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# **Comparative morphology of the Candoninae antennula, with remarks on the ancestral state in ostracods and a proposed new terminology**

(Crustacea, Ostracoda)

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The antennula in Ostracoda is usually considered uniramous. However, because of the clear presence of an exopod in Darwinulidae, it is supposed that this ramus existed once in the ostracod ancestor, and such antennula is presented in this paper. The remnants of the exopod, as well as protopodal and endopodal segments are recognized in some ostracod orders, especially Podocopida. In addition, the antennula of the Candoninae ancestor is proposed in the present paper, with a new setal terminology which is simpler and more appropriate to identify the position of setae on segments and appendages in general. The Candoninae ancestor's antennula consists of one segmented protopod, which comprises the fused coxa and basis; two setae of the exopod; and the six-segmented endopod, with a knee connection between the first and the second segments. Description, variability and a comparative analysis of the antennula in the 26 living genera of the subfamily Candoninae are given. The articulation is confirmed to have an important generic value, with the plesiomorphic six-segmented endopod found in 13 genera. Fusion of the endopodal segments which is mostly found between the second and third, and the fourth and fifth segments, is found in ten genera. The remaining three Candoninae genera have different fusions all of which are autapomorphies. Compared with the ancestor's antennula, the living representatives have reduced setae on the posterior side of segments and on the proximal, rather than the distal, end of the appendage. The most primitive setal pattern is found in the genus *Cryptocandona* Kaufmann, 1900, while the most derived one is found in the genera *Terrestricandona* Danielopol & Betsch, 1980 and *Deminutiocandona* Karanovic, 2003. Although the setal pattern tends to be constant within a genus, considerable variation occurs, and so the setation should be treated with caution on the generic level.

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## **Introduction**

Crustacea is a very ancient arthropod group with the fossil record dating back to the early Cambrian (McKenzie 1983, Martin & Davis 2001, Maas et al. 2003). What undoubtedly indicates its monophyly is the nauplius larva bearing three pairs of functional appendages: antennula, antennae and mandible

(McKenzie 1983, Boxshall 1997). In all Crustacean groups several body appendages have changed from the primitive biramous crustacean plan (containing three segmented protopod, two rami, endites and epipodites – see Forest 1994, Cohen et al. 1998; etc.) to highly specialized appendages. In recent crustaceans different appendages serve different functions (sensory, feeding, locomotion, copulation), show a

marked reduction in unnecessary parts, while the functional parts are strongly developed. Therefore, it is sometimes difficult to recognize the various components of a primitive crustacean limb part.

The antennula has retained a clearly recognizable biramous form in two crustacean classes, Remipedia and Malacostraca; while in four others (Branchiopoda, Maxillopoda, Cephalocarida and Ostracoda) it has undergone profound reductions (for the illustration of the antennula in different crustacean classes see Brusca & Brusca 1990). In Ostracoda the antennula has a maximum of eight articles and has sensory and locomotory functions. In the subclass Myodocopa the antennula of most species shows sexual dimorphism (see Poulsen 1962, 1965, Horne et al. 2002). Many authors, especially recent ones, consider the ostracod antennula to be uniramous, lacking any trace of protopod, endopod and exopod, and refer to all articles as podomeres (Maddocks 1982, 2000, Cohen et al. 1998, Horne et al. 2002). However, in the superfamily Cypridoidea distinction is sometimes made between protopod and endopod of the antennula (Martens 1986, 1988, 1992). While in the whole subclass Myodocopa (Fig. 1C) and most Podocopa superfamilies (including Cypridoidea) it is hard to trace any element of a biramous antennula, one podocopid family is an obvious exception. Namely, all recent Darwinulidae bear externally on the posterior end of the second segment of the antennula a distinct article (more or less fused with the second segment) which carries two or three setae (Figs 1A,B). This article clearly bears comparison with the exopod of the second antenna, and as such it is clearly illustrated repeatedly by Rossetti & Martens (1996, 1998, 1999), Martens & Rossetti (2002), and even labeled as an exopod (Rossetti & Martens 1996, 1999, Rossetti et al. 1998). Maddocks (2000) opposes the presence of an exopod in Darwinulidae, because of its posterior (ventral in Maddocks 2000) position. However, it must be pointed out that the antennulae in Ostracoda must have changed their orientation in the body, from a lateral location as found in many Crustacea, to an apical position, when this class enclosed its body between valves. In consequence, the position of the exopod would be expected to have changed.

In Müller's (1894) composite profile of the pra-ostracod, the antennula was presented as an eight-jointed sensory/locomotory organ such as found in Cyprididae (see also Maddocks 1982). Maddocks (1976) proposed a hypothetical ancestral podocopid antennula, and subsequently (Maddocks 2000) also proposed an antennula of an imaginary podocopid ostracod (with much less setae than in her previous paper), both without any trace of a biramous limb.

In the present paper, I propose an hypothetical ancestral ostracod antennula which is quite different from the "ground plan" ostracod limb proposed by Hartmann (1966) (comprising all three protopod segments, several endites and two epipodites, four segmented endopod and eight segmented exopod), however, in contrast to Maddocks (2000), with the clear presence of two rami (Fig. 3). The presence of the exopod remnants on the darwinulid antennula (Fig. 5) indicates that this ramus existed in the ostracod ancestor. Using topology as an important tool in the search for homology (Rieppel 1994), it would be possible to distinguish between protopod, endopod and exopod on the antennula in the recent Ostracoda.

To aid comparison between taxa and to facilitate the identification of homologous structures, a standard terminology was adopted (Huys & Boxshall 1991). However, in high systematic categories (like the ostracod subclasses are) it is difficult to identify all homologies, especially on a multiarticulated appendage (as antennula is) that carries large number of setae. Additionally, the setation in different ostracod orders is not conservative (unlike Copepods for example – see Huys & Boxshall 1991), what makes the identification of homologous structures even more difficult. When podocopid ostracods are considered, most appendages have their own terminology. Broodbakker & Danielopol (1982) proposed a terminology for the Cyprididae antenna, mandibula, first thoracopod and furca. They also labeled some setae on other appendages, but distinguished only "ya" seta and Rome's organ on the antennula. Martens (1987) revised the terminology for antenna, while Meisch (1996) named setae on the third thoracopod. Several setae on the antennula have been named also in Darwinulidae (see Rossetti and Martens 1998). Recently, Maddocks (2000) in "the intention to establish a comprehensive network of detailed homologies for the constituent podomeres and setae ..." labeled all the setae on the podocopid antennula with numbers from the proximal to the distal end. The most detailed model was given by Danielopol (1978a) who distinguished segments on the Candoninae antennula (from I to VII) and on each segment (except the terminal one) named anterior (a1, a2) and posterior setae (p1 and p2). However, Maddocks (2000) and Danielopol (1978a) did not recognize the remnants of an exopod on the Candoninae antennula. Based on the setal homology and the presence of the exopod on the antennula in Darwinulidae, the remnant of a biramous appendage is hypothesized in the supposed Candoninae ancestor and all 26 recent genera. Consequently, in the present paper I propose a new terminology for the

Candoninae antennula. For each genus the antennula is described along with the variability found until now. With the addition of a few setae this terminology could be used for all podocopid ostracods and it tends to be simple and to identify the position of a seta on a segment and the appendage in general.

## Material and Methods

For the observation under the light microscope, ostracods were dissected in a mixture of distilled water and glycerol (1:1) with fine entomological needles (mark 000). Dissected appendages were mounted in Faure's medium and observed on Leica DMLS microscope with C-plan achromatic objectives. All drawings have been prepared using a drawing tube attachment on the same microscope. For the Scanning Electron Microscopy (SEM), soft parts were taken from their valves and then dehydrated in graded ethanol: 70 %, 80 %, 95 % and 100 %. In each of the grades, soft parts were left for about 15 minutes. After that they were mounted on SEM stubs using double side adhesive tape ("Scotch"). All samples were sputter coated with gold and observed under the LEO FEG VPSEM microscope on the in-lens detectors, with working distance between 2 mm and 6 mm, and accelerating voltage between 2 kV and 5 kV.

## Abbreviations used in text and figures

a–anterior seta; A1–antennula; A2–antenna; AIBs–allobasis; b–anterior seta; Bs–basis; c–posterior seta; CB–coxobasis; CB1, CB2–setae on CB; Cx–coxa; d–posterior seta; En–endopod; Ex–exopod; Ex1, Ex2–exopodal setae; L–length; PCx–praecoxa; Pp–protopod; ya–aesthetasc on En6;  $\alpha$ –seta on En5.

Abbreviation for repositories: APC–author's private collection; CALM–Conservation and Land Management; RBINS–Royal Belgium Institute of Natural Sciences; NMNH–National Museum of Natural History, Washington; WAM–Western Australian Museum; ZMA–Zoological Museum Amsterdam.

## Material examined

1. *Darwinula stevensoni* (Brady & Robertson, 1870). Female, L=1.06 mm. Montenegro, village Gornje Malo Blato, Skadar Lake; collector I. Karanovic; 2.X.1994. APC.
2. *Vestalenula marmonieri* Rossetti & Martens, 1999. Female, L=0.5 mm. Australia, Western Australia, Great Sandy Desert, Mandora Soak near Eighty Mile Beach, Little Eil Eil Spring; collector S. Halse; 18. X.1999. CALM.
3. *Leptocythere pseudoproboscidea* Karanovic & Petkovski, 1999. Female, L=0.52 mm. Montenegro, Podgorica, Mareze Spring; collector I. Karanovic; 18.X.1994. APC.

4. *Paralimnocythere karamani* (Petkovski, 1960). Male, L=0.64 mm. Montenegro, Podgorica, Baloci, Matica River; collector I. Karanovic, 28.II.1994. APC.
5. *Acondona admiratio* Karanovic, 2003. Male, holotype, L=0.673 mm. Australia, Western Australia, Margaret River, Easter Cave, Tiffanys Lake; collector S. M. Eberhard; 12.III.2002. WAM C29395.
6. *Alatocandona gajewskajae* (Bronstein, 1947). Male, L=0.793 mm. USSR, Lake Baikal, Southern Basin, Bol'shie Koty; unknown collector and date. RBINS Oc1594.
7. *Baicalocandona ceratina* (Mazepova, 1982). Male, L=0.879 mm. USSR, Lake Baikal, Northern Basin, Tompuda; unknown collector and date. RBINS Oc 1601.
8. *Candona neglecta* Sars, 1889. Female, L=1.2 mm. Montenegro, Skadar Lake Valley, Village Beri (near town of Podgorica), Sitnica River; collector I. Karanovic; 24.V.1997. APC.
9. *Candonopsis tenuis* (Brady, 1886). Female, L=0.922 mm. Australia, Western Australia, Perth Basin, Eneabba; collector S. M. Eberhard; 5.VI.1998. WAM C28271.
10. *Danielocandona lieshoutae* Broodbakker, 1983. Male, allotype, L=0.39 mm. Venezuela, Edo. Guárcia, round open well of Nancy de Venega. unknown collector; 10.III.1982. ZMA Ost. 150. 792.
11. *Deminutiocandona mica* Karanovic, 2003. Male, holotype, L=0.319 mm. Australia, Western Australia, Pilbara Region, Weeli Wolli Spring; collector S. M. Eberhard; 16.XI.1998. WAM C28420.
12. *Eucandona intermedia* (Furtos, 1933). Male, paratype, L=1.9 mm. USA, Ohio, Newark, Cold Spring Run, collector N. C. Furtos; 25.V.1932. SM coll. no. 67873.
13. *Eucandona holzkampfi* (Hartwig, 1900). Female, L=1.08 mm. Australia, Western Australia, Perth Basin, Marbling Brook; collector S. Schmidt; 12.XII.2001. WAM C28449.
14. *Humphreyscandona adorea* Karanovic & Marmonier, 2003. Female, L=0.802 mm. Australia, Western Australia, Pilbara Region, Millstream Aquifer, Palm Springs; collectors W. F. Humphreys and S. M. Eberhard; 20.VII.1997. WAM C28219.
15. *Meischcandona boitani* Karanovic, 2001. Female, paratype, L=0.296 mm. Mali, Sangha River; collector L. Boitani; 9.XII.1973. APC.
16. *Meridiescandona lucerna* Karanovic, 2003. Male, holotype, L=0.596 mm. Australia, Western Australia, Pilbara Region, Fortescue River Valley, Roy Hill Station, Battle Hill Well, collectors W. F. Humphreys and J. M. Waldock; 8.IX.2000. WAM C28412.
17. *Notacandona Boultoni* Karanovic & Marmonier, 2003. Male, holotype, L=0.7 mm. Australia, Western Australia, Pilbara Region, Weeli Wolli Spring, collector S. M. Eberhard; 16.XI.1998. WAM C28266.
18. *Pilbaracandona eberhardi* Karanovic & Marmonier, 2003. Male, holotype, L=0.527 mm. Australia, Western Australia, Newman Borefield Area, bore Ex 895; collector S. M. Eberhard; 20.XI.1998. WAM C28240.
19. *Pseudocandona marchica* (Hartwig, 1899). Male, L=1 mm. Montenegro, Niksic, Krupac Reservoir; collector I. Karanovic; 12.VI.1997. APC.

20. *Pseudocandona* sp. Female, L=0.721 mm; Australia, Western Australia, Perth Basin, Marbling Brook, collector S. Schmidt; 19.XII.2000. WAM C28450.
21. *Trapezicandona coineauae* (Rogulj & Danielopol, 1993). Female, L=0.72 mm. Greece, Epirus, Arta, freshwater well, collector G. L. Pesce; 5.V.1977. APC.
22. *Myodocopa*, Halocypridina, Halocyprididae. Male. Italy, Salerno, Punta Licosa, Tyrrhenian Sea, 1-3 m depth; collector I. Karanovic; 18.VII.1999. APC.

## Terminology and Classification

The ostracod A1 is generally considered to be uniramous (see Introduction) and the terminology for the biramous one, proposed in the present paper, follows the model which is in standard use in other Crustacean groups (see Forest 1994, Huys & Boxshall 1991) and in Ostracoda for those appendages that are considered to be biramous (see Martens 1998). The setal terminology adopted in the present paper is original, except for two setae: ya and  $\alpha$ . The former is after Broodbakker & Danielopol (1983), while the latter one is after Danielopol (1978).

The recent Candoninae genera in "Results" are listed in alphabetical order. The setal pattern described for a genus is based on one species (not necessarily the type species). If any deviation from this pattern is noticed in the genus, either from the published papers or based on the personal observation, it is reported in the remarks that follow description.

## Results

### 1. Ancestral Candoninae A1

Fig. 4

**Description of A1.** Pp consists of fused Cx and Bs – forming CB. Anteriorly CB carries two setae: proximal CB1, distal CB2. Ex reduced and consisting of two long setae – Ex1 and Ex2. En six segmented. En1 with only one seta – En1a. En2 with two anterior setae (En2a, En2b), and two posterior ones (En2c, En2d). En3 also with two anterior (En3a, En3b) and two posterior setae (En3c, En3d). En 4 same with En4a, En4b, En4c and En4d. En5 with  $\alpha$ -seta and all four distal setae (En5a, En5b, En5c, En5d). Terminal segment with aesthetasc ya, and setae En6b, En6c, and En6d.

### 2. *Acandona* Karanovic, 2003

Fig. 11

**Description of A1.** Cx and Bs fused in CB, and with CB1 and CB2 setae present. Ex reduced to two setae Ex1 and Ex2. En six segmented. En1 only with En1a; En2 bare; En3 with En3a, En3b and En3c. En4 with En4a, En4b, and En4c. En5 with  $\alpha$ -seta, and En5a, En5b, En5c, En5d. En6 with ya, En6b, En6c, and En6d. Anterior setae (a and b) long on segments three to six; posterior setae (c, d) on same segments short, as is the  $\alpha$ -seta.

**Remarks.** Only two species have been described in the genus *Acandona* from the subterranean waters of Western Australia (Karanovic 2003a): *A. admiratio* Karanovic, 2003 and *A. memoria* Karanovic, 2003. The latter species lacks En5d seta (see Karanovic 2003a, Fig. 9a).

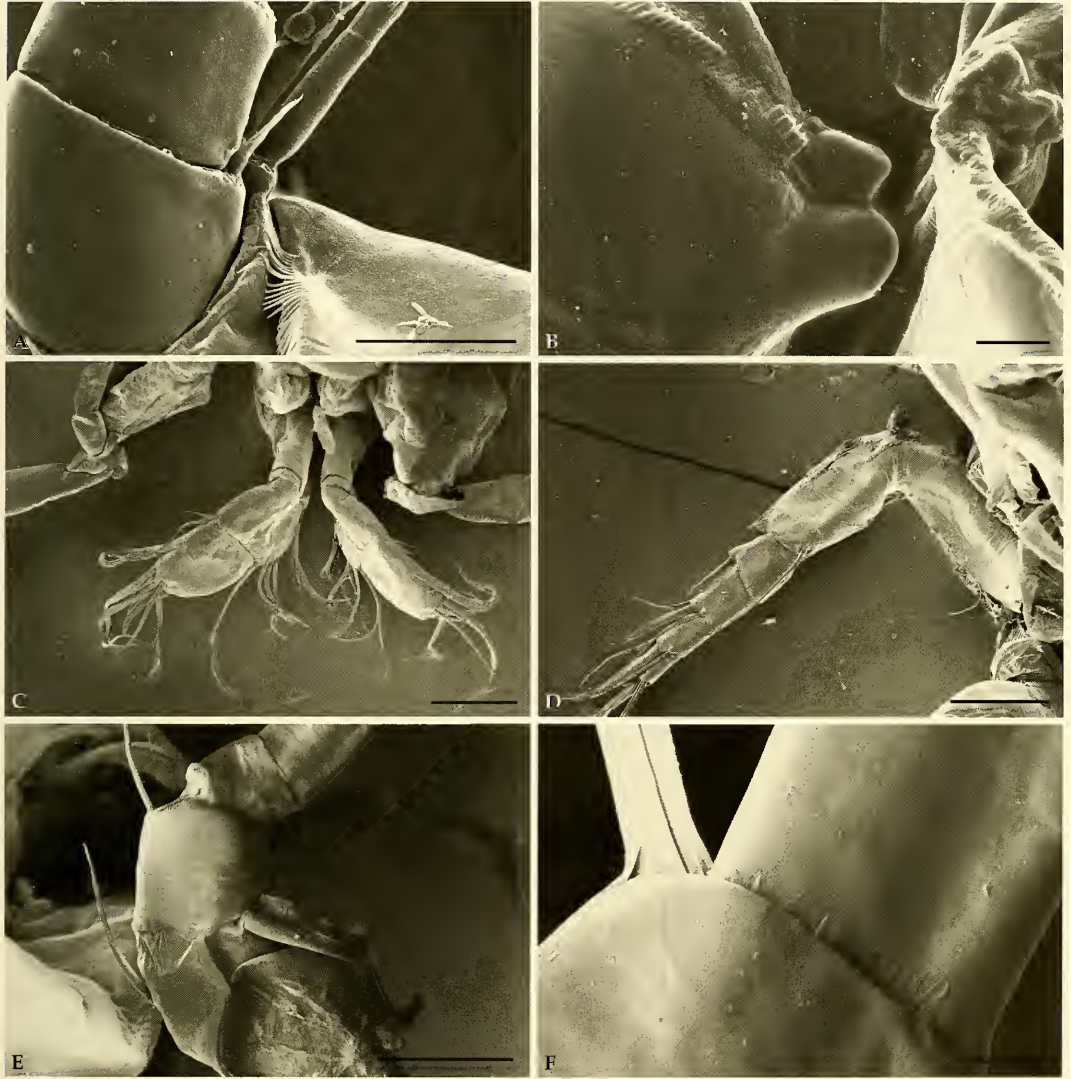
### 3. *Alatocandona* Carbonnel, 1969

Fig. 16

**Description of A1.** Cx and Bs fused, CB with both setae present. Ex reduced to long Ex1 and Ex2. En consists of four free segments. En1 with En1a; En 2, 3 and 4 fused, distally with En4a, En3d, and En 4d. En5 with short  $\alpha$ -seta, long En5a, and short En5d. En6 with ya, claw-like En6d, short En6c and long En6b.

**Remarks.** The genus *Alatocandona* was established by Carbonnel (1969) to accommodate two species: *A. gajewskajae* (Bronstein, 1947) and *A. bronsteini* Carbonnel, 1969. The latter species is a Miocene fossil. *Alatocandona gajewskajae* was originally described in the genus *Pseudocandona* Kaufmann, 1900 by Bronstein (1947), and it is one of the numerous *Pseudocandona* species described from the Baikal Lake (see Mazepova 1990). However, all *Pseudocandona* species described from Baikal differ from the rest of *Pseudocandona* by many very important features (see Mazepova 1990), and it is clear that they cannot belong into one genus. In addition the Baikal *Pseudocandona* are paraphyletic (Martens et al. 1992a,b) and many more described Baikal species could be assigned to the genus *Alatocandona*, but this is beyond the scope of the present paper.

The only specimen of *A. gajewskajae* I could examine has an asymmetry in the setal pattern of the two A1. The right A1 (Fig. 16) carries two postero-distal setae (En3d and En4d) on the fused En segments, while the left one lacks En3d. The similarity in the appearance and position of almost all setae on the En segments between closely related genera



**Fig. 1.** Scanning electron micrographs of A1. **A,B**, *Vestalenula marmonieri* Rossetti & Martens, 1999. **C**, *Myodocopida*, Halocypridina. **D**, *Leptocythere pseudoproboscidea* Karanovic and Petkovski, 1999. **E,F**, *Pseudocandona marchica* (Hartwig, 1899). **A,B**, Ex.; **C,D**, A1, general view; **E**, CB and Ex.; **F**, Detail of En4. Scales: **A**: 8.5  $\mu$ m, **B**: 2.7  $\mu$ m, **C**: 109  $\mu$ m, **D**: 77  $\mu$ m, **E**: 36  $\mu$ m, **F**: 3.6  $\mu$ m.

*Alatocandona* and *Baicalocandona* Mazepova, 1976 (Fig. 15) suggests that the seta En3d in the latter genus might be homologous with the inner postero-distal seta on fused segments in the former genus (labeled on Fig. 16 as En3d). In addition, the observed asymmetry in the appearance of A1 may indicate that the seta in question might be En3d. However, this is only a hypothesis which should be checked on more specimens and possibly be proven with the ontogenetic development.

#### 4. *Baicalocandona* Mazepova, 1976 Fig. 15

**Description of A1.** First segment represents CB with CB1 and CB2 setae. Ex reduced to Ex1 and Ex2 setae. En with five free segments. En1 with En1a; En2 and 3 fused and with En3a and En3d; En4 with En4a, En4b (claw-like), and En4d. En5 with five setae: En5a, En5b, En5c, En5d, and  $\alpha$ -seta. En5d and  $\alpha$ -seta short, while other setae on En5 long and more claw-like.

En6 with only three setae ya, En6b, and En6d (last two claw-like).

**Remarks.** The genus *Baicalocandona* was described by Mazepova (1976) to encompass all Candoninae-like species from the Baikal Lake with ornamented carapace and with the male sexual bristles on A2. The last feature, according to Mazepova (1976; 1990), distinguishes *Baicalocandona* from the Baikal species of the genus *Pseudocandona*. However, Karanovic (2001) proposed the transfer of all the Baikal *Pseudocandona* species into the genus *Baicalocandona*, because the absence of the male sexual bristles does not have a generic value. After rechecking the material of two Baikal Candoninae species (*Alatocandona gajewskajae* and *Baicalocandona ceratina*), both originally assigned to the genus *Pseudocandona*, it became clear that the morphological differences between them have a generic value. It must be pointed out that the number of species belonging to the actual genus *Baicalocandona* is unknown, and a revision of all the Baikal Candoninae is necessary. Unfortunately, incomplete descriptions and illustrations of almost all Candoninae species provided by Mazepova (1976, 1990) presently do not allow further comments on their relationships.

#### 5. *Candona* Baird, 1835

Figs 2A,B,C,F

**Description of A1.** Cx and Bs fused into CB, carrying two setae – CB1 and CB2. Ex reduced and with Ex1 and Ex2. En six segmented. En1 with En1a; En2 only with En2a; En3 and En4 each with two long anterior setae (a and b) and short posterior one (d). En5 with short  $\alpha$ -seta, long En5a and En5b and short En5c and En5d. En6 with ya, claw-like En6d and seta like En6c and En6b.

**Remarks.** The setal pattern described above is identical as in *Eucandona intermedia* shown on the Fig. 9. It is also consistent in the majority (if not all) of species of the genus *Candona*.

#### 6. *Candonopsis* Vavra, 1891

Fig. 14

**Description of A1.** Cx and Bs fused in CB, with CB1 and CB2. Ex reduced to Ex1 and Ex2 setae. En six segmented. En1 only with En1a; En2 with En2d; En3 and En4 each with two long anterior setae (a, b), and one short posterior seta (d). En5 with five distal setae:  $\alpha$ , En5a, En5b, En5c, En5d (c, d short, a, b long). En6 with ya, En6b, En6c and En6d.

**Remarks.** In the genus *Candonopsis* the number and length of individual setae vary greatly, especially in the Australian representatives (Karanovic & Marmonier 2002). The description above is of the A1 of *C. tenuis* (Brady, 1886). Segment En2 lacks any seta in the following two species: *C. williamsi* Karanovic & Marmonier, 2002, and *C. kimberleyi* Karanovic & Marmonier, 2002. Segment En3 has only setae En3a and En3d (both considerably shorter than in *C. tenuis*) in species *C. murchisoni* Karanovic & Marmonier, 2002; *C. williamsi*; *C. kimberleyi*; and *C. westaustraliensis* Karanovic & Marmonier, 2002. Segment En4 has only one long (En4a) and one short (En4d) seta in species *C. williamsi* and *C. westaustraliensis*. The former species additionally lacks  $\alpha$ -seta. It is worth noticing that *Candonopsis* species described from the Lake Tanganyika (see Rome 1962) as well as all *C. kingsleyi* (Brady & Robertson 1899) related species have much stronger and claw-like En6d. Unfortunately, many *Candonopsis* species lack the description of A1, so any additional deviation from the setal pattern described above could not be noticed.

#### 7. *Caribecandona* Broodbakker, 1983

Fig. 22

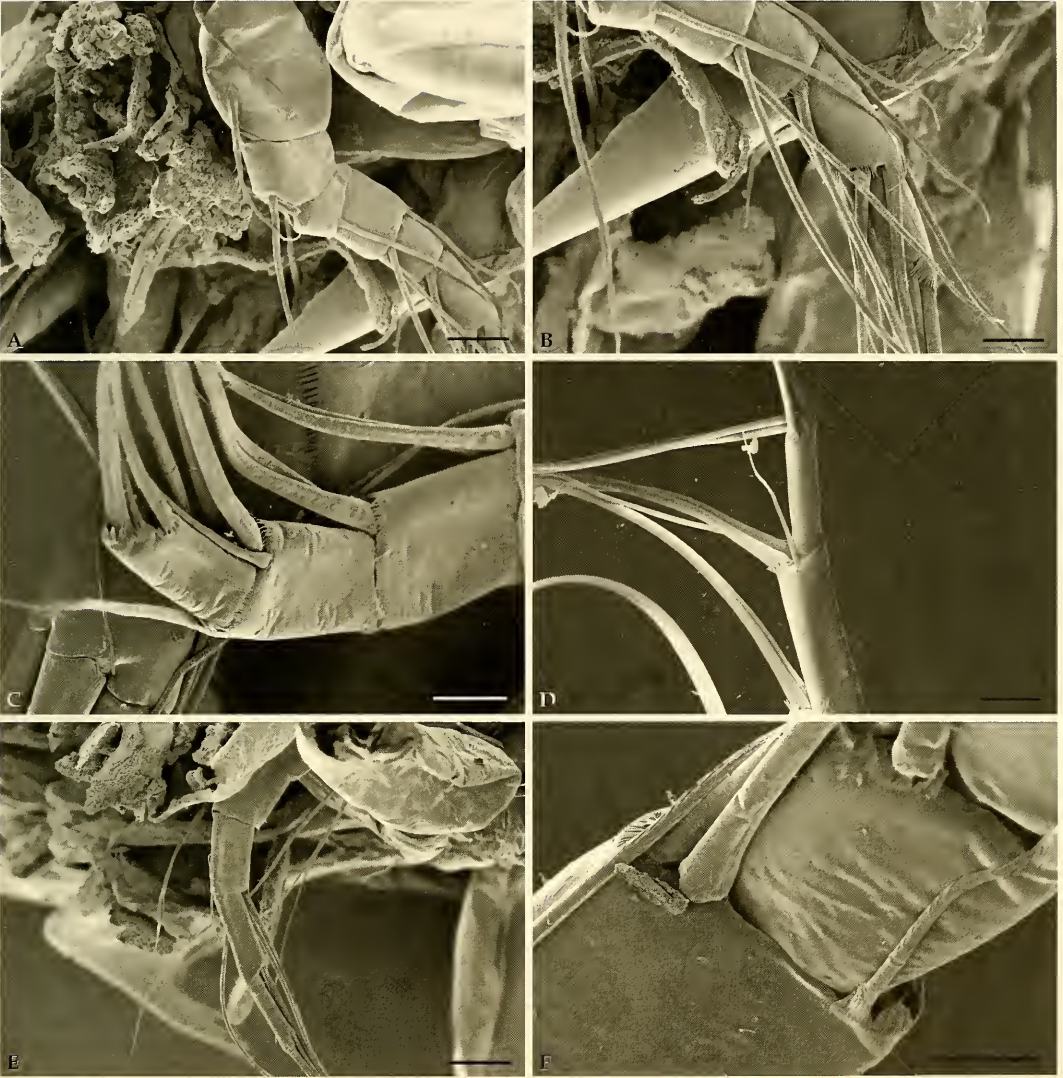
**Description of A1.** Cx and Bs fused in CB and with CB1 and CB2. Ex reduced to Ex1 and Ex2 setae. En composed of five free segments. En1 with En1a. En2 and En3 fused, distally with long En3a and En3b, and short En3d; En4 also with long anterior seta (a, b) and short posterior one (d). En5 with  $\alpha$ -seta, long En5a, En5b, and En5c, and short En5d. En6 with ya, long En6b and En6c, and short En6d.

**Remarks.** Three species are known so far, all with the same setal pattern of A1 (see Broodbakker 1983 Fig. 9b).

#### 8. *Cryptocandona* Kaufmann, 1900

**Description of A1.** Cx and Bs fused in CB with CB1 and CB2 present. Ex reduced and with Ex1 and Ex2 seta. En six segmented. En1 only with En1a; En2 with En2a and En2d (both short). En3 with long En3a and En3b, and short En3d. En4 with long anterior setae (a, b) and short posterior seta (d). En5 with  $\alpha$ -seta, long En5a, En5b, and En5c; short En5d. En6 with ya and three setae: En6b, En6c, and En6d. Only En6d short.

**Remarks.** The genus *Cryptocandona* is one of the best-defined genera in Candoninae with 12 recent species (Namiotko & Danielopol 2001). Recently,



**Fig. 2.** Scanning electron micrographs of A1. **A, B, C, F,** *Candonella neglecta* Sars, 1887. **D, E,** *Pseudocandona marchica* (Hartwig, 1899). **A, B,** Details of A1; **C,** En4, En5, and En6; **D,** En5 and En6; **E,** En3 to En6; **F,** En4. Scales: **A:** 22  $\mu\text{m}$ , **B:** 14  $\mu\text{m}$ , **C:** 17  $\mu\text{m}$ , **D:** 12  $\mu\text{m}$ , **E:** 25  $\mu\text{m}$ , **F:** 11  $\mu\text{m}$ .

several species have been redescribed in detail (Namiotko & Danielopol 2001; 2002), and the above setal pattern is based on these redescriptions. The majority of species show the same setal pattern described above, except that in some species some setae are slightly shorter or longer. Only the species *C. brehmi* (Klie, 1934) in an exception to this pattern because it has asymmetrical A1. Namely, left A1 has total of six setae on En5, while the right A1 has two postero-distal setae on En3, three antero-distal setae on the same segment, and no seta antero-distally on

En4. However, the redescription of *C. brehmi* was based on a single specimen (Namiotko & Danielopol 2002, Figs 3 and 4), and no other description of its A1 has been published, and so that this setal pattern is an abnormality cannot be excluded. However, it can be explained if we consider the L of En4 and En5. On the left A1 En4 and En5 are elongated and En4d seta has probably moved on En5, while on the right A1 En4 and En5 are considerably shorter and, probably due to compactness, En4a and En4d have moved proximally from En4 to En3. In addition, En4

has lost other long anterior seta (En4b). The "normal" setal pattern in *C. brehmi* would be according to this: En1 with En1a; En2 with En2a and En2d; En4 with En4a, En4b, En4c, and En4d; En5 with En5a, En5b, En5c, En5d,  $\alpha$ ; En6 with ya, En6b, En6c and En6d. This setal pattern is the most primitive in the subfamily Candoninae, and this support previous opinions that *Cryptocandona* represents a primitive lineage in the subfamily (Baltanás et al. 2000).

## 9. *Cubacandona* Broodbakker 1983

**Description of A1.** CB with both setae present. Ex reduced and with Ex1 and Ex2. En six segmented. En1 with En1a; En2 with En2d; En3 with long En3a and short En3d; En4 with long En4a and En4b; En5 only with long En5a and En5b plus small  $\alpha$ -seta; En6 with ya, two long setae En6b and En6c and short En6d.

**Remarks.** Broodbakker (1983) described *Cubacandona* as a subgenus of *Caribecandona*, but its elevation to generic rank was proposed by Karanovic & Marmonier (2002) partly because of the number of En segments of A1 (five in *Caribecandona*, six in *Cubacandona*). *Cubacandona* contains only the species *Cubacandona cubensis* and the setal pattern described above is based on the illustrations provided by Danielopol (1980, fig. 4a).

## 10. *Danielocandona* Broodbakker, 1983

Fig. 20

**Description of A1.** CB with only seta CB1. Ex reduced and only seta Ex1 present. En with four free segments. En1 with En1a; En2 and En3 fused and distally with En3a. En4 and En5 fused and distally with three long setae En5a, En5b, En5c. En6 with ya, long En6b and En6c and short En6d.

**Remarks.** The genus *Danielocandona* was described to accommodate *D. lieshoutae* Broodbakker, 1983 from subterranean waters of Venezuela. Martens & Behen (1994) transfer the species *Paracypris albida* Sars, 1901 into the genus *Danielocandona*. After re-checking the material of *Paracypris albida* (Zoological Museum of Oslo, collection number 11572, Mp. 498), it became clear that this species does not belong to the subfamily Candoninae, but to the subfamily Cypridopsinae. This species indeed needs a redescription, and this will be done elsewhere. Therefore,

*Danielocandona* is still a monospecific genus.

In the description of *Danielocandona* Broodbakker (1983) did not notice Ex1 in the holotype. However, the allotype male has this seta present and it has probably fallen off the holotype.

## 11. *Deminutiocandona* Karanovic, 2003

Fig. 25

**Description of A1.** CB without any seta present. Ex1 and Ex2 present. En with four free segments. En1 with En1a; En2 with En2a and En2d. En3 and En4 fused, distally with En4a and En4d (both short). En5 and En6 fused, distally with ya, long En6b and En6c and short En6d.

**Remarks.** Until now this genus has only one species *Deminutiocandona mica* Karanovic, 2003.

## 12. *Eucandona* Daday, 1900 s.l.

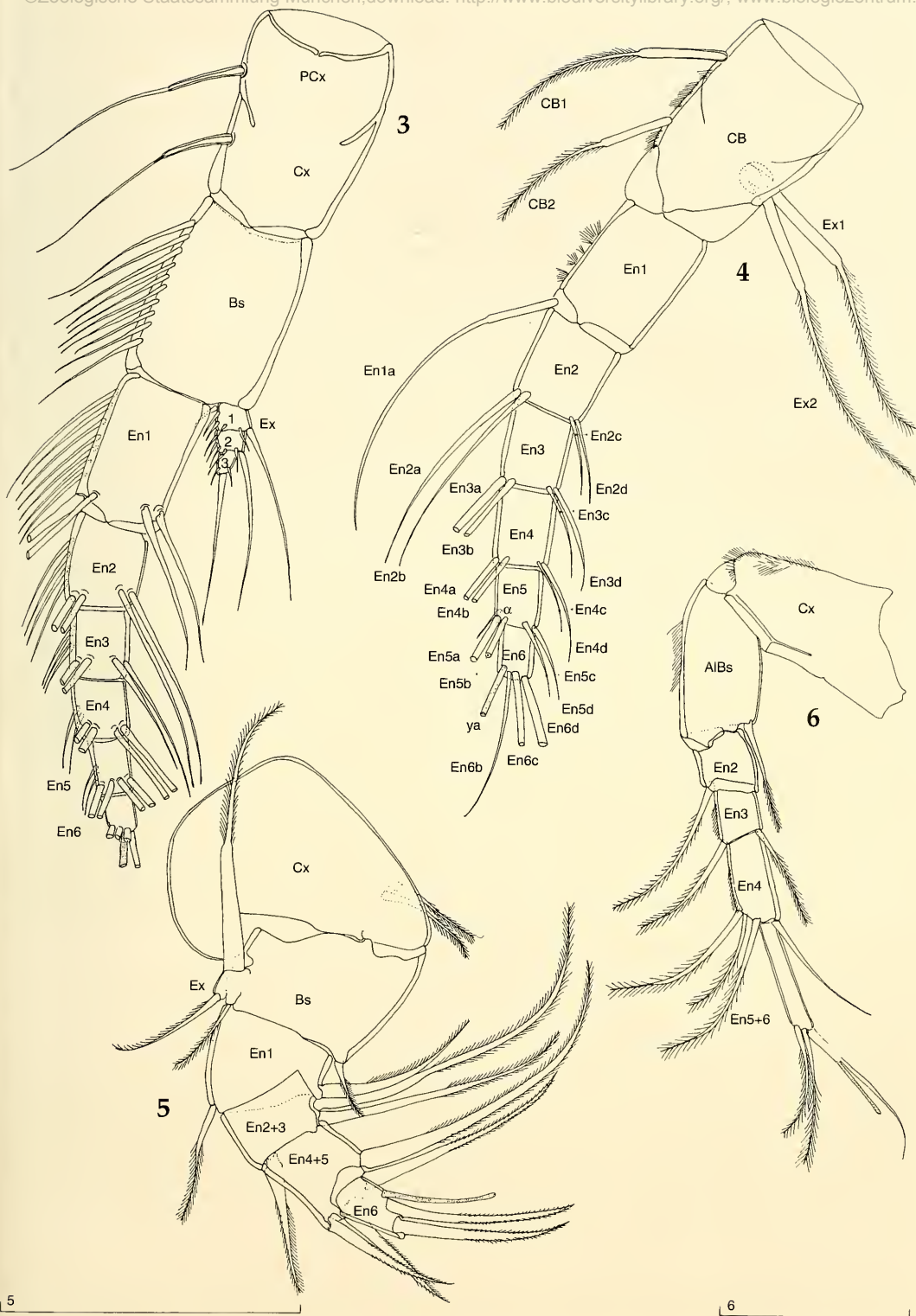
Figs 8, 9

**Description of A1.** CB with CB1 and CB2. Ex reduced and with Ex1 and Ex2 setae. En six segmented. En1 with En1a; En2 with En2a; En3 with long En3a and En3b, and short En3d; En4 also with two long anterior setae, En4a and En4b and one short posterior seta, En4d. En5 with short  $\alpha$ -seta, long En5a and En5b, and short En5c and En5d. En6 with aesthetasc ya, En6d which is claw-like and both En6b and En6c seta-like.

**Remarks.** There has been a discussion regarding the name priority between *Fabaeformiscandona* Krstic, 1972 and *Eucandona* Daday, 1900 (see Petkovski & Karanovic 2000). Although it is clear that the name *Eucandona* has priority, 50 recent species, described so far in this genus, do not represent a monophyletic taxon. Here I point out the differences in the setal pattern between all the species that today belong into the *fabaeformis*-group on one side, and those that belong to the *balatonica*- and *acuminata*-group on the other. Whereas species in the latter two groups have the most posterior seta on En5 present (Fig. 9), this seta is always missing in species of the former group of species (Fig. 8). This character, beside other morphological differences may indicate a separate generic status for the *fabaeformis*-group, in which case the generic name *Fabaeformiscandona* would be in use again.

There are several other exceptions to the two

**Figs 3-6.** Antennula. 3, Hypothetical Ostracod ancestor. 4, Hypothetical Candoninae ancestor. 5, *Darwinula stevensoni* (Brady & Robertson, 1870). 6, *Paralimnocythere karamani* (Petkovski, 1960). Scales = 0.1 mm. All originals.



setal patterns described above. However, they are all noticed only on one specimen, or only on one A1. Before drawing any conclusion, these exceptions should be checked on more specimens. For example, *Eucandona lapponica arctica* (Alm, 1914) has only En3a and En4a present on both A1. The holotype female of *E. indigena* (Hoff, 1942) has only En3a seta, while the allotype male has both antero-distal setae on En3. All these exceptions are based on my personal observations of these species and will be illustrated separately in the paper dealing with the North American Candoninae.

### 13. *Humphreyscandona* Karanovic & Marmonier, 2003

Fig. 18

**Description of A1.** CB with CB1 and CB2. Ex reduced and with both Ex1 and Ex2 present. En with four free segments. En1 with En1a; En2 and En3 fused, medially with En2a seta, distally with En3a and En3d setae; En4 and En5 fused, medially with En4a, distally with En5a, En5b, En5c and En5d,  $\alpha$ -seta missing. En6 with ya, short En6d and long En6b and En6c.

**Remarks.** The genus *Humphreyscandona* was described only recently (Karanovic & Marmonier 2003) and it has five recent species, all known from the subterranean waters of the Pilbara Region (Western Australia). All species have exactly the same setal pattern as described above. Only exception is one female of *H. adorea* Karanovic & Marmonier, 2003 which has one A1 with five free endopodal segment, i.e. En2 and En3 are completely divided.

### 14. *Indocandona* Gupta, 1984

**Description of A1.** En six segmented. En5 with five setae: En5a, En5b, En5c, En5d, and  $\alpha$ -seta. En6 with ya, En6b, En6c, and En6d.

**Remarks.** *Indocandona* is a monospecific genus, described from the subterranean waters of Bihar in India (Gupta 1984), and the above setal pattern is based on the illustrations provided by Gupta (1984, fig. 1c). The morphology of both furca and Zenker's organ leave no doubt regarding its generic status. However, some appendages (including A1) are very poorly described and illustrated. Relying on the Gupta's (1984) drawings CB is bare, Ex1 and Ex2 are

missing, and all En segments, except the last two are bare, what is very unlikely to be correct.

### 15. *Meischcandona* Karanovic, 2001

Fig. 21

**Description of A1.** CB with CB1 and CB2. Only Ex1 present. En with four free segments. En1 with En1a; En2 and En3 fused and without any seta; En4 and En5 fused, and distally with En5a, En5b and En5c. En6 with ya, short En6d and long En6b and En6c.

**Remarks.** *Meischcandona* is a monospecific genus described from two subadult females of *Meischcandona boitanii* Karanovic, 2001, collected in the river Sangha in Mali (Karanovic 2001). In this species setae on CB are positioned very close to each other, which may be because the specimens were juvenile. In addition, Karanovic (2001, fig. 7) erroneously drew Ex1 on the anterior, instead on the posterior side of A1.

### 16. *Meridiescandona* Karanovic, 2003

Fig. 17

**Description of A1.** CB with CB1 and CB2. Ex reduced and with Ex1 and Ex2 setae. En with five free segments. En1 with En1a; En2 and En3 fused and with En3a and En3d, both short; En4 with only one short seta, En4a. En5 with four setae En5d (short) and En5a, En5b, and En5c, all long ones. En6 with ya, long En6b and En6c, and short En6d.

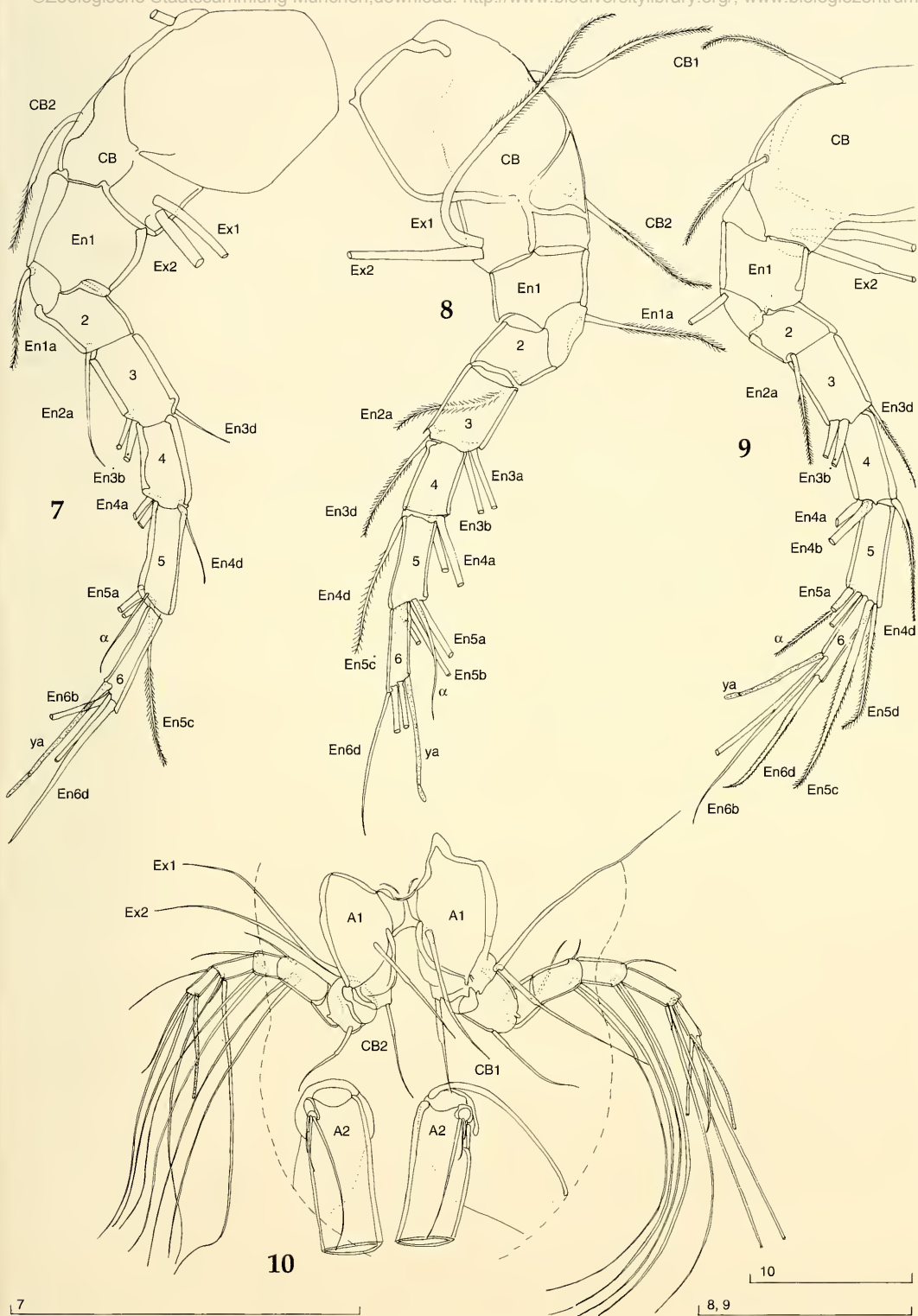
**Remarks.** The genus *Meridiescandona* has only two species (Karanovic 2003b): *M. lucerna* Karanovic, 2003 and *M. facies* Karanovic, 2003. The description above refers to the setal pattern of the former species, while the latter species lacks seta CB2 (Karanovic 2003b, fig. 31).

### 17. *Namibcypris* Martens, 1992

Fig. 24

**Description of A1.** CB with only seta CB1. Ex reduced and only with Ex1. En with four free segments. En1 bare; En2 and En3 fused, distally with long En3a; En4 and En5 also fused, distally with five setae:  $\alpha$ -seta, and long En5a, En5b, En5c and En5d. En6 with four setae: ya, long En6b and En6c and short En6d.

**Figs 7-10.** Antennula in recent Candoninae. 7, *Pseudocandona* sp. 8, *Eucandona holzkampfi* (Hartwig, 1900). 9, *Eucandona intermedia* (Furtos, 1933). 10, *Pseudocandona marchica* (Hartwig, 1899). Scales = 0.1 mm. All originals.



**Remarks.** *Namibcypripis* was described from spring waters of Namibia (Martens 1992) and until now it has only the species *N. costata*.

#### 18. *Nannocandona* Ekman, 1914

**Description of A1.** En1 fused with CB, both CB setae absent, En1a seta present. Ex reduced and only Ex1 seta present. En2 with En2a; En3 with En3a and En3d; En4 with En4a and En4b. En5 fused with En6, medially with En5a, distally with ya, En6b, En6c and claw like En6d.

**Remarks.** The genus *Nannocandona* was described with a four segmented A1 (Ekman 1914). Because of the very small dimensions of *Nannocandona faba* Eckman, 1914, the author overlooked the division between the two terminal segments, what was latter on corrected by Marmonier & Danielopol (1988). In addition, Ekman (1914) did not notice all existing setae on A1 (as well as on some other appendages). Although Sywula (1976) described a second species in the genus, *N. stygia* Sywula, 1976, from the subterranean waters of Poland, the differences between the type species and *N. stygia* fall in the range of variability of the type species, which suggests that the Polish species is a junior synonym of *N. faba*. There are some differences in the orientation of A1 between drawings provided by Sywula (1976, fig. 1b) and those provided by Marmonier & Danielopol (1988, figs 2b,c), however I would rather rely on the drawings of the latter authors, because they described A1 in details and have checked several specimens.

#### 19. *Notacandona* Karanovic & Marmonier, 2003

**Description of A1.** CB with only CB1 seta. Ex reduced, both Ex1 and Ex2 setae present. En with four free segments. En1 with En1a; En2 and En3 fused, medially with En2a, distally with En3a and En3d setae. Segments En4 and En5 fused, distally with En5a, En5b, En5c, and En5d;  $\alpha$ -seta absent. En6 with ya, long En6b and En6c, short En6d.

**Remarks.** *Notacandona* is another genus described from the subterranean waters of the Pilbara Region (Karanovic & Marmonier 2003). It has two species: *N. modesta* Karanovic & Marmonier, 2003 (which is type species) and *N. boultoni* Karanovic & Marmonier, 2003.

The setal pattern described above belongs to the former species. The A1 of the latter species (Fig. 23) differs by not having setae En1a, En2a, En3a and En3d. The first and the last two setae had probably fallen off during dissection. Unfortunately, only one adult male was collected (in addition to the two juvenile males), so it is not certain if the absence of the En2a is an intraspecific variability.

#### 20. *Paracandona* Hartwig, 1899

**Description of A1.** Unknown.

**Remarks.** *Paracandona* is a monospecific genus. The A1 of the type species, *P. euplectella* (Robertson 1889, see Meisch 2000), is unknown and I was not able to obtain material of this species.

#### 21. *Phreatocandona* Danielopol, 1978

**Description of A1.** Unknown.

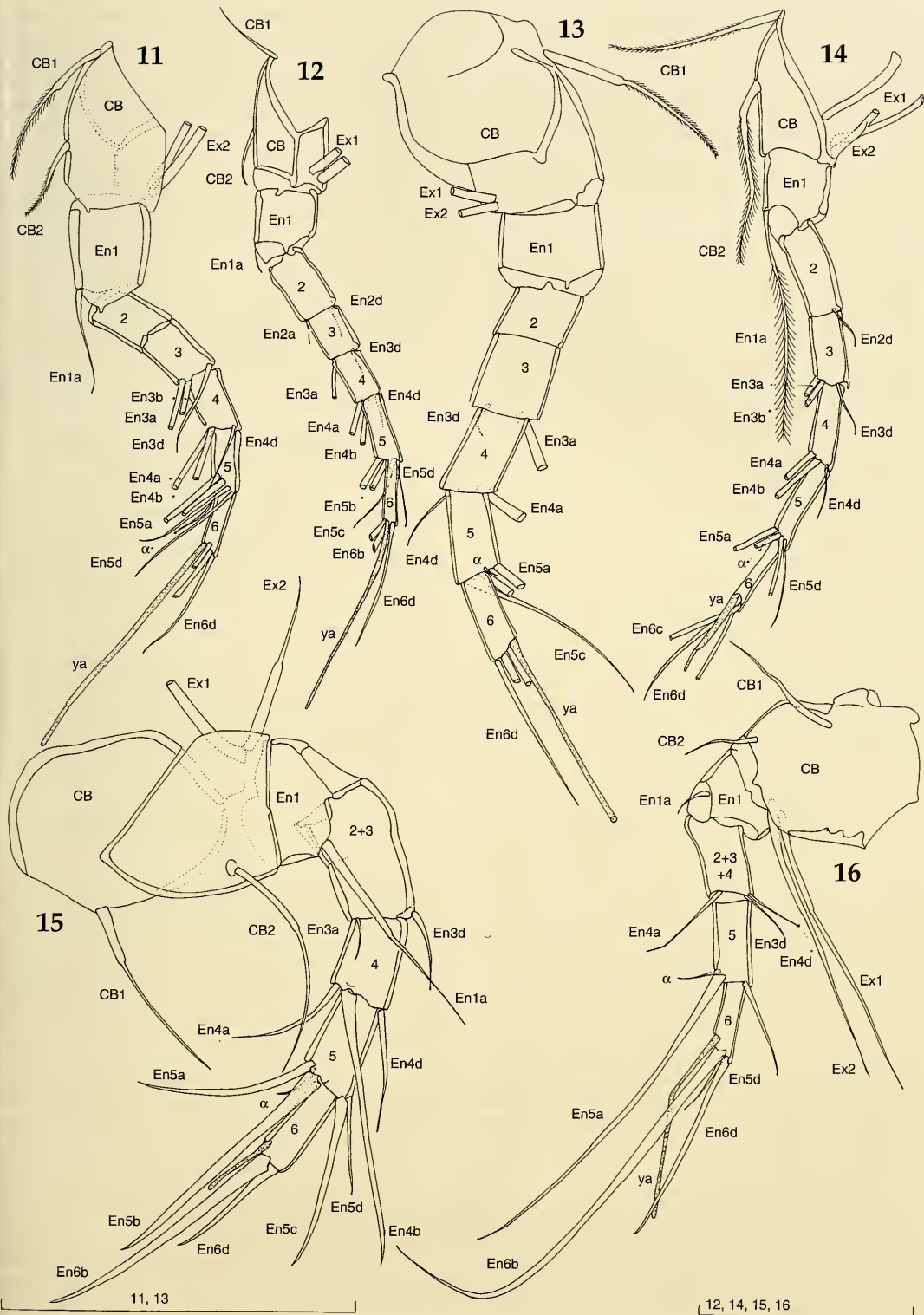
**Remarks.** *Phreatocandona* is another monospecific genus. The type species *P. motasi* was described by Danielopol (1978a, 1982a). The A1 is unknown and I was not able to obtain material of this species.

#### 22. *Pilbaracandona* Karanovic & Marmonier, 2003 Fig. 19

**Description of A1.** CB with both setae present. Ex with Ex1 and Ex2 setae. En with four free segments. En1 with En1a. En2 and En3 fused distally with En3a and En3d. En4 and En5 fused, medially with En4a, distally with En5a, En5b, En5c, and En5d;  $\alpha$ -seta missing. En6 with ya, long En6b and En6c, short En6d.

**Remarks.** Only two species are known so far from the subterranean waters of the Pilbara Region, Western Australia (Karanovic & Marmonier 2003). *Pilbaracandona eberhardi* (the type species of the genus) and *P. colonia* have identical setal pattern as described above.

**Figs 11-16.** Antennula in recent Candoninae. 11, *Acondona admiratio* Karanovic, 2003. 12, *Trapezicandona coineanae* (Rogulj & Danielopol, 1993). 13, *Trajanacandona natura* Karanovic, 1999. 14, *Candonopsis tenuis* (Brady, 1886). 15, *Baicalocandona ceratina* (Mazepova, 1982). 16, *Alatocandona gajewskajae* (Bronstein, 1947). Scales = 0.1 mm. All originals.



**23. *Pseudocandona Kaufmann, 1900 s.l.***

Figs 1E,F, 2D,E, 7, 10

**25. *Terrestricandona Danielopol & Betsch, 1980***

**Description of A1.** CB with only CB1 seta. Both Ex setae missing. En1 fused with CB. En with four free segments. En2 and En3 fused, armed with En3a and En3d setae. En4 bare. En5 with En5a and En5d. En6 with ya, En6b and En6c.

**Remarks.** Two species of *Terrestricandona* are described until now: the type species *T. minuta*, described from Madagascar (Danielopol & Betsch 1980) and *T. arborea* (Schornikov, 1980) from Solomon Islands (Schornikov 1980). *Terrestricandona minuta* lacks En3d on the fused segments En2 and En3 (see Danielopol & Betsch 1980, fig. 8a). On the other hand, this seta is present in *T. arborea* (see Schornikov 1980, fig. 4.4).

**26. *Trajancondona Karanovic, 1999***

Fig. 13

**Description of A1.** Only CB1 present. Both Ex1 and Ex2 present. En six segmented. En1 and En2 bare. En3 with long En3a and short En3d. En4 also with long En4a and short En4d. En5 with  $\alpha$ -seta, long En5a, En5b, and En5c. En6 with ya, long En6b, En6c, and short En6d.

**Remarks.** The genus *Trajancondona* contains two species (*T. natura* Karanovic, 1999 and *T. particula* Karanovic, 1999), both described from the subterranean waters of Montenegro, and both with the same setal patterns.

**27. *Trapezicandona Schornikov, 1969***

Fig. 12

**Description of A1.** CB with both setae present. Ex reduced and with Ex1 and Ex2. En six segmented. En1 with En1a; En2 with En2a and En2d (both short); En3 with long En3a and short En3d; En4 with long En4a and En4b and short En4d. En5 with En5a, En5b, En5c and En5d;  $\alpha$ -seta missing. En6 with ya, long En6b and En6c and short En6d.

**Remarks.** This genus contains about 20, exclusively hypogean recent species (Meisch 2000). The setal pattern is very variable between the species.

**Description of A1.** CB with both CB1 and CB2 setae. Ex reduced, Ex1 and Ex2 setae present. En six segmented. En1 with En1a; En2 with En2a; En3 and En4 with two long anterior setae (a,b) and one short posterior seta (d). En5 with  $\alpha$ -seta, En5a, En5b and En5c seta. En6 with ya, long En6b and En6c and short, claw-like En6d.

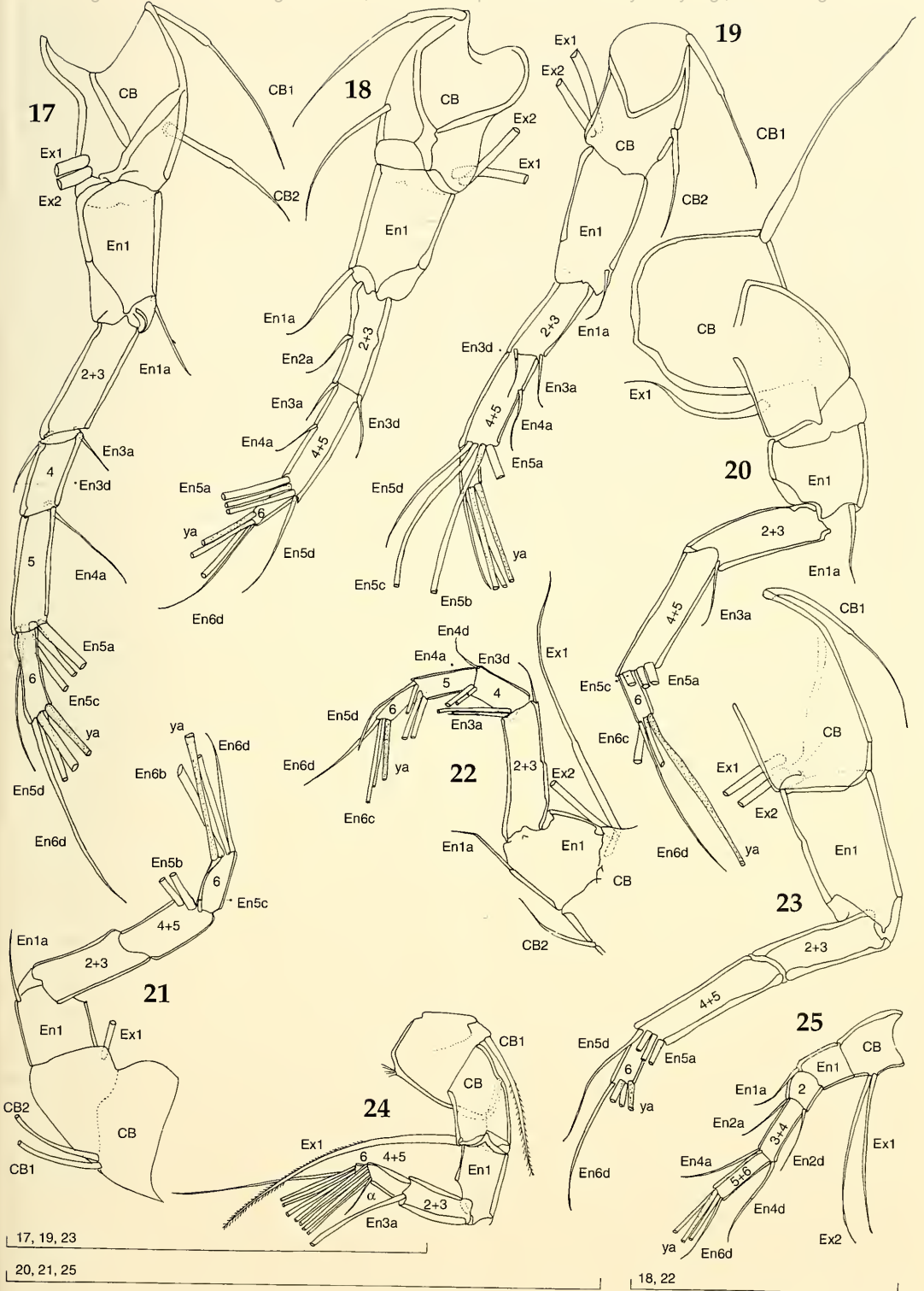
**Remarks.** The genus *Pseudocandona* is one of the largest Candoninae genera, containing about 75 recent species (Meisch 1996) divided into six species groups. Some of those groups probably deserve generic status. Despite differences in other morphological details between the groups, the setal pattern of A1 is uniform (see Danielopol 1978a, 1982b, Karanovic 1999, Meisch 2000, etc.). There are rare exceptions, but because they are recorded only on one A1, or only on one specimen, they could be an abnormality of specimen or variability within the species.

**24 *Schellencandona Meisch, 1996***

**Description of A1.** CB with CB1 and CB2. Ex reduced and with E1 and Ex2. En six segmented. En1 with En1a; En2 with En2a; En3 with two long anterior setae En3a and En3b, and short posterior one En3d; En4 with only two long anterior setae, En4a and En4b. En5 with  $\alpha$ -seta, and En5a, En5b and En5c. En6 with ya, En6b, En6c, and En6d.

**Remarks.** The genus *Schellencandona* was described only recently (Meisch 1996) with the type species *Candona schellenbergi* Klie, 1934. This genus encompasses a group of six species previously belonging to the *schellenbergi*-group of the genus *Pseudocandona*. The appearance of A1 is only known for two species: *S. simililampadis* (Danielopol, 1978) and *S. belgica* (Klie, 1937). The above described setal pattern is a compilation of setal patterns of the two species. *Schellencandona simililampadis* lacks En1a and En3a (see Danielopol 1978b, fig. 2a), while *S. belgica* lacks  $\alpha$ -seta on En5 (see Meisch 2000, fig. 63c). Seta En1a generally easily detaches from the A1, while  $\alpha$ -seta is usually very small and it can be easily overlooked. The absence of En3a should be confirmed on more species.

**Figs 17-25.** Antennula in recent Candoninae. 17, *Meridescandona lucerna* Karanovic, 2003. 18, *Humphreyscandona adorea* Karanovic & Marmonier, 2003. 19, *Pilbaracandona eberhardi* Karanovic & Marmonier, 2003. 20, *Danielocandona lieshoutae* Broodbakker, 1983. 21, *Meischcandona boitani* Karanovic, 2001. 22, *Caribecandona trapezoidea* Broodbakker, 1983. 23, *Notacandona boultoni* Karanovic & Marmonier, 2003. 24, *Namibcypris costata* Martens, 1992. 25, *Deminuticandona mica* Karanovic, 2003. Scales = 0.1 mm. 17-21 and 23 originals, 22 from Broodbakker (1983), 24 from Martens (1992). Note that fig. 24 does not have a scale bar, because Martens (1992) put wrong scales for A1 of *N. costata*.



Many lack En2d seta, which can be also overlooked because it is very tiny. *Trapezicandona chappuisi* (Klie, 1943), *T. pietrosani* (Danielopol & Cvetkov, 1979), *T. tabacarii* (Danielopol & Cvetkov, 1979), *T. botosaneanui* (Danielopol, 1978), *T. loffleri* (Danielopol, 1978), *T. lattingerae* (Rogulj & Danielopol, 1993), and *T. spandli* (Rogulj & Danielopol, 1993) all have two anterior setae on En3.

## Discussion

The newly proposed A1 of the ostracod ancestor (Fig. 3) had a protopod consisting of two segments: fused praecoxa and coxa and free basis. The endopod was six-segmented, while the exopod had three segments. The A1 had locomotory function, and because of that all epipods of a primitive crustacean limb were lost. Traces of endites could probably be found in the anterior setae of the protopod. This model is based on the fact that no recent ostracod has more than an eight segmented A1. Grygier (1987) also proposed that an eight segmented A1 was a synapomorphy of the class Maxillopoda, based on the presence of eight segmented A1 in Mystacocarida and Ostracoda, and on the appearance of eight segments during the ontogeny of Thecostraca.

In the subclass Myodocopa both protopodal segments are still present, and the exopod is lost but its remnants could probably be found in some external setae on the basis. The endopod has a maximum of six segments, and in some families the proximal segments still have numerous anterior setae (for illustration of A1 in different Myodocopa families see Poulsen 1962, 1965). It must be pointed out that not all the endopodal segments in Myodocopa and Podocopa are necessarily homologous. The articulation in Myodocopa and Podocopa may not be homologous with the ancestral A1, i.e. it is possible, for example that En2 and En3 in Podocopa derived from a divided ancestor's En2, while in Myodocopa En2 could be homologous with the same segment of the ancestral A1. On the other hand, at least in the subclass Podocopa, all endopodal segments are homologous.

The most obvious exopod is today present in the family Darwinulidae (Podocopa, Darwinulocopina). It consists of a small segment, more or less fused with a basis, and maximum of three setae (Fig. 5). In the same family the basis is separated from the coxa, while the endopod is four segmented, and probably has second and third, and fourth and fifth segments (of the ancestral Podocopid A1) fused. On the other hand, in the majority of representatives of two other Podocopid suborders, Cytherocopina and Sigillocopina, the coxa is free, while the basis is fused

with the first endopodal segment forming an allobasis (Fig. 6). In both suborders there is no clear trace of the exopod except for the seta (or setae in Sigillocopina) situated postero-medially on the external side of allobasis in some genera (for example *Gomphocythere* Sars, 1924, *Kovalenskiella* Klein, 1963, *Elpidium* Müller, 1880) and which could be its remnant. Seta which is placed postero-distally on the internal side (Figs 1D, 6) of the same segment might be seta of the first endopodal segment. The first endopodal segment could also be traced, if the remnant of the exopod is not clear, by the presence of a knee. Namely, the connection between En segments is without a knee, except between the first and the second one. This opinion contrasts that of authors who recognize two segments of protopod (here coxobasis and first endopodal segment) and five segments of endopod (see for example Martens 1986) in the superfamily Cypridoidea. However, a knee between the first and the second endopodal segments could be found on A2 and all thoracic appendages in Ostracods as well as in other Crustaceans, like in Copepods (see Huys & Boxshall 1991). In the majority of Cytheroidea the two terminal endopodal segments are fused. When those segments are not fused, the penultimate one is always bare and often very small (see illustrations on Text-Fig. 15 in Maddocks 2000). Coxa and basis also remained free in suborder Bairdocopina (Podocopida), where exopod is reduced to just one seta (see Maddocks 1969). In the suborder Cypridocopina (Podocopida) only in the representatives of the superfamily Macrocypridoidea and some of the superfamily Pontocypridoidea coxa and basis are free (see illustrations in Maddocks 2000). In addition, in some representatives of these two superfamilies, as well as in some representatives of the third Podocopid superfamily, Cypridoidea, the first endopodal segment is fused with the basis. In Cypridoidea that is often the case with the animals that inhabit semi-terrestrial environments. In all Cypridocopina there is a maximum of two setae, remnants of an exopod. They are situated on the external side of basis, and look very much like the exopodal setae in Darwinulidae (Fig. 5). The majority of Cypridocopina have fused coxa and basis and maximum of six endopodal segments, first and second one always jointed with an ankle. Some Cypridocopina families have specialized organs, for example Rome's organ positioned posteriorly on the first endopodal segment (Rome 1947), and a similar organ described by Wouters (1999) situated on the anterior side of coxobasis, which probably represents the CBI seta transformed, what is also noticed by Maddocks (2000). In addition, almost all representatives of Podocopida carry a sensory seta on the terminal segment of A1.

The representatives of the subfamily Candoninae fit well within in the general plan of the Podocypid A1. No member of the subfamily Candoninae has A1 with more than seven segments. The first one represents the fused coxa and basis, bearing one or two setae anteriorly, and two setae posteriorly which are the remnants of the exopod. Endopod consists of a maximum of six segments, and all setae (except  $\alpha$ -seta) are placed internally, with the long ones always located anteriorly, and short posteriorly on the segment (Fig. 10). On the sixth endopodal segment each species carry an aesthetasc. The plan of an hypothetical ancestral Candoninae A1 is based on those features (Fig. 4). However, it must be pointed out that there is no living Candoninae with all those setae present. For example, seta CB2 may be missing from the coxobasis, a character that has only specific value. In the genus *Meridiescandona*, for example, one species has both CB setae while the other one lacks CB2 seta (Karanovic 2003b). Only in the genus *Deminutiocandona* are both CB setae absent. All the other genera have both CB setae. The exopod is reduced to a single seta in four Candoninae genera (*Danielocandona*, *Meischcandona*, *Nannocandona* and *Namibcypis*) (Figs 20, 21, 24), while *Terrestricandona* has neither of Ex setae present (see Danielopol & Betch 1980). All the other Candoninae have both exopodal setae present, like on the ancestral A1. The endopod is still six-segmented in the following genera: *Acondona*, *Candona*, *Candonopsis*, *Cubacandona*, *Cryptocandona*, *Eucandona* s.l., *Indocandona*, *Paracandona*, *Phreatocandona*, *Pseudocandona*, *Schellencandona*, *Trajangcandona*, and *Trapezicandona*. Genera *Baicalocandona*, *Cubacandona*, and *Meridiescandona* have a five-segmented endopod, while *Alatocandona*, *Danielocandona*, *Deminutiocandona*, *Humphreyscandona*, *Meischcandona*, *Namibcypis*, *Nannocandona*, *Notacandona*, *Pilbaracandona*, and *Terrestricandona* have a four-segmented endopod. When the endopod has five free segments the fusion always lies between the second and the third segments. In the case of a four segmented endopod the fusion in the most cases lies between En2 and En3, and En4 and En5. *Humphreyscandona* has En2a and En4a setae still present, suggesting the fusion of two pre-existing segments. In *Pilbaracandona* only En4a seta is present, while in the genus *Notacandona* only the type species, *N. modesta*, has En2a. *Alatocandona* also has a four-segmented endopod, but three segments (En2+3+4) are fused in the row. In *Deminutiocandona* En3 and En4 are fused as well as En5 and En6. Segments En5 and En6 are also fused in *Nannocandona*. The fusion of En2 and En3, is a synapomorphy for four genera, while the fusion of En2 and En3 as well as En4 and En5 is a synapomorphy for six genera. All other fusions are autapomorphies. The first endopodal

segment in the recent Candoninae is most usually free and it carries only one anterior seta, as in the hypothetical Candoninae ancestor. Very rarely, as in genera *Nannocandona* and *Terrestricandona*, this segment is incorporated in the coxobasis. In *Trajangcandona*, in one species of *Notacandona*, and in *Namibcypis* (Figs 13, 23, 24) En1a seta is missing.

In Candoninae setae are inserted distally on all endopodal segments, except where there is a fusion of segments. The second segment carries maximum of two setae (one anterior and one posterior), third and fourth segments each carry three setae (two anterior and one posterior), with the exception of *Cryptocandona brehmi* where the fourth endopodal segment has two posterior setae (four setae altogether), which is a plesiomorphic character state. Fifth endopodal segment has maximum of five setae (of which one is external,  $\alpha$ -seta), and the sixth segment carries four setae distally. Alpha seta is absent in all Australian genera (except *Acondona*) and in *Danielocandona*, *Meischcandona*, *Nannocandona*, *Terrestricandona*, and *Trapezicandona*. In all species of the genus *Pseudocandona* and in the *fabaeformis*-group of the genus *Eucandona* s.l. the En5d seta is absent, which (in addition to other features) may support a generic status for the latter group of species.

The reduction of segments is probably not closely connected with a subterranean way of life. The examples are many small subterranean species in the genera *Schellencandona*, *Trajangcandona*, and *Trapezicandona* that still have clearly six-segmented endopods, and Baikal species (which are quite big) that have reduced endopodal segments. A better indication of a subterranean way of life, when A1 is considered, is the reduction of number and/or length of the long anterior setae on the third and fourth endopodal segments, as found in many *Candonopsis* species, *Trajangcandona*, *Trapezicandona*, and the Australian genera.

Candoninae A1 has an evolutionary trend towards the reductions of segments and setae. Compared with the ancestral Candoninae, the major reductions of setae occurred on the posterior side of segments and on the proximal rather than on the distal segments. While the reductions of segments have generic value, with majority being the synapomorphic character states, setal reductions are most often only a specific character. However, the presence of some posterior setae on proximal segments, such as En2d in some species of some genera (i.e. *Candonopsis*, *Cryptocandona*, and *Trapezicandona*) may indicate that these genera are on the lower branches of an assumed phylogenetic tree of the Candoninae, and probably this seta can be their symplesiomorphic character. In this paper a hypothetical ancestral A1 is used to aid clarification of phylogenetical relation-

ships between Candoninae genera and to highlight similarity due to the common descent, i. e. synapomorphies which are necessary for all further cladistic analysis. The features of A1 are only one of the numerous characters and many more should be applied in every such analysis.

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