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Notes on the genus *Pedionis* Hamilton (Hemiptera, Cicadellidae, Macropsinae), and with description of two new species from China

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Abstract

Two new species *Pedionis (Pedionis) nankunshanensis* Li, Dai & Li **sp. n.** and *P. (P.) tabulatus* Li, Dai & Li **sp. n.** from China are described and illustrated. A key is given to separate all species of this genus (except *P. (P.) oeroe* and *P. (P.) thyia*).

Keywords

Hemiptera, Macropsinae, *Pedionis*, new species, taxonomy, distribution, China

Introduction

The leafhopper genus *Pedionis* belongs to the tribe Macropsini, subfamily Macropsinae (Hemiptera: Cicadellidae) and was established by Hamilton (1980) with *Pediopsis garuda* Distant, 1916 as its type species. Hamilton separated two subgenera *Pedionis* and *Thyia* by anteapical cells and proposed six new combinations (one in subgenus *Thyia*) and described three new species. Later, 12 new species (Viraktamath 1981, 1996; Kuoh 1987; Huang and Virakatamath 1993; Liu and Zhang 2003; Zhang and Viraktamath 2010) were described and illustrated. Currently 20 species of the subgenus *Pedionis* and 1 species of the subgenus *Thyia* have been recorded, and 8 of the subgenus *Pedionis* from China.

Species of *Pedionis* are mainly distributed in the Oriental region, and almost half of them (all belong to subgenus *Pedionis*) are found in southern of China (Oriental region) and most *Pedionis* species are associated with shrubs and trees.

In this paper, two new Chinese species of the genus from Guizhou and Guangdong Province are described and illustrated. 23 species of the genus and a key to species from the world is provided (except *P. (P.) oeroe* and *P. (P.) thyia*). The type specimens of the new species are deposited in the Institute of Entomology, Guizhou University, Guiyang, China (GUGC).

Taxonomy

Genus *Pedionis* Hamilton

Pedionis Hamilton 1980: 891.

Type species: *Pediopsis garuda* Distant, 1916.

Diagnosis. Following Hamilton (1980).

Subgenus *Pedionis (Pedionis)* Hamilton

Pedionis (Pedionis) Hamilton 1980: 892.

Type species: *Pediopsis garuda* Distant, 1916: 239.

Diagnosis. Following Hamilton (1980).

Distribution. Oriental region, Palaearctic region, Northern Australia.

Subgenus *Pedionis (Thyia)* Hamilton

Subgenus *Pedionis (Thyia)* Hamilton 1980: 894.

Type species: *Macropsis thyia* Kirkaldy, 1907: 36.

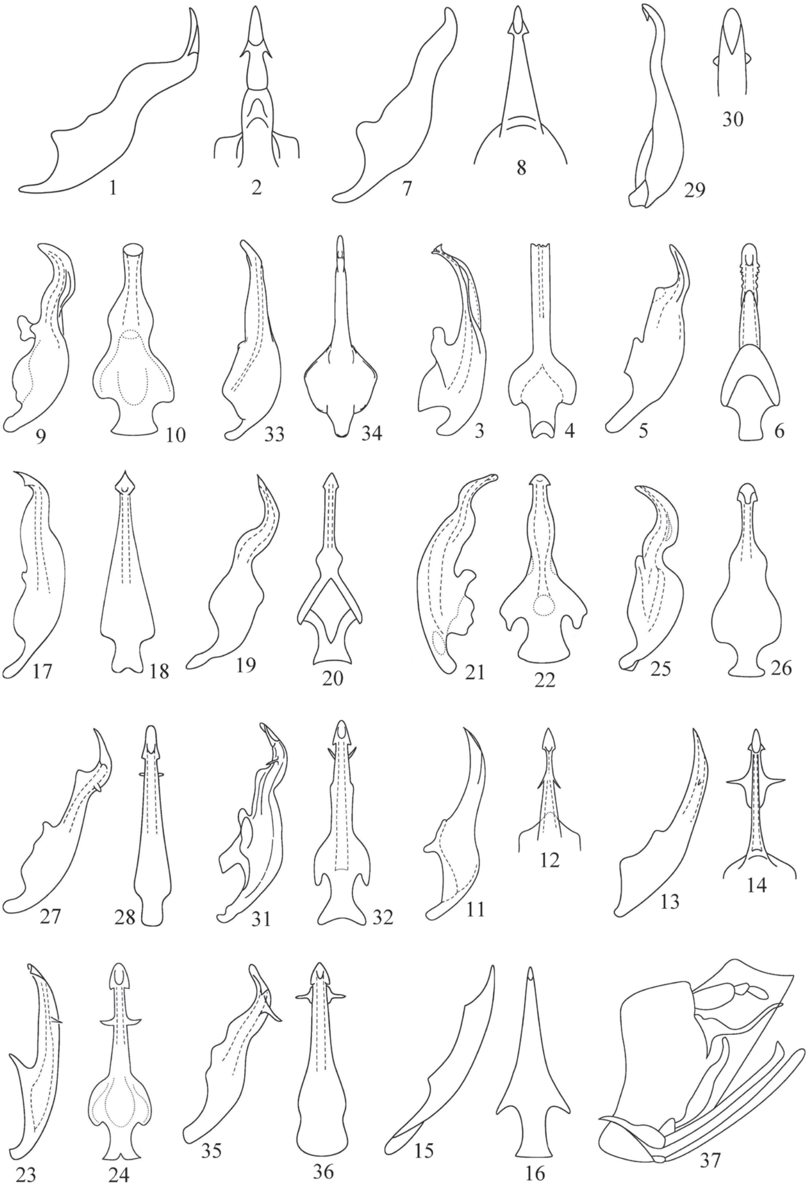
Diagnosis. Following Hamilton (1980).

Distribution. Northern Australia.

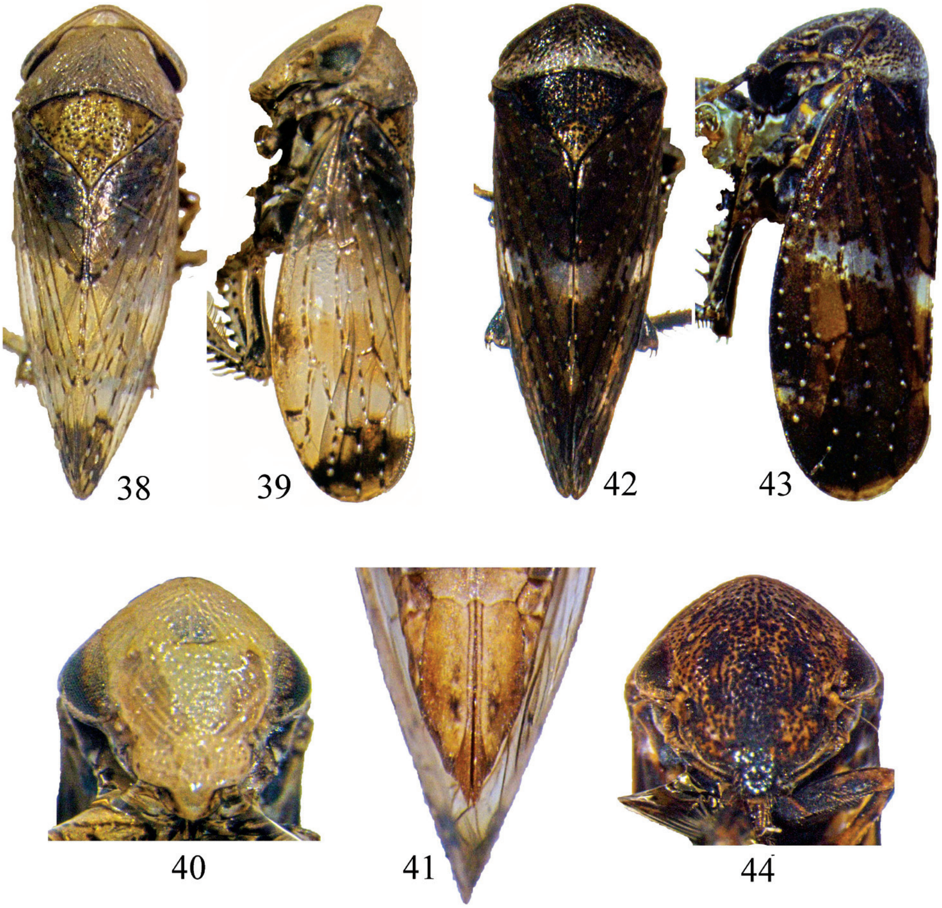
Key to male species of genus *Pedionis* (except *P. (P.) oeroe* and *P. (P.) thyia*)

Notes: The species *P. (P.) oeroe* should belong to the subgenus *Pedionis* by tegmina with only 2 subapical cells and veins dark fuscous multiannulate with whitish according to the original description, but no male genitalia manuscript (Kirkaldy 1907), the species *P. (P.) thyia* is distinguished from others by amount of anteapical cells (non-genitalic characters), therefore, the key don't encompass these two species.

1 Aedeagal shaft without any processes (Figs 9–10, 15–16, 33–34, 37)..........**2**
– Aedeagal shaft with 1–2 processes (Figs 1–8, 11–14, 17–32, 35–36, 47–48, 55–56)..........**5**
2 Aedeagus broader basally and tapering apically (Figs 9–10, 33–34)..........**3**
– Aedeagus less broader basally and about the end (Figs 15–16, 37)..........**4**
3 Gonopore opening on the apex of adeagal shaft (Figs 9–10)... ***P. (P.) curvata***
– Gonopore opening on the subapical of adeagal shaft (Figs 33–34)..........***P. (P.) venosa***
4 Aedeagal shaft strongly sinuated (Fig. 37)..........***P. (P.) minuta***
– Aedeagal shaft less sinuated and with protuberance in middle-dorsal aspect (Figs 15–16)..........***P. (P.) koghiensis***
5 Aedeagal shaft with one pair of processes (Figs 1–8, 17–22, 25–26, 29–30).... **6**
– Aedeagal shaft with two pairs of processes (Figs 11–14, 23–24, 27–28, 31–32, 35–36, 47–48, 55–56)..........**14**
6 This one pair of processes produced on the apex of aedeagal shaft (Figs 3–4, 17–22, 25–26, 29–30)..........**7**
– This one pair of processes produced on the subapical of aedeagal shaft (Figs 1–2, 5–8)..........**12**
7 The processes situated on the ventral margin of apical aedeagal shaft (Figs 3–4, 17–22, 25–26)..........**8**
– The processes situated on the dorsal margin of apical aedeagal shaft (Figs 29–30)..........***P. (P.) stigma***
8 The apex of aedeagus as arrow-like (Figs 17–20)..........**9**
– The apex of aedeagus as curved-like or serrated (Figs 3–4, 21–22, 25–26)... **10**
9 Aedeagal shaft with a bulbous (Figs 19–20)..........***P. (P.) mecota***
– Aedeagal shaft without any bulbous, tapering apically (Figs 17–18) ***P. (P.) lii***
10 Apex of aedeagal shaft as curved-like (Figs 21–22, 25–26)..........**11**
– Apex of aedeagal shaft as serrated-like (Figs 3–4)..........***P. (P.) cherraensis***
11 Aedeagal shaft with a bulge nearly base, the lateral aspect of aedeagus strongly sinuated (Figs 25–26)..........***P. (P.) serrate***
– Aedeagal shaft with a bulge nearly middle, the lateral aspect of aedeagus less sinuated (Figs 21–22)..........***P. (P.) palniensis***
12 The pair processes wide and as serrated (Figs 5–6).......... ***P. (P.) clypellata***
– The pair processes narrow and as lamella (Figs 1–2, 7–8)..........**13**



Figures 1–37. Aedeagus of *Pedionis* species, lateral view and ventral view. **1, 2** *P. astrala* Hamilton **3, 4** *P. cherraensis* Viraktamath **5, 6** *P. clypellata* Huang & Viraktamath **7, 8** *P. contrasta* Hamilton **9, 10** *P. curvata* Viraktamath **11, 12** *P. garuda* (Distant) **13, 14** *P. kagoshimensis* (Matsumura) **15, 16** *P. koghiensis* (Evans) **17, 18** *P. lii* Zhang & Viraktamath **19, 20** *P. mecota* Liu & Zhang **21, 22** *P. palniensis* Viraktamath **23, 24** *P. rufoscutallata* Huang & Viraktamath **25, 26** *P. serrate* Viraktamath **27, 28** *P. spinata* Zhang & Viraktamath **29, 30** *P. stigma* Kouh **31, 32** *P. sumatrana* Viraktamath **33, 34** *P. venosa* Hamilton **35, 36** *P. yunnana* Zhang & Viraktamath **37** *P. minuta* (Evans). (**1–2, 7–8, 13–14** after Hamilton 1980; **3–4, 31–32** after Viraktamath 1996; **5–6, 23–24** after Huang and Viraktamath 1993; **9–12, 21–22, 25–26** after Viraktamath 1981; **15–16** after Evans 1974; **17–18, 27–28; 35–36** after Zhang and Viraktamath 2010; **19–20** after Liu and Zhang 2003; **29–30** after Kuoh 1987; **33–34** after Okudera 2009; **37** after Evans 1971)



Figures 38–44. *Pedionis (Pedionis) nankunshanensis* Li, Dai & Li sp. n. **38** Dorsal view, (♂) **39** Lateral view, (♂) **40** Facial view, (♂) **41** Seventh sternite ventral view. **42–44** *Pedionis (Pedionis) tabulatus* Li, Dai & Li sp. n. **42** Dorsal view, (♂) **43** Lateral view, (♂) **44** Facial view, (♂).

13 Aedeagal shaft with a constriction in middle, the lateral aspect of aedeagus strongly sinuated (Figs 1–2) .... ***P. (P.) astrala***

– Aedeagal shaft without any constriction in any position, the lateral aspect of aedeagus less sinuated (Figs 7–8)..***P. (P.) contrasta***

14 Two pairs of processes without connection, separated (Figs 23–24, 27–28, 31–32, 35–36, 55–56)...**15**

– Two pairs of processes with a membranous connection (Figs 11–14, 47–48).... ....**19**

15 The first pair of processes produced on the dorsal margin of apical aedeagal shaft, the second wide (Figs 55–56) ....***P. (P.) tabulatus* Li, Dai & Li sp. n.**

– The first pair of processes produced on the ventral margin of apical aedeagal shaft, the second narrow (Figs 23–24, 27–28, 31–32, 35–36)...................**16**

16 The second pair of processes closely to the first (Figs 35–36)... ***P. (P.) yunnana***

– The second pair of processes away from the first (Figs 23–24, 27–28, 31–32).. **17**

17 Dorsal aspect of aedeagal shaft with protuberance in middle (Figs 27–28, 31–32).. **18**

– Dorsal aspect of aedeagal shaft without protuberance (Figs 23–24).............. .... ***P. (P.) rufoscutallata***

18 Aedeagal shaft with a bulge nearly middle, the second pair of processes towards dorsal aspect (Figs 31–32).. ***P. (P.) sumatrana***

– Aedeagal shaft without a bulge nearly middle, the second pair of processes towards ventral aspect (Figs 27–28).. ***P. (P.) spinata***

19 The first pair of processes produced on the dorsal margin of aedeagal shaft as serrated, the second have reflexed ventral aspect view (Figs 47–48).............. .... ***P. (P.) nankunshanensis*** **Li, Dai & Li sp. n.**

– The first pair of processes produced on the ventral margin of aedeagal shaft, the second have no reflexed ventral aspect view (Figs 11–14).................... **20**

20 The second pair of processes wide basally, aedeagal shaft strongly sinuated (Figs 13–14).. ***P. (P.) kagoshimensis***

– The second pair of processes slender, aedeagal shaft less sinuated (Figs 11–12)... .... ***P. (P.) garuda***

Pedionis (Pedionis) nankunshanensis **Li, Dai & Li sp. n.**

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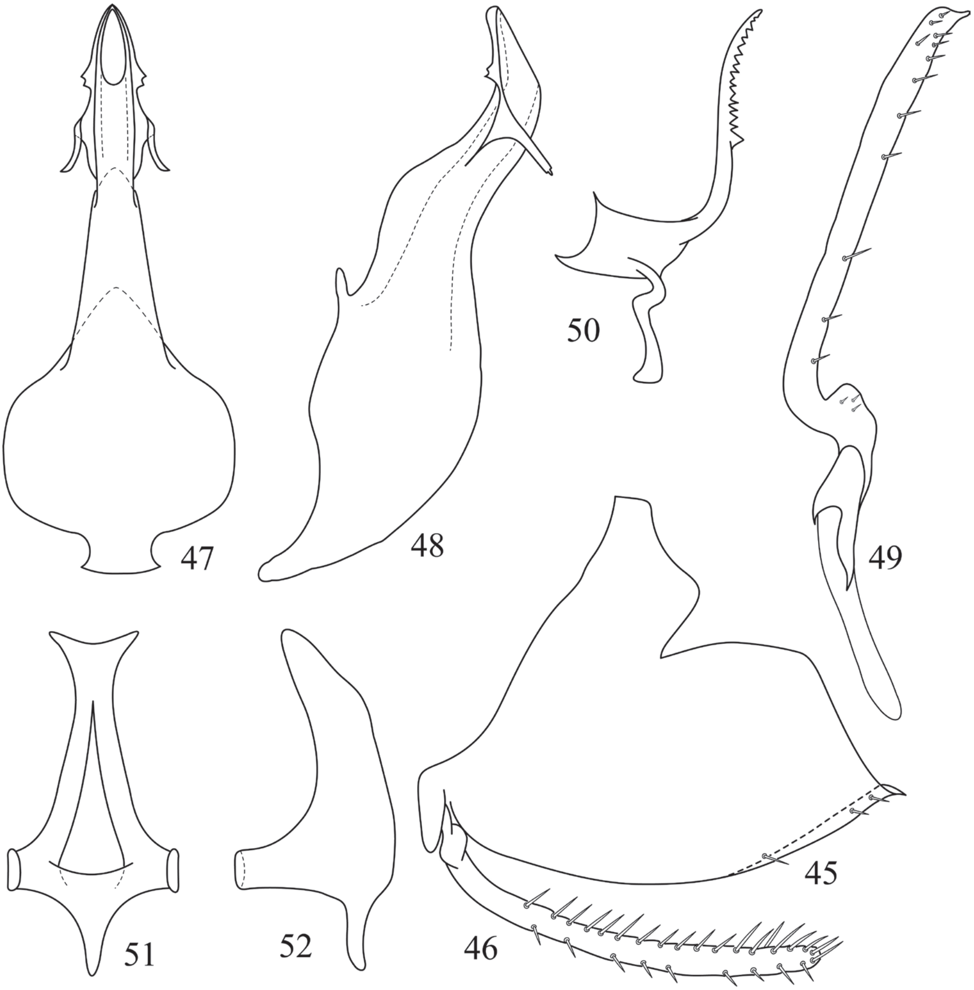
http://species-id.net/wiki/Pedionis_(Pedionis)_nankunshanensis
Figs 45–52

Description. Body yellowish-brown (Fig. 38). The vertex inverted "V" shaped, as wide as pronotum (Fig. 38), weakly curved in profile, slightly away from the pronotum (Fig. 39); eyes brown; ocelli located between the eyes, its surrounding yellow, below gray (Fig. 40). The pronotum pale-yellow, anterior margin curved prominent, posterior margin slightly concave. Scutellum triangular, yellowish, scatter dark notches, base-lateral sides gray, post-middle region with one deep notch (Fig. 38). Forewings hyaline, end area chocolate-brown, veins fuscous white spots distinctly (Fig. 39).

Male genitalia Pygofer broad, the apex acute in lateral view and produced several setae on the ventral margin (Fig. 45). Subgenital plate slender with many marginal setae (Fig. 46). Aedeagus broader basally, shaft strongly sinuate in lateral view, apex tapering, and with two pairs of processes, the apical processes located dorsal margin, serrated, the subapical processes located lateral margin, reflexed in ventral aspect view, apex digitation, the processes with a membranous connection (Figs 47–48). Style parallel-margined and angled on the apical third, the apex obliquely truncate, produced a narrow truncate process on dorsal margin (Fig. 49). Dorsal connective complex and sinuate, apex bulbous, produced a long process



Figures 45–52. *Pedionis (Pedionis) nankunshanensis* Li, Dai & Li sp. n. **45** Male pygofer side, lateral view **46** Subgenital plate, lateral view **47** Aedeagus, ventral view **48** Aedeagus, lateral view **49** Style, dorsal view **50** Dorsal connective **51** Connective, dorsal view **52** Connective, lateral view.

from caudal margin to dorsad, and mesal-ventral apical margin minutely serrated (Fig. 50). Connective broader basally, a finger-like protrusion in middle, both sides bent to the inside (Figs 51–52).

Female. Similar to male in coloration and appearance. The seventh sternite 1.5 times the sixth sternite, carved in middle-posterior margin (Fig. 41).

Measurement. Length (including tegmen): ♂, 3.2–3.5 mm; ♀, 3.8–4.0 mm.

Type material. Holotype ♂, China: Guangdong Prov., Nankunshan, 24 August 2010, collected by Hu Li (GUGC). Paratypes: 1♂1♀, same data as holotype; 2♀♀, Guangdong Prov., Nankunshan, 22 August 2010, collected by Junqiang Ni (GUGC).

Diagnosis. This species is similar to *P. (P.) yunnana* Zhang & Viraktamath, 2010 but can be distinguished from the latter by having the apical processes on aedeagal shaft serrated; the subapical processes reflexed ventral aspect view, apex digitations.

Etymology. The new species name refers to the type locality.

Pedionis (Pedionis) tabulatus Li, Dai & Li sp. n.

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http://species-id.net/wiki/Pedionis_(Pedionis)_tabulatus
Figs 53–60

Description. Body coloration and appearance similar to *P. (P.) lii* Zhang & Viraktamath, 2010 but more dark and pronotum slightly concave, with a white belt on posterior margin (Figs 42–44).

Male genitalia. Pygofer broad, obliquely truncate, the apex obtuse in lateral view, produced regularly spike-spines and setae on the ventral margin (Fig. 53). Subgenital plate slender with many setae, several especially long in the end (Fig. 54). Aedeagus broader basally, shaft strongly sinuated, angled heavily on apical third and bulge occurred in middle-dorsal in lateral view; apex tapering, and with two pairs of processes, the apical processes small and produced on dorsal margin, the subapical processes located lateral margin, broad as lamella (Figs 55–56). Style (Fig. 57), dorsal connective (Fig. 58) and connective (Figs 59–60) similar to *P. (P.) nankunshanensis* **sp. n.** but differs by mesal-dorsal serration.

Female. Unknown.

Measurement. Length (including tegmen): ♂, 5.2mm.

Type material. Holotype ♂, China: Guizhou Prov., Kuankuoshui Nature Reserve, Baishaogou, 7 June 2010, collected by Hu Li (GUGC).

Diagnosis. This species is similar to *P. (P.) yunnana* Zhang & Viraktamath, 2010 but differs markedly from the latter in having the apical processes on aedeagal shaft occurred in dorsal margin; the subapical processes broad, lamella-like; the pygofer with regularly spike-spines and setae on the ventral margin.

Etymology. Th e species name is derived from the Latin words "*tabulatus*", indicating the subapical processes of adeagal shaft are lamella-like.

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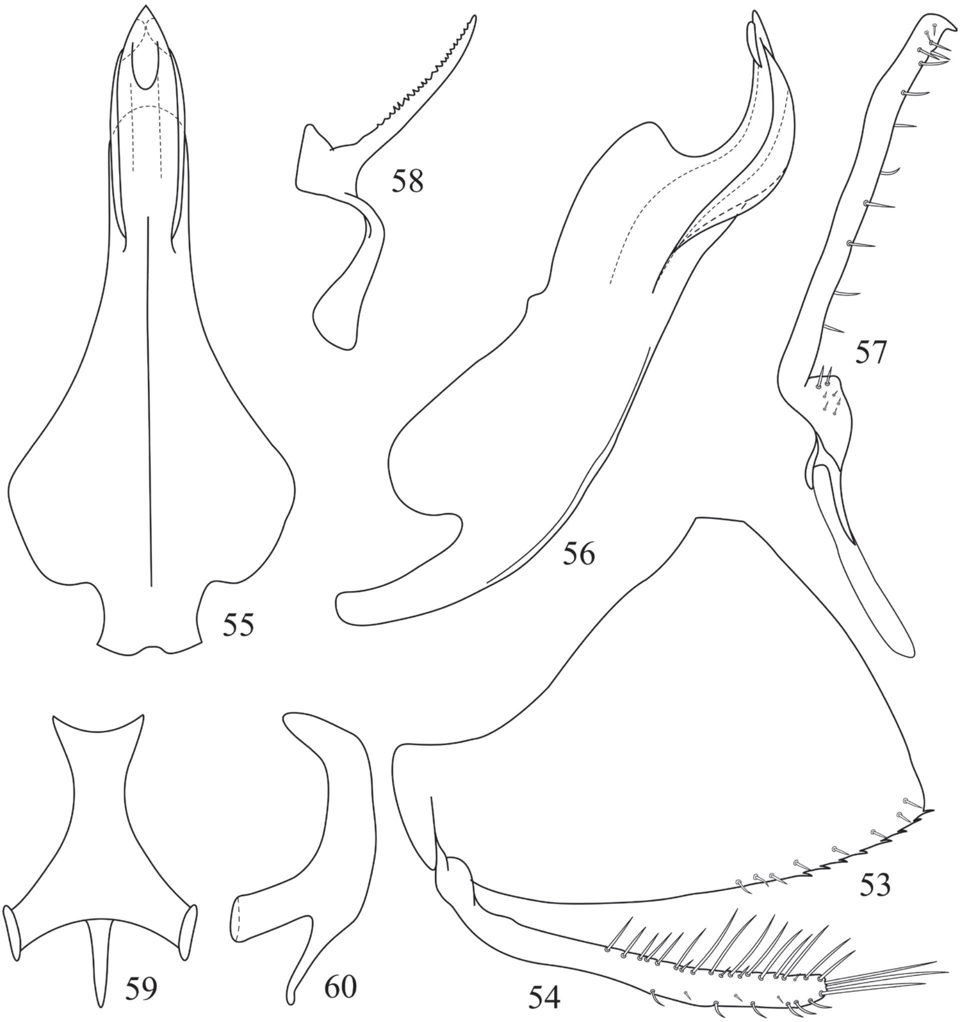

Figures 53–60. *Pedionis (Pedionis) tabulatus* Li, Dai & Li sp. n. **53** Male pygofer side, lateral view **54** Subgenital plate, lateral view **55** Aedeagus, ventral view **56** Aedeagus, lateral view **57** Style, dorsal view **58** Dorsal connective **59** Connective, dorsal view **60** Connective, lateral view.

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RESEARCH ARTICLE

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Miocene honey bees from the Randeck Maar of southwestern Germany (Hymenoptera, Apidae)

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Abstract

The Miocene Randeck Maar (southwestern Germany) is one of the only sites with abundant material of fossil honey bees. The fauna has been the focus of much scrutiny by early authors who recognized multiple species or subspecies within the fauna. The history of work on the Randeck Maar is briefly reviewed and these fossils placed into context with other Tertiary and living species of the genus *Apis* Linnaeus (Apinae: Apini). Previously unrecorded specimens from Randeck Maar were compared with earlier series in an attempt to evaluate the observed variation. A morphometric analysis of forewing venation angles across representative Recent and Tertiary species of *Apis* as well as various non-Apini controls was undertaken to evaluate the distribution of variation in fossil honey bees. The resulting dendrogram shows considerable variation concerning the wing venation of Miocene Apini, but intergradation of other morphological characters reveals no clear pattern of separate species. This suggests that a single, highly variable species was present in Europe during the Miocene. The pattern also supports the notion that the multiple species and subspecies proposed by earlier authors for the Randeck Maar honey bee fauna are not valid, and all are accordingly recognized as *Apis armbrusteri* Zeuner.

Keywords

Apoidea, Anthophila, Apinae, *Apis*, honey bees, taxonomy, Tertiary, morphometrics

Introduction

Honey bees (Apini Latreille: *Apis* Linnaeus) are among the most familiar of animals, with a tight association with humans since their domestication and use worldwide in agricultural ecosystems as crop pollinators (e.g., Partap 2011) and for the honey they produce. Species of *Apis*, particularly the familiar Western Honey Bee, *Apis mellifera* L., have been transported throughout the globe and are today cosmopolitan, with intensive research programs focusing on apiculture and related topics in every corner of the world. However, like most groups of Apoidea, little attention has been paid to the historical record of honey bees, outside of their most recent history since domestication. The more ancient, fossil record of *Apis* has become the focus of more critical research efforts only within the last 10–15 years (e.g., Engel 1998, 2006; Nel et al. 1999). This is partly owing to a dearth of material but also to the slow development of paleomelittology which has expanded significantly during the last two decades (Engel 2011).

The earliest definitive members of the tribe Apini are known from the Oligocene of France and Germany. These comprise *A. henshawi* Cockerell, and under some classificatory schemes *A. vetusta* Engel, from Rott and Enspel, Germany (e.g., Cockerell 1907; Statz 1931, 1934; Engel 1998, 1999; Wedmann 2000), and *A. cuenoti* Théobald from Céreste, France (Théobald 1937; Nel et al. 1999), the latter of which is sometimes considered a synonym of *A. henshawi* (Engel 1999). Generally the forewing venation of these Oligocene honey bee populations resembles that of Recent *A. dorsata* Fabricius, but the species are distinctly smaller, more typical of the averaged-sized *A. mellifera* and *A. cerana* Fabricius (e.g., Nel et al. 1999, Wedmann 2000). Apini from the Oligocene and Miocene are known from Spain and France (e.g., Arillo et al. 1996, Nel et al. 1999), Italy (Handlirsch 1907), Germany (e.g., Zeuner 1931; Pongrácz 1931; Armbruster 1938a; Prokop and Fikáček 2007), Austria (Nel et al. 1999), the Czech Republic (Říha 1973; Prokop and Nel 2003), China (Hong 1983; Zhang 1989, 1990), Japan (Engel 2005, 2006), and most surprisingly the western United States (Engel et al. 2009). For most of the Late Oligocene and Miocene forms, the specific status remains questionable (Nel et al. 1999; Engel 2006). There are no unquestionable fossils of *Apis* from the Pliocene, and only records of modern *A. mellifera* in East African copal of Late Pleistocene or younger age (e.g., Foord 1890; Cockerell 1909; Zeuner and Manning 1976) as well as petrified combs of *A. cerana* from the Malay Peninsula (Stauffer 1979). Among all of these records, the honey bees from Rott and the Randeck Maar in Germany are the most abundant, particularly from the latter deposit.

William Scheuthle was the first to discover honey bees at the Randeck Maar (Early Miocene, southwest Germany) in 1926, and in 1928 he and Ludwig Armbruster, a prominent apiculturist of the day, excavated more material. Finally, in 1938 the accumulated material was first formally described based on an examination of 72 specimens (Armbruster 1938a, 1938b, 1938c). Armbruster (1938a) classified the material into three species of a then new genus, dubbed *Hauffapis*, although he himself pointed to the obvious similarities of *Hauffapis* to *Apis* and especially to Recent *A. dorsata* and the contemporaneous fossil species *A. armbrusteri* Zeuner from the nearby Böttingen Marmor (Zeuner 1931). The generic name *Hauffapis*, unfortunately, was not validly proposed and so is not nomenclaturally available (Michener 1990, 1997; Engel 1999). Armbruster (1938a) also noted that some specimens resembled *A. mellifera* in terms of forewing venation (*vide infra*), which further convinced him that he was dealing with multiple species and which he named *Hauffapis scheuthlei*, *H. scheeri*, and *H. scharmanni* (naming them for his collecting partners, along with various infraspecific forms). Subsequently, Zeuner and Manning (1976) united all of these taxa, including that from Böttingen Marmor, into a single species and under the name *A. armbrusteri*, considering Armbruster's three forms to be separate subspecies. The fossil bees from the Böttingen Marmor are preserved only as hollow imprints and, while they can be attributed to *Apis*, many features remain unknown from the type series (Zeuner 1931, Zeuner and Manning 1976). In order to stabilize the application of names for these bees a petition has been submitted to the ICZN to conserve universal usage of the name *A. armbrusteri* by designation of a neotype (Engel et al. in press).

The abundance of material from Randeck Maar represents a wonderful opportunity to evaluate more critically these fossil honey bees, since from most localities only one or a very few specimens are typically available. Unfortunately, several of the diagnostics used for the determination of extant *Apis* species or subspecies cannot be used for the differentiation of fossil Apini, even when excluding the obvious biochemical attributes. For example, *A. cerana*, *A. mellifera*, and their subspecies, along with *A. koschevnikovi* Enderlein and *A. nigrocincta* Smith, are generally recognized from differences in size, coloration of setae and integument, distribution and proportions of setal bands on the metasoma, length of the proboscis, sternal and leg podite proportions, the presence or absence of a distal abscissa to M in the hind wing (absent in *A. mellifera*), structure of the drone legs and endophallus, and behavioral aspects such as the time of drone mating flights, structure of brood cell caps, or the position of a worker while wing-flapping in front of the hive (e.g., Ruttner 1988; Verma et al. 1994; Hadisoesilo and Otis 1996, 1998; Damus and Otis 1997; Sheppard et al. 1997; Sheppard and Meixner 2003; Radloff et al. 2010, 2011). Several of these are highly variable (e.g., size, coloration, time of drone flights), while more consistent traits such as those from the hind wing are infrequently preserved in fossil *Apis*. Moreover, behavioral aspects are rarely detectable in the fossil record unless they leave a discrete trace or physical structure suitable for fossilization [e.g., traces of leaf-cutter bees (Wappler and Engel 2003; Wedmann et al. 2009), fossilized nests (Stauffer 1979)]. To date no fossil of a drone honey bee has been recovered and, indeed, male bees of any tribe or family are exceptionally rare as fossils (e.g., Camargo et al. 2000; Engel 2001a; Hinojosa-Díaz and Engel 2007). Thus, using only the typical criteria for segregating species such as *A. cerana*, *A. mellifera*, or their relatives, and particularly subspecies within each of these forms, it would be nearly impossible to distinguish these taxa in the fossil record. This has greatly hampered any understanding of fossil *Apis*.

In order to circumvent these extreme limitations in studying fossil Apini, herein we follow the approach of DuPraw (1965), Ruttner (1988), Rinderer et al. (1989, 1995), Wedmann (2000), and other apiculturists to analyze forewing venation angles (hereafter "FWVA"), i.e., the angles between specific landmarks (vein and crossvein bifurcations or fusions) in the forewing remigium. Given that the forewing is often very well preserved in fossil insects it permits a more meaningful comparison between Recent and fossil Apini. The approach to measure FWVA is the least complicated method for recording numerous wing characteristics (DuPraw 1965, Ruttner 1988). We agree with Engel (2006) that the recognition of taxa in Apini based solely on morphometric measurements of the forewing venation should be regarded with caution (*vide etiam* Radloff and Hepburn 1998; Hepburn 2000; Hepburn and Radloff 2002). However, forewings are one suite of morphological features that can permit the assignment of individuals to genera or sometimes even species for numerous kinds of insects, even if all other attributes are missing. For example, automatic bee identification systems that are based on forewing analyses (e.g., Steinhage et al. 2006) have met with some success. In addition, Tofilski (2008) has shown that identification of *A. mellifera* subspecies based on forewing morphometry is >80% successful. In contrast with some other morphological features such as setal length or lengths of extremities, FWVA are probably not associated with environmental parameters such as elevation, rainfall, temperature, and latitude, as has been demonstrated for Recent populations of *A. cerana* (Tan et al. 2003), although note that the relative proportion of presence of some wing features do occur along weak latitudinal or longitudinal clines (e.g., the proportion of individuals with an adventitious Rs_2 in the forewing: Tan et al. 2008). Naturally, any consideration of fossil wings must also take into consideration possible deformation resulting from fossilization or subsequent tectonic activity. Fortunately, deformations of wing venation are relatively easy to recognize, and the approach of Rinderer et al. (1989, 1995) and Wedmann (2000), which includes the complete wing venation, is more objective and less bias-prone than the methods employed by earlier authors who studied only a few cells (e.g., Armbruster 1938a, 1938b, 1938c). Thus, despite its obvious limitations, we believe FWVA analysis is perhaps the most reliable suite of data currently available for statistically comparing living and fossil Apini.

While we are well cognizant of the fact that dendrograms resulting from cluster (phenetic) analyses cannot be equated with phylogenies owing to the inability of such methods to distinguish plesiomorphic and apomorphic features or homologies from analogies, and that these are more useful at the level of tokogenetic relationships (e.g., Hennig 1966; Wiley 1981; Schuh 2000), such analyses are nonetheless informative heuristic methods for evaluating the general similarity of populations and lineages and may provide novel insights for fossil *Apis*. Accordingly, herein we evaluate the forewing morphometrics of the Randeck Maar honey bees, including the three subspecies of Armbruster, and provide descriptive notes and analysis of previously unstudied specimens.

Recent honey bee species

The number of Recent species of *Apis* and their respective diagnoses has been a matter of debate over the last couple of decades. Interpretations vary between six or seven species on the conservative end (Alexander 1991a, 1991b, Engel and Schultz 1997, Engel 1999: Fig. 1) and 10 or 11 (e.g., Arias and Sheppard 2005; Lo et al. 2010), or even as many as 24 (Maa 1953) at the higher extreme. Most of the controversy surrounds the status of some Southeast Asian populations (Koeniger et al. 2010; Radloff et al. 2011). While several analyses have examined *Apis* phylogeny, most recent investigations have relied solely on DNA sequence data and sometimes with exceptionally small samples across the diversity of honey bee populations (e.g., Willis et al. 1992; Tanaka et al. 2001; Arias and Sheppard 2005; Raffiudin and Crozier 2007; Lo et al. 2010). Only one analysis has synthesized data from multiple sources – adult morphology, larval morphology, DNA sequences, and behavior (Engel and Schultz 1997). The species recognized in the Engel and Schultz (1997) combined analysis were *A. mellifera*, *A. florea* Fabricius, *A. andreniformis* Smith, *A. koschevnikovi*, *A. cerana*, and *A. dorsata* (these authors did not consider *A. nigrocincta* specifically distinct from *A. cerana* at that time). *Apis nigrocincta* was subsequently added to this list of honey bee diversity (Hadisoesilo et al. 1995; Hadisoesilo and Otis 1996, 1998; Engel 1999; Smith et al. 2000, 2003) (Fig. 1). While the species recognized in the diversity of phylogenetic treatments varies under the biological, phylogenetic, or evolutionary species concepts, there remains broad congruence as to the principal clades within the genus and their interrelationships (e.g., Engel and Schultz 1997; Engel 1998, 1999, 2006; Leelamanit et al. 2004; Arias and Sheppard 2005; Raffiudin and Crozier 2007; Lo et al. 2010). These studies agree that the lineage of dwarf honey bees, *A. florea* and *A. andreniformis*, diverged early on from the remainder of Recent *Apis* clades, with the giant honey bees, *A. dorsata* and its predecessors, diverging from the common ancestor of a clade comprising *A. mellifera* and the "*cerana*" group of species (i.e., *A. cerana*, *A. koschevnikovi*, *A. nigrocincta*). These three groups are sometimes accorded subgeneric status as *Micrapis* Ashmead, *Megapis* Ashmead, and *Apis* s.str. (e.g., Engel 1999, 2001b, 2002, 2006; Engel et al. 2009; Koeniger et al. 2011), although some less widely employed classifications have considered them as separate genera in their own right (e.g., Ashmead 1904; Maa 1953; Wu and Kuang 1987). *Apis mellifera* is the most widespread of these species, occurring throughout Europe, Africa, northernwestern Asia (e.g., Ponto-Caspian and as far East as the Tien Shan), the Levant, Caucasia, and the Iranian Plateau (Ruttner 1988, 1992; Ruttner et al. 1985; Sheppard and Meixner 2003), as well as adventive in the Americas and Australia (e.g., Kerr 1957; Sheppard 1989; Engel 1999; Moritz et al. 2005). The remaining Recent honey bees are largely restricted to Asia (Michener 2007; Radloff et al. 2011), with the exception of *A. florea* which is known also from Jordan, the eastern Arabian Peninsula, and northeastern Africa (Lord and Nagi 1987; Mogga and Ruttner 1988; Engel 1999; Michener 2007; Dathe 2009; Haddad et al. 2009; Moritz et al. 2010). The precise distributions of the remaining Asian spe-

Figure 1. Modern honey bee diversity (all bees are workers and to the same scale). **A** *Apis mellifera* Linnaeus **B** *A. koschevnikovi* Enderlein **C** *A. nigrocincta* Smith **D** *A. cerana* Fabricius **E** *A. dorsata* Fabricius **F** *A. florea* Fabricius **G** *A. andreniformis* Smith. After Engel et al. (2009).

cies and morphotypes are summarized by Otis (1996), Engel (1999), Oldroyd and Wongsiri (2006), and Hepburn and Radloff (2011). We did not attempt to evaluate the morphometrics of the complete suite of forewing variation in modern *Apis* species, which is well beyond the scope of the current study. Instead, for the purposes of our analyses (*vide infra*), it was most critical to simply represent the broadest sample of variation across the genus. Accordingly, we employed representatives of the three principal clades, or subgenera, of *Apis*.

Geological setting

The Randeck Maar is located in southwest Germany, southeast of Stuttgart at the escarpment of the Swabian Alb (48°71'N, 9°31.8'E, 750m elevation) and originated during the Miocene. During this epoch, the Mesozoic rocks of the Swabian Alb were penetrated by numerous volcanic dykes leading to phreatomagmatic eruptions when the rising nepheline-melilithitic magma contacted groundwater (Bleich 1988). The Maar deposits consist of volcanoclastic limestones overlain by Miocene sediments (Krautter and Schweigert 1991), which are dated as Early/Middle Miocene (Burdigalian, Karpatian, MN 5, ca. 16–18 Ma) after the mammal fauna (Heizmann 1983). In one phase of sedimentation, bituminous laminites ('dysodiles') and laminated, varve-like limestones were deposited. These limestones contain exceptionally well preserved fossil insects (e.g., Armbruster et al. 1938a, 1939; Schawaller 1986; Kotthoff 2005; Kotthoff and Schmid 2005).

Material and methods

The fossil material studied originates from the Staatliches Museum für Naturkunde, Stuttgart (SMNS), the Heimatmuseum Göppingen Jebenhausen (HMJ), and the Paläontologisches Museum Nierstein (PMN) (Figs 2–5). Additional *A. armbrusteri* specimens are present in the Urwelt-Museum Hauff but were already considered in detail by Armbruster (1938a). A re-examination of the majority of the specimens described in Armbruster (1938a) was impossible since many of these were covered in Canada balsam, ironically used by Armbruster to preserve the bees (Armbruster 1938a, 1939), but which has darkened over time. Removing the balsam likely will lead to the destruction of many important features. In total, 18 not yet described specimens of *A. armbrusteri* are introduced in this work (Table 1).

Table 1. List of not-yet described specimens of *Apis armbrusteri* presented in this work.

Museum/number		**body length (mm)**	**forewing length (mm)**	**hindwing length (mm)**	**Sediment/Annotations**
Wing venation not well preserved:					
HMJ	A 817	12.6	7.5	-	light varve layer
SMNS	64674/17a	21.6	-	-	dark grey limestone
SMNS	64674/21a/b	16.9	8.9*	6.0*	dark grey limestone
SMNS	64674/28	15.0	-	-	dark varve layer
SMNS	64674/31	13.9	-	-	dark varve layer
SMNS	64674/38	16.0	-	-	light limestone
SMNS	64674/50a	24.3	>15	-	dark varve layer
PMN	SSN10RM12	16.9	9.1	-	light varve layer
Wing venation well preserved:					
SMNS	64674/11a	13.2	>7.9	-	light varve layer
SMNS	64674/11b & 11c	14.1	>8.7*	-	dark varve layer
SMNS	64674/12a & 12b	15.7	9.9	7.3	dark grey calcareous marl
SMNS	64674/18	17.4	9.7*	7.8*	dark varve layer
SMNS	64674/19	17.0	>10.3	-	dark varve layer
SMNS	64674/30	-	8.4	-	dark varve layer
SMNS	64674/35	>15.0**	>11.2		dark varve layer
SMNS	64674/36	>14.7**	10.0		dark varve layer
SMNS	64674/49	9.9**	>9.0		light varve layer
SMNS	64675	14.3	8.1		dark varve layer

* distal part reconstructed based on similar complete wings of other specimens

** head missing

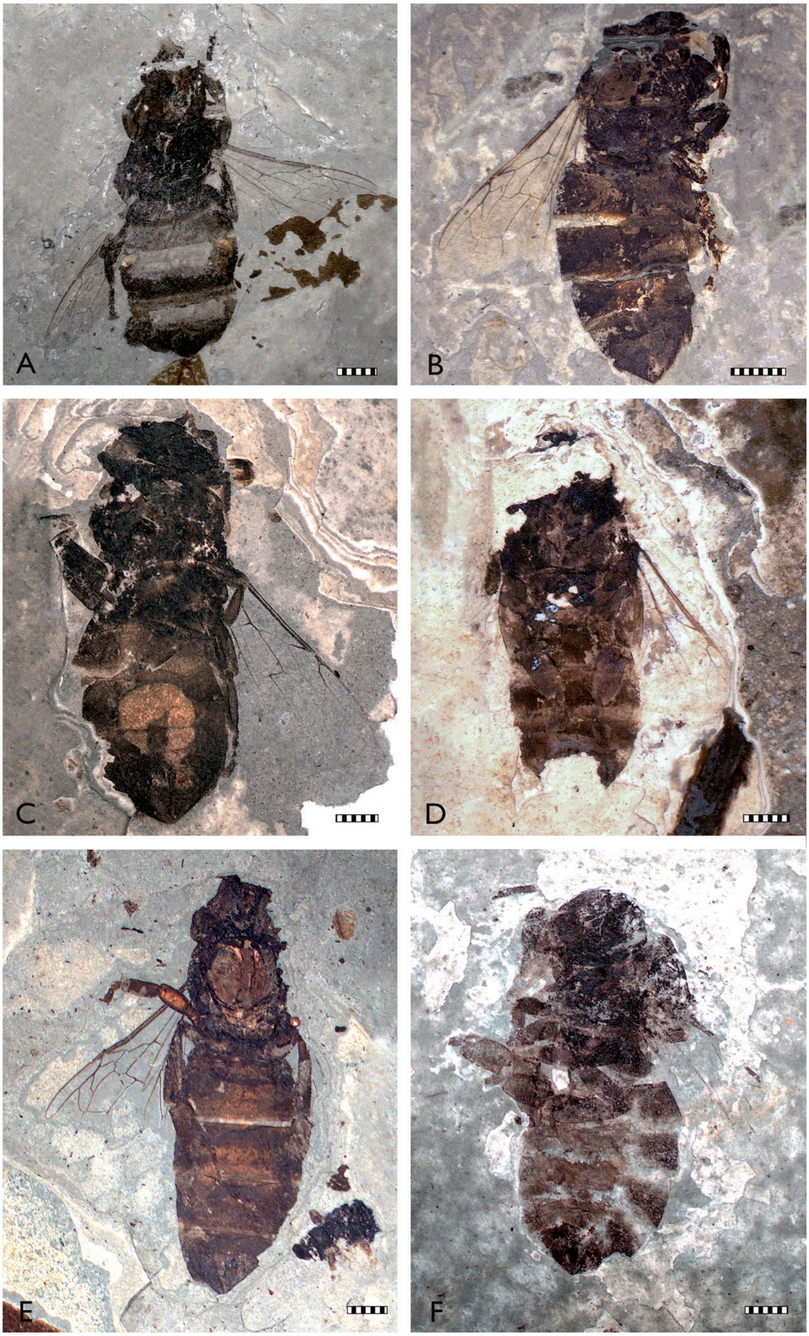

Figure 2. Photomicrographs of representative Randeck Maar honey bees (*Apis armbrusteri* Zeuner). **A** SMNS 64675 (neotype) [Morphotype D] **B** SMNS 64674/12 [Morphotype D] **C** SMNS 64674/11b [Morphotype D?] **D** SMNS 64674/11a [Morphotype CM] **E** SMNS 64674/21 **F** SMNS 64674/28. Scale bar = 2 mm.

Fossils were examined with a stereomicroscope, while drawings were prepared using a camera lucida. Photographs were taken with a digital camera and the software "Analysis Pro Version 3.1" (SIS) used for distance and angle measurements. The software "PAST" version 1.75b (Hammer et al. 2001) was used for cluster analyses. Nomenclature of wing veins and cells follows that of Engel (2001a), while landmarks and angles for FWVA analysis follow those of previous authors (e.g., Ruttner 1988; Rinderer et al. 1989, 1995; Wedmann 2000).

FWVA measurements of all specimens documented herein and with well-preserved forewings were subjected to a cluster analysis together with measurements of representative Recent Apini from Europe (*A. mellifera*; eleven specimens) and Asia (*A. florea* Fabricius; four specimens; *A. dorsata*; twelve specimens; *A. cerana*; 14 specimens). So as to expand our comparative treatment we included other Miocene and Oligocene honey bees that had sufficiently well-preserved forewings to permit meaningful measurement and comparison. These included the European material of *A. henshawi* (ten specimens; Cockerell 1907; Wedmann 2000); *A. cuenoti* (two specimens; Théobald 1937; Nel et al. 1999); Arillo et al. (1996) and Nel et al. (1999) Oligocene and Miocene *A. aquisextana* (two specimens; erroneously as "*A. aquisextusensis*" in the latter publication: Engel 2006), and forms B, C, E, F, G, H, I, and J (twenty specimens; Nel et al. 1999); *A. lithohermaea* Engel from Japan (Engel 2006); and *A. nearctica* Engel et al. from North America (Engel et al. 2009). For comparative purposes, we included FWVA measurements from other Eocene Apidae (*Electrapis* Cockerell, *Electrobombus* Engel, *Succinapis* Engel, *Thaumastobombus* Engel, *Melikertes* Engel, and *Pygomelissa* Engel and Wappler; one or two specimens per taxon), as well as other tribes of Recent corbiculate (*Bombus* Latreille, *Euglossa* Latreille, *Eufriesea* Cockerell; one specimen each) and non-corbiculate Apinae (*Centris* Fabricius, *Epicharis* Klug, *Xeromelecta* Linsley, and *Zacosmia* Ashmead; one specimen each). In total, 97 forewings were analyzed, and additionally, 19 measurements taken by Wedmann (2000) were added for the cluster analysis (see Appendix I).

While it would have been ideal to make the analysis more robust with the inclusion of more of Armbruster's original material, this was not possible. Most of the specimens described by Armbruster (1938a) are now lost and many of the few remaining are rendered useless for examination owing to the unfortunate application of Canadian balsam (Armbruster 1939). As such, only Armbruster's (1938a) photographs and illustrations were of use.

Although the venation of drones does not differ significantly from that of workers, in order to completely eliminate potential caste differences two drones of *A. cerana* from Pakistan were added to the analysis as a control. While the drones were separated from workers, they were still more similar to conspecific workers than to specimens of any other taxon. Further tests which included drones of *A. mellifera* found similar results (Kotthoff 2002). Thus, gender did not introduce any bias into the results even though all fossil *Apis* discovered to date are workers (Engel 1998, 2006; Nel et al. 1999; Engel et al. 2009; herein).

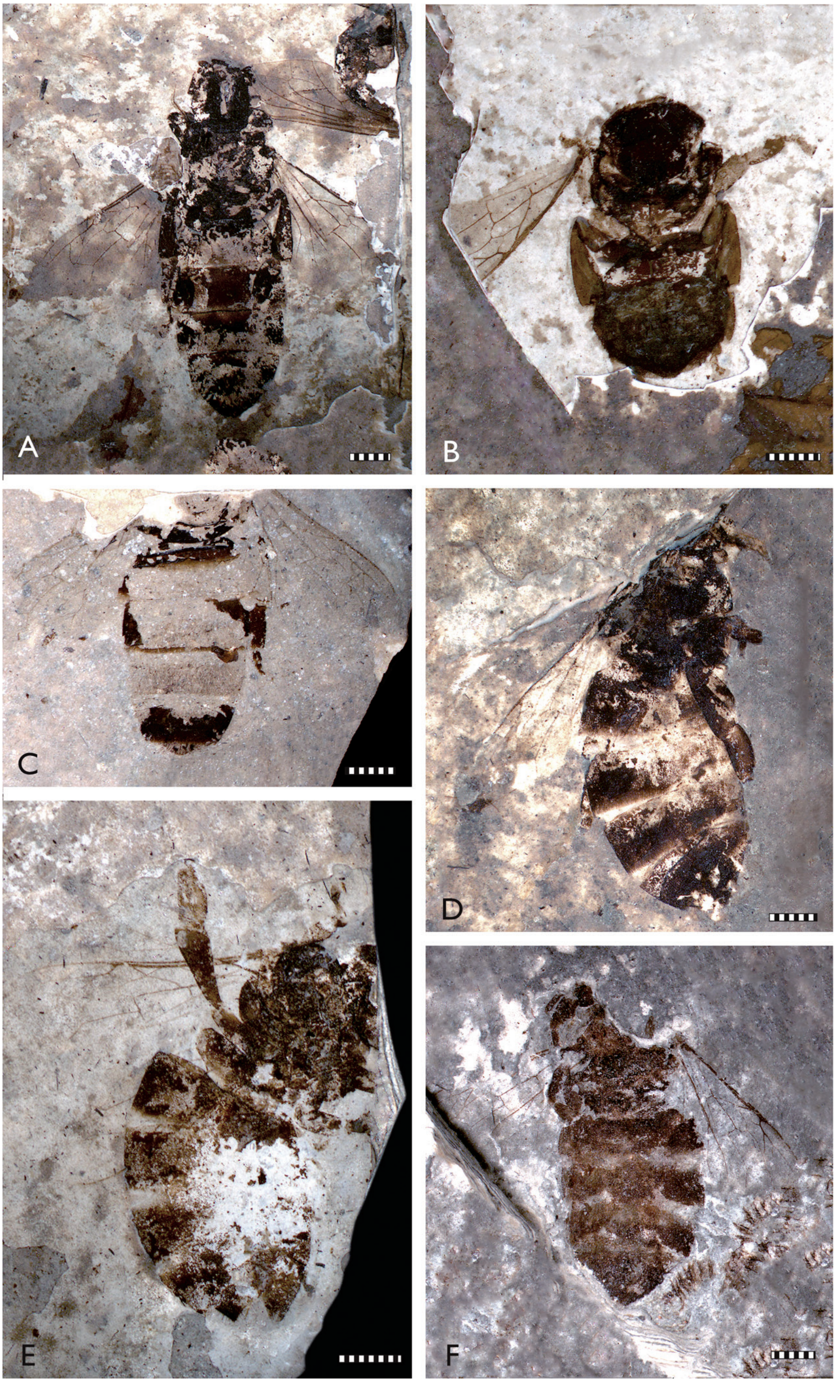

Figure 3. Photomicrographs of representative Randeck Maar honey bees (*Apis armbrusteri* Zeuner). **A** SMNS 64674/18 [Morphotype D] **B** SMNS 64674/49 [Morphotype D] **C** SMNS 64674/30 [Morphotype D] **D** SMNS 64674/35 [Morphotype D] **E** SMNS 64674/19 [Morphotype D] **F** SMNS 64674/36 [Morphotype CM]. Scale bar = 2 mm.

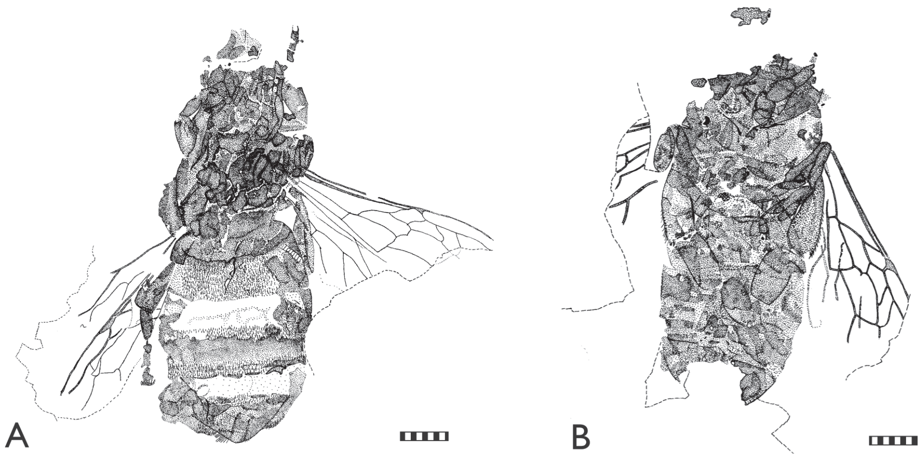

Figure 4. Representative Randeck Maar honey bees (*Apis armbrusteri* Zeuner). **A** SMNS 64675 (neotype) [Morphotype D] **B** SMNS 64674/11a [Morphotype CM]. Scale bar = 2 mm.

Systematic paleontology

Genus *Apis* Linnaeus
Apis armbrusteri Zeuner

Refer to Engel et al. (2009) for a complete taxonomic summary for the species, and to Engel et al. (in press) for details on the neotype (SMNS 64675: Figs 2a, 4a). Herein we provide descriptive notes for a series of specimens not previously documented by earlier authors. For those that are most completely preserved we have noted whether the specimens are of a *cerana*/*mellifera*-like morphotype (CM) or a *dorsata*-like morphotype (D). All metrics are provided in millimetres.

Specimens with poorly-preserved or missing wings

HMJ A 817. *Metrics*: body length 12.6; metasoma 7.3; mesosoma 3.2; head 1.8; forewing 7.5. *Descriptive notes*: Ventral view on light varve layer; preservation exceptionally poor; legs missing except for a few fragments, apparently preserving only metatibiae, which are relatively long and slender; wings only fragmentarily preserved, fragments match forewings of other *A. armbrusteri*; no counterpart.

SMNS 64674/17a. *Metrics*: body length 21.6. *Descriptive notes*: Ventral view on dark grey limestone; fossil re-crystallized and fragmented; metasoma highly deformed and obviously swollen, resulting in extra-ordinary high body length; forewing venation poorly preserved; left hind leg positioned parallel to metasoma, revealing a slender metabasitarsus; head ventrally directed; compound eyes small in proportion to head and far apart from each other; counterpart is SMNS/17b, which is even more poorly preserved.

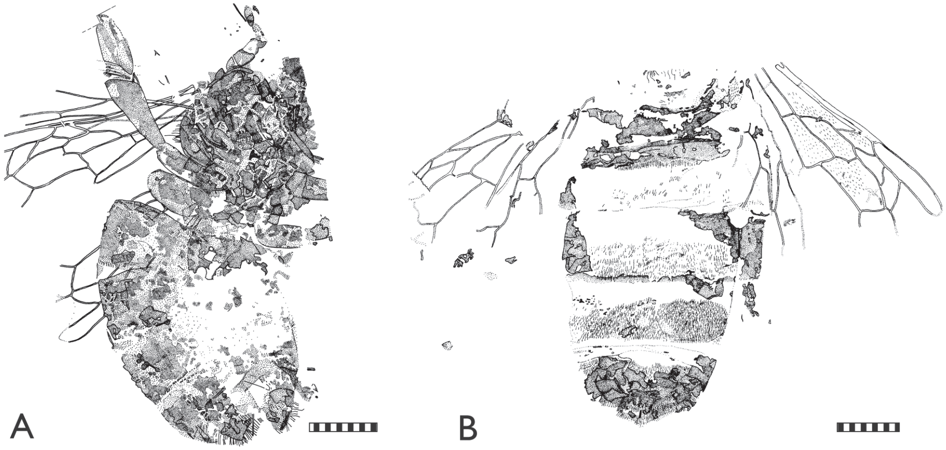

Figure 5. Representative Randeck Maar honey bees (*Apis armbrusteri* Zeuner). **A** SMNS 64674/19 [Morphotype D] **B** SMNS 64674/30 [Morphotype D]. Scale bar = 2 mm.

SMNS 64674/21a. *Metrics*: body length 16.9; metasoma 9.9; mesosoma 4.7; head 2.8; mesofemur 1.2; mesotibia 1.6; mesobasitarsus 1.6; metafemur 2.1; metatibia 3.2; metabasitarsus 2.7; forewing (reconstructed) 8.9; hind wing (reconstructed) 6.0. *Descriptive notes*: Ventral view on dark grey limestone; parts of dorsal cuticle apparent; right forewing well preserved, but folded; metasoma very long (probably resulting from swelling in water after death) and well preserved, but not completely exposed from matrix; sting apparatus apparent; left metatibia long and slender; metabasitarsus very long and broadened; setae preserved in some areas of metabasitarsus; glossa and galeae evident between mandibles; counterpart is SMNS 64674/21b.

SMNS 64674/28. *Metrics*: body length 15.0; metasoma 9.0; mesosoma 4.7; head 2.1; glossa 2.9; profemur 2.2; protibia 1.6; probasitarsus 1.3; mesofemur 2.3; mesotibia 1.9; metabasitarsus 2.5. *Descriptive notes*: Lateral view of inner surface on dark varve layer; fossil slightly turned ventral; right forewing venation only partly visible; fragment of left forewing preserved; metatibia and metabasitarsus appear flattened and short; mesoscutum broken; mandibles well preserved; glossa appears protruded; counterpart (SMNS, not registered) exhibits a few dorsal elements, fragments of left forewing, and parts of the other lateral side.

SMNS 64674/31. *Metrics*: body length 13.9; metasoma 7.6; mesosoma 3.8; head 3.1; metafemur 2.8; metatibia 2.9; metabasitarsus 1.8. *Descriptive notes*: Laterally embedded on dark varve layer; head turned upwards; mandibles well preserved; right hind leg exposed above metasoma; metatibia and metabasitarsus appear short and broadened; metabasitarsus partly covered by metasoma; wings not preserved; no counterpart.

SMNS 64674/38. *Metrics*: body length 16.0; metasoma 9.0; mesosoma 5.5; head 2.8; metatibia 2.7; metabasitarsus 1.8. *Descriptive notes*: Laterally embedded on light limestone; fragmentary preservation of head and mesosoma; metabasitarsus of presumably left hind leg flat and short; metasoma obviously swollen and compressed; wings not preserved.

SMNS 64674/50a. *Metrics*: body length 24.3; forewing >15; mesosoma+head 8.8. *Descriptive notes*: Largest specimen known among Miocene honey bees from Randeck Maar; preserved on dark varve layer; metasoma, especially first metasomal segment, very well preserved; mesosoma poorly preserved except for slightly arched mesoscutum; legs missing; wings oriented parallel to metasoma, wing venation not apparent; compound eyes especially well preserved; counterpart is SMNS 64674/50b. *Remarks*: Even though the metasoma may have swollen due to postmortem processes, the specimen is extraordinarily large. Additionally, the forewing length indicates that this specimen approximated an *A. dorsata* worker in size. The average forewing length of the specimens presented here is 9.6 mm, thus the wing of SMNS 64674/50 is >50% longer. The second largest forewing length of specimen SMNS 64674/35 is more than 3 mm shorter. Due to this difference in size, we believe SMNS 64674/50 may have been an *A. armbrusteri* queen. According to Ruttner (1988), in Recent Apini the size difference between the female castes are greatest in the dwarf honey bee *A. florea* (worker: 6.26±0.10 mm forewing length, queen: ~35% longer), slightly less in *A. cerana* (worker: 7.54±0.14 mm forewing length, queen: ~24% longer) and significantly lower in *A. mellifera* and the giant honey bee *A. dorsata*. An unequivocal identification of SMNS 64674/50 as a queen is not possible. However, we believe that the occurrence of a queen among the >90 *Apis* specimens from the Miocene Randeck Maar is more probable than the presence of one isolated giant honey bee worker. SMNS 64674/50 may be the first honey bee queen from the fossil record. The specimen is not a drone as evidenced by the relatively small size of the compound eyes rather than the nearly holoptic eyes of male honey bees.

PMN SSN10RM12. *Metrics*: body length 16.9; metasoma 10.0; mesosoma 4.8; head 2.5; mesofemur 1.5; mesotibia 1.8; metafemur 2.2; metatibia 2.7; metabasitarsus 1.9; scape (reconstructed) 0.6; flagellum 2.6; forewing 9.1. *Descriptive notes*: Dorsoventrally embedded and very well preserved on light varve layer; antennae very well preserved; third submarginal cell of forewing broader than that of *A. cerana* or *A. mellifera* (unfortunately the wings could not be analyzed in detail); metatibiae and metabasitarsi rather slender; specimen somewhat resembles *A. henshawi*.

Specimens with well preserved forewings

SMNS 64674/11a [Morphotype CM]. *Metrics*: body length (reconstructed) 13.2; metasoma 7.0; mesosoma 3.7; head 2.4; mesofemur 2.1; metafemur 1.7; metabasitarsus 2.3; forewing >7.9 (most distal part not apparent). *Descriptive notes*: Dorsoventrally compressed, ventral view on light varve layer (Figs 2d, 4b); posterior metasoma not preserved, head only partially preserved; a fragment, possibly part of head, lies next to specimen; mesosoma, left forewing, and legs completely preserved; extremities ventrally exposed; one setal row of left metabasitarsus evident, number of setae estimated at 28–30; metatibia and metabasitarsus laterally flattened and short in proportion to width; some setae of rastellum preserved at metatibial apex; forewing with third submarginal cell extraordinarily long; 1m-cu with a small distal process in second medial cell; hind wing with a distal process of vein M preserved; no counterpart. *Remarks*: This specimen is small in comparison to other bees from the Randeck Maar. The forewing length of SMNS 64674/11a (>7.9, but probably not >8.5 mm) is similar to a small *A. cerana* worker (7.5–9 mm) and shorter than the average forewings from the Miocene honey bees from Randeck (9.6 mm). The long third submarginal cell is reminiscent of *A. cerana*, *A. mellifera*, and their relatives, but the process of 1m-cu is not present in these modern species, while this aberrant veinal stub appears in several individuals of *A. armbrusteri*. The distal process of M in the hind wing does not occur in *A. mellifera* but is present in all other Recent *Apis* species (Alexander 1991a; Engel 1999). The number of setae (28–30) in one of the setal comb rows of the metabasitarsus is similar to *A. mellifera* (Maa 1953). *Apis mellifera* has ten setal comb rows, of which the median has about 30 setae (Maa 1953; Nitschmann and Hüsing 1987; Lutz 1993). By contrast *A. henshawi* only has 24 setae in the medial comb (Zeuner and Manning 1976). In this regard, the specimen is more similar to *A. mellifera* and the '*cerana*' group than to *A. dorsata* and *A. henshawi*. Accordingly we ascribe the specimen to the CM morphotype.

SMNS 64674/11b [Morphotype D?]. *Metrics*: body length 14.1; metasoma 8.5; mesosoma 3.5; head 2.5; metatibia 2.2; metabasitarsus 1.9; forewing (reconstructed) > 8.7; mandible 1.5. *Descriptive notes*: Dorsoventrally compressed on dark varve layer (Fig. 2c); anterior part (head in particular) slightly rotated around axis of body length; mandibles, compound eyes, and antennae well preserved; antennae with at least nine, perhaps 10, flagellomeres preserved; parts of the legs compressed close to body; left hind leg positioned lateral of metasoma; metatibia and metabasitarsus do not appear flattened or shortened in respect to homologous appendages of SMNS 64674/11a; part of metasoma re-crystallized, probably pyritized; parts of sting apparatus apparent; forewing 1m-cu with a very short process; counterpart is SMNS 64674/11c. *Remarks*: The wing venation of this specimen is generally similar to that of *A. dorsata*; however, the third submarginal cell is not completely preserved. The shape and relative length of the metatibia and metabasitarsus are also similar to those of *A. dorsata* but the specimen is smaller than typical workers of this species.

SMNS 64674/12b [Morphotype D]. *Metrics*: body length 15.7; metasoma 9.7; mesosoma 4.3; head 1.8; profemur 1.5; protibia 1.5; probasitarsus 1.1; mesofemur 1.6; mesotibia 1.6; metatibia 2.4; metabasitarsus 1.8; forewing 9.9; hind wing 7.3. *Descriptive notes*: Laterally compressed on dark grey calcareous marl (Fig. 2b); body parts well preserved except for head; wing venation outstandingly well preserved; third submarginal cell rather short and meeting 2m-cu strongly distad; 1m-cu broken, with a short medioapical process projecting into second medial cell; mesosomal cuticle partly fragmented; distal five segments of metasoma stressed horizontally owing to postmortem processes; metabasitarsi fragmented but revealing a relatively slender shape; setae clearly preserved distally on metasoma; counterpart 64674/12a not preserving further details. *Remarks*: The shape of the short submarginal cell and relatively slender shape of the metabasitarsi are reminiscent of those of *A. dorsata*. While the length of the forewing exceeds the typical length of *A. mellifera*, it does not reach the length of *A. dorsata*.

SMNS 64674/18 [Morphotype D]. *Metrics*: body length 17.4; metasoma 10.2; mesosoma 3.8; head 3.3; metafemur 2.4; metatibia 3.2; metabasitarsus 2.3; metabasitarsal width 0.9; forewing (reconstructed) 9.7 (minimal); hind wing (reconstructed) 7.8 (minimal). *Descriptive notes*: Ventral aspect on dark varve layer, very well preserved but metasoma probably swollen during rest in water column and subsequently compressed during compaction, with metasoma appearing artificially lengthened and broadened; specimen length was probably ~15 mm in life (reaching general size of *A. dorsata*); forewing venation well preserved (Fig. 3a); third submarginal cell short and broad; process of 1m-cu present; rastellum of left metatibia apparent; setal comb rows of right metabasitarsus consist of 20–25 setae; left metabasitarsus shorter and broader than that of SMNS 64674/11b but more slender than that of 64674/11a; sting very well preserved; no counterpart; next to head is wing of *Bombylius* sp. (Kotthoff 2005). *Remarks*: The short, broad third submarginal cell is similar to that of *A. dorsata* and *A. henshawi*. The number of setae in the setal comb rows of the right metabasitarsus are also somewhat similar to that of *A. henshawi* (Lutz 1993).

SMNS 64674/19 [Morphotype D]. *Metrics*: body (without head) 17.0; metasoma 8.3; mesosoma 5.6; metatibia 2.9; metabasitarsus 2.3; forewing (reconstructed) >10.3. *Descriptive notes*: Partly laterally, partly dorsoventrally compressed on dark varve layer (Figs 3e, 5a); head missing; right hind leg extended laterally; right metatarsus not completely excavated from matrix; rastellum well preserved; wing venation of right forewing well preserved except for apicalmost area; third submarginal cell short; 1m-cu with long medioapical process projecting into second medial cell; one hind wing compressed under right forewing; distal abscissa of M apparently present; left forewing obscured by metasoma; sting preserved but sting device not apparent owing to recrystallization in center of metasoma; no counterpart. *Remarks*: The body size of this individual is quite large and cannot be explained solely by broadening and lengthening of the metasoma from postmortem swelling given that the terga are positioned close to and largely overlapping each other. The right forewing has a short, broad third submarginal cell somewhat similar to *A. henshawi*, with a general length presumably reaching a similar proportion to that of *A. dorsata*. The forewing is generally similar to the forewing of SMNS 64674/18. The metabasitarsus is relatively slender.

SMNS 64674/30 [Morphotype D]. *Metrics*: metasoma 9.1; metabasitarsus 1.8; forewing 8.4. *Descriptive notes*: Parts of metasoma and fragments of mesosoma, legs and wings preserved on dark varve layer (Figs 3c, 5b); metasoma mainly represented by setae and tergal fragments, presumably ventral view of dorsal elements; no counterpart. *Remarks*: The wings are similar to those of *A. dorsata* and *A. henshawi*, and the fragments of the hind legs indicate that the metatibia and metabasitarsus were slender, similar to those of *A. dorsata*.

SMNS 64674/35 [Morphotype D]. *Metrics*: body length (metasoma + mesosoma) 15.0; metasoma 9.5; mesosoma 4.8; metatibia 3.3; metabasitarsus 1.9; forewing >11.2. *Descriptive notes*: Laterally compressed, with head missing, on dark varve layer (Fig. 3d); mesosoma fragmentarily preserved; mesoscutum turned upwards; one forewing well preserved in basal part; one hind leg obscured by dorsal part of metasoma; other hind leg positioned on top of ventral part of metasoma; metatibia slender; metabasitarsus apparently broad and short, but more slender than that of SMNS 64674/11a. *Remarks*: The complete forewing was perhaps 12 mm long in life and therefore as long as an *A. dorsata* forewing.

SMNS 64674/36 [Morphotype CM?]. *Metrics*: body (metasoma + mesosoma) 14.7; metasoma 9.7; mesosoma 4.9; forewing (reconstructed) 10.0. *Descriptive notes*: Laterally compressed, with head missing, on dark varve layer; mesosoma and hind legs only fragmentarily preserved; right (presumably, could be left) metabasitarsus positioned along ventral part of metasoma, very broad and short; metasoma not well preserved; terga not in contact with each other; one forewing very well preserved (Fig. 3f), revealing long third submarginal cell; distal absicssa of vein M apparently present in hind wing; no counterpart. *Remarks*: The forewing of this specimen is very similar to those of *A. cerana* and *A. mellifera*. The shape of the metabasitarsus is also reminiscent of these species but possibly the metabasitarsus was deformed during fossilization. The size of the specimen exceeds the typical size of both *A. cerana* and *A. mellifera*.

SMNS 64674/49 [Morphotype D]. *Metrics*: body length (without head) 9.9; metasoma 4.7; mesosoma 4.6; mesofemur 1.9; mesotibia 1.6; mesobasitarsus 1.6; metafemur 1.8; metatibia 2.9; metabasitarsus 1.6; forewing (reconstructed) >9.0. *Descriptive notes*: Interior apparent in ventral view on light varve layer (Fig. 3b); head not preserved; terga still connected (indicating that metasoma was barely swollen); terga slightly laterally inflected; sting apparatus well preserved; setae of a single setal comb row evident in basal part of left mesobasitarsus, consisting of ~25 setae; metabasitarsus slender and somewhat triangular in shape; forewing venation preserved except for distalmost part; no counterpart. *Remarks*: While the lengths of the mesosoma and forewings are comparable to those of other bees from the Randeck Maar, the metasoma is noticeably shorter. The forewing length and venation appear similar to that of *A. dorsata*. In addition, the slender metabasitarsi are reminiscent of *A. dorsata*, even though the specimen does not approximate this species in size.

SMNS 64675 (neotype) [Morphotype D]. *Metrics*: body length 14.3; metasoma 8.1; mesosoma 3.4; head 2.6; metatibia 2.4; metabasitarsus 1.1; forewing 8.1. *Descriptive notes*: Dorsoventrally compressed on dark varve layer (Figs 2a, 4a); sterna fragmentarily preserved, setae of sterna nearly completely preserved; wax mirrors apparent as orange-brown areas (cf. Ansorge and Kohring 1995: fig. 5.1), evident on third metasomal sternum; mesosoma revealing dorsal elements; legs fragmentarily preserved; hind legs positioned next to metasoma; very slender metatibiae and metabasitarsi; metabasitarsi probably not completely preserved; some wing areas not apparent, but all cells of right forewing visible; compound eyes evident; clypeus and frons not discernible (gap in matrix separates parts of mandibles and right protarsus from remainder of specimen); fossil leaf preserved behind metasoma; another leaf positioned in same varve layer at right side of bee; wing not preserved in contact zone of leaf and wing, perhaps result of earlier preparation. *Remarks*: The forewing of this individual was probably

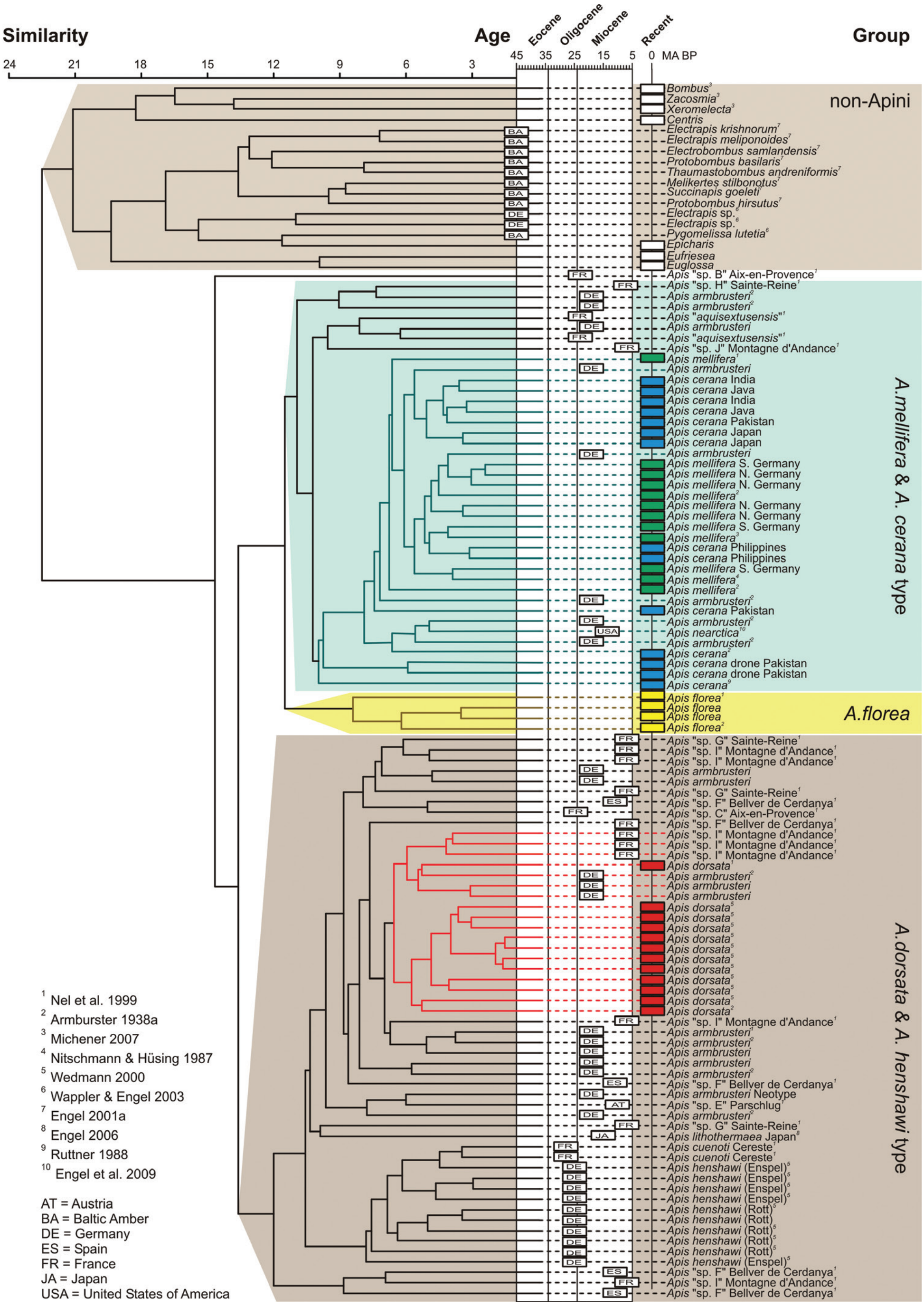

Figure 6. Dendrogram resulting from FWVA cluster analysis described in the text. Recent specimens of *Apis* and associated clusters are marked in the following colors: red, *A. dorsata* Fabricius; yellow, *A. florea* Fabricius; green, *A. mellifera* Linnaeus; blue, *A. cerana* Fabricius; cyan, *cerana*/*mellifera*, morphotype.

longer than 8.1 mm, presumably reaching a length of 9.5–10 mm, and is similar to that of *A. dorsata*. Although all phylogenetic evidence indicates that fossil *Apis* built combs like their modern counterparts (Ruttner 1988; Engel 1998), the wax mirrors confirm that the honey bees from the Miocene Randeck Maar constructed combs. The presence of leaves in the same layer may indicate that the specimen died in Autumn.

Results

As to be expected given the unique venation of honey bees, all non-Apini were grouped together relative to *Apis* in the FWVA cluster analysis (Fig. 6). Among the Apini, all Recent forms were grouped in general accordance with their systematic position, and independent of whether the measurements were based on the literature or newly measured forewings. This underlines both the utility of the method and the quality of metrics and drawings made by different authors (e.g., Armbruster 1938a; Nel et al. 1999; Engel 2006).

The dendrogram (Fig. 6) reveals two main clusters, the first of which comprises the FWVAs of *mellifera*/*cerana* and, on a subbranch of their own, the specimens of *A. florea*. The second major cluster consists of FWVAs of *A. dorsata* and *A. henshawi*, with both species well segregated from each other. These groups do not necessarily represent clades given that undoubtedly some grouping is based on symplesiomorphies. In regard to the specimens of *A. armbrusteri*, most specimens group with *A. dorsata*, while some specimens (e.g., SMNS 64674/11a and SMNS 64674/36) are positioned within the *cerana*/*mellifera* group (Fig. 6). The dendrogram supports the observations described above, that at least some of the specimens newly documented herein are superficially more similar in forewing venation to *cerana*/*mellifera*-like bees than to *A. dorsata*, the latter phylogenetically outside of the *Apis* s.str. clade (Engel and Schultz 1997; Engel 2006; Raffiudin and Crozier 2007; Lo et al. 2010).

Apis henshawi from the Oligocene grouped nearest to those *A. dorsata* and *dorsata*-like fossils (Fig. 6). Not surprisingly, *A. cuenoti* from the Oligocene of Céreste groups within *A. henshawi*, generally supporting the synonymy of these taxa (Engel 1999).

The probably Late Oligocene-aged specimens from Aix-en-Provence, however, showed a different clustering pattern. Some of the specimens of the debated species "*A. aquisextana*" (Arillo et al. 1996; Nel et al. 1999; Engel 2006) grouped with the *mellifera*/*cerana* branch, while another specimen ("B" of Nel et al. 1999) grouped outside all other Apini. However, Nel et al. (1999) noted that for this material the apical portions of the wings were destroyed and it is, therefore, very possible that the wing venation was altered by postmortem processes. As such, this specimen may represent merely a damaged individual of *A. armbrusteri* of the "CM" morphotype and its current clustering position should be considered dubious. A fourth specimen ("C" of Nel et al. 1999) was positioned on a branch together with other Miocene bees whose FWVA are generally similar to *A. dorsata* and *A. armbrusteri* of the "D" morphotype (Fig. 6).

The Apini from the Miocene are, independent of their geographical origin, scattered across the principle clusters (i.e., the branches on which either *mellifera/cerana* or *A. dorsata* and *A. henshawi* are positioned). In addition to the specimens SMNS 64674/11a and 64674/39, six other individuals from the Miocene of Randeck showed a forewing venation more similar to that of *cerana/mellifera*-like bees than to that of *A. dorsata*. The distribution of Armbruster's specimens (based on his 1938a photographs and figures) in the dendrogram was independent of the "*Hauffapis*"-species designated by Armbruster (1938a). For example, forewings of "*H. scheuthlei*" occur next to both the *cerana/mellifera* and *A. dorsata* clusters, indicating that the subdivisions of *A. armbrusteri* into the several species or subspecies as advocated by Armbruster (1938a) and Zeuner and Manning (1976) are effectively meaningless. The pattern was the same for the other European Miocene fossillagerstätten, namely that the *Apis* from Montagne d'Andance and Sainte-Reine (Miocene, France) are positioned on both major branches as for the material from Randeck (Fig. 6).

Discussion

Naturally, as noted previously, dendrograms cannot be interpreted as phylogenies owing to an inability to distinguish homology from analogy and plesiomorphy from apomorphy. This is immediately evident in that, while all *Apis* group together, the corbiculate Apinae do not form a cluster, nor do the Centridini, or other well-defined taxa based on larger suites of characters (Fig. 6). Moreover, *A. florea* phylogenetically lies outside of an *Apis* s.str.+*Megapis* clade (Alexander 1991a, 1991b; Engel and Schultz 1997; Engel 2006; Raffiudin and Crozier 2007; Lo et al. 2010), while nonetheless sharing more plesiomorphic similarities in FWVA with *Apis* s.str. relative to *Megapis* and thereby resulting in the grouping of *Micrapis* with *Apis* s.str. in a cluster analysis (Fig. 6). Despite this inability to equate the dendrogram with a phylogeny, the FWVA analysis supports the general systematic division of the Oligocene and Recent honey bees as well as the three principle lineages of modern *Apis* (*Megapis*, *Micrapis*, and *Apis* s.str.) (e.g., Engel 1998, 1999, 2006).

The newly documented honey bees from the Randeck Maar exhibit, similar to the specimens described by Armbruster (1938a), a considerable variability in size, body shape, and forewing venation. Among the ten specimens newly considered in detail, two are remarkably similar to the *cerana/mellifera* group. Specimen 64674/11a in particular probably could not be differentiated from a fossil of *A. cerana* in many respects, although the presence of the small process of 1m-cu is not found in the former species. However, other specimens such as 64674/19 are seemingly more similar to *A. henshawi* and *A. dorsata*, but putatively only in plesiomorphic features. However, there are also specimens for which the assignment to one or the other of the two morphotypes employed herein must remain questionable and, in general, when characters other than wing venation are examined there is gradation between these morphological extremes. It is thus not entirely clear whether the environment around the Randeck Maar hosted two different *Apis* species [or even more, as suggested by Armbruster (1938a)], or only one variable species, a phenomenon known in modern taxa such as *A. mellifera*, *A. cerana*, *Accipiter tachiro* (Daudin) (e.g., Hepburn and Radloff 1998; Radloff et al. 2010; Louette 2007), and particularly for variable wing morphologies in species of lower termites, bark lice, halictine bees, and many other insect lineages (e.g., Emerson 1933; Coaton 1949, 1958; Kučerová 1997; Grimaldi et al. 2008; Gibbs 2010). A clear division into two species would make sense if there were other supporting characters (e.g., leg shape, size, hind wing venation). Though, as noted, this cannot be demonstrated for any of the bees from the Miocene of Randeck. Additionally, other European sites also show the presence of different morphotypes within the same locality, particularly Montagne d'Andance and Sainte-Reine (Miocene, France) (*vide supra*). Conversely, Recent honey bees in Asia, while broadly overlapping, tend not to occur in the same microhabitats. For example, *A. dorsata* is more common at higher elevations, and *A. florea* uses a special ecological niche in the stratum of dense bushes and small trees in tropical areas (e.g., Wu and Kuang 1987; Ruttner 1988). *Apis mellifera* and *A. cerana* do not occur in the same regions naturally, and where *A. mellifera* is introduced, it can result in the competitive exclusion of *A. cerana* (Ruttner 1988), depending on which subspecies are involved (e.g., Manila-Fajardo and Cleofas 2003).

We conservatively suggest that European Apini of the Miocene exhibited a considerable morphological diversity, even somewhat more so than in modern congeners. This is supported by the fact that among the specimens from Randeck, even those within morphotype D, showed a remarkable variation in body size, which cannot be explained solely by postmortem effects, by caste differences, or biological phenomena. The heterogeneity is further supported by the considerable variability in leg shape and the varying presence or absence of the small process of 1m-cu, all of which are apparently independent of the two morphotypes recognized on the basis of FWVA.

Noteworthy, our results show a much lower variability for the Oligocene Apini from Germany and France. As shown by the Honeybee Genome Sequencing Consortium (2006), the rate of evolution in *Apis* is slow compared to other insects. This may perhaps explain how European populations of *Apis* maintained such hyper-variability within an otherwise single evolutionary species for such a considerable time throughout the Miocene. Consequently, the various morphotypes observed across these European populations would perhaps all represent a single, widespread species, much like modern widespread species such as *A. mellifera* and *A. cerana*. The historical biogeography and nest evolution of the genus shall be discussed elsewhere (Kotthoff et al. in prep.).

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Appendix I

Forewing venation angle measurements. (doi: 10.3897/zookeys.96.752.app) File format: Microsoft Word.

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RESEARCH ARTICLE

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First descriptions of copepodid stages, sexual dimorphism and intraspecific variability of *Mesocletodes* Sars, 1909 (Copepoda, Harpacticoida, Argestidae), including the description of a new species with broad abyssal distribution

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Abstract

Mesocletodes Sars, 1909a encompasses 37 species to date. Initial evidence on intraspecific variability and sexual dimorphism has been verified for 77 specimens of *Mesocletodes elmari* sp. n. from various deep-sea regions, and ontogenetic development has been traced for the first time. Apomorphies are a strong spinule-like pinna on the mx seta that is fused to the basis, P2–P4 exp3 proximal outer seta lost, P1–P4 enp2 extremely elongated, furcal rami elongated, female body of prickly appearance, female P2–P4 enp2 proximal inner seta lost. Intraspecific variability involves spinulation, ornamentation and size of the body and setation and spinulation of pereiopods. Sexually dimorphic modifications of adult females include prickly appearance of the body, P1 enp exceeds exp in length, P1 coxa externally broadened, seta of basis arising from prominent protrusion, hyaline frills of body somites ornate. Sexual dimorphism in adult males is expressed in smaller body size, haplocer A1, 2 inner setae on P2–P4 enp2 and on P5 exp, P5 basendopodal lobe with 2 setae. Some modifications allow sexing of copepodid stages. The female A1 is fully developed in CV, the male A1 undergoes extensive modifications at the last molt. P1–P4 are fully developed in CV. *Mesocletodes faroerensis* and *Mesocletodes thielei* lack apomorphies of *Mesocletodes* and are excluded.

Keywords

ANDEEP, CROZEX, DIVA, Great Meteor Bank, meiofauna, *Mesocletodes elmari* sp. n., NODINAUT, ontogeny, Porcupine Abyssal Plain

Introduction

Expeditions to the Southeast Atlantic (DIVA-1 [Balzer et al. 2006], DIVA-2 [Türkay and Pätzold 2009] and part of ANDEEP III [Fahrbach 2006]), the Southern Ocean (ANDEEP I and II [Fütterer et al. 2003]), the South Indian Ocean (CROZEX [Pollard and Sanders 2006]), the central Pacific (NODINAUT [Galéron and Fabri 2004], the North Atlantic (Porcupine Abyssal Plain, PAP [see Kalogeropoulou et al. 2010 for summary] and the Great Meteor Bank [Pfannkuche et al. 2000]) (Fig. 1) provided numerous specimens of the genus *Mesocletodes* Sars, 1909a. Belonging to the family of Argestidae Por, 1986a, *Mesocletodes* is considered to be a typical and primarily deep-water dwelling taxon (compare overview in George 2004 and George 2008). The total number of *Mesocletodes* in deep-sea samples amounts to almost 50% of all Argestidae Por, which in turn form one of the most abundant taxa of harpacticoid copepods therein. Due to the high frequency in deep-sea samples and conspicuous morphological characters, *Mesocletodes* is informative for chorological, faunistic and biogeographic research. The number of specimens as well as species diversity are substantial, but species are well discernible.

Mesocletodes nowadays comprises 36 species (Menzel and George 2009; Wells 2007). All allied species show characteristic morphological features that allow rapid recognition in metazoan meiofauna samples: body of cylindrical shape, A1 segment 2 with conspicuous protrusion bearing a strong seta, md gnathobase with broad grinding face, P1 exp2 without inner seta, P1 exp3 without proximal outer spine, spines of this segment with subterminal tubular extensions, P2–P4 exp1 without inner seta, P2–P4 enps at most 2-segmented, telson square in dorsal and ventral view and furcal rami long and slender (cf. Menzel and George 2009).

The sex ratio of harpacticoid copepods in the deep sea is strongly biased towards females (e.g. Shimanaga et al. 2009; Shimanaga and Shirayama 2003; Thistle and Eckman 1990) and it is very difficult or nearly impossible to connect males and females of some species (e.g. Menzel and George 2009; Seifried and Veit-Köhler 2010; Vasconcelos et al. 2009; Willen 2006; Willen 2009; Willen and Dittmar 2009), indicating extremely poecilandric populations (Por 1986b). Concerning Argestidae, males could be connected to females for *Eurycletodes* Sars, 1909b, *Argestes* Sars, 1910, and *Hypalocletodes* Por, 1967 (cf. original descriptions). Since the establishment of *Mesocletodes* early in the 20th century (Sars, 1909a), this has been possible only for two species plus the herein described species. For 32 species of this genus only females are known, while exclusively males are known for two species.

Most of the species descriptions of *Mesocletodes* are based on few adult specimens (29 descriptions contain one to five type specimens, three descriptions are based on six to ten specimens, four descriptions are based on 11 to 16 specimens). Thus, neither intraspecific variability nor the process of ontogenetic development is reported for any species of *Mesocletodes*. Expeditions during the DIVA and ANDEEP campaigns yielded 54 out of 66 adults of *Mesocletodes elmari* sp. n. (more than 80%). The comparatively high frequency of specimens is probably explicable by the greater sampling effort in contrast to the CROZEX, NODINAUT, OASIS expeditions and

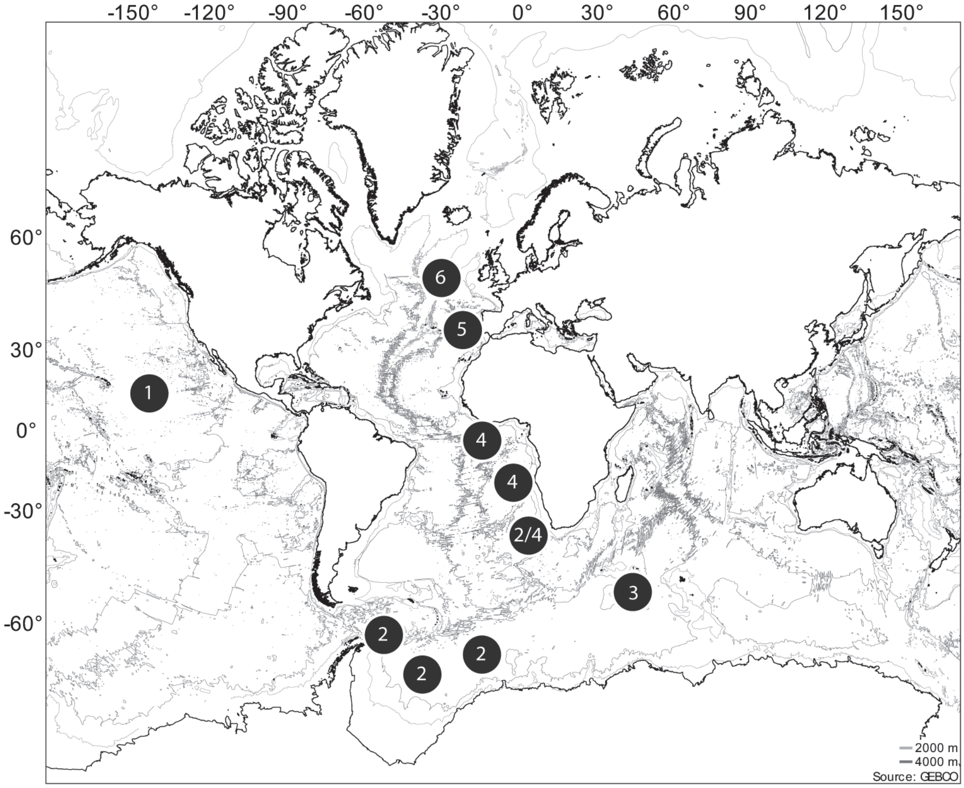

Figure 1. Positions of the sampled stations containing the species studied. **1** NODINAUT **2** ANDEEP **3** CROZEX **4** DIVA **5** GMB **6** PAP.

sampling at the PAP as well as during previous campaigns. Repeated multicorer sampling of the same station (Martínez Arbizu and Schminke 2005; Rose et al. 2005) greatly enhances, for the first time, the opportunity of finding the same species again in one station or region. This implies that more specimens of one species are available, making investigations on intraspecific variability, specification of sexually dimorphic modifications and retracing of the ontogenetic development possible for the first time (cf. George 2008).

The aim of this publication is to convey an initial impression of the extent of sexually dimorphic modifications, ontogeny and intraspecific variability for the genus *Mesocletodes*, using *Mesocletodes elmari* sp. n. as an example.

Material and methods

Sediment samples were taken with a multicorer (Barnett et al. 1984) in different oceanic regions: Southeast Atlantic (DIVA-1, DIVA-2 and part of ANDEEP III), Southern Ocean (ANDEEP I and II), South Indian Ocean (CROZEX), central Pacific (NODINAUT), North Atlantic (PAP and Great Meteor Bank) (Fig. 1, Table 1). Adult Harpacticoida were extracted from all samples, whereas copepodid stages are only available from the campaigns DIVA-1, DIVA-2 and ANDEEP.

Altogether 77 specimens (56 adult females, 10 adult males, 2 CV females, 3 CV males, 5 CIV males and 1 CIII) were found. The type material of *Mesocletodes elmari* sp. n. consists of 7 specimens (2 females plus 1 each of the other discovered stages). The type material was deposited in the collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (Germany). The remaining 70 specimens are mounted on slides and kept in the collection of the DZMB in Wilhelmshaven (Germany).

The material was mounted on separate slides using glycerol as the embedding medium. Identification at the species level and drawings were carried out using a Leica microscope DM2500 equipped with a camera lucida and interference contrast with a maximum magnification of 1600x.

The CLSM photograph of a Congo-red stained female was taken with a Leica TCS SP5 mounted in a Leica DM5000. Preparations and settings were made according to Michels and Büntzow (2010).

Abbreviations used in the present paper are: A1 (antennula), A2 (antenna), aes (aesthetasc), benp (baseoendopod), CI–CV (copepodid stages 1–5), cphth (cephalothorax), enp (endopod), exp (exopod), FR (furcal rami), GF (genital field), md (mandibula), mx (maxilla), mxl (maxillula), mxp (maxilliped), P1–P6 (pereiopods 1–6), STE (Subterminal Tubular Extension, according to Huys 1996).

I could examine other material for comparison: Type material of *M. parabodini* Schriever, 1983, (1 dissected female, ZMK Cop. No. 1319). *M. farauni* Por, 1967 (1 female, dissected, HUJ Cop no. 69 plus one additional specimen), *M. glaber* Por, 1964a (1 female, dissected, HUJ Cop no. 33) and *M. monensis* (Thompson, 1893) (3 females, dissected, on one slide each, HUJ Cop no. 63, 93, 138).

Taxonomy

Argestidae Por, 1986a

Mesocletodes Sars, 1909a

http://species-id.net/wiki/Mesocletodes

Type species: *Mesocletodes irrasus* (T. and A. Scott, 1894), (described as *Cletodes irrasa*)

Additional species: *Mesocletodes* contains 37 species (Boxshall and Halsey 2004; Menzel and George 2009; Wells 2007), including the type species and the herein described new species: *M. abyssicola* (T. and A. Scott, 1901), *M. angolaensis* Menzel and George, 2009, *M. bathybia* Por, 1964b, *M. bicornis* Menzel and George, 2009, *M. brevifurca* Lang, 1936, *M. dolichurus* Smirnov, 1946, *M. dorsiprocessus* Menzel and George, 2009, *M. katharinae* Soyer, 1964, *M. meteorensis* Menzel and George, 2009,

Table 1. Specimens of *Mesocletodes elmari* sp. n. discovered, containing information on gender, number of eggs, ontogenetic stage, body length and remarks on intraspecific variability. f = female; m = male.

	Project	**Expedition**	**Station**	**gender**	**number of eggs**	**ontogenetic stage**	**body length [mm]**	**remarks on intraspecific variability**
	ANDEEP I	PS61	43/4-6	f		adult	0.70	
	ANDEEP I	PS61	46/4-1	f	ca. 15	adult	0.82	
	ANDEEP I	PS61	46/4-5	f		adult	0.63	P2 enp2 with outer seta
	ANDEEP I	PS61	46/4-8	f		adult	0.70	hyaline frill not ornate
	ANDEEP I	PS61	46/6-5	m		CV	0.50	
	ANDEEP I	PS61	46/6-3	f		adult	0.80	P2-P4 enp2 with outer seta
	ANDEEP I	PS61	46/6-3	f		adult	0.87	
	ANDEEP I	PS61	129/5-4	f	4	adult	0.78	
	ANDEEP II	PS61	131/11-A	f	4? 20?	adult	0.62	
	ANDEEP II	PS61	138/11-4	f		adult	0.71	
Paratype 6	ANDEEP II	PS61	138/11-4			CIII	0.47	
	CROZEX	D300	15773/31	f	11	adult	0.80	
	CROZEX	D300	15775/32	f		adult	0.92	FR: setular tuft near seta VII
	CROZEX	D300	15775/36	m		adult	0.43	
	DIVA-1	M48/1	325/6-2	f		adult	?	FR lost
	DIVA-1	M48/1	342/2-1	f		adult	0.71	FR: setular tuft near the base
	DIVA-1	M48/1	346/1-3	m		adult	0.68	
	DIVA-1	M48/1	346/1-7	m		adult	0.54	
	DIVA-1	M48/1	346/2-3	f		adult	0.83	
	DIVA-1	M48/1	346/2-3	f	12	adult	0.87	
	DIVA-1	M48/1	346/2-8	f	17	adult	0.86	
	DIVA-1	M48/1	346/2-9	f	3?	adult	0.74	
	DIVA-1	M48/1	346/2-11	f		adult	0.82	FR: setular tuft near seta VII, P1-P4 enp shorter
	DIVA-1	M48/1	346/3-9	f		adult	0.91	

	Project	Expedition	Station	gender	number of eggs	ontogenetic stage	body length [mm]	remarks on intraspecific variability
	DIVA-1	M48/1	346/4-10	f		adult	0.85	FR: setular tuft near seta VII, P1-P4 enp shorter
	DIVA-1	M48/1	346/5-3	f		adult	0.80	hyaline frill not ornate
	DIVA-1	M48/1	346/5-9	f		adult	0.82	
	DIVA-1	M48/1	346/5-10	f	10	adult	0.66	
	DIVA-1	M48/1	346/6-2	f		adult	0.82	
	DIVA-1	M48/1	346/7-7	f		adult	0.85	
	DIVA-1	M48/1	346/7-8	f		adult	0.79	
	DIVA-1	M48/1	346/7-10	f		adult	0.78	
	DIVA-1	M48/1	346/7-10	f		CV	0.75	
Paratype 4	DIVA-1	M48/1	346/7-10	m		CV	0.59	
	DIVA-1	M48/1	346/8-3	f		adult	0.86	
Paratype 2	DIVA-2	M63/2	CAPE/35-7	f		adult	0.90	FR: setular tuft near seta VII
	DIVA-2	M63/2	CAPE/36-10	f	3	adult	0.57	
	DIVA-2	M63/2	CAPE/36-11	f		adult	0.66	
	DIVA-2	M63/2	CAPE/36-11	m		adult	0.40	
	DIVA-2	M63/2	CAPE/36-11	m		CV	0.40	FR: setular tuft near the base, P2-P4 enp2 with only 1 inner seta
	DIVA-2	M63/2	GUINEA E/56-5	m		adult	0.53	
	DIVA-2	M63/2	GUINEA E/57-1	f	2?	adult	0.70	FR: setular tuft near the base
	DIVA-2	M63/2	GUINEA E/57-8	f		adult	0.67	
	DIVA-2	M63/2	GUINEA E/58-10	f	7	adult	0.75	
	DIVA-2	M63/2	GUINEA E/58-12	f	5	adult	0.63	
	DIVA-2	M63/2	GUINEA E/59-10	f		adult	0.64	
	DIVA-2	M63/2	GUINEA E/59-12	m		adult	0.51	
	DIVA-2	M63/2	GUINEA E/61-4	m		adult	0.50	
	DIVA-2	M63/2	GUINEA E/62-6	f		adult	0.81	
	DIVA-2	M63/2	GUINEA E/62-6	m		adult	0.53	

	Project	Expedition	Station	gender	number of eggs	ontogenetic stage	body length [mm]	remarks on intraspecific variability
	DIVA-2	M63/2	GUINEA W A/74-4	f		adult	0.78	hyaline frill not ornate, FR longer
Holotype	DIVA-2	M63/2	GUINEA W A/75-7	f		adult	0.78	
	DIVA-2	M63/2	GUINEA W A/76-6	f	7	adult	0.80	
	DIVA-2	M63/2	GUINEA W A/78-6	f		adult	?	FR lost
Paratype 1	DIVA-2	M63/2	GUINEA W A/78-7	m		adult	0.42	
	DIVA-2	M63/2	GUINEA W A/79-4	f		adult	?	Abdomen lost
Paratype 3	DIVA-2	M63/2	GUINEA W A/79-4	f		CV	0.55	P1 0-0 0,1,1, P2 0-0 0,2,0
	DIVA-2	M63/2	GUINEA W B/95-10	m		adult	0.43	
	DIVA-2	M63/2	GUINEA W B/96-8	f		adult	0.80	FR: setular tuft near the base, hyaline frill not ornate, FR longer
	DIVA-2	M63/2	GUINEA W B/97-6	f		adult	0.87	
	DIVA-2	M63/2	GUINEA W B/97-7	m		CIV	0.52	FR: setular tuft near the base, P1–P4 enp2 with outer seta
	DIVA-2	M63/2	GUINEA W B/97-7	m		CIV	0.49	FR: setular tuft near the base, P1–P4 enp2 with outer seta
	DIVA-2	M63/2	GUINEA W B/97-7	m		CIV	0.64	FR: setular tuft near the base, P1–P4 enp2 with outer seta
	DIVA-2	M63/2	GUINEA W B/97-7	m		CIV	0.47	FR: setular tuft near the base, P1–P4 enp2 with outer seta
Paratype 5	DIVA-2	M63/2	GUINEA W B/97-7	m		CIV	0.43	FR: setular tuft near the base, P1–P4 enp2 with outer seta
	DIVA-2	M63/2	GUINEA W B/99-10	f	10	adult	0.71	FR: setular tuft near the base, P2-P4 enp2 with outer seta, denticulation of hyaline frill more dense
	DIVA-2	M63/2	GUINEA W B/100-6	f		adult	0.87	
	DIVA-2	M63/2	GUINEA W B/100-7	f	5	adult	0.90	
	GMB	M42/3	505	f		adult	0.61	
	GMB	M42/3	505	f		adult	0.61	

	Project	**Expedition**	**Station**	**gender**	**number of eggs**	**ontogenetic stage**	**body length [mm]**	**remarks on intraspecific variability**
	GMB	M42/3	566	f		adult	0.76	FR: setular tuft near the base
	NODINAUT		1599/7-2	f	4	adult	0.65	
	NODINAUT		1599/7-3	f		adult	0.66	
	NODINAUT		1602/10-7	f	5	adult	0.69	
	NODINAUT		1602/10-8	f	5	adult	0.67	
	NODINAUT		1603/11-1	f		adult	1.06	
	PAP		Mar 1997/13077-12	f	1?	adult	0.63	FR: setular tuft near the base

M. monensis, *M. opoteros* Por, 1986b, *M. quadrispinosa* Schriever, 1985, *M. robustus* Por, 1965, *M. soyeri* Bodin, 1968, *M. ameliae* Soyer, 1975, *M. arenicola* Noodt, 1952, *M. bodini* Soyer, 1975, *M. carpinei* Soyer, 1975, *M. commixtus* Coull, 1973, *M. duosetosus* Schriever, 1985, *M. farauni*, *M. faroerensis* Schriever, 1985, *M. fladensis* Wells, 1965, *M. glaber*, *M. guillei* Soyer, 1964, *M. inermis* Sars, 1921, *M. irrasus*, *M. kunzi* Schriever, 1985, *M. langi* Smirnov, 1946, *M. makarovi* Smirnov, 1946, *M. parabodini* Schriever, 1983, *M. parirrasus* Becker, Noodt and Schriever, 1979, *M. sarsi* Becker, Noodt and Schriever, 1979, *M. thieli* Schriever, 1985, *M. trisetosa* Schriever, 1983, *M. variabilis* Schriever, 1983, *M. elmari* sp. n.

Generic diagnosis (amended from Sars 1909a and Soyer 1964): Body of cylindric form, distal edge of body somites with many spinules close to hyaline frill, integument thin and flexible. Cphth not longer than first 2 free prosomites together, rostrum small. Telson as long as 2 last urosomites together, square from lateral and ventral view. FR longer than wide, seta VII in the proximal third. A1 6–8-segmented in females, second segment with strong protrusion bearing 1 strong bipinnate seta pointing backwards. A2 with basis or allobasis, without abexopodal seta, exp at most 1-segmented with at most 2 setae. Md palpus with at most 1-segmented exp and enp, blades of gnathobase forming broad grinding face. Mxl palp enp segment incorporated into basis or absent, exp segment present, incorporated into basis or absent. Mx proximal endite with 1 seta. Mxp prehensile, with strong claw distally. P1–P4 exps 3-segmented, of P1 small, of P2–P4 long and slender. P1 exp3 with 4 setal elements, spines with STEs. P1–P4 enps at most biarticulate. P5 exp longer than wide, endopodal lobe barely protruding. 1 egg sack with 2–40 eggs.

Mesocletodes elmari sp. n.

urn:lsid:zoobank.org:act:
http://species-id.net/wiki/Mesocletodes_elmari
Figs 2–14

Etymology: The name is dedicated to the author's father, Elmar Menzel.

Locus typicus: Guinea Basin, RV "Meteor", Cruise M63/2 (DIVA-2), station 75/7 (0°50.0'N, 5°35.0'W, 5139m), March 19, 2005.

Type material: 7 individuals Holotype: 1 female, dissected, mounted on 17 slides, coll. no. SMF 37012/1–17, RV "Meteor", Cruise M63/2 (DIVA-2) at station 75/7 (0°50.0'N, 05°35.0'W, 5139m), March 19, 2005.

Paratypes: Paratype 1 (Allotype): 1 male, dissected, mounted on 9 slides, coll. no. SMF 37013/1–9, RV "Meteor", Cruise M63/2 (DIVA-2) at station 78/7 (0°50.1'N, 05°35.1'W, 5136m), March 19, 2005.

Paratype 2: 1 female, mounted on 1 slide, coll. no. SMF 37014, RV "Meteor", Cruise M63/2 (DIVA-2) at station 35/7 (28°6.8'S, 7°20.7'E, 5033m), March 03, 2005.

Paratype 3: 1 CV female dissected, mounted on 6 slides, coll. no. SMF 37015/1–6, RV "Meteor", Cruise M63/2 (DIVA-2) at station 79/4 (0°50.0'N, 05°35.1'W, 5140m), March 19, 2005.

Figure 2. *Mesocletodes elmari* sp. n., adult female, paratype 2. CLSM photograph of a Congo-red stained specimen, lateral view. Scale bar: 100 µm

Paratype 4: 1 CV male dissected, mounted on 2 slides, coll. no. SMF 37016/1–2, RV "Meteor", Cruise M48/1 (DIVA-1) at station 346-7/10 (16°17.0'S, 05°27.0'E, 5389m), July 27, 2000.

Paratype 5: 1 CIV male dissected, mounted on 8 slides, coll. no. SMF 37017/1–8, RV "Meteor", Cruise M63/2 (DIVA-2) at station 97/7 (0°37.2'N, 06°28.1'W, 5168m), March 23, 2005.

Paratype 6: 1 CIII dissected, mounted on 7 slides, coll. no. SMF 37018/1–7, RV "Polarstern", Cruise PS61 (ANT-XIX/4 (ANDEEP II)) at station 138-11/4 (62°58.03'S, 27°54.08'W, 4541m) March 18, 2002.

Description of adult female holotype. (Figs 2–8) Habitus (Figs 2 [paratype], 3 A – B) of cylindrical shape, no clear distinction between prosome and urosome. Body length including FR 0.78 mm. Distal margins of cphth, prosomites and urosomites with conspicuous coarsely ornate and denticulated hyaline frill with many setules (Fig. 3 E). Body with several remarkably long sensilla. Distal margins of prosomites with long spinules: only dorsally in prosomites and first urosomite, in urosomites also laterally and ventrally. Distal margin of last urosomite without sensilla. Rostrum not protruding, with 2 sensilla. Body of prickly appearance, caused by small protrusions bearing one setule each, protrusions in urosomites and telson coarser than in prosomites (Fig. 3 D, F). Notch-like pores ventrolaterally on P4 – P5 bearing somites. Genital double somite fused ventrally. Telson (Fig. 3 A–C) as long as 2 preceding urosomites together, almost square from lateral and dorsal view. Ventrally with 2 rows of 6 long spinules each and on the outer edges, close to hyaline frill of last urosomite. 1 ventral notch-like pore on each side at inner edge near insertion of FR. Operculum with several denticles (Fig. 3 A).

A1 (Fig. 4 A, A') 7-segmented, reticulated as shown for proximal part of A2 enp1 (Fig. 4 B). Segments 4 and 7 with aes. Second segment of paratype 2 (A') large, with 1 protrusion bearing 1 bipinnate seta (seta lost during preparation of holotype). Spines with STEs. First and second segment bear inner and outer spinules, third segment with outer spinules. Setal formula: 1: 0; 2: 8; 3: 5; 4: 2+aes; 5: 1; 6: 2; 7: 9+acrothek (=11+aes).

A2 (Fig. 4 B) with basis, reticulate ornamentation as shown for part of enp1. Exp 1-segmented, with 1 terminal and 1 subterminal seta. Enp 2-segmented, both segments with strong outer spinules. Enp2 with 2 bipinnate spines subterminally. 3 geniculate and 2 pinnate spines, and 1 naked seta terminally. Naked terminal seta fused basally to 1 outer pinnate spine. The innermost element is a reduced seta. Spines with STEs.

Labrum (Fig. 5 A) with 1 medial and 2 lateral rows of spinules, setules at oral surface.

Md (Fig. 5 B, C) gnathobase formed by 5 tooth-like projections: 1 dentate, 1 broad tooth, 3 strong teeth partly fused to broad grinding face. Strong seta close to grinding face. Md palpus 3-segmented, exp and enp articulated. 1 strong basal seta terminally, exp with 2 terminal and 1 subterminal setae, enp with 3 terminal setae.

Paragnaths (Fig. 5 D) on each side with 2 rows of traverse arranged brush-like setae orally and 1 row of long spinules at the surface.

Mxl (Fig. 5 E) praecoxal arthrite terminally with 6 strong elements: 3 hooks with 1 strong spinule each, 1 brushlike seta fused to arthrite and 2 unipinnate setae. Subterminally with another pinnate spine and 2 bare setae aborally. Coxa with 4

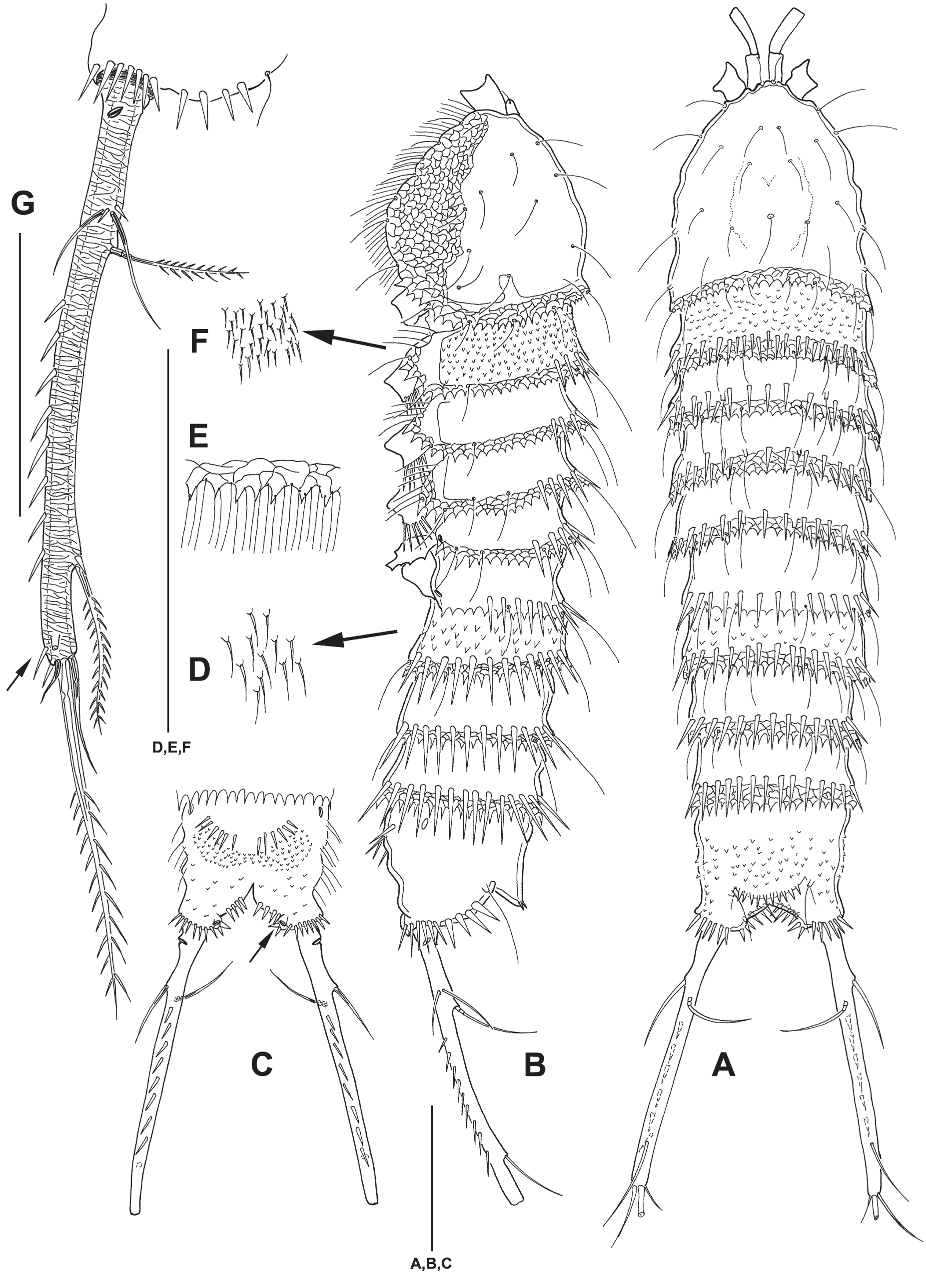

Figure 3. *Mesocletodes elmari* sp. n., adult female, holotype. **A** habitus dorsal view **B** habitus lateral view **C** telson ventral view, internal notch-like pores indicated by arrow **D** detail of urosomal setules **E** detail of hyaline frill **F** detail of prosomal setules **G** FR lateral view, tube pores indicated by arrow. Scale bars: **A–C**: 100 µm; **D–G**: 50 µm

elements terminally: 1 strong seta fused to coxa and 3 bare setae. Basis with 2 bare setae. Enp incorporated into basis, with 2 bare setae, exp 1-segmented with 2 pinnate setae.

Mx (Fig. 5 F) syncoxa with 2 endites, the proximal one bearing 1 seta. Distal endite with 3 setae, the biggest one fused to segment. 2 strong setae fused to basis, distal one shows a suture, proximal one with 1 conspicuous strong spinule-like pinna (indicated by arrow in Fig. 5 F). Basis additionally with 1 bare seta. Enp 1-segmented, with 2 bipinnate setae of equal length (dash-depicted seta supplemented from paratype 2).

Mxp (Fig. 5 G, G1–G3) prehensile, syncoxa (Fig. 5 G1) slightly shorter than basis (proximal part of Fig. 5 G2), with 2 setae and several spinules. Basis slender, with spinules of different sizes. Enp 2-segmented. Enp1 (distal part of Fig. 5 G2) small, bare of setae. Enp2 (Fig. 5 G3) terminally fused to strongly pinnate claw, suture visible.

P1 (Fig. 6 A) with 3-segmented exp and 2-segmented enp. Intercoxal sclerite long and bow-like. Coxa 1/3 broader than basis, with several spinules on ventral margin. Basis with outer spine, outer pore, long inner spine ventrally oriented and several rows of spinules. Exp1 and exp2 without inner seta. Exp3 with 4 elements. Enp1 short, with strong inner spine inserted medially. Enp2 extremely long, surpassing exp in length, with 1 outer, 1 terminal and 1 inner seta. Enp2 with 1 peculiar spinule subterminally. For setal formula see Table 2.

P2–P4 (Figs 6 B, 7 A, B) with 3-segmented exps and 2-segmented enps. Intercoxal sclerites long and bow-like. Coxae little larger than bases. Bases twice as broad as long. Bases with outer spines, at inner margin with setular tufts. Outer margins of coxa with

Table 2. *Mesocletodes elmari* sp. n., setal formula of P1–P4 of adults and copepodid stages. Pereiopodal setation of CV female and CV male is analogous to adults. – = segment is missing

		exp1	exp2	exp3	enp1	enp2
P1	adult female	I-0	I-0	I,I1,1	0-1	1,1,1
	adult male	I-0	I-0	I,I1,1	0-1	0,1,1
	CIV male	I-0	2,I1,1	–	0-1	1,1,1
	CIII	I-0	2,I1,1		0-1	0,1,1
P2	adult female	I-0	I-1	II,I1,2	0-1	0,2,1
	adult male	I-0	I-1	II,I1,2	0-1	0,2,2
	CIV male	I-0	III,I1,3	–	0-1	1,2,1
	CIII	I-0	III,I1,2	–	0-1	0,2,1
P3	adult female	I-0	I-1	II,I1,2	0-1	0,2,1
	adult male	I-0	I-1	II,I1,2	0-1	0,2,2
	CIV male	I-0	III,I1,3	–	0-1	1,2,1
	CIII	I-0	II,I1,2	–	0-1	0,2,0
P4	adult female	I-0	I-1	II,I1,2	0-1	0,2,1
	adult male	I-0	I-1	II,I1,2	0-1	0,2,2
	CIV male	I-0	III,I1,3	–	0-1	1,2,1
	CIII	III,I1,0	–	–	0,2,0	–

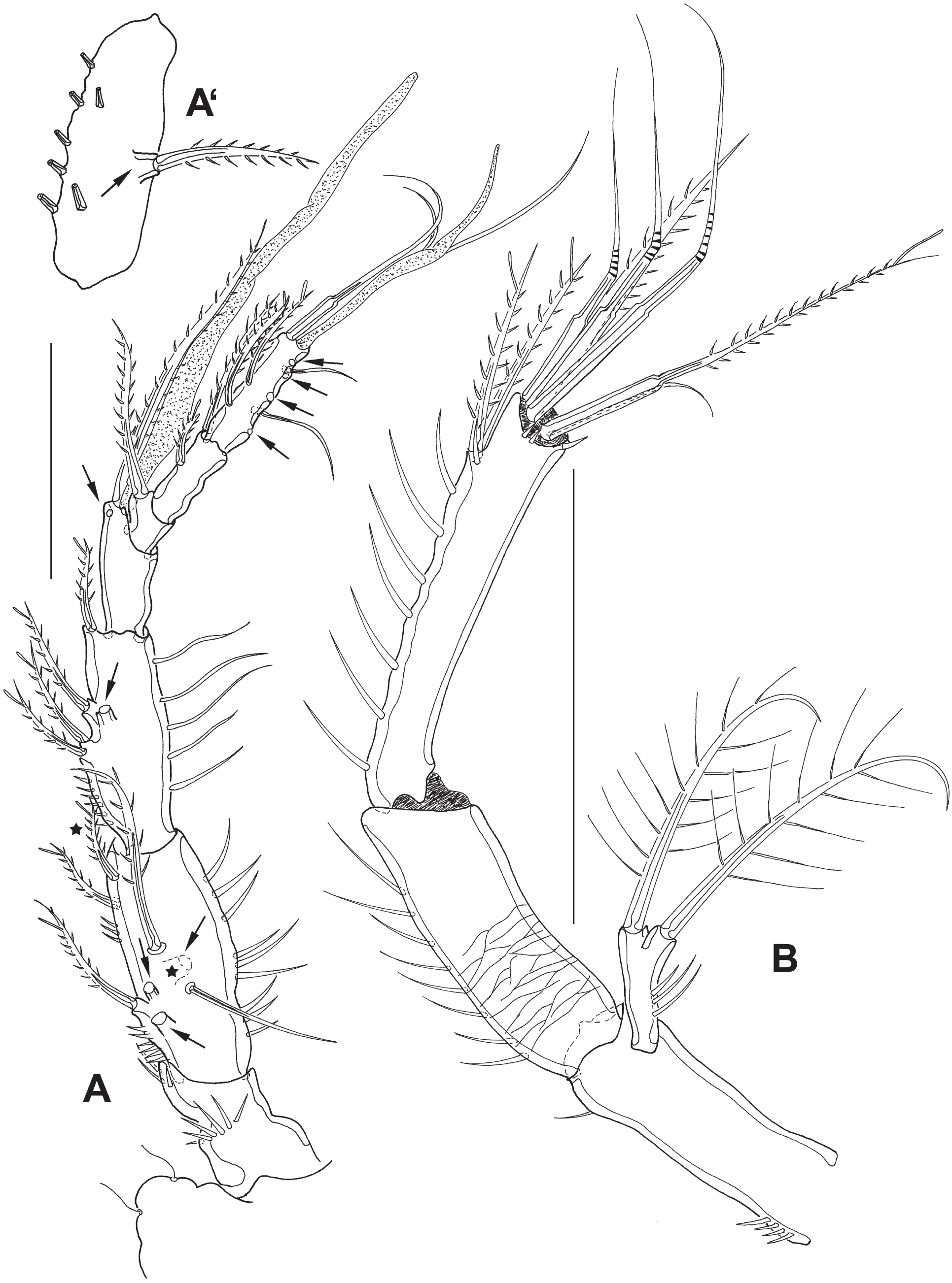

Figure 4. *Mesocletodes elmari* sp. n., adult female. **A** A1, holotype, dorsal view. Missing setae indicated by arrows. Asterisks mark the 2 setae presumably occurring in CV. **A'** second A1 segment, paratype 2, ventral view, arrow indicates characteristic protrusion with seta **B** A2 holotype. Scale bars: 50 µm

strong spinules, inner margins of coxa and basis with setules. Exp1 as long as exp2 and exp3 together. Exp1 without inner seta. Exp3 terminally with cuticular hooks. Enp1 short. Enp2 extremely long, decreasing in length from P2-P4, measured in relation to exp1. Enp2 with 1 strong, short spinule subterminally. Outer terminal seta of enp2 decreasing in length from P2–P4. Inner terminal seta in P2 enp2 lost during preparation (indicated by arrow in Fig. 6 B). Setation of exp and enp as in Table 2.

P5 (Fig. 8 A) benp with setophore with 2 spinules and 1 long bipinnate seta. Endopodal lobe not protruding, with 3 setae. Exp about 2 times as long as broad at base, bearing 3 outer, 1 terminal and 1 inner seta (dash-depicted setae supplemented from paratype 2).

P6 integrated into GF (Fig. 8 B), reduced to a fused opercular plate, armed with 1 short spine on each side (see asterisk in Fig. 8 B). GF with single aperture, accompanied by 1 row of spinules on each side.

FR (Fig. 3 G) long and slender, ornate, ventral spinules between seta VII and III. Approximately 13 times as long as broad (measured at base). Close to base ventrolaterally with 1 notch-like pore at external side (Fig. 3 G, C). Extremely elongated between setae VII and III. Seta I close to seta II. Seta VII triarticulate. Seta III located on dorsal side subterminally. Setae IV–VI located terminally. FR laterally with subterminal tube pore (see arrow in Fig. 3 G).

Description of adult male paratype (Allotype) (Figs 8–11) The adult male corresponds to the adult female in all morphological characters unless deviations are mentioned below.

Habitus (Fig. 9 A, B) much smaller than adult female, body length including FR 0.40 mm. Body not of prickly appearance (Fig. 9 A–C), hyaline frill (Fig. 9 D) not ornate. Distal margins of first and second urosomites with long spinules dorsally, of third urosomite dorsally, laterally and ventrally, of last 2 urosomites only laterally and ventrally. With 2 spermatophores: first one inside first urosomite, second one inside second and third prosomite. Gut empty. FR (Fig. 9 E) as described for female.

A1 (Fig. 10 A) 9-segmented, haplocer. Segments 5 and 9 with aes. Second segment large, with 1 protrusion bearing 1 bare seta. Segments 5, 6 and 7 with modified setae. Setae of most segments bare. Setal formula: 1: 0; 2: 8; 3: 4; 4: 2; 5: 4+aes; 6: 2; 7: 2; 8: 2; 9: 9+acrothek (=11+aes).

A2, Md, Mxl, Mx and Mxp as described for adult female.

P1–P4 (Fig. 11 A–D) intercoxal sclerites, coxae, bases and segmentation of enp and exp as described for adult female, but with fewer spinules. P1 exp3 with 1 spine and 3 setae, the 2 innermost of wreathed appearance. P2–P4 inner exopodal setae long. P2–P4 enp2 with 2 long inner setae. Basal seta of P3 and P4 broken (indicated by arrow in Fig. 11 C, D). For setal formula see Table 2.

P5 (Fig. 8 D) with setophore (seta lost during dissection, see arrow in Fig. 8 D) with few spinules and 1 notch-like pore laterally. Endopodal lobe barely protruding, with 2 setae, outermost very short. Exp about twice as long as broad (measured at base), bearing 3 outer, 1 terminal and 2 inner setae.

P6 (Fig. 8 D1) with 2 setae.

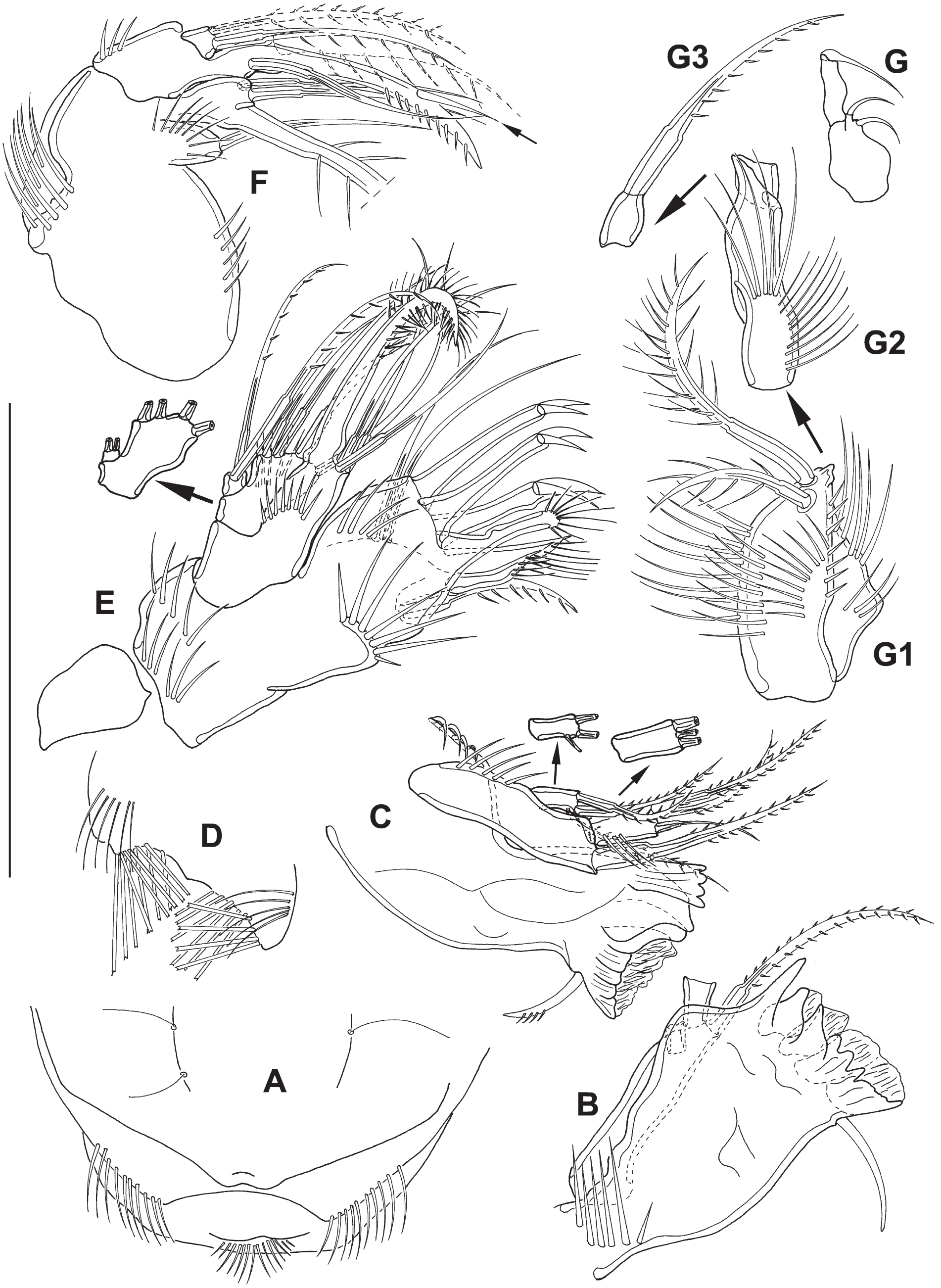

Figure 5. *Mesocletodes elmari* sp. n., adult female. **A** labrum, holotype **B+C** md, holotype, **D** paragnaths, holotype **E** mxl, holotype **F** mx, holotype, basal seta supplemented after counterpart, dash-depicted endopodal seta supplemented after paratype 2. Arrow dicates the peculiar spinulelike pinna **G** mxp, paratype 2, unfragmented, **G1–G3** mxp details, holotype. Scale bar: 50 µm

Description of copepodid stages (paratypes 3–6) (Figs 8, 10, 12–14) CV female (Fig. 12 C, C1): body length including FR 0.58 mm. Body not of prickly appearance. Penultimate urosomite is not formed. Distal margins of body somites with smooth hyaline frill and, except penultimate one, with sensilla. Extremities A1–P4 (not depicted) as described for adult female but smaller. P5 (Fig. 8 C) exp not separated from benp, setation of exp and basendopodal lobe as in adult female but smaller. P6 (Fig. 8 C1) with 2 setae. GF not expressed.

CV male: body as in CV female. A1 (Fig. 10 B) 6-segmented. Segments 3 and 6 with aes. Second segment large, with a protrusion bearing 1 seta. Setal formula: 1: 0; 2: 8; 3: 9+aes; 4: 2; 5: 2; 6: 9+acrothek (=11+aes). A2–mxp as described for adult female. P1–P4 (not depicted) and P6 (Fig. 8 E1) as described for adult male but smaller. P5 (Fig. 8 E) exp not separated from benp, setation of exp as in adult male but smaller. Right basendopodal lobe with 2 setae and 1 cuticular protrusion, which is missing on the counterpart (see asterisk in Fig. 8 E).

CIV male (Fig. 12 B, B1): body length including FR 0.50 mm. Body not of prickly appearance. 2 penultimate urosomites not formed. Distal margins of body somites with smooth hyaline frill and, except the penultimate one, with sensilla. A1 (Fig. 14 A) 6-segmented. Segments 3 and 6 with aes. Setal formula: 1: 0; 2: 6; 3: 6+aes; 4: 1; 5: 2; 6: 9+acrothek (=11+aes). A2–mxp (not depicted) as described for adult female but smaller P1–P4 (Fig. 13 A–D) with 2-segmented enp and 2-segmented exp. P1–P4 enp2 with 1 inner seta and 1 subterminal, outer seta. For setal formula see Table 2. Setal elements developed as in adult male, P5 (Fig. 8 F) exp not separated from benp. Basendopodal lobe with 2 setae and 1 cuticular protrusion, P5 not fused in the middle. P6 (Fig. 8 F1) with 2 setae. GF not expressed. FR with setular tuft (Fig. 12 B1) close to insertion in telson.

CIII (Fig. 12 A, A1): body length including FR 0.42mm. Body not of prickly appearance. 3 penultimate urosomites not formed. Distal margins of body somites with smooth hyaline frill. A1 (Fig. 14 F) 5-segmented. Setal formula: 1: 0; 2: 8+aes; 3: 1; 4: 2; 5: 9+acrothek (=11+aes). A2–mxp (not depicted) as described for adult female but smaller.

P1–P3 (Fig. 14 B–D) with 2-segmented enp and 2-segmented exp. Exp1 longer than exp2. P4 (Fig. 14 E) exp and enp 1-segmented. For setal formula see Table 2. P5 lost during preparation, P6 not expressed.

Morphological variability (cf. Table 1). The body length including FR is variable: for adult females between 0.57 and 1.06 mm (the majority measured 0.7 to 0.9 mm), for adult males between 0.4 and 0.7 mm, for CV females between 0.5 and 0.75 mm, for CV males between 0.5 and 0.59 mm, for CIV males between 0.4 and 0.64 mm.

The spinulation also seems to be highly variable: the row of spinules ventrally at the telson ranges from numerous, long and slender to few, short and stout. In total, 16 specimens show setular tufts in the FR: six adult females, one CV male and the five CIV males bear setular tufts close to the telson, four adult females close to seta VII. The amount of spinules in A1 segment 3 varies. Four out of 56 adult females,

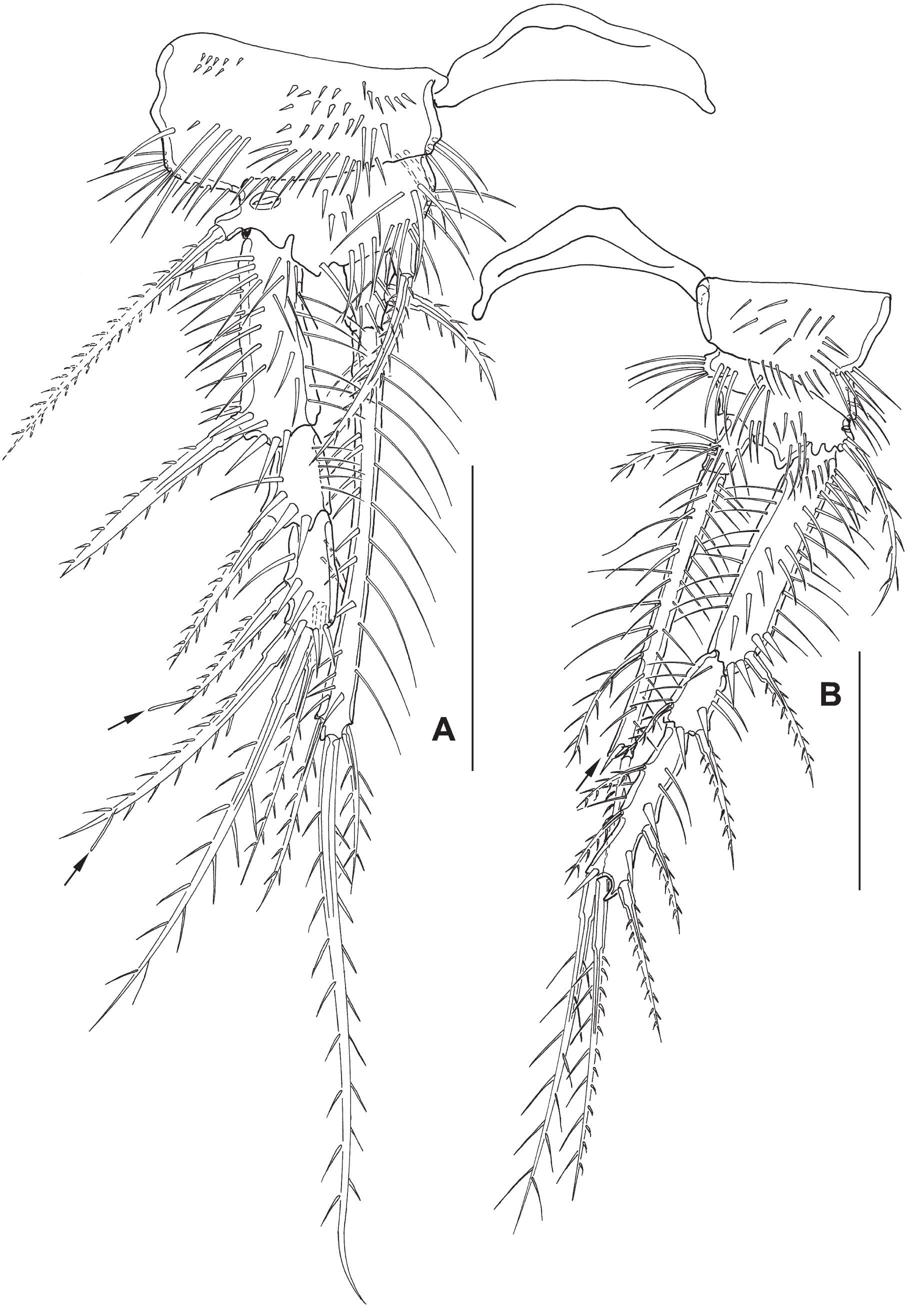

Figure 6. *Mesocletodes elmari* sp. n., adult female, holotype. **A** P1, tube pores indicated by arrows **B** P2. Scale bars: 50 µm

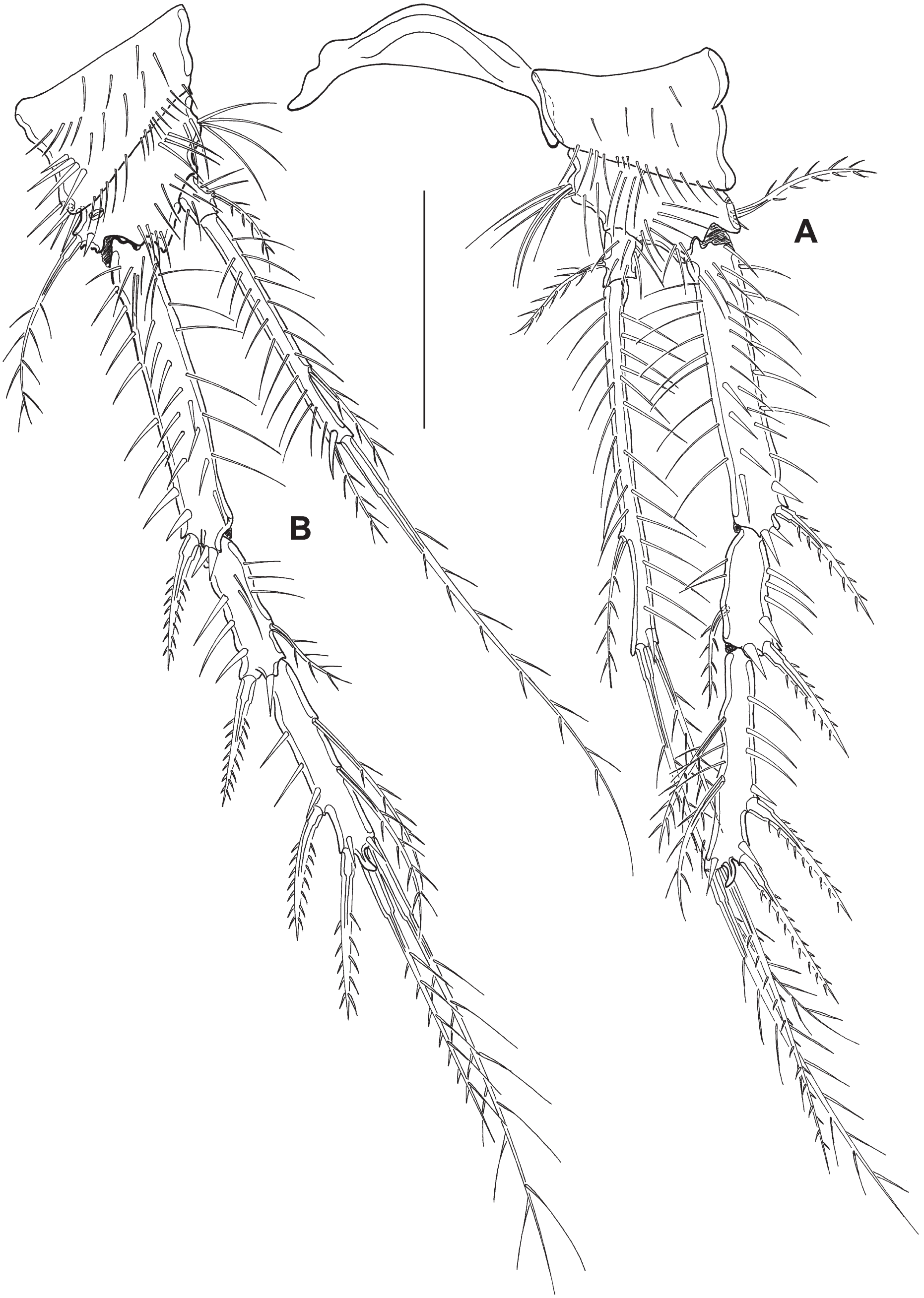

Figure 7. *Mesocletodes elmari* sp. n., adult female, holotype. **A** P3 **B** P4. Scale bar: 50 µm

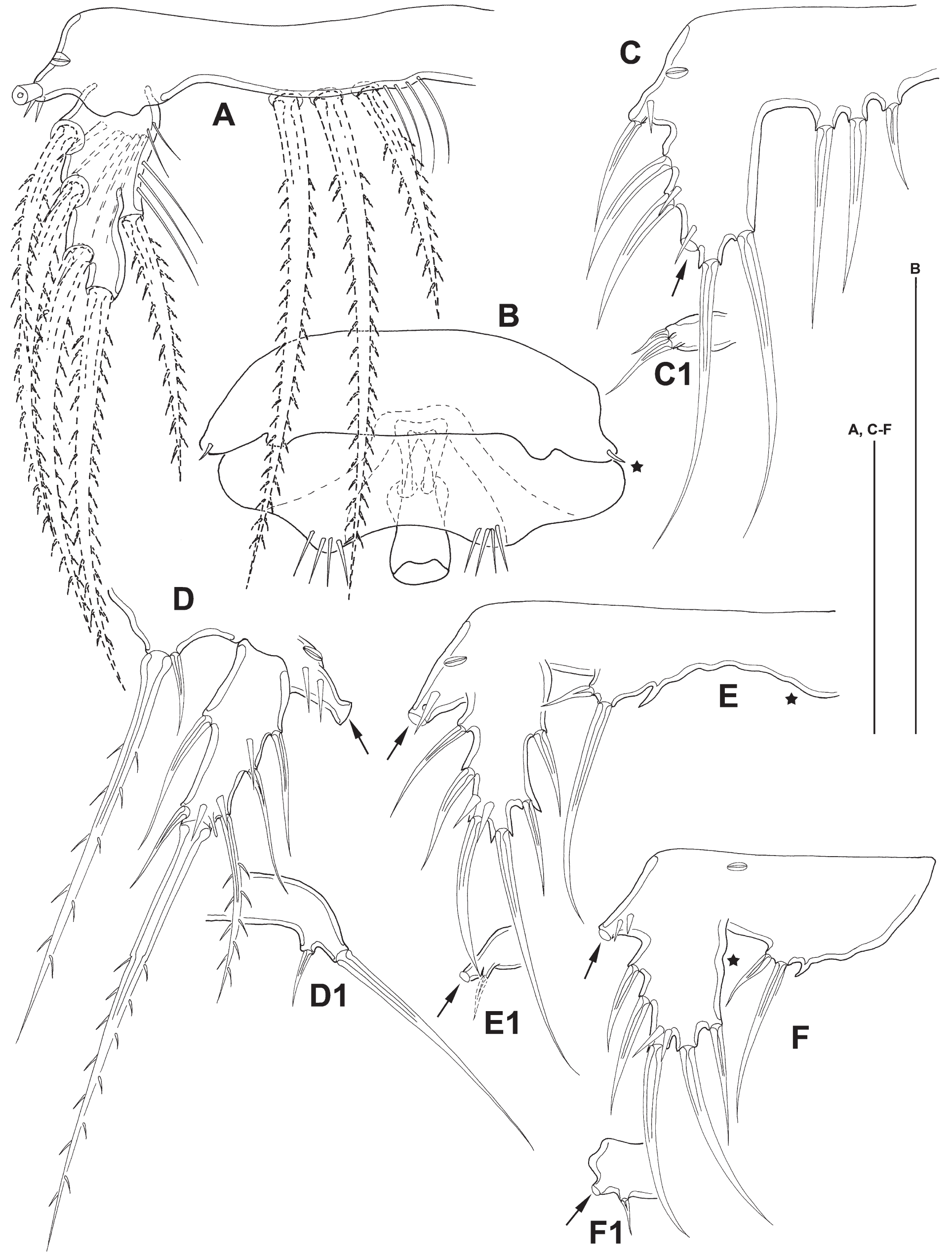

Figure 8. *Mesocletodes elmari* sp. n. **A** adult female holotype, P5, dorsal view **B** adult female holotype, GF, P6 indicated by asterisk **C** CV female paratype 3, P5 ventral view **C1** CV female paratype 3, P6 ventral view **D** adult male paratype 1, P5 ventral view **D1** adult male paratype 1, P6 ventral view **E** CV male paratype 4, P5 ventral view, asterisk on the right side of the endopodal lobe indicates where a cuticular protrusion analogous to the one on the left side can be expected **E1** CV male paratype 4, P6 ventral view **F** CIV male paratype 5, P5 ventral view, asterisk marks the inner depression on P5 exp **F1** CIV male paratype 5, P6 ventral view. Missing setae indicated by arrows. Scale bars: 50 µm.

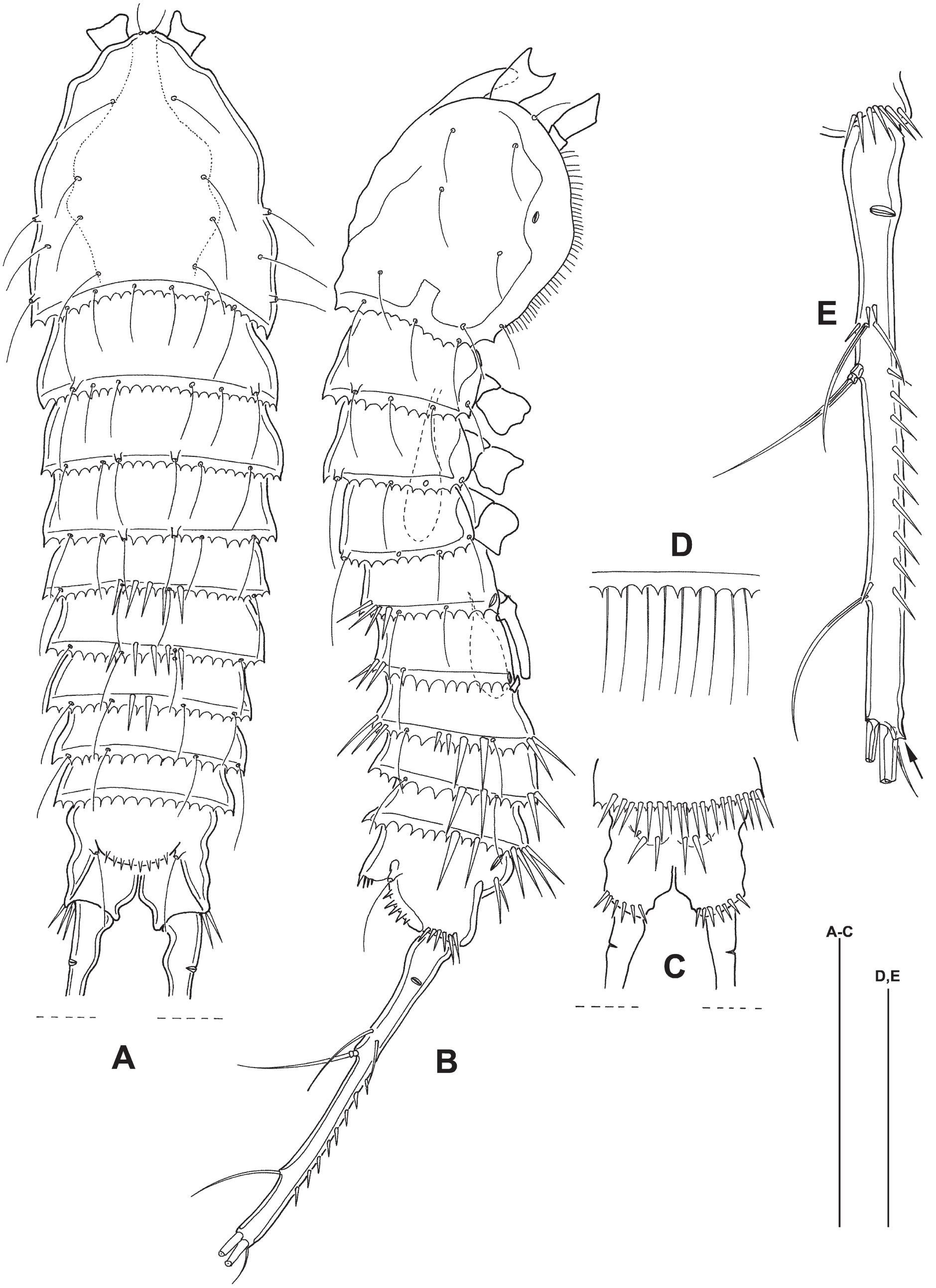

Figure 9. *Mesocletodes elmari* sp. n., adult male paratype 1. **A** habitus dorsal view **B** habitus lateral view **C** telson ventral view **D** detail of hyaline frill **E** FR, lateral view, arrow indicates terminal tube pore. Scale bars: **A–C** 100 µm, **D+E** 50 µm.

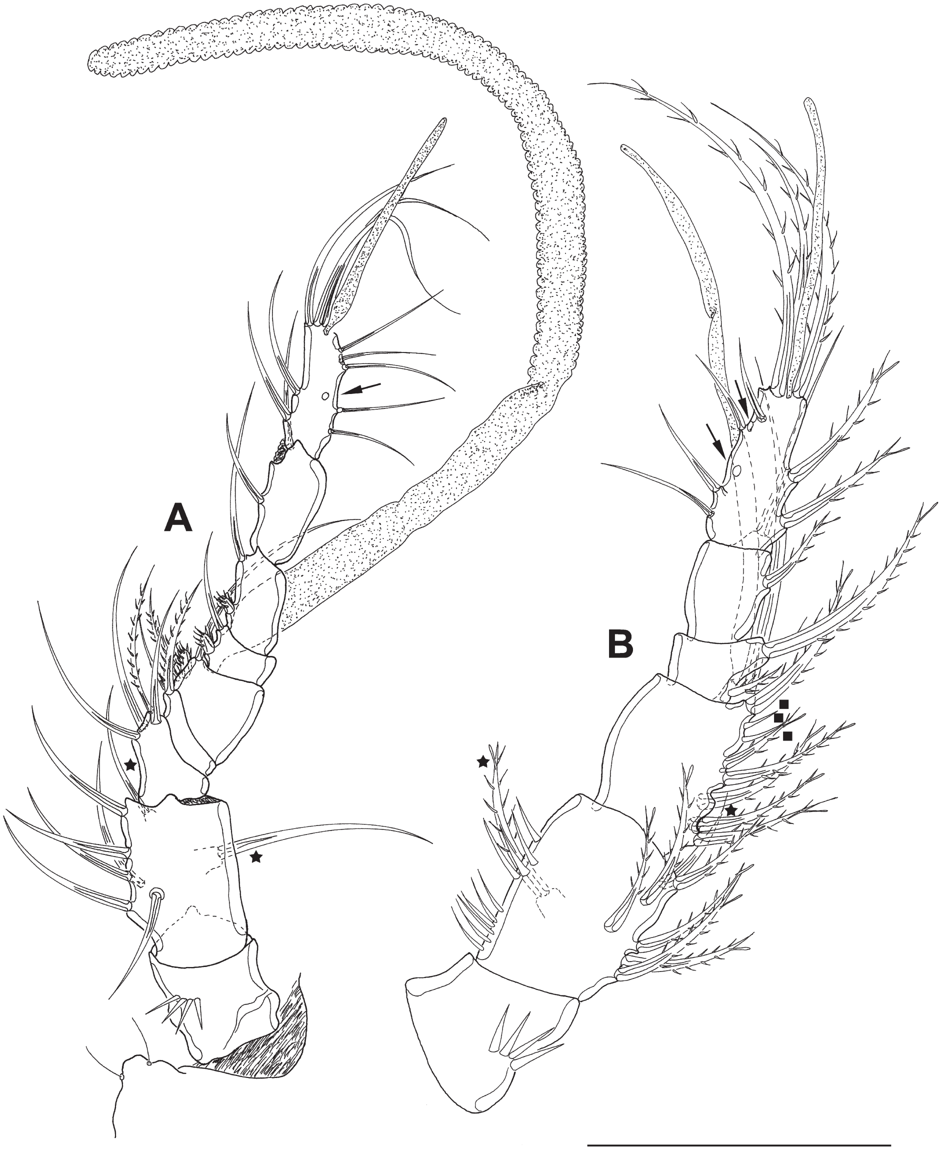

Figure 10. *Mesocletodes elmari* sp. n. **A** adult male paratype 1, A1 dorsal view **B** CV male paratype 4, A1 dorsal view, minute setae on third segment highlighted by solid squares. Asterisks mark the 2 setae occurring in CV. Missing setae indicated by arrows. Scale bar: 50 µm.

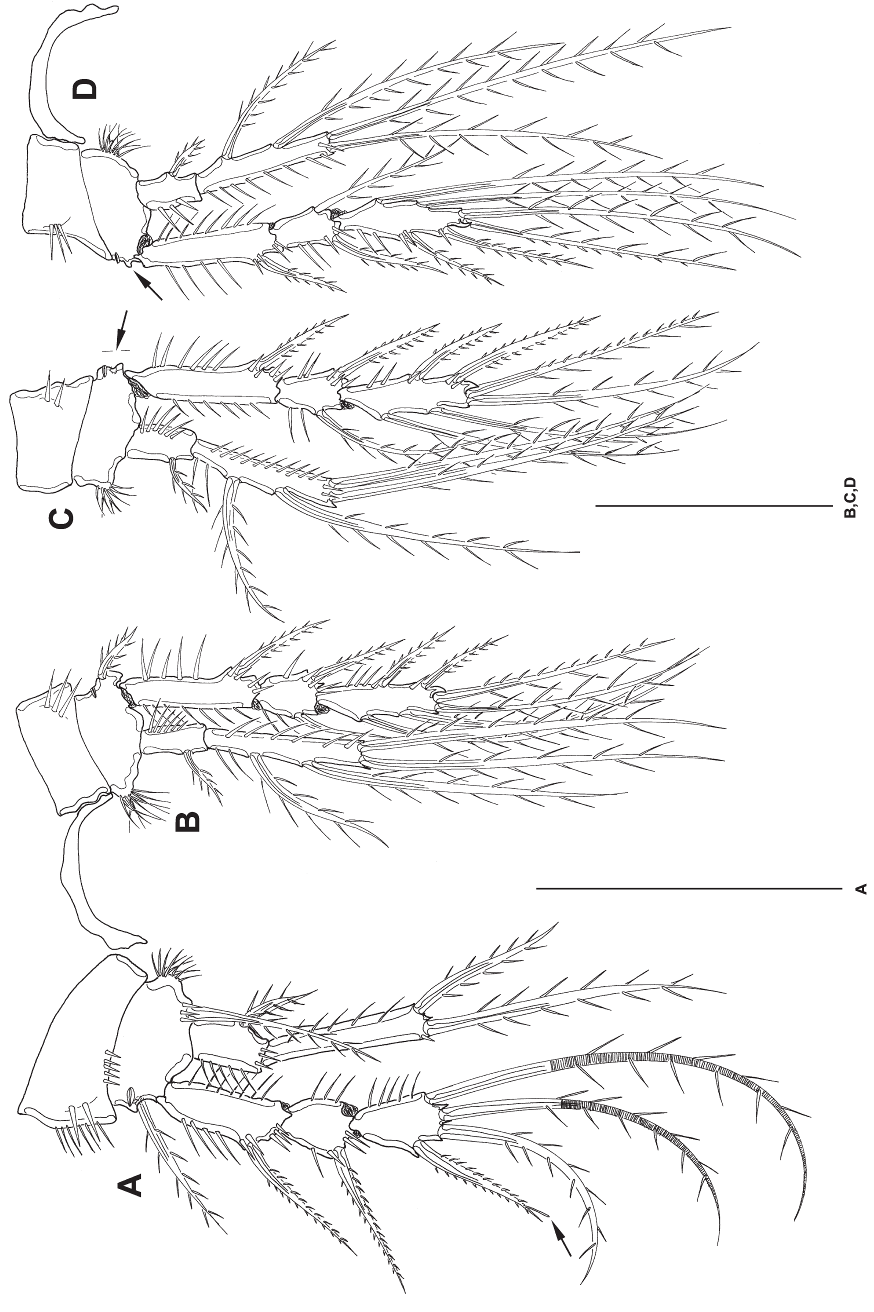

Figure 11. *Mesocletodes elmari* sp. n., adult male paratype 1. **A** P1 **B** P2 **C** P3 **D** P4. Missing setae indicated by arrows. Scale bars: 50 µm.

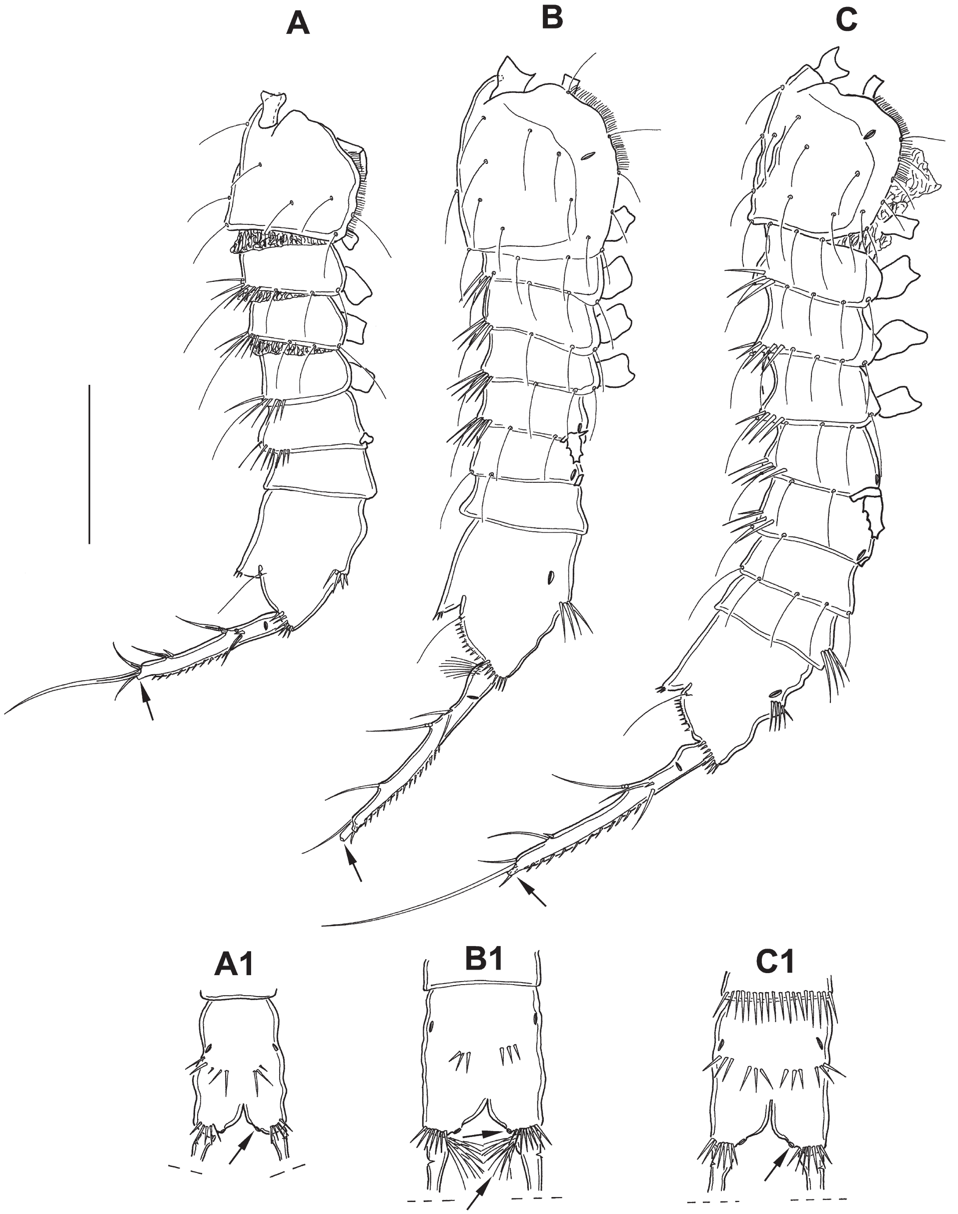

Figure 12. *Mesocletodes elmari* sp. n. **A** CIII paratype 6, habitus lateral view, terminal TP on FR indicated by arrow **A1** CIII paratype 6, telson ventral view, internal notch-like pores indicated by arrow **B** CIV male paratype 5, habitus lateral view, terminal TP on FR indicated by arrow **B1** CIV male paratype 5, telson ventral view, internal notch-like pores and setular tuft on FR indicated by arrows **C** CV female paratype 3, habitus lateral view, terminal TP on FR indicated by arrow **C1** CV female paratype 3, telson ventral view, internal notch-like pores indicated by arrow. Scale bar: 100 µm.

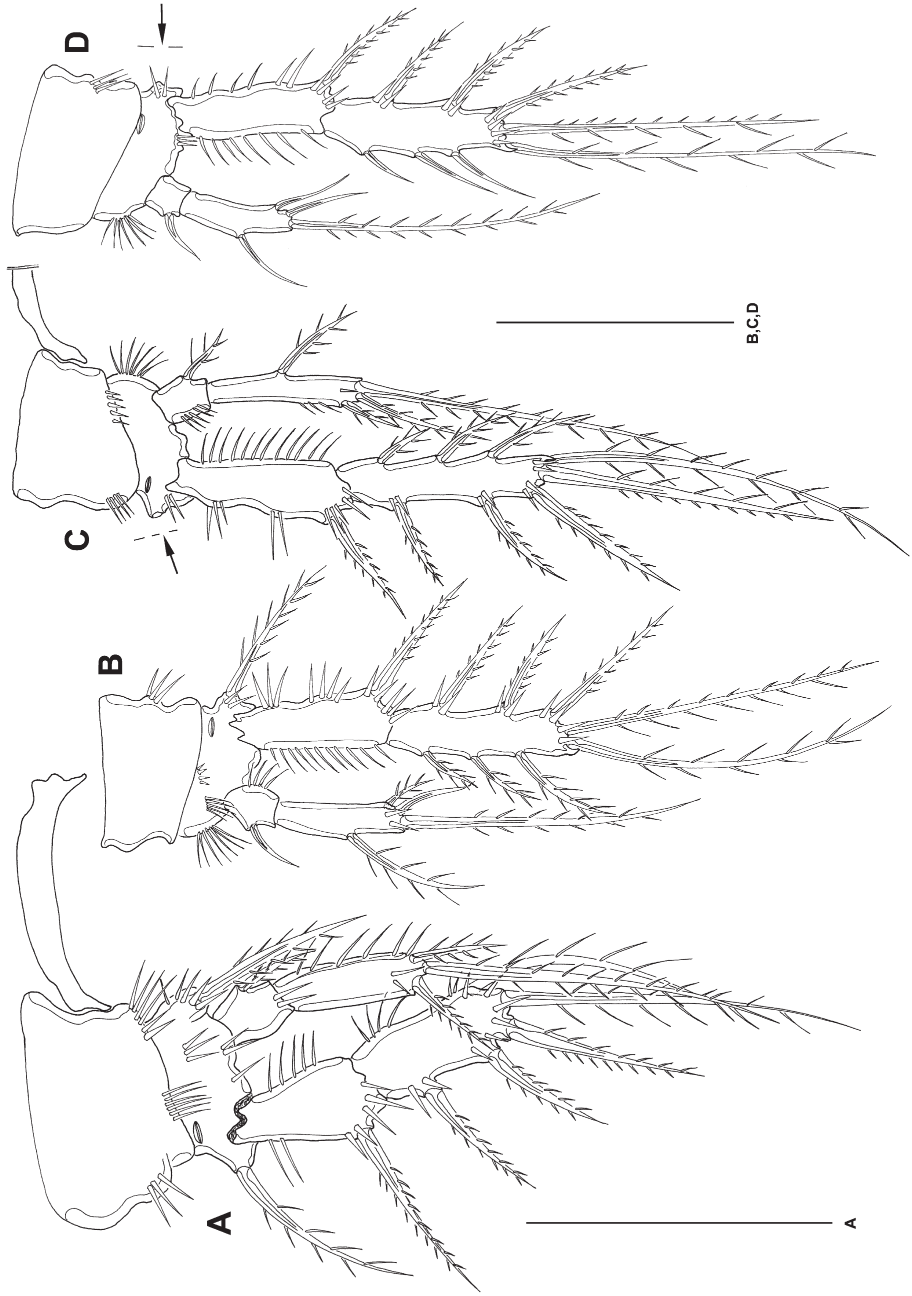

Figure 13. *Mesocletodes elmari* sp. n., CIV male paratype 5. **A** P1 **B** P2 **C** P3 **D** P4. Missing setae indicated by arrows. Scale bars: 50 µm.

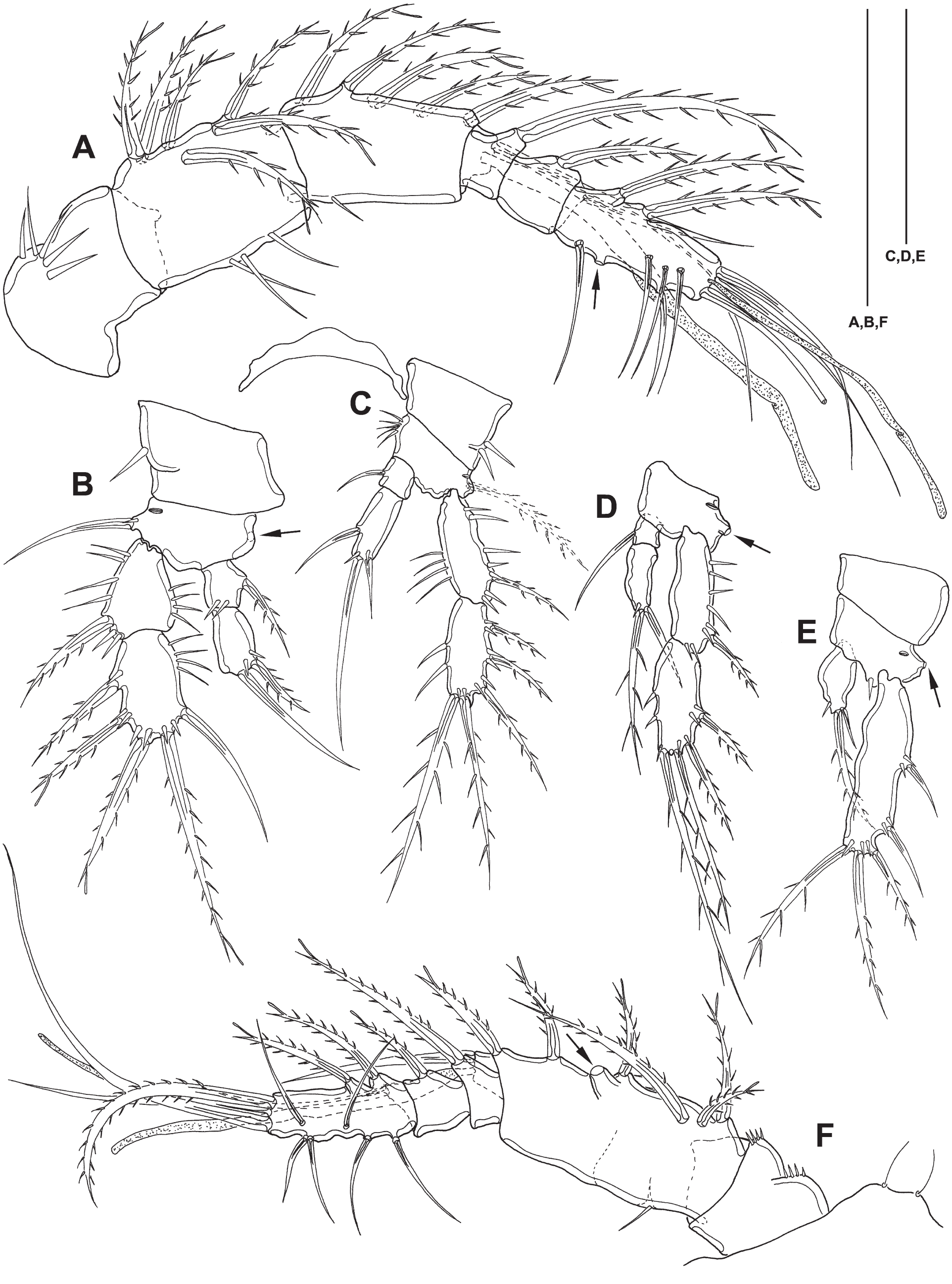

Figure 14. *Mesocletodes elmari* sp. n. **A** CIV male paratype 5, A1 dorsal view **B** CIII paratype 6, P1 **C** CIII paratype 6, P2, outer basal seta supplemented according to counterpart **D** CIII paratype 6, P3 **E** CIII paratype 6, P4 **F** CIII paratype 6, A1. Missing setae indicated by arrows. Scale bars: 50 μm.

all adult males and copepodid stages possess a non-ornate hyaline frill. A very rare feature (in two adult females, all CIV males) is also the presence of outer setae in P2–P4 enp2 or just in P2 enp2 (one adult female). The number of eggs (2–20) is variable, too.

Discussion

Allocation of *Mesocletodes elmari* sp. n. to *Mesocletodes* and its position within this genus

Allocation of *M. elmari* sp. n. to the taxon *Mesocletodes* is indisputable since all specimens show the apomorphies recognized by Menzel and George (2009): 1) second A1 segment with a strong protrusion bearing 1 strong, bipinnate seta, 2) proximal outer spine of P1 exp3 reduced, 3) spines of P1 exp3 equipped with STE and 4) blades of md gnathobase forming a strong, grinding tooth.

The phylogenetic relationships within *Mesocletodes* are still under discussion. However, a first approach is possible: *M. elmari* sp. n. is considered to belong to the "*Mesocletodes inermis* group" as it lacks the characteristic cuticular processes on cephalothorax and telson that are regarded to be autapomorphic to the *M. abyssicola*-group (Menzel and George 2009). The extreme elongation of the FR is assumed to be convergent in the new species and the *M. abyssicola*-group because several recently observed, but as yet undescribed species of *Mesocletodes* without cuticular processes on cephalothorax and telson also show elongated FR (personal observation). Future investigations, however, will have to prove the phylogenetic relevance of the elongated FR for the *M. abyssicola*-group.

M. elmari sp. n. shows a distinct mxl exopodal segment, and the enp is incorporated into the basis. By contrast, a distinct endopodal segment is described for the mxl of *M. bodini* (Soyer 1964; Soyer 1975) and *M. irrasus* (T. and A. Scott 1894), whereas the exp is considered to be absent. According to Huys and Boxshall (1991) and Seifried (2003), however, the distinct segments of *M. elmari* sp. n., *M. bodini* and *M. irrasus* are homologous to the exp of other Harpacticoida. The description for *M. irrasus* and *M. bodini* is therefore erroneous because they show an articulated exp instead of an articulated enp.

Justification of *Mesocletodes elmari* sp. n. as a new species

From a morphological point of view *M. elmari* sp. n. is similar to *M. bodini* and *M. parabodini* as these three are the only species of *Mesocletodes* with elongated P1–P4 enp2. *M. elmari* sp. n., however, shows clear autapomorphies [plesiomorphic states in brackets] that justify it as a new species:

1) mx seta that is fused to the basis, bears a conspicuously strong spinule-like pinna [seta without spinule-like pinna]
2) P2–P4 exp3 proximal outer seta lost [seta present]
3) P1–P4 enp2 extremely elongated [not elongated]
4) FR strongly elongated between setae III and VII [not elongated]
5) female body of a prickly appearance created by setules that are widened at their bases [no prickly appearance]
6) female P2–P4 enp2 proximal inner seta lost [seta present]

Character 1): The mx seta that is fused to the basis carries a conspicuously strong spinule-like pinna in *M. elmari* sp. n. The corresponding seta in other species of *Mesocletodes* is usually bipinnate with the pinnae of equal size. The loss of all pinnae except one at the anterior side plus the modification of this pinna towards a spinule-like appearance is not recorded for any other species of *Mesocletodes* or Argestidae and is therefore regarded here as derived. This modification thus is considered to be autapomorphic to *M. elmari* sp. n.

Character 2): *M. elmari* sp. n. lacks the proximal outer seta on P2–P4 exp3. The reduction of outer pereiopodal ornamentation is considered to be derived according to the rule of oligomerization (Huys and Boxshall, 1991), but various harpacticoid taxa, including species of Mesocletodes lack this seta convergently. The loss of the proximal outer seta on P2–P4 exp3 is thus considered to be species-specific and therefore autapomorphic to *M. elmari* sp. n.

Character 3): Endopodal segments of species of *Mesocletodes* are very short and there are never more than two of them in this genus, many species even have only one single segment. The extreme elongations in P1–P4 enp2 are unique for *M. elmari* sp. n. and are considered to be the result of lengthening of the distal endopodal segment. Ontogenetic stages of males do not show a suture that might indicate a fusion of the distal segment with the preceding. Extreme elongations of P1–P4 enp2 are therefore considered here to be autapomorphic to *M. elmari* sp. n. A less extreme elongation of these segments, however, occurs also in *M. bodini* and *M. parabodini*.

Character 4): The FR of *Mesocletodes* are longer than wide, with setae IV, V and VI located terminally, whereas setae I, II, III and VII are located closer to or in the proximal part of the ramus. An extreme elongation between setae III and VII has been discussed as an apomorphy for the *Mesocletodes abyssicola*-group (Menzel and George, 2009). However, lacking cuticular processes on cephalotorax and/or telson, *M. elmari* sp. n. does not show the other two apomorphies of the *Mesocletodes abyssicola*-group. The extreme elongation of FR thus is considered here to occur convergently in *M. elmari* sp. n. and species belonging to the *M. abyssicola*-group.

Character 5): Females of *M. elmari* sp. n. are characterized by the prickly appearance of the body somites dorsally and laterally. Such coverage is absent in other species of *Mesocletodes* and is therefore regarded here as derived, i.e. an autapomorphic character for *M. elmari* sp. n.

Character 6): Endopodal segments do not seem to be fused in *M. elmari* sp. n. (see character 3). The proximal inner seta on P2–P4 enp2 in males is considered to be reduced in females. The lack of the proximal inner seta on P2–P4 enp2 is therefore considered here to be autapomorphic to females of *M. elmari* sp. n.

Intraspecific variability in *Mesocletodes elmari* sp. n.

Intraspecific variability in deep-sea harpacticoids has recently been revealed to be extremely high. For instance, George (2008), Seifried and Martínez Arbizu (2008) as well as Gheerardyn and Veit-Köhler (2009) were able to show that neither setation nor segmentation, nor total length of appendages has to be a reliable character for species discrimination in deep-sea Harpacticoida. Variability in Argestidae has only been recorded for the pereiopodal chaetotaxy of *Argestes angolaensis* George, 2008 (George 2008 and personal observations), and for the shape and number of ventral spinules on the telson in the argestid genus *Eurycletodes* Sars, 1909b (Menzel in press).

For *Mesocletodes* intraspecific variability has not yet explicitly been recorded. However, five species were redescribed at least once, indicating that detected specimens deviate minimally from the type specimen: *M. abyssicola* (T. and A. Scott 1901; Sars 1921; Lang 1936), *M. bathybia* (Por 1964b; Soyer 1964), *M. irrasus* (Scott 1893; T. and A. Scott 1894; Lang 1936; Sars 1909; Soyer 1964) *M. monensis* (Thompson 1893; Sars 1921; Lang 1936; Por 1964b;) and *M. robustus* (Por 1965; Menzel and George 2009).

Although clear apomorphies were recognized for *M. elmari* sp. n., careful morphological examination of the 77 specimens revealed high intraspecific variability (cf. Table 1). The total length of FR, the number and the shape of spinules in various parts of the body, the ornamentation of the hyaline frill and the setation of P2–P4 enp2 is variable. Moreover, few specimens bear setular tufts in various positions on the FR. Setular tufts on the FR near seta VII have only been recorded for *M. bodini* (Soyer 1975) and *M. parabodini* (Schriever 1983), but corresponding structures near the basis seem to be unique in *M. elmari* sp. n. Although setular tufts on the FR seem to be species-specific for *M. bodini* and *M. parabodini*, the importance of those cuticular structures for species discrimination or even for unraveling phylogenetic relationships remains unclear.

Sexual dimorphism in *Mesocletodes*

Many morphological characters of species belonging to *Mesocletodes* are entirely different in both genders. Nevertheless, the identification keys for *Mesocletodes* are exclusively based on the morphology of females (e.g. Wells 2007), possibly due to the fact that merely two males have been described to date. With the aid of these keys, it is nearly impossible to connect a male of *Mesocletodes* to the corresponding female. Consequently the number of species in any deep-sea sample is overestimated, which means faunistic and ecological analyses at the species level are subject to a strong bias. As follows, it appears urgent to quantify the sexually dimorphic modifications in *Mesocletodes*.

Sexual dimorphism in adults. The descriptions of *Mesocletodes* contain only females, with the exception of four species: exclusively the male is described for *M. angolaensis* and *M. fladensis* (the latter description is poorly detailed). Both genders are described for *M. faroerensis* and *M. thielei*. However, these two species bear a proximal outer spine in P1 exp3 and 3 inner setae on P3 exp3. Moreover, *M. faroerensis* bears an inner seta on P1 exp2 and 3 inner setae on P3 exp3, and the md gnathobase of *M. thielei* does not form a strong grinding face. Consequently, both species lack autapomorphies of *Mesocletodes* (cf. Menzel and George 2009). Even though the descriptions are poorly detailed and the type material of both species is not available any more, the characters in question are not to be misinterpreted. Thus, *M. faroerensis* and *M. thielei* have to be excluded from *Mesocletodes*. Future investigations will have to unveil their generic attribution within Argestidae. Consequently, *M. elmari* sp. n. is the only known species with matching males and females and therefore convenient for investigations on sexually dimorphic modifications in *Mesocletodes*.

Sexually dimorphic modifications in males of basal Argestidae, such as *Argestes* (George 2008), and *Bodinia* George, 2004 (George 2004) include the A1, P5, P6, and the body size, whereas males of *Mesocletodes* show many more affected characters. The modifications in *M. elmari* sp. n. males are comparable to the ones observed in *M. angolaensis* and numerous undescribed males from deep-sea samples (personal observation) and are therefore considered to be a good representation of male sexual dimorphism in *Mesocletodes*. 1) The body tapers distally and the setation especially in P1–P4 is very rich and strongly developed in comparison to females. These morphological characters are likely adaptations that help males to stay in the bottom currents once resuspended (cf. characteristics of "typical emergers" [Thistle and Sedlacek 2004; Thistle et al. 2007]) and thus would allow them to explore the sediments for mates. 2) The gut of adult males of *Mesocletodes* is generally empty (personal observation), but the body is filled with several spermatophores instead of food as is reported for several Harpacticoida (cf. Menzel and George 2009; Shimanaga et al. 2009; Wells 1965; Willen 2005). Since the gut of CIV males and CV males of *M. elmari* sp. n. is well filled with sediment or detritus, feeding seems to be abandoned at the last molt. It has not been investigated yet whether the gut and digestive tissue are present in adult males. However, the abandonment of feeding and the production of extremely large and numerous spermatophores might be an adaptation to the sparsely populated and oligotrophic deep-sea environments and is therefore considered to represent a derived character state. 3) Mouthparts are either absent, strongly reduced or complete, but apparently not utilized for feeding. Along with the complete reduction of mouthparts, the cephalothorax of *M. angolaensis* is slightly depressed in the lateral view and lacks the part that encloses the mouthparts in females. Although the mouthparts of the male of *M. elmari* sp. n. do not differ from the female, the ventral edge of the male cephalothorax is less rounded than in the female, but less reduced than in *M. angolaensis*.

However, not only the empty gut or the reduction of mouthparts indicates the abandonment of feeding in adult males, but also the A1: most setae on the A1 of the adult male of *M. elmari* sp. n. are smooth, merely some in the grasping region of the A1 (segments 3–6) are bipinnate (Fig. 10 A). However, all setae that are smooth in the adult male are strongly pinnate in the two preceding copepodid stages (Figs. 10 B, 14 A). Thus, the loss of pinnae is regarded as another sexually dimorphic modification in adult males since the regression or poorer development of setal elements is typical of non-feeding male copepods (Boxshall and Huys 1998).

Females are generally considered to show the whole character set of a species while the modifications in males are considered to be due to sexual dimorphism (but see George 1998; George 2006a for Ancorabolidae). It is likely, however, that adult females, too, show characters that are connected to the gender because the CV females of *M. elmari* sp. n. do not show characters that are typical of adult females: prickly appearance of the body created by setules that are widened at their bases, coxa of P1 externally widened and basal inner seta arising from a prominent protrusion, strongly bent outwards and overlying the enp, P1 enp exceeding exp in length, all extremities bearing conspicuously numerous and strong spinules, and hyaline frill of body somites ornate.

Sexual dimorphisms in juveniles. Sexually dimorphic modifications expressed in copepodid stages of *M. elmari* sp. n. allow sexing during ontogenetic stages, at least from CV onwards; it is only partially resolved for this species if sexing of CIV is possible because all discovered CIV seem to be of the same gender. A similar constraint applies to the single individual of CIII. This copepodid stage, however, is assumed not to show sexual dimorphism (e.g. Dahms 1990) and is therefore not discussed here.

Sexing of CV. The male CV and the female CV of *M. elmari* sp. n. are distinguishable from the adults by virtue of the overall smaller body size, the lack of the penultimate urosomite and the non-articulated P5 exp. Moreover, the female CV lacks the GF, the male CV lacks the spermatophores and shows strong differences from the adult male in the A1 (Fig. 15 B, C): only six out of nine A1 segments are articulated and several setae are lacking. The position and number of developed setae in these segments, however, resemble the adult male A1 more than the adult female A1 (compare Figs 4 A, 10 A, B, 15 A–C).

Sexing of CIV. Careful examination of the A1 and the P5 suggests sexing of the discovered CIV as males.

The five inner setae on the third segment of the CIV A1 (Figs 14 A, 15 D) are almost evenly distributed as is the case in the CV male (Figs 10 B, 15 C). The CV female A1 (cf. Fig. 4 A) has the aes on the fourth segment, while it is on the third in the CV male (Figs 10 B, 15 C). As follows, if the CIV were females, a separation of the aes-bearing segment from the third segment should happen at the next molt. This does not seem plausible, however, because four setae on female segment 3 (Figs 4 A, 15 A) are close to each other in the middle of the segment, the fifth seta inserts distally. An elongation proximally and distally of the evenly distributed four setae in CIV segment 3, plus shortening of the distances between these setae, is not likely. However, an addition of three inner setae at the molt from CIV (Figs 14 A, 15 D) to CV (Figs 10 B, 15 C) in the distal part of this segment (see solid squares in Figs 10 B, 15 C) and maintenance of the distances between the five setae addressed above appear likely. The A1 of the CIV is therefore considered herein to show male characteristics.

The P5 endopodal lobe of the four CIV (Fig. 8 F) has one short, outer seta, one long medial seta and one inner cuticular protrusion, and is therefore in accordance with the CV male (Fig. 8 E). The setation of P5 exp, however, resembles the CV female. Nevertheless, the small depression on the proximal inner edge of the exp (see asterisk in Fig. 8 F) might indicate the emergence of a seta at the next molt, which is only present in males. It is unclear, however, whether harpacticoid CIV show sexually dimorphic modifications in P5 exp. It seems that the CIV of *M. elmari* sp. n. do, whereas the opposite is reported for the CIV of an undescribed species of *Orthopsyllus* Brady and Robertson, 1873 (Huys 1990).

P2–P4 enp2 of the discovered CIV bear one inner seta, which is in accordance with female adults and CV. The male adult and CV bear two inner setae in these segments, with the distal seta being homologous to the single seta in the adult female. However, previous studies suggest that endopodal setation is not complete in harpacticoid CIV (Dahms 1990; Dahms 1993; Huys 1990). Thus, the addition of the proximal inner seta at the molt to CV is considered to be likely.

Ontogenetic development of *Mesocletodes elmari* sp. n.

Although copepodid stages amount to between 30% and more than 50% of the total deep-sea harpacticoid assemblage, they are excluded from faunistic analyses because confident specific allocation is not possible for many families. For investigations on phylogeny, however, juveniles may be the key to plausible theories (e.g. Ferrari 1988; Fiers 1998; Huys and Boxshall 1991).

Many species descriptions contain short remarks on *Mesocletodes* relationships with other genera and species within the genus. Phylogenetic investigations have been subject to one study to date (Menzel and George 2009), whereas ontogenetic studies on *Mesocletodes* are pending. However, not all copepodid stages of *M. elmari* sp. n. are available, and a comparison with juvenile stages of other species of *Mesocletodes* is impossible due to the lack of knowledge. The ontogeny of *M. elmari* sp. n. is therefore presented here in a rather descriptive way, but with the purpose to serve as a background for future studies.

A2, mouthparts and FR of Harpacticoida are complete with respect to segmentation and setation from CI onwards (cf. Dahms 1990; Dahms 1992; Dahms 1993). A1 and pereiopods, by contrast, develop gradually by every molt, which is also the case for the habitus: at each molt from CI to adult, one body somite is added anterior to the telson. CV thus shows seven free trunk segments, CIV shows six, and CIII shows five free trunk segments between cephalotorax and telson. Reproductive organs (GF in females and spermatophores in males) are developed at the molt to adult.

A1. The female A1 of *M. elmari* sp. n. is complete at least at CV, whereas the male A1, which is available from CIV onwards, undergoes extensive modifications at each molt. Segments 3 to 5 of the adult male are part of the third compound segment in CIV males, three setae (marked by solid squares in Figs 10 B, 15 C) are added to this compound segment at the molt to CV. The strongest modifications appear at the molt to adult: the third compound segment is simultaneously separated into segments 3, 4 and 5. Segment 6 of the adult male is distinct at least from CIV onwards, but the proximal seta is added at the molt to CV. Segment 7, directly preceding the geniculation, is not present prior to the molt to adult male.

The characteristic *Mesocletodes* seta (strong, bipinnate, arising from a conspicuous protrusion, see Menzel and George 2009) and a subterminal seta occur at CV in males (compare setae marked by asterisks in Figs 4 A, 10 A, B, 15 A–C). This is likely the case for females, too, as the second A1 segment does not show sexually dimorphic modification regarding the number and position of setae.

Although sexing of the single discovered CIII was impossible, its A1 provides valuable ontogenetic information for *M. elmari* sp. n. with respect to the first and the last two A1 segments. These segments, moreover, are not sexually dimorphically modified in CIV or later stages.

Segment 1 lacks a seta at least from CIII onwards (Figs 4 A, 10 A, B, 14 A, F). The presence of a seta on this segment in CI and CII, but the loss at the molt to CIII is discussed to be the case for some harpacticoid species (cf. Boxshall and Huys 1998; Dahms, 1989). This, however, could not be followed for *M. elmari* sp. n due to the lack of earlier stages than CIII. A similar constraint applies to the development of the last two segments, which are complete at least at CIII (see schematics in Fig. 15), but should also be since CI, as it would be the case in many harpacticoids (cf. Dahms 1989 and references therein).

P1–P5. Copepodid development of CI to CV implies extensive changes in P2–P5 with respect to segmentation and setation at each molt. P1 exopodal setation, however, is complete from CI, endopodal setation from CII (Dahms 1993). Changes from the last copepodid stage to adults are restricted to the increase in size (e.g. Dahms 1993; Ferrari 1988). Although earlier stages than CIII have not been found, the investigations on *M. elmari* sp. n. are considered to provide an adequate insight into postnaupliar development of P2–P4 in *Mesocletodes* since the progress of the P4 in CIII is comparable to the P2 in CI (Dahms 1993).

Outer elements on the pereiopods of *M. elmari* sp. n. occur earlier during ontogeny than inner setae, exps and enps are affected likewise (see P2–P4 of CIII and CIV, Figs 13 B–D, 14 C–E) (cf. Dahms 1993; Ferrari 1988; George 2001). The development of setae in *M. elmari* sp. n. is complete at the latest in CIII for P1 (however, it should already be complete in CI, see above), or in CIV for P2–P4 respectively. The separation of the second and third exopodal segments of P1–P4, however, occurs at

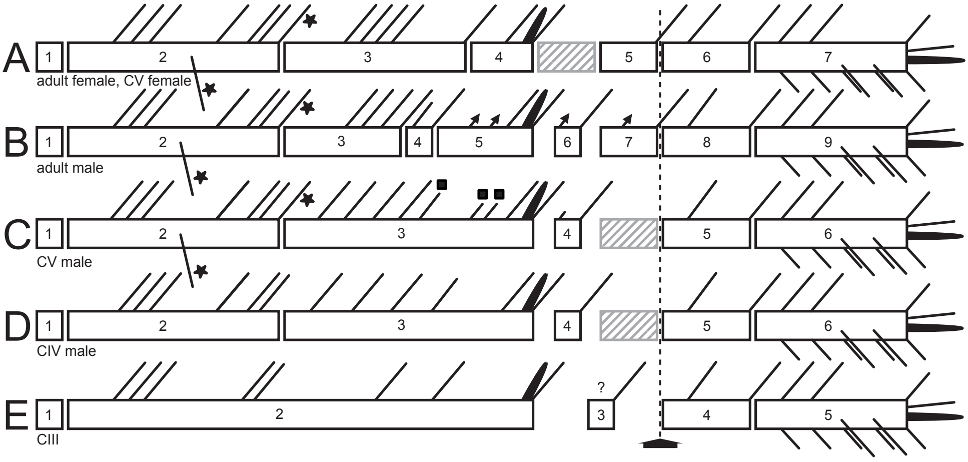

Figure 15. Schematic showing the A1 segmentation and setation of both genders and different copepodid stages of *M. elmari* sp. n. **A** adult female and CV female **B** adult male **C** CV male **D** CIV male **E** CIII. Crosshatched segments are considered to be missing or not formed. Solid triangles: sexually dimorphically modified setae, solid squares=setae added at the molt to CV male, solid asterisks=characteristic *Mesocletodes* seta and the subterminal seta in segment 2 in CV and adults. Arrow marks geniculation.

the molt to CV. P1–P3 endopodal segmentation is complete at the latest in CIII of *M. elmari* sp. n., whereas P4 still shows a 1-segmented enp at this stage.

In CIV males the P5 endopodal lobe corresponds to the one in CV and adult, whereas the P5 exp lacks the proximal inner seta (Fig. 8 D, E, F) (see section *Sexual dimorphisms in juveniles*).

On the basis of adult specimens, Menzel and George (2009) recognized four apomorphies for *Mesocletodes* (see above). The above addressed ontogenetic development of *M. elmari* sp. n. shows that none of them is characteristic of adults only, but rather appear already during juvenile development.

The characteristic *Mesocletodes* seta on the second A1 segment is developed from CV onwards of both genders. This segment does not show sexually dimorphic modification, except that the setae of females are bipinnate, whereas males bear bare setae. All investigated stages of *M. elmari* sp. n. lack the proximal outer spine on P1 exp3. According to Ferrari (1988), this is caused by suppression and further indicates pedomorphosis for this character, i.e. the maintenance of juvenile characters in adults. Considering the harpacticoid pattern of leg development (Dahms 1993; Ferrari 1988), the distal part of the single P1 segment in CI or the second segment in CII–CIV is homologous to the third segment in CV and adult. These parts are fully equipped with all elements characteristic of the third segment. STEs arising from spines on P1 exp3 are only traced from CIII on for *M. elmari* sp. n. However, it seems likely that these extensions exist from CI as the setae they are associated with do so. The same applies to the strong grinding tooth at the md gnathobase. This is developed at least at CIII of *M. elmari* sp. n., but according to Dahms (1990), for example, this should be the case from CI onwards.

Brief remarks on the geographic distribution of *Mesocletodes elmari* sp. n.

Various taxa of benthic harpacticoid copepods show distribution ranges at the species level that extend over thousands of kilometers across Atlantic, Southern Ocean and Pacific abyssal plains: Ancorabolidae Sars, 1909a (George 2006b; Gheerardyn and George 2010), Argestidae (Menzel and George 2009; Menzel in press), Canthocamptidae Sars, 1906 (Mahatma 2009), Ectinosomatidae Sars, 1903 (Seifried and Martínez Arbizu 2008), Paramesochridae Lang, 1944 (Gheerardyn and Veit-Köhler 2009; Plum and George 2009).

In the case of *Mesocletodes*, as well, the sampling localities known up to now suggest an extremely wide distribution of this genus: the North Atlantic (Scandinavian coast [Lang 1948; Pesta, 1927; Por 1964a; Por 1965; Sars 1909; Sars 1921], Irish, English and Scottish coasts [T. Scott, 1900; T. Scott, 1906; Thompson 1893; Wells 1965], Porcupine Abyssal Plain [Gheerardyn 2007; Gheerardyn et al. 2010], Spitzbergen coast [Lang 1936], Arctic Ocean [T. and A. Scott 1901; Smirnov 1946], Icelandic coast and Iceland Faroe Ridge [Schriever 1983; Schriever 1985], Greenlandic coast [Jespersen, 1939], off North Carolina [Coull 1973] Nova Scotia Rise [Thistle and Eckman 1990], French Atlantic coast [Bodin 1968], Iberian Basin [Becker et al. 1979], Great Meteor Bank [George and Schminke 2002]), the Mediterranean Sea (Guidi-Guilvard et al. 2009; Por 1964b; Soyer 1964; Soyer 1975), the Red Sea (Por 1967), the Pacific Ocean (Peru Trench [Becker et al. 1979], off Hawaii [Mahatma 2009], off the Californian coast [Thistle et al. 2007], off the Japanese coast [Shimanaga et al. 2004]), the Indian Ocean (Por 1986a), the South Atlantic Ocean (Southwest Atlantic [George 2005], the Southeast Atlantic [Menzel and George 2009]). However, the distribution of *Mesocletodes* at the species level has been addressed briefly (Menzel and George, 2009), and is subject to ongoing studies.

The record of *M. elmari* sp. n. in the North Atlantic Ocean and South Atlantic Ocean, the Southern Ocean, the Pacific Ocean and the South Indian Ocean extends the knowledge on the distribution of *Mesocletodes* and points a worldwide distribution at the species level. Future studies will have to deal with the means of dispersal as well as ecological and biological needs of species belonging to *Mesocletodes* to help explain the distributional patterns.

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