BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE, BIOLOGIE, 73: 107-113, 2003
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN, BIOLOGIE, 73: 107-113, 2003

Vestigial structures in pontoporeiid and stegocephalid amphipods (Crustacea, Amphipoda, Gammaridea)

by Cédric d' UDEKEM d' ACOZ & Jørgen BERGE

Abstract

Two kinds of previously overlooked vestigial structures in amphipods are here described and illustrated by SEM photographies. A rudimentary dactylus, reduced to a tiny bud terminated by a seta has been detected on the second and the fifth pereiopod in *Bathyporeia* spp. (Pontoporeiidae), and a minute setiform structure representing the remnant of the mandibular palp has been observed in most stegocephalid genera. Their evolutionary significance is briefly discussed.

Key words : *Bathyporeia*, Pontoporeiidae, Stegocephalidae, *Eualus*, Caridea, mandibular palp, dactylus, vestigial, morphology.

Résumé

Deux types de structures vestigiales présentes chez certains amphipodes sont décrits ici pour la première fois, et illustrés par des photographies en microscopie électronique à balayage. Un dactyle minuscule et rudimentaire prolongé par une soie a été détecté sur le second et le cinquième péreiopode de *Bathyporeia* spp. (Pontoporeiidae). De même, une très petite structure sétiforme représentant l'ultime vestige d'un palpe mandibulaire a été observé chez la plupart des Stegocephalidae. Leur signification évolutive est brièvement discutée.

Mots clés : *Bathyporeia*, Pontoporeiidae, Stegocephalidae, *Eualus*, Caridea, palpe mandibulaire, dactyle, vestigial, morphologie.

Introduction

As a consequence of evolutionary pressure, some appendages or structures may regress and finally disappear. Such regressive processes are usually gradual, and vestigial remnants of these structures often persist for very long periods before their complete disappearance. During our respective studies on pontoporeiid and stegocephalid amphipods, both authors independently discovered two kinds of vestigial structures, which are here presented in a joint paper: the occurrence of a rudimentary dactylus on the second and fifth pereiopod in the genus *Bathyporeia* (Pontoporeiidae) and that of a rudimentary mandibular palp in stegocephalid amphipods. Those structures, which have previously been overlooked, are described here for the first time.

The dactylus of the second and fifth pereiopod in *Bathyporeia* spp. (Pontoporeiidae)

The very homogeneous genus *Bathyporeia* LINDSTRÖM, 1855 includes about 20 species living in sandy intertidal and coastal bottoms in the Atlantic and the Mediterranean Sea (D'UDEKEM D'ACOZ, submitted). Their antennae, pereiopods and uropods are deeply modified (G.O. SARS, 1891) in direct relationship with their fossorial habits (NICOLAISEN & KANNEWORFF, 1969). Previous authors such as e.g. G.O. SARS (1891) concluded that the dactylus was lacking on the second and the fifth pereiopods, and indeed at first glance they seem to be absent. However, when studying the taxonomy of the northwestern European species under a high power light microscope, the first author had the surprise to detect minute structures between the apical propodal setae of the second and the fifth pereiopods, which are obviously vestigial dactyli. They were observed in all northwestern European *Bathyporeia* species: *B. elegans* WATKIN, 1938; *B. gracilis* G.O. SARS, 1891; *B. guilliamsoniana* (BATE, 1857); *B. nana* TOULMOND, 1966; *B. pelagica* (BATE, 1856); *B. pilosa* LINDSTRÖM, 1855; *B. sarsi* WATKIN, 1938 and *B. tenuipes* MEINERT, 1870, as well as in the northeastern American *B. parkeri* BOUSFIELD, 1973, and that disposition is presumably characteristic of the whole genus. A closer examination in scanning electron microscopy (SEM) revealed that the rudimentary dactylus of the second pereiopod, which arises from the ventral surface of the propodus, consists of a discoid tiny bud fused to the propodus, terminated in a longer, strongly setulose seta (Fig. 1). Despite its very small size, the fifth dactylus appears to be in a less advanced stage of morphological regression. It consists of a minute cylinder, distinctly articulated with the anteroventral part of the propodus and terminated in a scarcely setulose seta (Fig. 2).

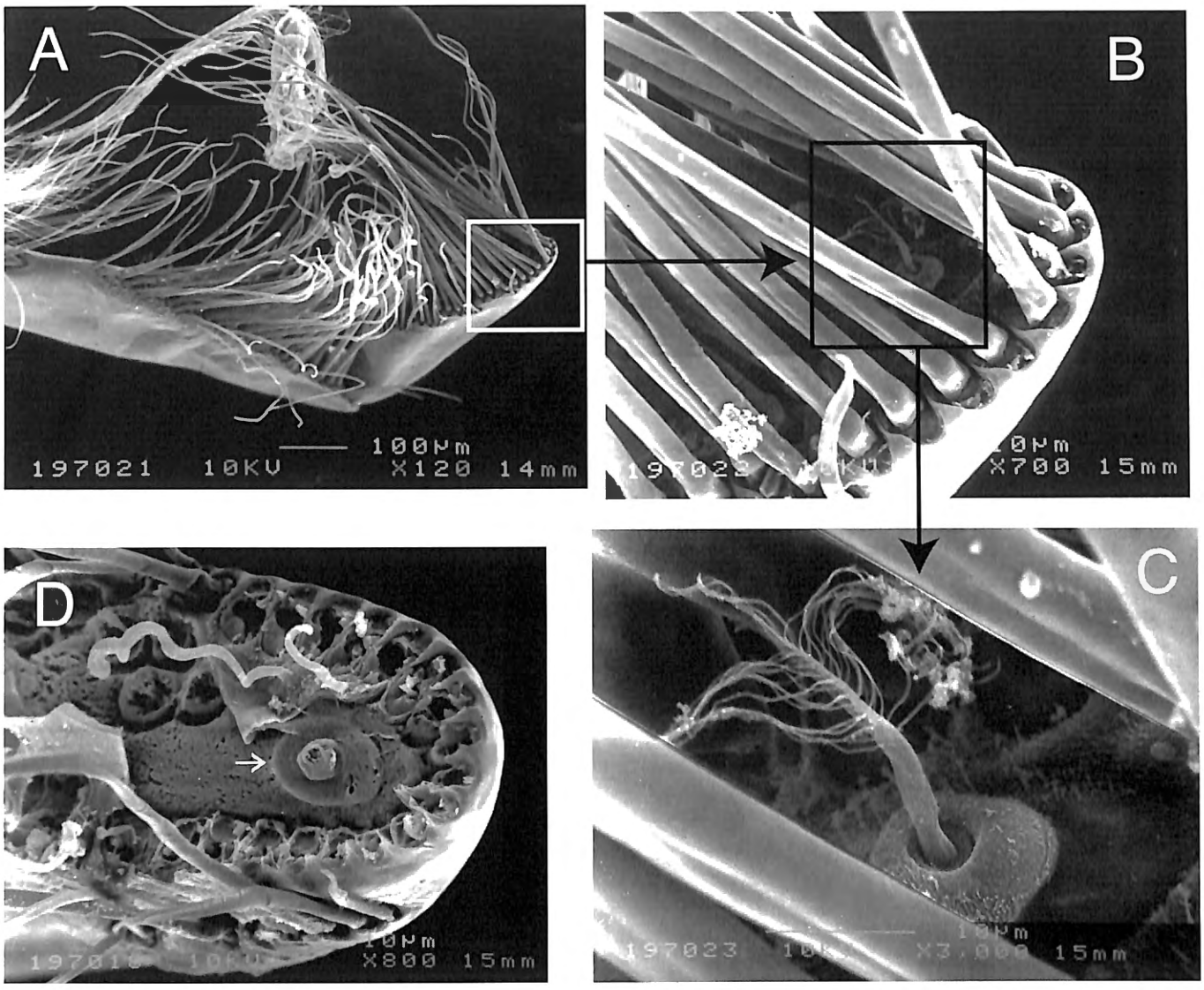

Fig. 1. *Bathyporeia guilliamsoniana* (BATE, 1857), male, the Netherlands, second pereiopod. A, carpus and propodus; B, D, tip of propodus + vestigial dactylus; C, vestigial dactylus. On fig. D, the apical seta of the vestigial dactylus has been rubbed off during the removal of the propodal marginal setae.

In related genera like *Pontoporeia* and *Amphiporeia*, the dactylus of the second pereiopod, although not always large, remains well developed and forms a subchela with the propodus (e.g. G.O. SARS, 1891; SHOEMAKER, 1933; BOUSFIELD, 1973; GLENNON, 1979). In contrast, *Bathyporeia* possesses an elongate and deeply modified propodus with a vestigial bud-like dactylus.

As concerns the fifth pereiopod, its general shape remains basal in *Pontoporeia*, whilst in *Amphiporeia* it is highly modified, with a blade-like merus, and morphologically very close to that of *Bathyporeia*. However both in *Pontoporeia* and *Amphiporeia*, the dactylus of the fifth pereiopod, albeit small, remains conspicuous and is much bigger than in *Bathyporeia*. So, if the second and the fifth pereiopod are considered alone, there is apparently a kind of evolutionary gradation : *Pontoporeia* (P2 and P5 basal) > *Amphiporeia* (P2 basal; P5 modified but with conspicuous dactylus) > *Bathyporeia* (P2 and P5 modified, both with very reduced dactyli).

The stegocephalid mandible and its vestigial palp

So far, all authors dealing with either the morphology and/or the taxonomy of the amphipod family Stegocephalidae DANA, 1852 have concluded that the mandible of the family is always devoid both of palp and molar process; see especially BERGE & VADER (2001) in their recent revision of the family. However, a careful examination of representatives of all five subfamilies of the Stegocephalidae: Andaniexinae, Andaniopsinae, Bathystegocephalinae, Parandaniinae and Stegocephalinae in SEM has revealed the existence of a tiny, more or less setiform structure at the exact position where a palp does occur in other amphipod families. That structure is herein interpreted as a rudimentary palp.

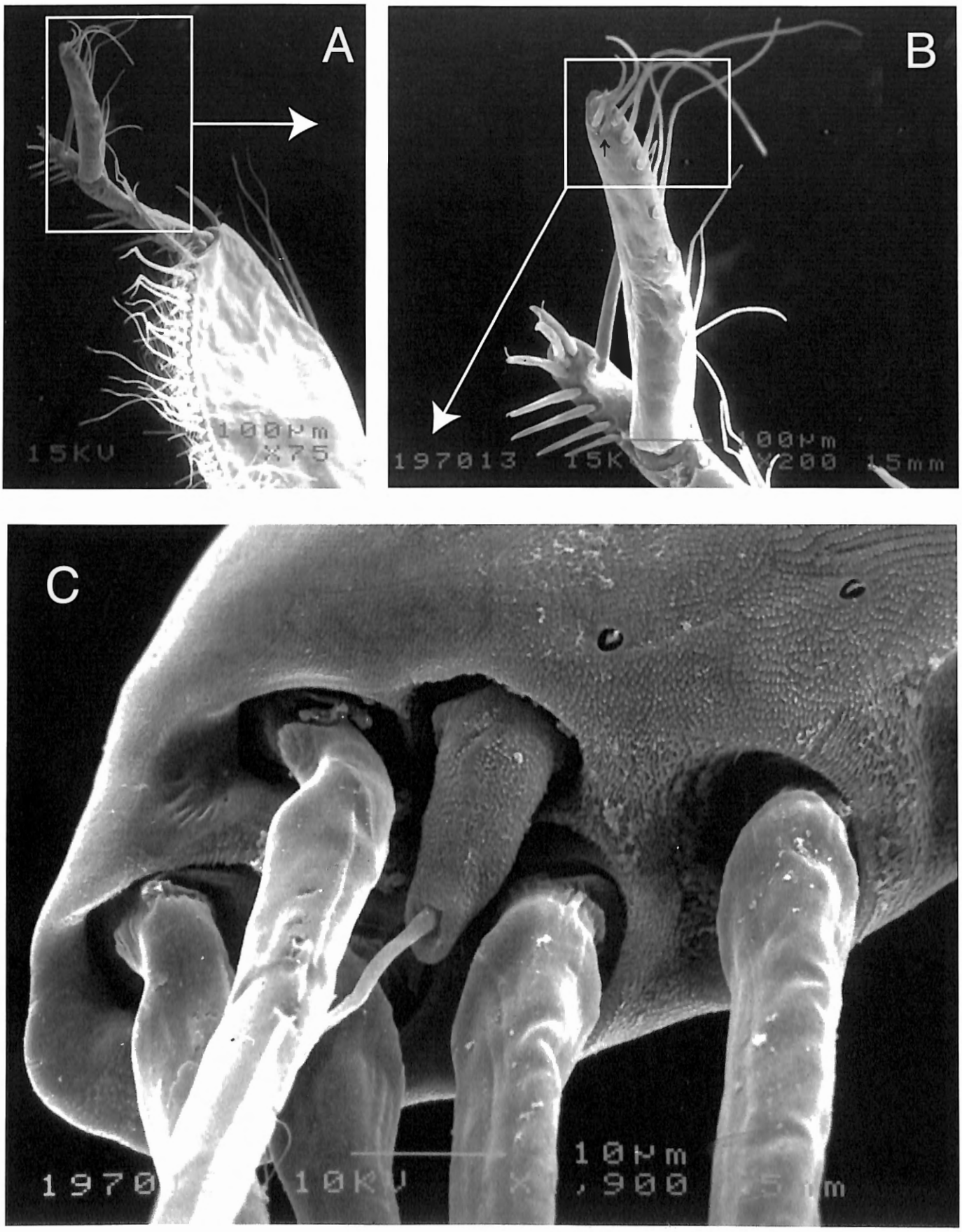

Fig. 2. *Bathyporeia guilliamsoniana* (BATE, 1857), male, the Netherlands, fifth pereiopod. A, merus to tip; B, propodus + scarcely distinct dactylus; C, tip of propodus + vestigial dactylus.

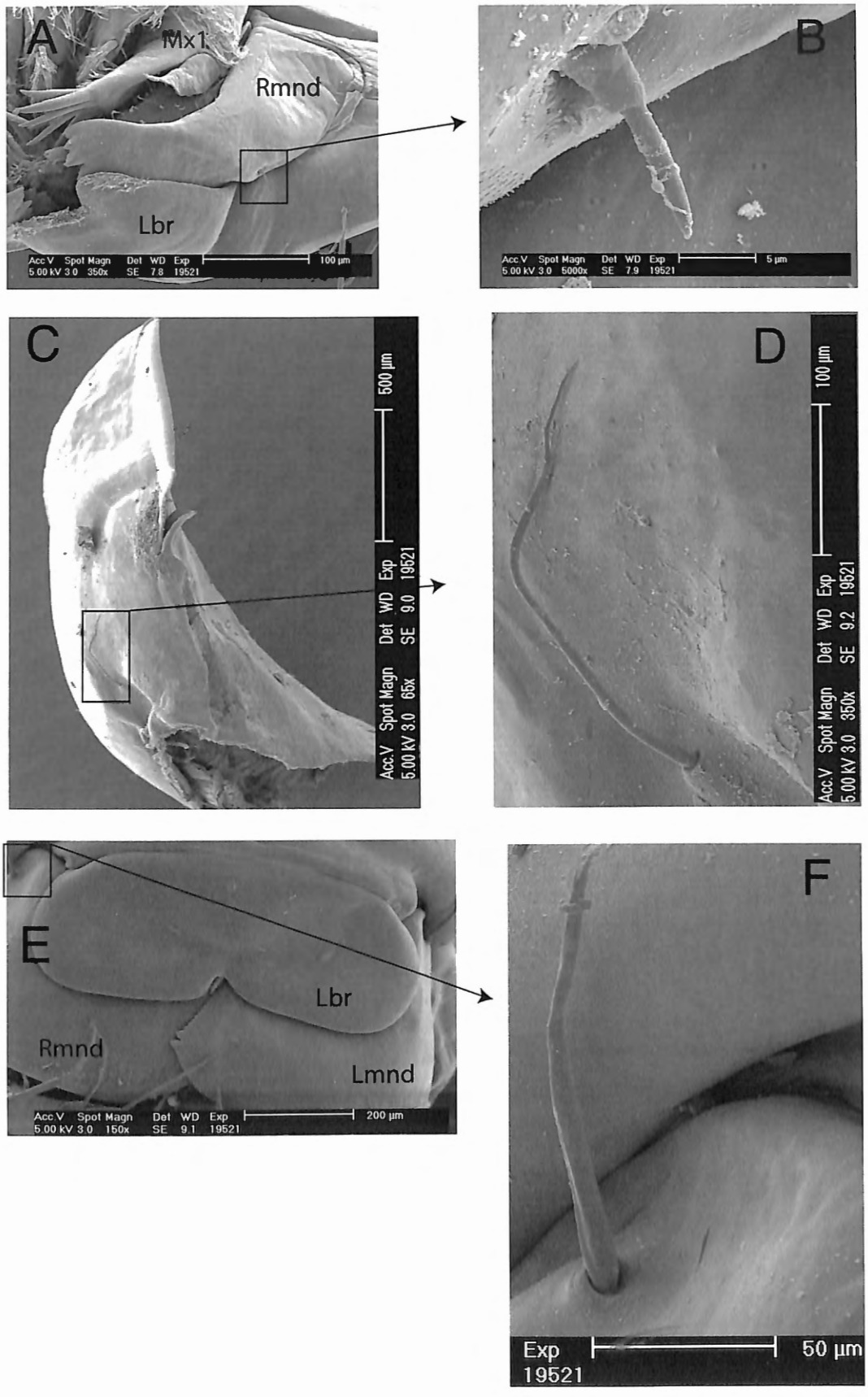

Fig. 3. A, B: *Stegonomadia biofar* (BERGE & VADER, 1997), Iceland; C, D: *Parandania gigantea* (STEBBING, 1888), Southern Ocean, E, F: *Bathystegocephalus globosus* WALKER, 1909, Indian Ocean. A, C, E, mandible and oral field; B, D, F, vestigial mandibular palp.

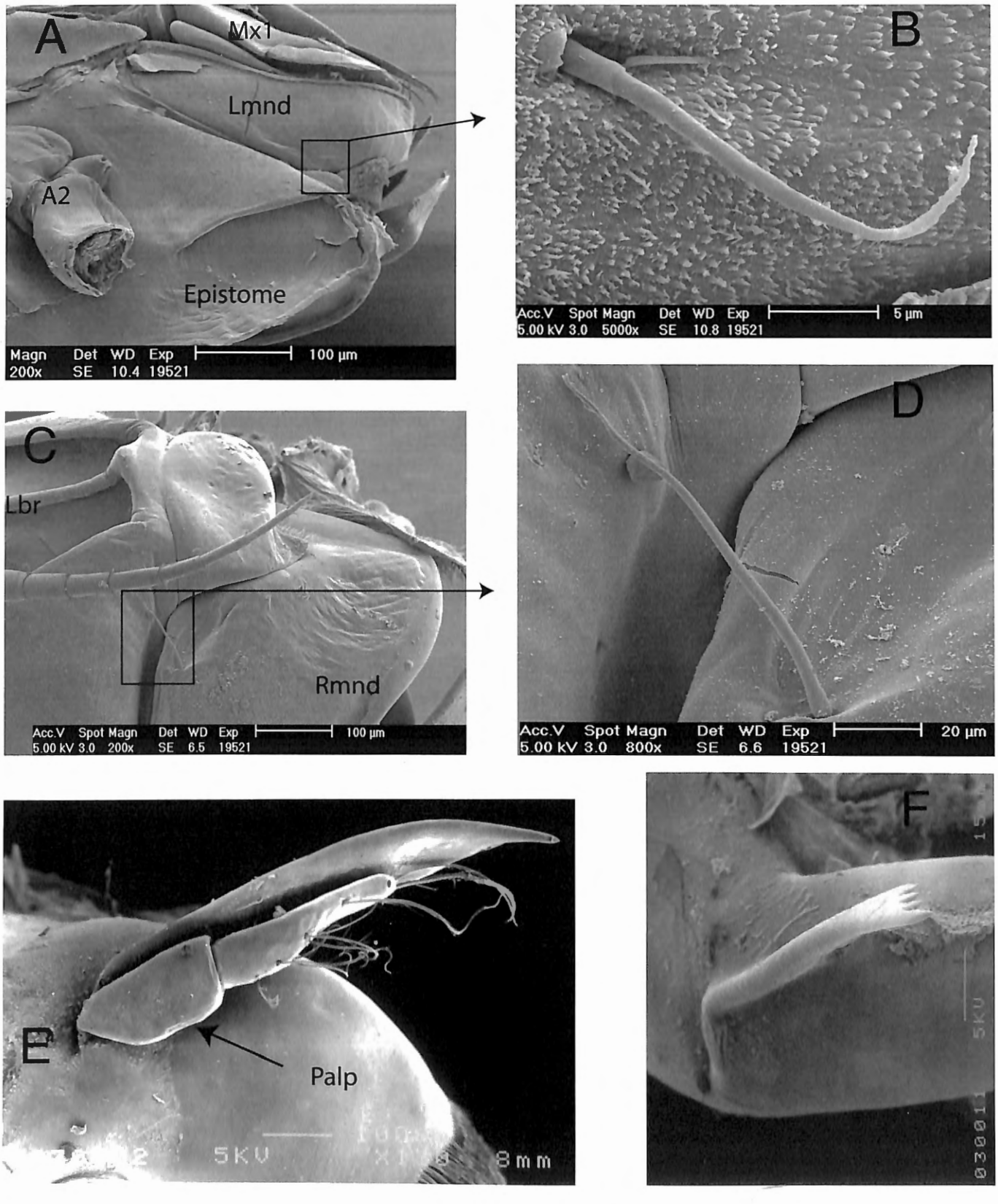

Fig. 4. A, B: *Andaniopsis nordlandica* (BOECK, 1871), Northern Norway; C, D: *Andaniotes linearis* K.H. BARNARD, 1930, Southern Ocean; E: *Eualus occultus* (LEBOUR, 1936), female, NW France, île Callot; F: *Eualus cranchii* (LEACH, 1817), female, Belgium, Zeebrugge. A, C, mandible and oral field; B, D, vestigial mandibular palp; E, F, left mandible (respectively with and without palp).

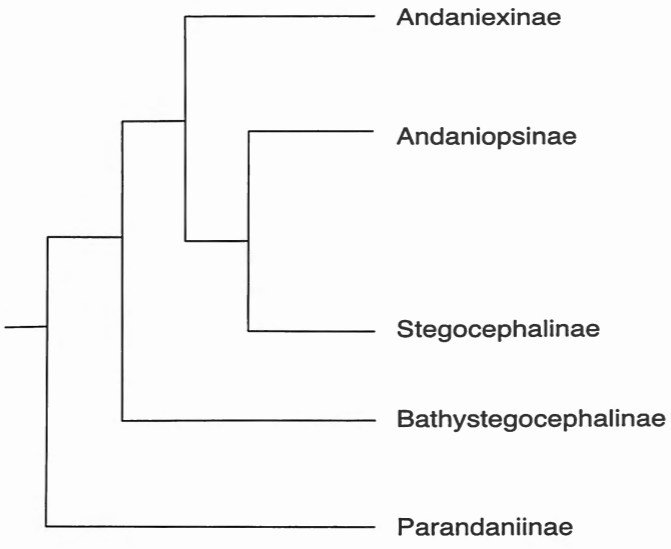

Fig. 5. Phylogenetic relationships among the subfamilies of Stegocephalidae as hypothesised by BERGE & VADER (2001).

Its distribution across all five subfamilies clearly indicates this being a plesiomorphic character state. Indeed, all members of the two most plesiomorphic subfamilies (Bathystegocephalinae and Parandaniinae, see Fig. 5), which together consist of merely 4 species (*Bathystegocephalus globosus* WALKER, 1909, *Parandania boecki* (STEBBING, 1888), *P. gigantea* (STEBBING, 1888) and *P. nonhiata* ANDRES, 1985), possess a rudimentary palp (Fig. 3 C-F), as do all examined species of the subfamily Andaniexinae (*Andaniexis lupus* BERGE & VADER, 1997, *Andaniotes linearis* K.H BARNARD, 1930, *A. pseudolinearis* BERGE, 2001, *Glorandaniotes eilae* BERGE & VADER, 1997, *Mediterexis mimonectes* (RUFFO, 1975), and *Stegosoladidus simplex* (K.H. BARNARD, 1930)), here represented by *Andaniotes linearis* (Fig. 4 C-D). In all these three subfamilies, the palp remnant consists of a relatively elongated structure, very similar to a long simple seta, but eventually with a slight basal thickening (Figure 3 B). In the majority of the Andaniopsinae (*Andaniopsis nordlandica* (BOECK, 1871), *Andaniopsis* sp. nov, BERGE in press and *Steleuthera maremboca* BARNARD, 1964) a rudimentary palp, similar to that of *Andaniopsis nordlandica* (Fig. 4 A-B), is present. However, among the remaining three Andaniopsinae species, two (*Andaniopsis pectinata* G.O. SARS, 1883 and *Steleuthera africana* BERGE, DE BROYER & VADER, 2001) are shown to have no palp at all, whereas the corresponding character state is still unknown for the last Andaniopsinae species, *Andaniopsis integripes* (BELLAN-SANTINI & LEDOYER, 1986).

In the fifth stegocephalid subfamily, the Stegocephalinae, at least six genera are known to possess a rudimentary palp (*Austrocephaloides australis* (K.H. BARNARD, 1930, *Pseudo bioice* (BERGE & VADER, 1997), *Stegocephalina wagini* (GURJANOVA, 1936), *Stegocephalus inflatus* KRØYER, 1842, *Stegonomadia biofar* (BERGE & VADER, 1997) and *Tetradeion crassum* (CHILTON, 1883), herein represented by *Stegonomadia biofar* (Fig. 3 A-B). However, within the clade consisting of the four genera *Austrophippsia, Phippsia, Schellenbergia* and *Tetradeion*, it seems that most species in fact do not possess any palp, but that it has been retained in some *Tetradion* species.

Thus, it seems that within the three most basal stegocephalid subfamilies (Fig. 5), a rudimentary palp is present in all species (at least, all species examined hitherto have been confirmed to possess a palp), whereas the homologous feature is not present in all species of the two more derived subfamilies (Andaniopsinae and Stegocephalinae, see Fig. 5).

Discussion and conclusion

Interestingly, both in the case of the vestigial dactyli and in that of the mandibular palp, a hair-like element is present. Indeed the dactyli of *Bathyporeia* spp. consist of a bud-like structure terminated by a proportionately large seta, and the stegocephalid palp as a whole is setiform. Maybe, the stegocephalid condition is a more advanced stage or regression. This is supported by the fact that the vestigial condition is the rule in the family, whilst various character states are found amongst Pontoporeiidae.

Although, in the cases described above, the regression appears to be a gradual process, with a long-persisting vestige, there are probably exceptions to that rule in crustaceans. Recently, we have examined the mandible of the caridean shrimp *Eualus cranchii* (LEACH, 1817) which was also supposed to be devoid of a mandibular palp. Scanning electron microscopy examination confirmed that it was completely absent as previously stated, without any vestigial remnant (Fig. 4 F). Very closely related species such as *Eualus occultus* (LEBOUR, 1936) exhibit a well-developed palp (Fig. 4 E). Because of the great similarity between the two species, it is likely that the regressive process has been very fast, unlike in Stegocephalidae.

Finally, our observations clearly demonstrate that very careful examination is necessary before claiming the complete disappearance of a structure, and it would not be surprising if other supposedly lacking dactyli, palps or spines will prove to have persisted in a vestigial condition in other crustaceans.

Acknowledgments

The authors are grateful to Prof Wim VADER (Tromsø Museum) for his help with earlier drafts of the manuscript, and to Tom Ivar EILERTSEN (Tromsø University), Chris JONES and Prof. Geoff BOXSHALL (The Natural History Museum in London) for their help and support in preparing the SEM pictures, and Dr. David M. KNOTT, Southern Regional Taxonomic Center, Charleston for providing us with material of *Bathyporeia parkeri* BOUSFIELD, 1973.

The second author was funded by the Norwegian Research Council, project number 145384/432.

References

BERGE, J. & W. VADER, 2001. Revision of the amphipod (Crustacea) family Stegocephalidae. *Zoological Journal of the Linnean Society*, 133: 531-592.

BOUSFIELD, E.L., 1973. Shallow-water gammaridean Amphipoda of New England. Comstock Publishing Associates, a division of Cornell University Press, Ithaca & London: 1 frontispiece + i-xii + 1-312.

GLENNON, T.A., Jr., 1979. Description of the Male of *Amphiporeia gigantea* BOUSFIELD (Amphipoda, Haustoriidae). *Crustaceana*, 37(3): 304-310.

NICOLAISEN, W., & E. KANNEWORFF, 1969. On the burrowing and feeding habits of the amphipods *Bathyporeia pilosa* LINDSTRÖM and *Bathyporeia sarsi* WALKER. *Ophelia*, 6: 231-250.

SARS, G.O., 1890-1895. An account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. 1. Amphipoda. Christiana and Copenhagen, published by Alb. CAMMERMEYER (reprinted 1966 by Universitetsforlaget, Bergen and Oslo): 1-711 + pl. 1-240 + pl. i-viii.

SHOEMAKER, C.R., 1933. A new amphipod of the genus *Amphiporeia* from Virginia. *Journal of the Washington Academy of Sciences*, 23(4): 212-216.

UDEKEM D'ACOZ, C. d', submitted. The genus *Bathyporeia* LINDSTRÖM, 1855 in Western Europe (Crustacea, Amphipoda, Pontoporeiidae). *Zoologische Verhandelingen, Leiden*

Cédric D'UDEKEM D'ACOZ
Tromsø Museum (Department of Zoology)
University of Tromsø
9037 Tromsø, Norway
E-mail : cdudekem@tmu.uit.no

Jørgen BERGE
Associate Professor, Marine Biology
UNIS, Pb 156
9171 Longyearbyen, Norway
E-mail : jorgen.berge@unis.no