fig. 30), similar in male and female, with a rugose posterior margin of the merus. Palmer angle spine not as long as in *N. pachypus*.

Gnathopod 2 (fig. 31), similar in male and female, with about 8 groups of setae on the posterior margin of the propodus, against 4 in *N. pachypus*. Palmer
**Table I Inter- and intraspecific variability**

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<td>2) Mandible, labium, right</td>
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<td>3) Maxilla 1, armature of distal spines on outer lobe</td>
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<td>4) Gnathopod 2, carpus</td>
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<td>5) Gnathopod 3, ratio of carpus</td>
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<td>6) Claw P7, unguis</td>
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<td>7) Uropod 3, ratio of antedistal segment</td>
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<td>8) Uropod 3, length/width ratio of eca-</td>
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<td>9) Telson, cleat</td>
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<td>10) Shape medial</td>
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<td>505 511 520 524 546 548 551 559 561 562 587 617 620 640 646 658 659 661 678 512 533 565 568 573 582</td>
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<td>2) Mandible, labium, right</td>
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<td>3) Maxilla 1, armature of distal spines on outer lobe</td>
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<tr>
<td>10) Shape medial</td>
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</tbody>
</table>

1 The characters used in this table are selected from **TABLE 1** in Stock & Gledhill (1977)

Station number represents one individual. From each station the largest individual was
taken.

Only those characters which have clear discriminating value have been used. Telson emargination and shape, maxilla 1 armature, antenna
peduncle length and female gnathopod configuration prove to be the best discriminating characters.

\[=\] intermediate character state

\[0\] = *Niphargus kochianus kochianus*

\[1\] = *Niphargus pachypus*
Table II: Morphometric Differences

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</table>

A ratio is taken to compare the robustness of the pereopod 7 basis of *N. pachypus* with that of the hybrid. Although there is considerable variation—also between the individuals of the same length from the same population (*)—a difference is noticed: *N. pachypus* has a wider basis of P7 than the hybrid. *Niphargus k. kochianus* is not included in these measurements for P7 is lacking in most cases.

angle spine not as long, but the setae on posterior margin of the basis are twice as long as in *N. pachypus*.

To facilitate comparison with *N. pachypus* from other parts of Europe most appendages of the hybrid are illustrated (figs. 14-31).

RESULTS AND DISCUSSION

In order to test the supposed hybrid status of *Niphargus k. kochianus* × *Niphargus pachypus*, four criteria were used.

1. Inter- and intraspecific variability.

From table I it can be seen that the individuals from the last 6 stations (512 to 582) have mostly characters corresponding with *N. pachypus* but that character 3 deviates significantly (bold print). This character is intermediate (figs. 6,7,10,11) and in two populations (533 and 582) its expression is characteristic for *N.k.kochianus* (figs. 8,9). The *N.k.kochianus* populations from Aquitaine have at least 4 denticles on the spines on the outer lobe of maxilla 1, while *N.pachypus* has forked spines with 1 denticle except for the innermost spine which bears 4 or 5 fine denticles.

The shape of the claw of pereopod 7, character 8 (figs. 2-5), can in both species from the sampled zone be called "subchelate". In this respect *N.pachypus* from Aquitaine differs from *N.pachypus* found in the eastern
### Table III

#### Intrapopulational variability

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Members of four populations have been screened on their variability. Character states correspond with those in Table I. The individuals of one station are here considered as one population.
Pyrenees (Stock & Gledhill, 1977), in eastern France (Ginet, 1971) and in the Netherlands.

2. Morphometric differences.
The form of the basis of pereopod 7 proved to be a discriminating character between \textit{N. pachypus} and the hybrid. A ratio was taken by dividing the overall body length of the animals by the width of the basis of pereopod 7 (table II).

3. Intrapopulational variability.
The variability within populations was measured to enhance the value of the previous results. Station 533 contained many undamaged animals, therefore 8 individuals were studied instead of 3 or 2 from other stations (table III).

\textit{Niphargus k. kochianus} \times \textit{Niphargus pachypus} seems confined to a narrow zone between two main rivers, the Dordogne and the Lot (see map 1). In the north the hybrid borders upon \textit{N.k. kochianus}, in the south and the east upon \textit{N.pachypus}.

The specific boundary between \textit{N.k. kochianus} and \textit{N.pachypus} is not sharp. The supposed hybrid has some intermediate characters and is also geographically intermediate between the two species (Map 1). Supposedly introgressive hybridization occurred in these populations. The shape of the basis of pereopod 7 and the armature of maxilla 1 can be considered in some cases as intermediate, grading into those of each parental species, while in other cases (table I, stations 533, 582) it actually has the form of one of the parental species.

Of course occurrence of introgressive hybridization between \textit{N.k. kochianus} and \textit{N.pachypus} populations in the contact zone cannot be proved without genetic analysis. However, it seems likely that a group of populations, which in almost all aspects resemble \textit{N.pachypus}, developed through crossbreeding character states similar to those of neighbouring \textit{N.k. kochianus}.

The next step in explaining the possible existence of an intergradation zone is to look for the cause of breakdown of isolating mechanisms between \textit{N.k. kochianus} and \textit{N.pachypus} in the Dordogne area.

It looks as if members of the \textit{N.kochianus}-group are capable of migrating best through fluviatile terraces of the great river systems. In the Netherlands \textit{N.pachypus} is restricted to the drainage system of the river Meuse (Stock & Gledhill, 1977; Notenboom, pers. comm.). Bou (1968) found that the habitat of \textit{N.pachypus} in the area he investigated was restricted to the lower terraces of the river Tarn. As to the hydrological situation in the Aquitanian Basin one can recognize it as a meeting area of several long rivers. The present courses of these rivers were gradually acquired, for various tectonic deformations took place until the end of the Pleistocene (B.G.R.M. Atlas, 1974). Supposedly the Charente reached its final position during the last Ice-age; another river originating in the Massif Central, the Dordogne, was captured by the Garonne—originating in the High Pyrenees—during the last interglacial.
Ma pp  1 . South-Western France. Distribution pattern of the *Niphargus kochianus*-group.

* = *Niphargus kochianus kochianus*
★ = *Niphargus pachypus*
● = hybrid

............. = boundary between Cretaceous (right) and Tertiary (left)
---- = coastline during Aquitanian transgression

Such events may help in installing a secondary zone of contact between two formerly isolated populations that did not acquire complete reproductive isolation during the preceding period of geographic isolation. There is, however, much difficulty in distinguishing, even in principle, primary from secondary contact (Barton & Hewitt, 1985) and we can only point toward the possibility of geographic isolation of the Aquitanian stygofauna in the lower Miocene, when the last great marine transgressions formed large gulfs in the area, destroying the freshwater stygofauna between the western Pyrenees and the Perigord. The Burdigalian transgression reached as far as Agen (Gourinard, Magné & Wallez, 1987). On maps 1 and 2 the Aquitanian transgression coastlines are shown, based on the B.G.R.M. Atlas, 1974.
The higher northern parts of the basin were not inundated during the marine incursions from the West. These parts are covered with Cretaceous deposits. When the distribution of *N. k. kochianus* and *N. ladmiraulti* is superimposed on a geological map a relation between species distribution and these deposits becomes visible (Map 1). Less clear is the relation between the extensive deposits of early Tertiary sediments and the distribution of *N. pachypus* and *N. longicaudatus plateaui*. Noteworthy is the occurrence of *N. pachypus* inside the former seafloor area (Aquitanian and Burdigalian transgression seas) west of Agen. This points toward dispersion of the species after final regression of the sea.

Intrapopulational variation is small (Table III) and differences are probably
due to allometric growth except for those in number of teeth on the right lacinia mobilis: these numbers vary within populations and are discarded as a character useful for species delimitation.

*N.k.kochianus* has also been found in the department Var in south-eastern France (Notenboom, unpublished). Examination of this material shows no important differences from specimens from Aquitaine or from the type-specimens from England.

**CONCLUSIONS**

Geographical and character distribution point toward introgressive hybridization between two species of the *Niphargus kochianus*-group in the Aquitanian Basin. The northern *Niphargus kochianus kochianus* has a geographical distribution associated with Cretaceous deposits while the southern *Niphargus pachypus* is found in Tertiary sediments and also colonized the emergent Lower Miocene seafloor area West of Agen. In the meeting area of the two species, an assumed hybrid was found. It is likely that isolation of northern and southern populations during Miocene marine transgressions and tectonic deformations and change of river courses during the Pleistocene glacial periods played a role in the origin of this hybrid.

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**REFERENCES**


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