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**Discovery of Superornatiremidae Huys
 (Copepoda, Harpacticoida)
 outside anchialine caves, with the description
 of *Gideonia noncavernicola* gen. et sp. nov.
 from the Patagonian continental slope (Chile)**

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Abstract

A new harpacticoid species is described from the Patagonian continental slope southern off Tierra del Fuego (Chile). *Gideonia noncavernicola* gen. et sp. nov. belongs to the Superornatiremidae Huys, 1996 based on the following apomorphic characters: gonopores displaced laterally, inner setae of enp2 of P4 transformed into strong spines and, in particular, presence of an outer seta on enp2 of P1. This is the first species of the family known to live outside anchialine caves. This record, together with the discovery of additional new superornatiremid species in the central Atlantic and the Barents Sea, leads to the rejection of the hypothesis of Superornatiremidae as being an exclusively cavernicolous taxon with an amphiatlantic/mediterranean distribution.

Keywords: Superornatiremidae, *Gideonia noncavernicola*, biogeography, Magellan Region, anchialine caves

Introduction

Anchialine caves are considered as “bodies of haline waters, usually with a restricted exposure to open air, always with more or less extensive subterranean connections to the sea, and showing noticeable marine as well as terrestrial influences.” (Stock et al. 1986: p. 91). During the last 20 years an increasing number of scientific publications have been written about organisms of such anchialine caves. The study of anchialine cave fauna has re-

sulted in the description of a large number of protozoan and metazoan organisms (for review see Iliffe 2000), among them a considerable number of new and remarkable crustaceans, like e.g. the Remipedia (cf. Yager 1981, Yager & Carpenter 1999), a representative of Mictacea (Bowman & Iliffe 1985), and in particular the Copepoda (Calanoida: e.g. Barr 1984, Fosshagen & Iliffe 1989, 1991, 1994; Platycopioidea: e.g. Fosshagen & Iliffe 1988; Misophrioida: e.g. Boxshall & Iliffe 1986, 1987, 1990, Jaume & Boxshall 1996a, b, Jaume et

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al. 1998; Harpacticoida: Huys 1988, 1996, Huys & Iliffe 1998, Jaume 1997). These records have led to the hypothesis that anchialine caves are characterised by a high degree of endemic and highly specialized taxa even at supraspecific level (Huys 1996). Recent descriptions of Rotundiclepidae Huys, 1988, Superornatiremidae Huys, 1996, and Novocriniidae Huys & Iliffe, 1998 seemed to confirm this assumption even for Harpacticoida (Huys 1996, Huys & Iliffe 1998). For the Novocriniidae, however, the hypothesis was falsified in the same year as the establishment of the family, when an additional species of the family was described from the Barents Sea (Martínez Arbizu & Moura 1998). Superornatiremidae were largely believed to inhabit exclusively anchialine caves at both sides of the North Atlantic Ocean (Jaume 1997). However, discovery of three new superornatiremid species from the Arctic Ocean, from the top of a seamount in the north-eastern Atlantic Ocean, and from the Patagonian continental slope (south-western Atlantic) but not associated with caves, changes the nature of the distribution of the Superornatiremidae in a fundamental way. *Gideonia noncavernicola* gen. et sp. nov. is described in the present contribution; the other two species will be described elsewhere.

Material and methods

Eight specimens (4 females, 4 males) were collected in the meiobenthic material of station 40/110 from the Patagonian Continental Slope (Magellan Region, Chile), which was sampled during expedition ANT XIII/4 of German RV "Polarstern" (cf. Fahrback & Gerdes 1997, George 1999) (Fig. 9). As described by George (1999), the specimens were fixed in 5 % buffered formalin, separated from the substrate by centrifugation, and sorted out using a stereo microscope. For the illustrations some specimens were placed on slides with glycerol as embedding medium. Illustrations were made using a Leica-DMLB microscope with an interference contrast 1500 times objective and equipped with a camera lucida.

Abbreviations used in the text: A1: antennule, A2: antenna, aes: aesthetasc, benp: basendopodite, cphth: cephalothorax, CR: caudal ramus/rami, enp/exp: endopodite/exopodite, GDS: genital double somite, md: mandible, mxl: maxillule, mx: maxilla, mxp: maxilliped, P1-P6: pereopods 1 to 6.

The type material is stored in the UNIOLO collection of the AG Zoosystematik und Morphologie at the Carl-von-Ossietzky-Universität, D-26111 Oldenburg, Germany.

Gideonia gen. nov., generic diagnosis

Superornatiremidae. Generic diagnosis is identical with that of the type species *G. noncavernicola* gen. et sp. nov.

Description of *Gideonia noncavernicola* gen. et sp. nov.

Holotype: female, dissected and mounted on 13 slides (UNIOLO-2000.47/1-13). **Paratypes:** male (allotype), dissected and mounted on 14 slides (UNIOLO-2000.48/1-14), 4 females and 2 males, mounted on 14 slides (UNIOLO-2000.49/1-6, 2000.50/1-4, 2000.51/1, 2000.52/1, 2000.53/1, 2000.54/1).

Locus typicus: Patagonian[‡] continental slope, 55°26.4'S/66°14.0'W, 101m depth (station 40/110 of expedition ANT XIII/4 of RV "Polarstern" in 1996).

Etymology: The generic name *Gideonia* is given in dedication to Gideon Calvin George, son of KHG. The specific name *noncavernicola* refers to the first record of an superornatiremid species outside of anchialine caves.

Female

Habitus (Fig. 1A,B) long, body length in average approximately 380 µm. Urosome as long as prosome. Cphth dorsally and laterally with sensilla. Free thoracic somites at distal margin also with sensilla. P5-bearing thoracic somite also with a row of small spinules. Urosome completely covered with small spinules, as indicated in Figs. 1A, 7A). Former articulation between last thoracic and first abdominal somite indicated by an inner cuticular bulge, and the dorsolateral position of 2 sensilla. GDS and abdominal somites except telson distally with hyaline frill, GDS and first abdominal somite in addition dorsally and laterally with sensilla.

Telson (Figs. 1A, 2B) with weak anal operculum which shows no ornamentation. Operculum covered by hyaline frill of preceding somite. Tel-

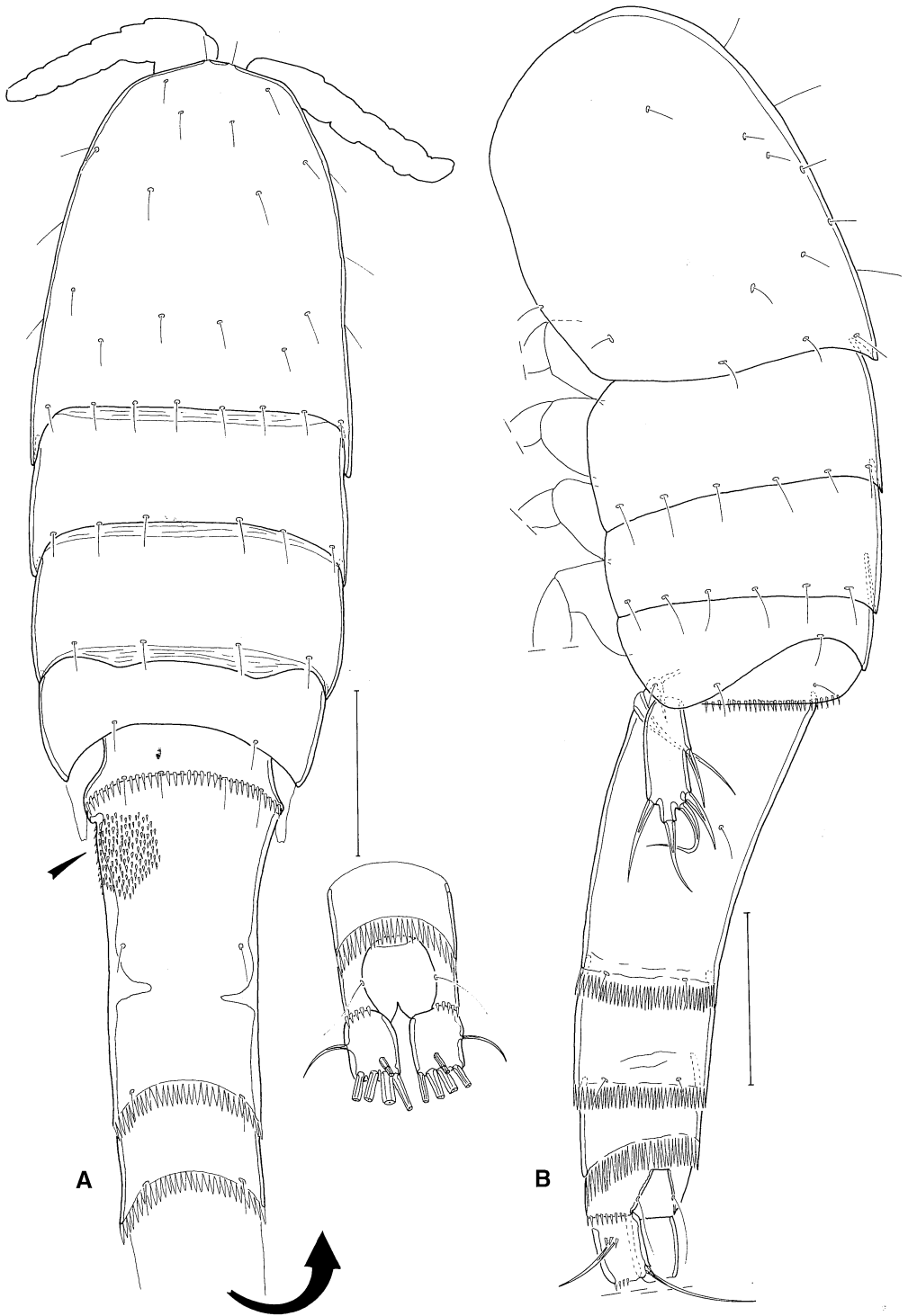


Fig. 1. *Gideonia noncavernicola* gen. et. sp. nov., female habitus. A. dorsal view, B. lateral view. Scales: 100 μm. Triangular arrow indicating spinules covering whole urosome.

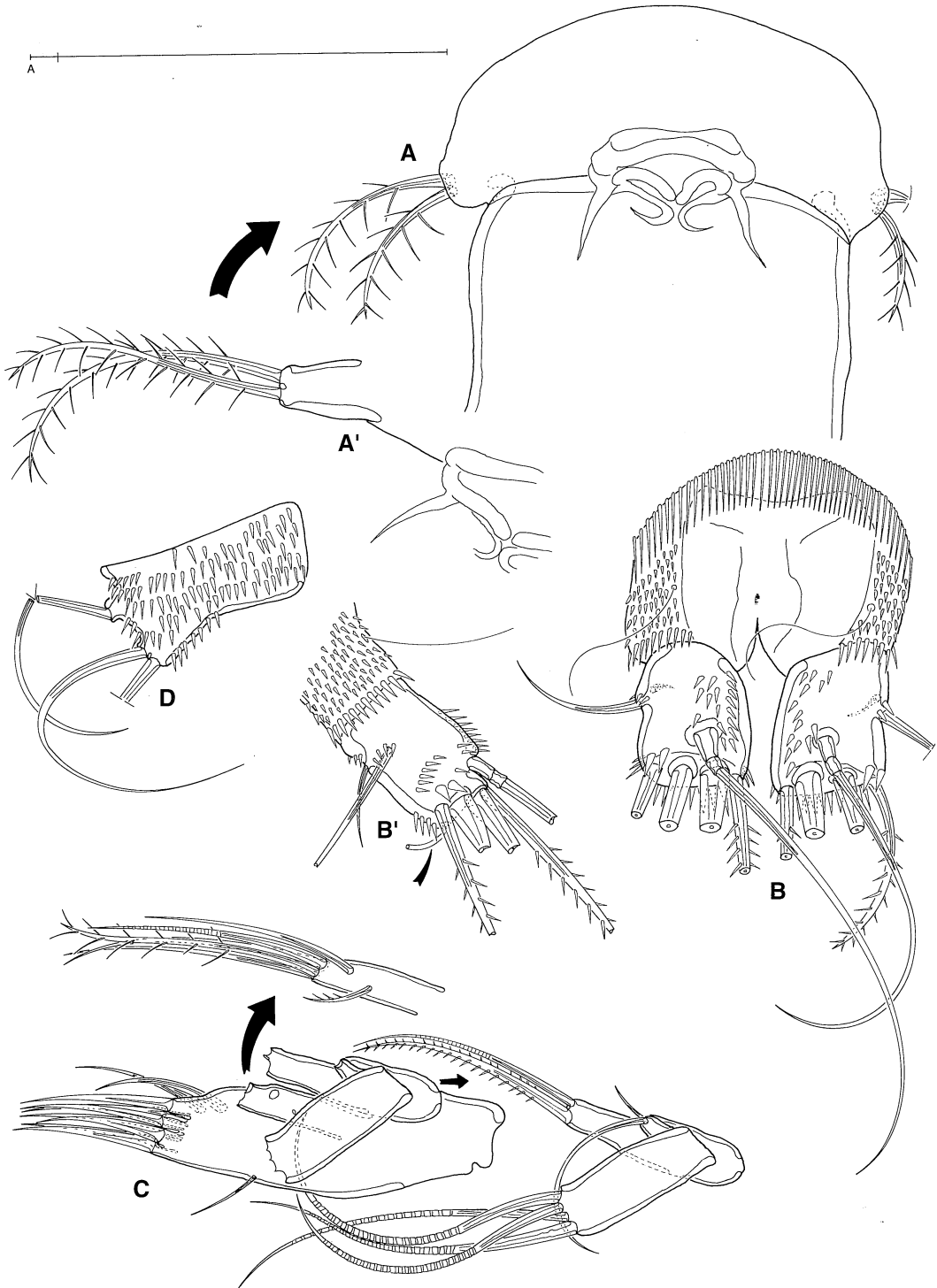


Fig. 2. *Gideonia noncavernicola* gen. et. sp. nov. A,A'. genital field with P6, B. telson and CR, dorsal view, B'. CR, lateral view, triangular arrow indicating tube pore, C. mxl, D. P6 male. Scales: 50 μ m.

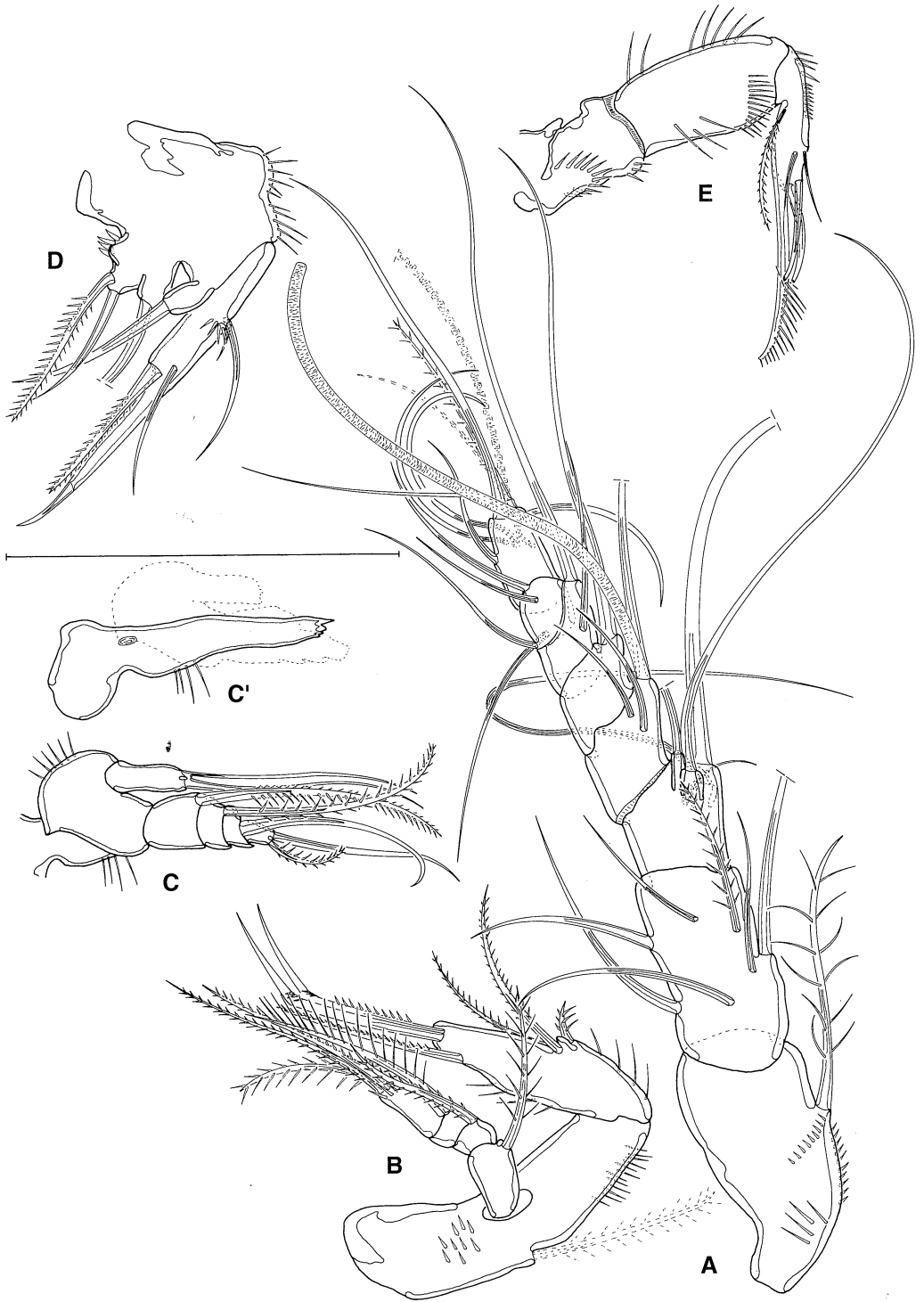


Fig. 3. *Gideonia noncavernicola* gen. et sp. nov., female. A. A1, dotted seta and aes completed according to counterpart, B. A2, C. md palp, C'. md, D. mx, E. mxp. Scale: 50 μ m.

son dorsally with pair of very long sensilla (Figs. 2B,B').

CR (Figs. 2B,B') covered with spinules, with 7 setae. I displaced ventrally (Fig. 2'). II longer than I, inserting laterally, surrounded by several spinules. III to VI terminally. III and VI of nearly the same length and bipinnate, inserting II at outer, and VI at inner terminal margin. IV and V also bipinnate, reaching almost length of abdomen. V slightly longer than IV. VII bi-articulated, inserted subterminally at the dorsal side. CR distally with row of spinules and long tube pore on ventral side (cf. triangular arrow in Fig. 2B'). Genital field (Fig. 2A,A') P6 displaced laterally (Fig. 2A'), reduced to small projection with 2 bipinnate setae. Gonopores paired, laterally displaced and separated (Fig. 2A). Copulatory pore not discernible.

A1 (Fig. 3A) 8-segmented. First segment with several rows of spinules and 1 biplumose seta. Second segment as long as first, with 6 bare setae and 1 bipinnate seta. Adjoining segments of almost same length and shorter than first 2 segments. Third segment with 4 bare setae, all of which inserting from knob-like projections. Fourth segment with 3 bare setae and 1 long and slender aes. Fifth segment with 1 bare seta, sixth segment with 2 bare setae. Seventh segment with 4 bare setae. Eighth segment with 6 bare setae and 1 bipinnate seta. Terminally with aes.

Setal formula: I-1/II-7/III-4/IV-3 + aes/V-1/VI-6/VII-4/VIII-5 + aes.

A2 (Fig. 3B) with allobasis covered with several spinules and 1 abexopodal seta. Enp 1-segmented, with 1 row of spinules each on its anterior and posterior side. At anterior margin with 1 small and 2 longer bipinnate setae. Terminally with 2 geniculate setae, one of which unipinnate. Subterminally at posterior margin with 1 unipinnate seta. It has to be remarked that not all females show the here described holotypic setation; some of them present an ornamentation as in the males (cf. Fig. 8B). Exp 4-segmented, first segment with 1 bipinnate seta, second and third segment together as long as first, each with 1 bipinnate seta. Seta of third segment with long pinnae. Fourth segment as long as first, terminally with 3 bipinnate setae.

Md (Fig. 3C,C') with stiletto-like gnathobase (Fig. 3C') bearing a few small teeth. Md palp (Fig. 3C) biramous. Basis without setae but row of spinules at inner margin. Enp 1-segmented, terminally with 2 bare setae, which are fused

basally. Exp 4-segmented, first and second segment each with 1 bipinnate seta. Third segment with 1 bare seta, fourth segment terminally with 1 bipinnate and 1 bare seta.

Mxl (Fig. 2C). Praecoxa slender. Arthrite terminally with 7 bare setae, subterminally with 2 setae, and laterally with 1 small seta. Coxa terminally with 2 bare setae, as well as with 1 biplumose and 1 articulated seta. Subterminally with 1 bare and 1 unipinnate seta. Basis with distal endite bearing terminally 1 bipinnate and 1 articulated seta. Enp small, with 2 bare and small setae. Exp massive, terminally with 4 long setae, showing all an articulation in their distal part.

Mx (Fig. 3D). Syncoxa distally with row of spinules and 2 endites. Proximal endite trilobate: First lobe weak developed, but clearly discernible, with 4 proximally directed spinules. Second lobe bearing 1 bare and 1 bipinnate seta, third lobe with 1 bare seta. Distal endite with 1 bare seta. Allobasis transforming into long claw, which is accompanied by 1 bipinnate and 1 bare seta. Enp incorporated into allobasis, bearing 1 long and 1 small bare seta, also with 4 spinules.

Mxp (Fig. 3E) prehensile. Syncoxa with row and additionally with small group of spinules. Basis with long spinules, without setation. Enp long, slender, at inner margin with row of spinules, transforming in unipinnate claw, which is accompanied by 4 bare setae and 1 bipinnate seta.

P1 (Fig. 4A) with 3-segmented exp and enp. Basis with bare inner and outer seta. Intercoxal sclerite longer than broad. Exp1 and exp2 without inner seta, each with 1 outer seta. Exp3 with 5 setae, the innermost with long pinnae. Enp1 longer than exp, inner seta in the middle of segment, with long pinnae. Enp2 with each 1 inner and 1 outer bare seta. Enp3 approximately half as long as enp2, with 1 inner seta and 4 geniculate terminal bare setae.

P2-P4 (Fig. 4B, 5A, 6A) with 3-segmented exps and 2-segmented enps. Intercoxal sclerites longer than broad. Inner margin of basis strongly convex, with very long spinules. Exp1 shortest of exopodal segments, without an inner seta, but with an outer seta and collars of fine spinules at distal margins. Exp2 about twice as long as exp1, with each 1 inner and 1 outer seta, and also with fine and long spinulose collars. Exp3 longest exopodal segment, with 3 outer and 2 terminal setae as well as 1 inner seta. Enp1 P1-P3 with an inner seta at mid-length; enp1 P4 with 3 spinules

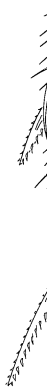


Fig. 4

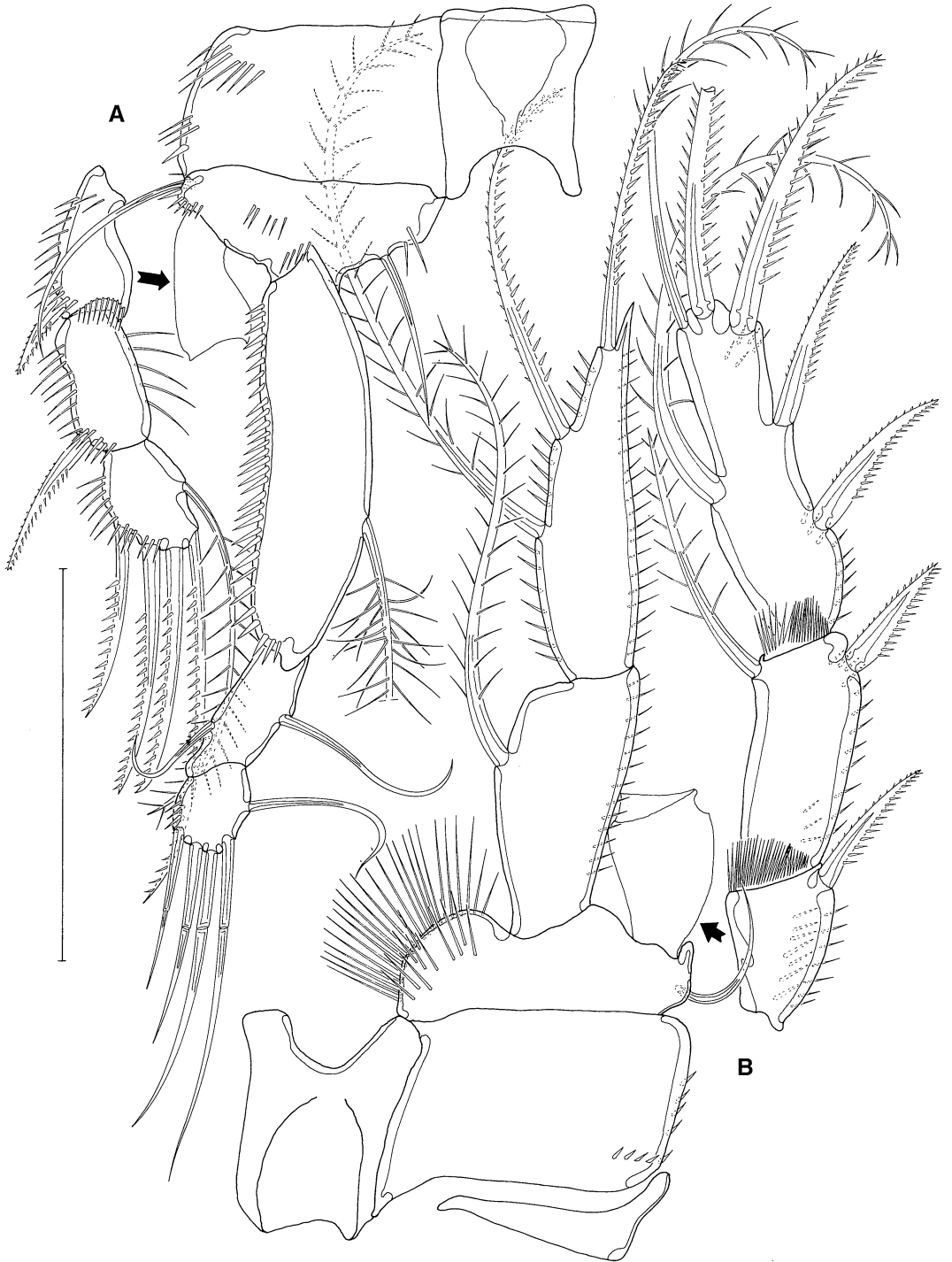


Fig. 4. *Gideonia noncavernicola* gen. et. sp. nov., female. A. P1, B. P2. Scale: 50 μ m.

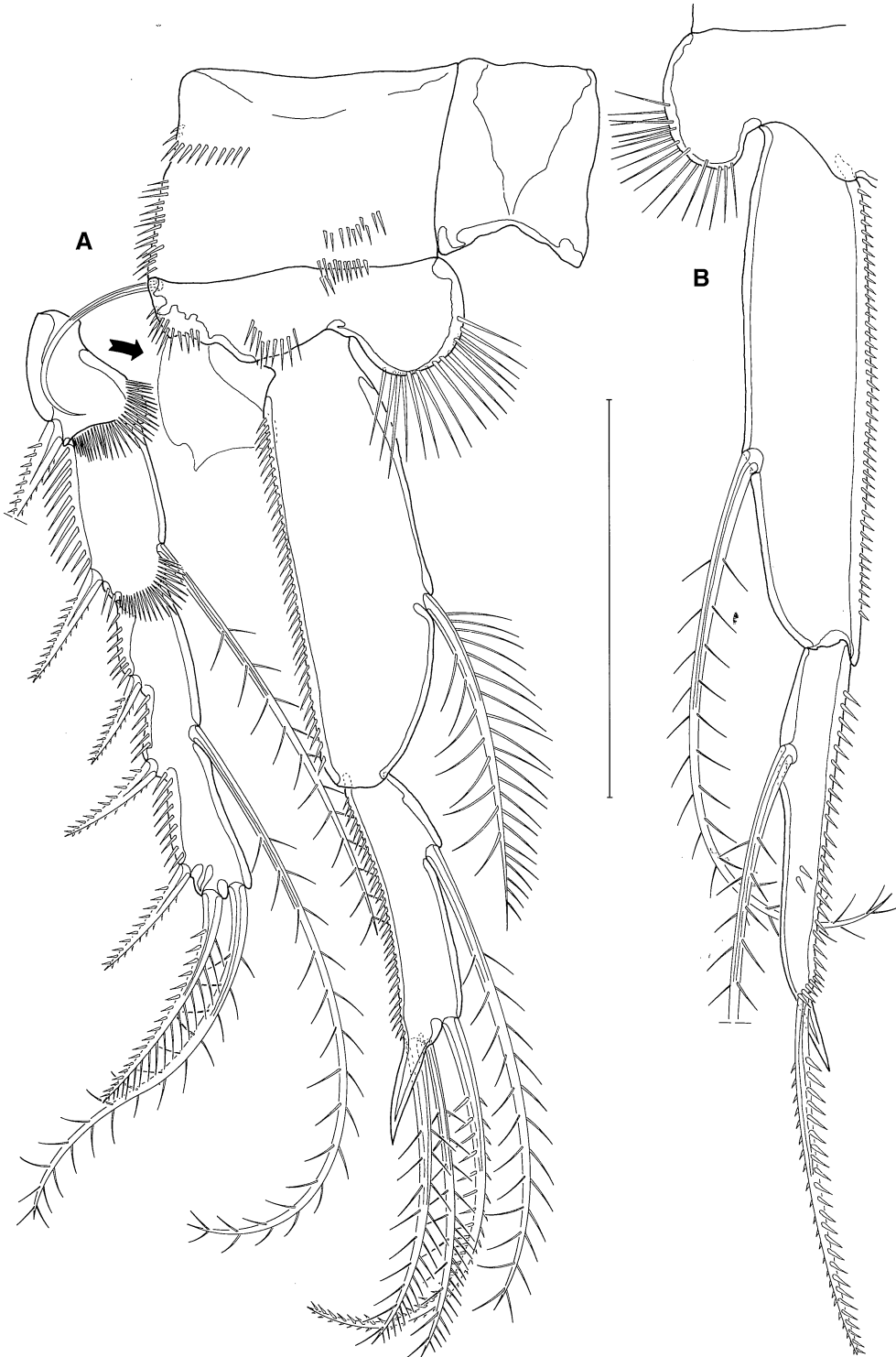


Fig. 5. *Gideonia noncavernicola* gen. et. sp. nov. A. P3 female, B. P3 enp male. Scale: 50 μ m.

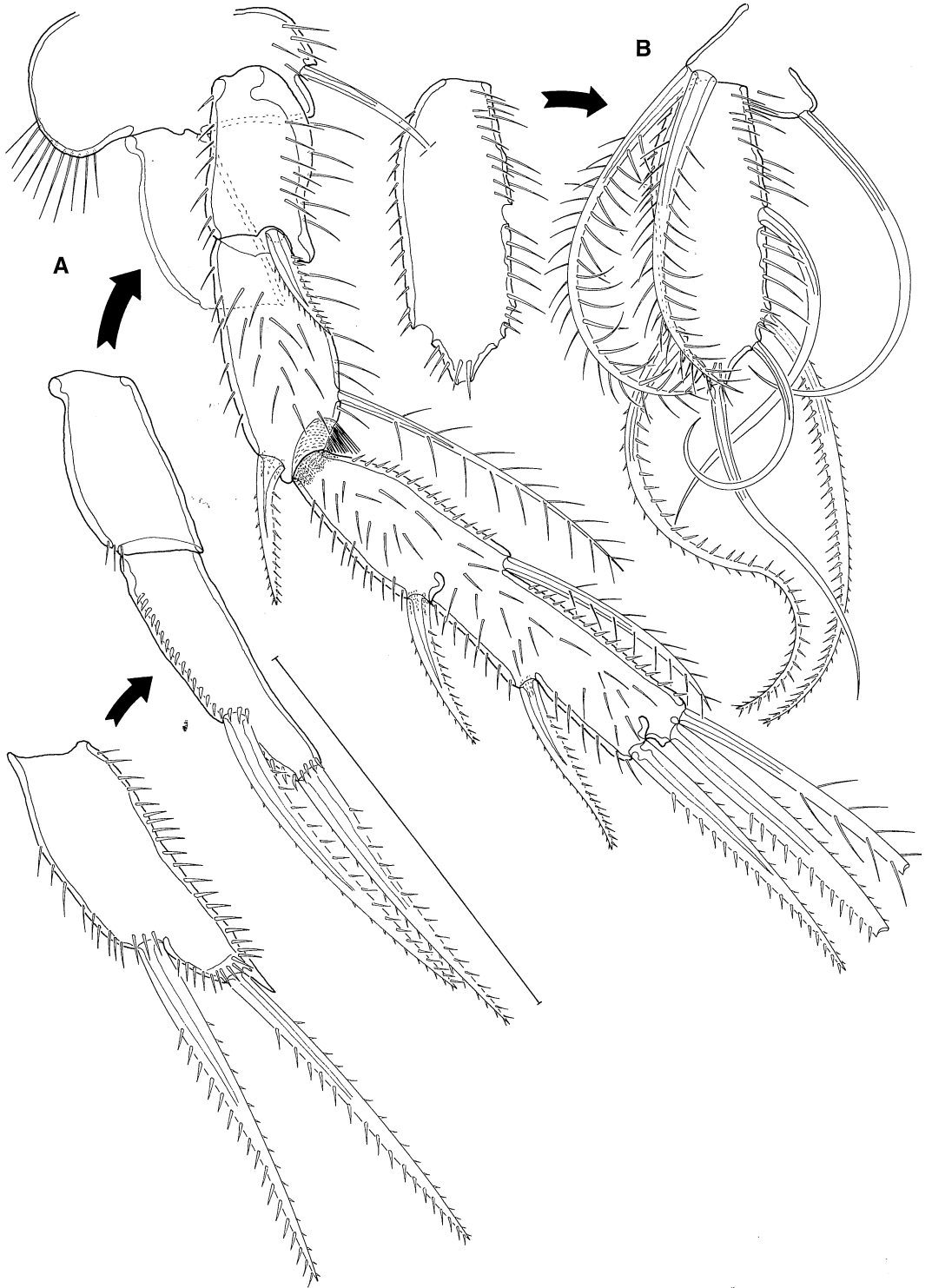


Fig. 6. *Gideonia noncavernicola* gen. et .sp. nov., female. A. P4, B. P5. Scale: 50 μ m.

at subterminal inner margin. Enp2 P2-P4 with terminal apophysis, which is best developed on enp2 P3. Enp2 P2 (Fig. 4B) with row of spinules at each its inner and outer side, in addition with 2 inner setae and 1 terminal seta. Enp2 P3 (Fig. 5A) with row of spinules at outer margin, and with 2 inner and 2 terminal setae. Enp P4 (Fig. 6A) with 1 inner and 1 terminal seta.

P5 (Fig. 6B). Benp. Small, with 2 thick bipinnate setae. Exp long, with 3 outer setae, the middle of which bipinnate. Terminally with 1 bare seta, and additionally with 1 large bipinnate seta at inner margin.

Male

With approximately 370 μm body length, the male shows nearly the same length as the female. It differs in the following characters:

Habitus (Fig. 7A,B) more slender than female, genital somite laterally slightly bi-convex. First 2 free thoracic somites and genital somite dorsally with single remarkable long sensillum.

A1 (Fig. 8A) showing sexual dimorphism, 10-segmented, haplocer. First segment longest, with some spinules and 1 bipinnate seta. Second segment very small, with 1 bare seta. Third segment almost as long as first, with 6 bare setae. Fourth segment small, with 5 bare setae and 1 large aes constricted in the middle. Fifth segment with 2 bare setae, one of which inserting distally from distinct pedestal. Sixth segment smallest, with 2 bare setae and 1 large, constricted aes. Seventh and eighth segment each with 1 bare seta. Ninth segment with 4 bare setae. Tenth segment subterminally with 5 bare setae, one of which inserting from a pedestal, a second seta inserting from a knob-like projection. Additionally with small aes.

Setal formula: I-1/II-1/III-6/IV-5 + aes/V-2/VI-2 + aes/VII-1/VIII-1/IX-4/X-5 + aes.

A2 (Fig. 8B) as in female, except the enp, which bears always 4 geniculate subterminal setae. Additionally with 1 bare and 1 bifid seta, and 1 small bare seta at its outer margin. As remarked above, a similar ornamentation was also detected in some females.

P3 (Fig. 5B) enp more slender than in female. Enp2 with apophysis, but with 2 setae only.

P5 (Fig. 8C). Benp very small, without ornamentation. Exp 2-segmented, first segment with several spinules and 1 bare outer seta. Exp2 as long as exp1, also bearing several spinules. Seta-

tion: 3 bare outer setae, 1 bare terminal seta, and 1 bipinnate inner seta.

P6 (Fig. 2D) covered with spinules. At outer side with 3 bare setae.

Report of two additional superornatiremid species outside caves

During RV "Polarstern" expedition ARK IX/4 (1993), four specimens of a new superornatiremid species were collected from the continental slope in the Barents Sea, locality 82°07.42'N/42°32.35'E at 534 m depth. The species is identified here provisionally as "Superornatiremid sp. nov. 1" (Fig. 9C).

A third benthic-living species was sampled from Seine Seamount (northeast Atlantic) with 3 specimens, during RV "Meteor" cruise M60/1 "OASIS" in 2003 (station #760, 33°46.2'N/14°23.0'W, 181 m depth). It is identified provisionally as "Superornatiremid sp. nov. 2" (Fig. 9B).

Discussion

Assignment of *Gideonia noncavernicola* gen. et sp. nov. to Superornatiremididae. According to Huys (1996), Superornatiremididae is characterized by the following autapomorphies: (1) formation of an oral cone in combination with transformation (elongation) in particular of md and mx1, (2) modification of proximal maxillar endite as well as formation of proximal projection carrying inwardly directed spinules, (3) development of additional setae on P1 (here: additional outer seta on enp2), (4) modification of distal setae on last segment of enp P4 into strong spines, (5) displacement of gonopores and female P6 laterally. According to Seifried (2003) the formation of an oral cone and elongation of mouthparts cannot be considered an autapomorphy of Superornatiremididae, but a synapomorphy of Palinarthra Seifried 2003, a taxon including Novocriniidimorpha Seifried 2003 and Tisboidea Stebbing 1910. The remaining characters mentioned above seem to be potential autapomorphies of the Superornatiremididae, shared also by *Gideonia noncavernicola* gen. et sp. nov. In particular the possession of an additional outer seta on P1 enp2 is considered by us as very important diagnostic character, because it is uniqueness within the Copepoda as a whole (Huys & Boxshall 1991).



Fig. 7. *Gideonia noncavernicola* gen. et .sp. nov., male habitus. A. dorsal view, B. lateral view. Scale: 100 μ m. Triangular arrow indicating spinules covering whole urosome.

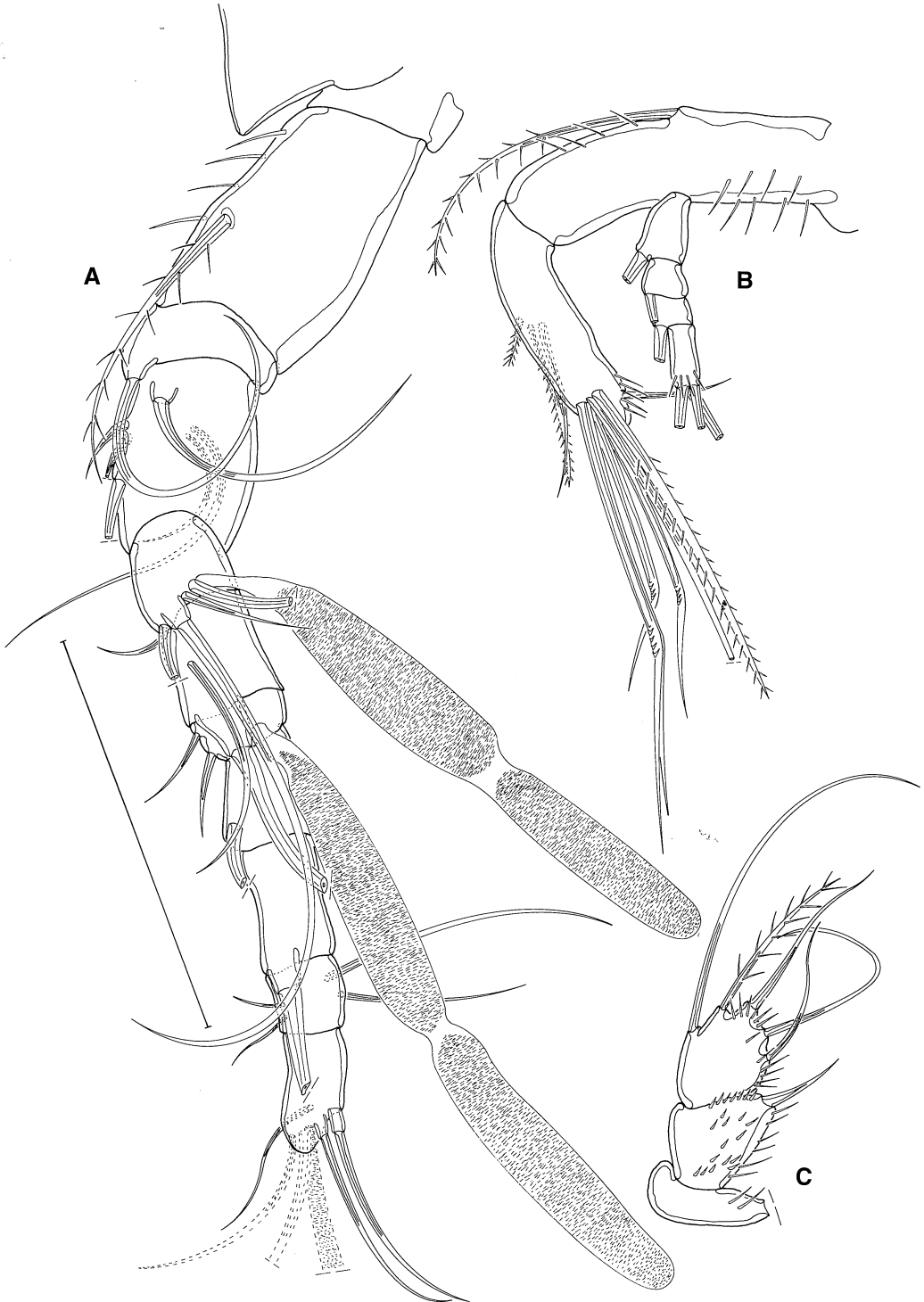


Fig. 8. *Gideonia noncavernicola* gen. et .sp. nov., male. A. A1, dotted setae and aes completed according to counterpart, B. A2, C. P5. Scale: 50 μ m.

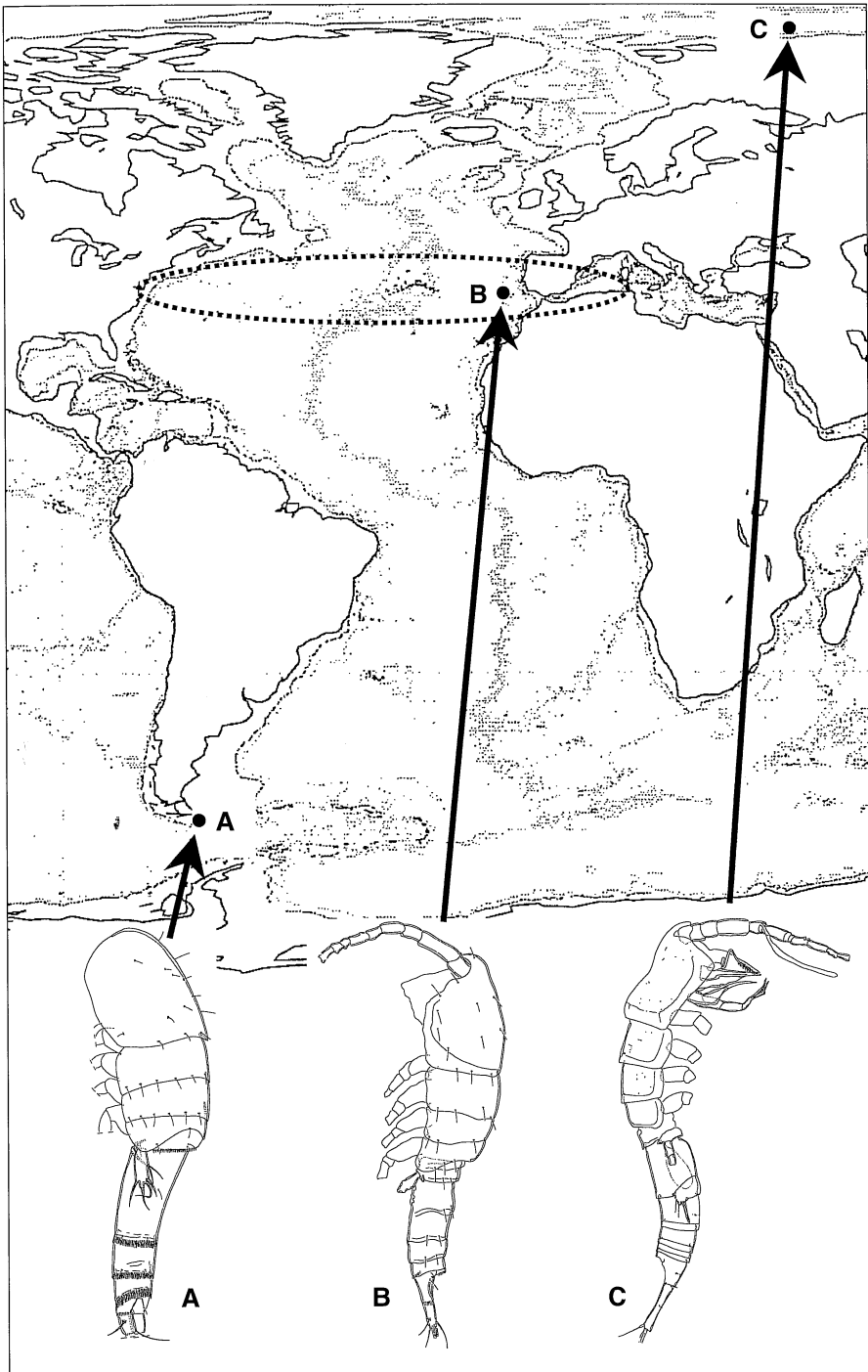


Fig. 9. Map indicating the records of the new Superornatiremidae. A. *Gideonia noncavernicola* gen. et sp. nov., Patagonian continental slope, B. "Superornatiremidae sp. nov. 2", Seine Seamount, C. "Superornatiremidae sp. nov. 1", Barents Sea. Dotted ellipse: distribution area of formerly recorded Superornatiremidae (Huys 1996, Jaume 1997).

Systematic position within Superornatiremidae. The genera *Superornatiremis* Huys, 1996, *Neoechinophora* Huys, 1996 and *Intercrusia* Huys, 1996 show several apomorphic characteristics not present in *Gideonia noncavernicola* gen. et sp. nov.: (6) more additional setae on exp P1, (7) enp3 of P1 with 7 setae (5 setae in *G. noncavernicola* gen. et sp. nov.), (8) development of characteristic seta at md basis (missing in *G. noncavernicola* gen. et sp. nov.), (9) distal setae of enps P2-P3 transformed into spines (normal shape in *G. noncavernicola* gen. et sp. nov.), (10) formation of an epicopulatory plate (absent in *G. noncavernicola* gen. et sp. nov.). These apomorphies confirm the existence of a derived monophyletic group within Superornatiremidae comprising the genera proposed by Huys (1996), but excluding the new species, which appears to be the sister-group of this cluster of genera. *G. noncavernicola* gen. et sp. nov. shows several features which may be considered as apomorphies: (11) A1 with reduced no. of segments (A1 female 8-segmented, A1 male 10-segmented), (12) reduction of 1 endite in mx1, (13) reduction of 1 seta in mx1, (14) distal projection of proximal maxillary endite with 1 seta, (15) distal endite mx with 1 seta, (16) P1 exp2 without inner seta, (17) bases P2-P4 at inner side strongly vaulted, (18) enp P2-P4 2-segmented, (19) sexual dimorphism on enp P3 and probably also on A2.

Distribution. The discovery of non-cavernicolous Superornatiremidae in northern and southern Atlantic waters has implications for the biogeography and the ecology of this taxon.

Former records of Superornatiremidae from Canary Islands, Bermuda and Balearic Islands lead to the assumption that, as other anchialine taxa (cf. Iliffe 2000), this taxon also shows an ampho-Atlantic/Mediterranean distribution (Huys 1996, Jaume 1997). Based on this assumption Jaume (1997) even speculated on the origin of the family concluding that it must be Tethyan as regarded for many stygobiont crustaceans (Stock 1993, Iliffe 2000). This distribution pattern suggests that such organisms are very old and that they inhabited the former Tethys Sea in the early Cretaceous before the opening of the Atlantic Ocean (Stock 1993). However, our findings of *Gideonia noncavernicola* gen. et sp. nov. in the Magellan Region, and of "Superornatiremidae sp. nov. 1" in the polar Barents Sea do not confirm this assumption but suggest a much wider distribution of Superornatiremidae. Such apparently selective

and "complex zoogeographic relationships" (Iliffe 2000, p. 71) are not as unusual as they may appear. For instance, Boxshall & Iliffe (1987, 1990) reported the misophrioid *Expansophria* Boxshall & Iliffe, 1987 from the Galapagos Islands and Palau (both Pacific Ocean), as well as from the Canary Islands (Atlantic).

Recognition that the family is largely distributed in shallow waters on the continental shelf and slopes of South and North Atlantic (and probably in other oceans too) also does not support a "Tethyan origin" for the Superornatiremidae, which means that the present distribution of the family in anchialine habitats may be the result of recent colonization events, rather than very old ones.

Further the discovery of the relatively primitive species *G. noncavernicola* gen. et sp. nov. makes clear that the Superornatiremidae did not evolve in subterranean habitats but from a benthic, shallow-water inhabiting and non-cavernicolous ancestor and the family may have diversified outside cave habitats. During the process of dispersal, descendants may have colonized anchialine caves, among other habitats. At this time, the derived cluster of genera had already evolved its characteristic autapomorphies (like additional setae on exp1 on leg 1), as verified by the non-cavernicolous and derived "Superornatiremidae sp. nov. 1" and "Superornatiremidae sp. nov. 2".

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