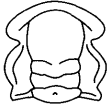# Homology of Holocene ostracode biramous appendages with those of other crustaceans: the protopod, epipod, exopod and endopod

ANNE C. COHEN, JOEL W. MARTIN AND LOUIS S. KORNICKER

LETHAIA

Unambiguously biramous appendages with a proximal precoxa, well-defined coxa and basis, setose plate-like epipod originating on the precoxa, and both an endopod and exopod attached to the terminal end of the basis are described from several living Ostracoda of the order Halocyprida (Myodocopa). These limbs are proposed as the best choice for comparison of ostracode limbs with those of other crustaceans and fossil arthropods with preserved limbs, such as the Cambrian superficially ostracode-like *Kunmingella* and *Hesslandona*. The 2nd maxilla of *Metapolycope* (Cladocopina) and 1st trunk limb of *Spelaeoecia*, *Deeveya* and *Thaumatoconcha* (all Halocypridina) are illustrated, and clear homologies are shown between the parts of these limbs and those of some general crustacean models as well as some of the remarkable crustacean *s.s.* Orsten fossils. No living ostracodes exhibit only primitive morphology; all have at least some (usually many) derived characters. Few have the probably primitive attribute of trunk segmentation (two genera of halocyprid Myodocopa, one order plus one genus of Podocopa, and the problematic *Manawa*); unambiguously biramous limbs are limited to a few halocyprids. Homologies between podocopid limbs and those of the illustrated primitive myodocopid limbs are tentatively suggested. A setose plate-like extension, often attached basally to a podocopid protopod, is probably homologous to the myodocopid epipod, which was present at least as early as the Triassic. Somewhat more distal, less setose, and plate-like extensions, present on some podocopid limbs (e.g., mandible), may be homologous instead to the exopod (clearly present on myodocopid mandibles). The coxa (or precoxa) is by definition the most basal part of the limb. A molar-like tooth is present proximally on the mandibular protopod of many ostracodes; it is the coxal endite and projects medially from the coxa (or proximal protopod). The Ostracoda is probably a monophyletic crustacean group composed of Myodocopa and Podocopa. All have a unique juvenile (not a larva) initially with three or more limbs. Except that juveniles lack some setae and limbs, they are morphologially similar to the adult. Thus the following suite of characters *in all instars* may be considered a synapomorphy uniting all Ostracoda: (1) Each pair of limbs is uniquely different from the others. (2) The whole body is completely enclosed within a bivalved carapace that lacks growth lines. (3) No more than nine pairs of limbs are present in any instar..(4) The body shows little or no segmentation, with no more than ten dorsally defined trunk segments. No other crustaceans have this suite of characters. A probable synapomorphy uniting the Podocopa is a 2nd antenna with exopod reduced relative to the endopod. □*Ostracoda, Myodocopa, Crustacea, Podocopa, homology, morphology.*

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Hou *et al.* (1996) recently published an important good description of the first known appendages of a fossil taxon, the Bradoriida, previously known only from bivalved carapaces and often consigned to the crustacean class Ostracoda. The limbs of *Kunmingella*, a well-preserved early Cambrian bradoriid from the soft-bodied 'Chengjiang' Lagerstätte of China, identify the group as arthropods, but neither as ostracodes nor even as crusta-

ceans *s.str.* by their definition of these taxa. We agree with Hou *et al.* that Phosphatocopina (Müller 1979) (another group of bivalved fossils with limbs), also are not Ostracoda (see below). All other Cambrian fossils presently assigned to the Ostracoda are known only from bivalved shells and lack any diagnostic characters that could assign them to a particular Holocene ostracode taxon. We agree with Hou *et al.* (1996) that all such

Cambrian records of Ostracoda are presently doubtful; no one knows what strange, possibly non-ostracode, limbs once lay within their carapaces.

We applaud Hou *et al.* (1996) for presenting a remarkable description of difficult material and for being suitably cautious in some of their conclusions. However, we regret a need to clarify the homologies of Holocene ostracode limbs, confusingly exemplified in their single figure showing the limbs of a Holocene ostracode with relatively derived limb characters (Hou *et al.* 1996, Fig. 8). The first problem is the unfortunate choice for this figure of an ostracode suborder, Bairdiocopina (Bythocyprididae, Maddocks 1976, p. 195), that is a typical ostracode in the sense of abundant distribution, but not representative of relatively primitive limb characteristics within the Ostracoda. The second problem is that in the same figure the black color used to indicate the 'exopodite' is unfortunately almost an imperceptibly lighter black than the black used to indicate the 'coxa'. In addition, those confusing labels appear to be incorrectly applied to three of the limbs.

We agree with Hou *et al.* (1996) that the Ostracoda is an important group of Crustacea, and because the affinities of Ostracoda to other Crustacea are still unclear, we present more information on the homology of the limbs of some Holocene ostracodes. Ostracodes live worldwide in the ocean (most species) from intertidal to abyssal depths (7,000 m), as well as in a variety of freshwater and a few terrestrial habitats. This large group comprises the vast majority of crustacean fossils. So common and diverse are the calcareous ostracode shells in fossil deposits and in marine sediments today that they have been called accessory minerals of the biosphere (Kaesler 1987).

We agree with Boxshall (1998, p. 166) that appendage characters are important in understanding phylogenetic relationships. Thus, we focus here on illustrations of some of the most primitive limb character states present in extant ostracodes with some interpretations of their crustacean homologies. Many of our figures and interpretations were first given in an oral presentation (Kornicker & Cohen 1993), which included preliminary results of a cladistic analysis of the Myodocopa and certain Podocopa, an analysis which is still incomplete. This paper is one step toward completion of that project. No one knows what outgroup is appropriate for Ostracoda; proposing homologies between many ostracode characters and those of possible outgroups is basically still guesswork. A new crustacean ground plan and model ancestral ostracode are also far beyond the scope of our paper and for the same reasons. We limit ourselves in this paper to demonstrating those limb characters that we can with some confidence label as homologous with crustacean limb parts and character states that we can reasonably propose as primitive/symplesiomorphic within the Ostracoda.

Are ostracodes, as currently defined, monophyletic?

We acknowledge the possibility that the Myodocopa and Podocopa might not comprise a monophyletic group (e.g., Vannier & Abe 1995, Text-fig. 18; Spears & Abele 1998), but regard it more parsimonious and useful to assume that they do, considering the many similarities between them, at least some of which are probably derived. In particular, no other crustaceans have nauplii or hatching juveniles that so closely resemble adult ostracodes in limb and carapace morphology.

The presence of the following suite of ostracode characters in all instars is proposed as a synapomorphy uniting all Ostracoda: (1) Each pair of limbs is uniquely different from the others. (2) The whole body is completely enclosed within a bivalved carapace that lacks growth lines. (3) No more than nine pairs of limbs (plus furcae; see below) are present in any instar (including copulatory limbs, and sometimes limb-like 'brush organs', Cohen & Morin 1997); the last adult limb (usually the 8th pair) is always the copulatory limb. (4) The body shows little or no segmentation; trunk segmentation is present in some primitive ostracodes only, none of which have more than ten dorsally defined trunk segments. In podocopid (but not myodocopid) ostracodes, the paired furcae are ventroanterior to the anus and are accordingly considered by some experts to be homologous to crustacean uropods, i.e. a 10th pair of ostracode limbs (Maddocks 1982; Athersuch *et al.* 1989); however, the furcae of the crustacean *s.s.* 'maxillopod' fossils *Bredocaris* and *Skara* have the same position, according to Walossek & Müller (1992). Segmentation of the head is indicated only by the five paired limbs of that region (see below). The first instars of ostracodes differ from adult ostracodes only in lacking some limbs and setae. First instars of some Podocopida have as few as three limbs, and are probably homologous with crustacean naupliar larvae in that respect, but cannot be termed larvae, because they resemble adult ostracodes and undergo no metamorphosis.

Thus we assume, as have most previous workers, that Ostracoda is a monophyletic assemblage. Presently, ostracodes are sometimes provisionally assigned to the Class Maxillopoda (which also includes the Copepoda and Thecostraca and a varying number of additional taxa) on the basis of some perhaps homologous morphological features: a medial naupliar eye with three cups and tapetal layer (present in most Myodocopida and many Podocopida) and reduction in body size and limb number. Recent molecular analysis (published since submission of this paper) indicates (but with little support) that both Ostracoda and Maxillopoda may be paraphyletic, that Myodocopa may possibly be related to Copepoda, and that Podocopa may be related to Branchiura and Pentastomida or may not be Crustacea (Spears & Abele 1998).
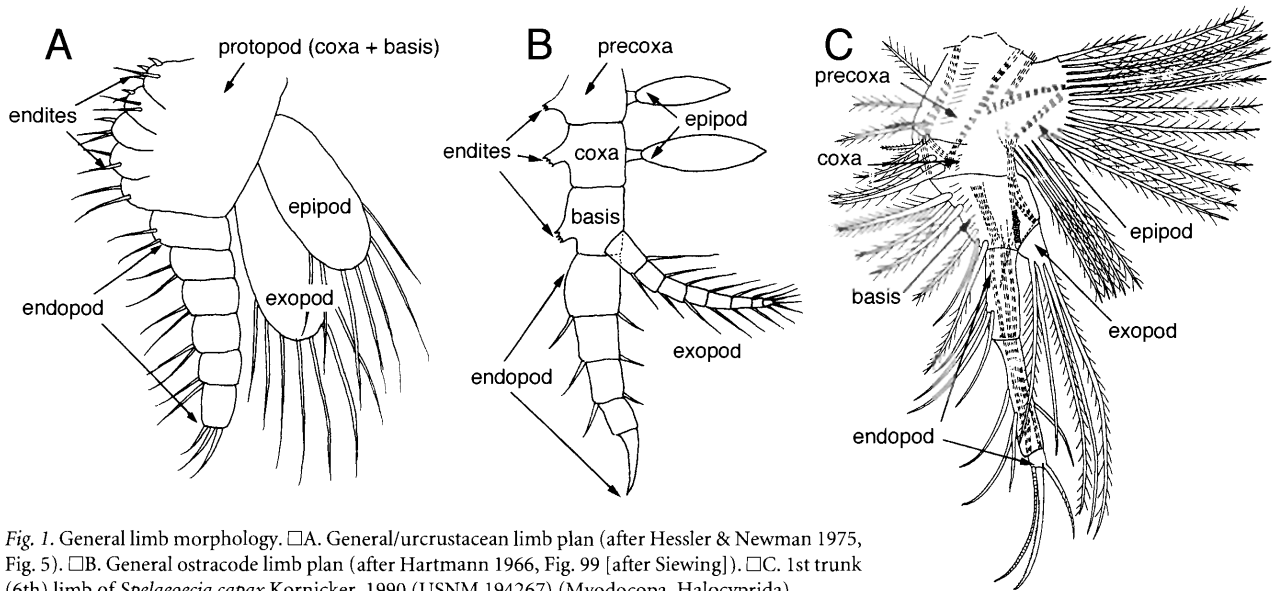
Fig. 1. General limb morphology. □A. General/urcrustacean limb plan (after Hessler & Newman 1975, Fig. 5). □B. General ostracode limb plan (after Hartmann 1966, Fig. 99 [after Siewing]). □C. 1st trunk (6th) limb of *Spelaeoecia capax* Kornicker, 1990 (USNM 194267) (Myodocopa, Halocyprida).

What are the most 'primitive' limb characters of the Holocene Ostracoda?

Given the above assumption of monophyly, which of the two subclasses, Podocopa and Myodocopa, exhibits the most plesiomorphic characters that might most appropriately be compared to other Crustacea and Arthropoda? All living ostracodes have at least some (usually many) derived character states (e.g., Maddocks 1982, p. 225), but some ostracodes exhibit more apparently primitive character states, e.g., dorsal trunk segmentation and at least some biramous limbs.

Primitive biramous limbs

A biramous limb is an appendage that bears a subdivided protopod (i.e. showing some indication of the coxa and basis) and a clearly identifiable endopod, exopod, and medial endites (and perhaps an epipod). We assume that a biramous limb is the more primitive ostracode limb state, because postantennular limbs are biramous in the Cambrian Orsten fossils which have been proposed both as stem-line Crustacea (Walossek & Müller 1990) and Crustacea *s.s.*, e.g., *Rebachiella* (Walossek 1995), *Skara* (Müller & Walossek 1985a) and *Bredocaris* (Müller & Walossek 1988). In *Rebachiella* (Walossek 1995), *Bredocaris* (Müller & Walossek 1988) and *Skara* (Müller & Walossek 1985a) the 1st maxilla has an exopod with apparently one or perhaps two articles (exopod interpreted as unjointed by Müller & Walossek 1985a, 1988 and Boxshall 1998, but with apparent division of the basis in Müller & Walossek's illustrations) and endopod with apparently three to perhaps five articles (*Skara* with three

in Müller & Walossek 1985a and Boxshall 1998; *Bredocaris* with four in Müller & Walossek 1988). The Remipedia, often considered basal in crustacean phylogeny (Schram 1986; Brusca & Brusca 1990), also have biramous trunk limbs; recent analyses indicate that this group is less basal and perhaps related to cephalocarids and mystococarids (based on molecular data; Spears & Abele 1998) and to 'maxillopod' taxa (based on limb morphology; Boxshall 1998).

A biramous limb has often been depicted as ancestral or primitive, as in Hessler & Newman's (1975) reconstruction of the 'urcrustacean' limb (Fig. 1A), a figure which did not incorporate the subsequent discoveries of Orsten crustacean fossils. The Hessler & Newman hypothetical limb, which closely resembles that of living cephalocarids, exhibits a well-developed endopod, exopod, and epipod, and has several medial endites arising from a common protopod. From this hypothetical limb, one can easily derive what Hartmann (1966) referred to as the ostracode 'ground plan' limb, bearing essentially the same features but with a divided protopod and multisegmented exopod (Fig. 1B), perhaps more like that of some stem crustacean Orsten fossil limbs of Walossek & Müller (1990). Although no extant ostracode has limbs exactly like that of stem-group crustacean fossils or like that of a hypothetical limb plan, some limbs of some species among the Myodocopa approach their morphology; the 1st trunk limb of one such species (the halocyprid *Spelaeoecia capax*) is shown in Fig. 1C. This, then, might suggest that biramous myodocope limbs are less derived than uniramous ones. The partial division of the coxa and presence of an epipod in *Spelaeoecia* may be a primitive character within the Ostracoda, but not the Crustacea.

Dorsal trunk segmentation

By dorsal trunk segmentation we mean at least some indication of serially similar somites, a state presumed to be ancestral because it is present in most Crustacea *s.s.* and stem-line fossils. Within the Podocopa, only the Platycopida and *Saipanetta* (Table 1) exhibit any dorsal trunk segmentation; however, they lack unambiguously primitive biramous limbs. Within the Myodocopa, some members of the Cladocopina have both definite indications of dorsal trunk segmentation as well as some biramous limbs (Table 1). Remnants of dorsal trunk segmentation are visible in a few of those halocyprid species that also have clearly biramous limbs (see below and Fig. 3B). Thus, once again, we are drawn to Myodocopa rather than Podocopa in our search for the most plesiomorphic Holocene ostracode character states.

Table 1. Classification of Ostracoda showing taxa discussed (other families excluded) (classification from Morin & Cohen 1991; Martens 1992 and in press). * = contains taxa with dorsal trunk segmentation; + = contains taxa with 'primitive' (unambiguously biramous) limbs; *+ = contains taxa with both dorsal trunk segmentation and 'primitive' limbs; † = extinct taxon (period of earliest fossil appearance). References: [1] = Siveter et al. 1987, Pl. 84:1; [2] = Kornicker & Sohn 1976; [3] = Weitschat 1983a, b; [4] = Kaesler 1987; [5] = Rossetti & Martens 1996; [6] = Maddocks 1969, p. 1. All remaining unlabelled taxa are recent Holocene.

Myodocopa (?Silurian[1], Devonian[2])
  *+Order Halocyprida
    *Suborder Cladocopina (Devonian[2])
      *+Polycopidae (Polycopsisinae)
        *+*Metapolycope*
    *+Suborder Halocypridina
      *+Thaumatocypridoidea (Permian[2])
        *+*Thaumatoconcha*, +*Danielopolina*
        †*Thaumatomma* (Permian[2])
      Halocypridoidea
        Halocyprididae
          +Deeveyinae
            +*Deeveya*, *Spelaeoecia
          Halocypridinae
            Euconchoecia
  Order Myodocopida (?Silurian[1], Triassic[3])
    †Triadocyprididinae (Triassic[3])
      †*Triadocypris* (Triassic[3])

Podocopa (Ordovician[4, 5])
  *Order Platycopida (Ordovician[4])
    *Cytherella
  *Order Podocopida (Ordovician[5])
    *Sigillocopina (Silurian)
      *Saipanetta
    Cypridocopina
    Darwinulocopina (Ordovician[5])
    Bairdiocopina (Devonian[6])
      Bythocyprididae
        Zabythocypris
    Cytherocopina

cf. Podocopa?
    *Manawa

Fossil evidence in Ostracoda

The earliest fossil representatives of Holocene ostracode taxa are probably Paleozoic (references in Table 1). A split between the subclasses Podocopa and Myodocopa may have occurred as early as the Silurian (e.g., 'Cypridinid' gen. et sp.nov. A, which generally appears to resemble shells of some Holocene Myodocopida; Siveter *et al.* 1987, Pl. 84-1), but it certainly had occurred by the Triassic. A Triassic fossil with some limbs having derived characters of the order Myodocopida has been described (Fig. 4; Weitschat 1983a, b).

Hesslandona

Hesslandona (Müller 1979, 1982; Müller & Walossek 1985b) is in several respects the most ostracode-like limb-bearing fossil among the Cambrian Phosphatocopina. As Müller (1979) noted, *Hesslandona* does share with the Ostracoda a possible synapomorphy, i.e. the release of juveniles or larvae with no more than seven limbs and those being completely enclosed within a bivalved shell. We agree with Hou *et al.* (1996) and Boxshall (1998) that *Hesslandona* is not an ostracode, because *Hesslandona* has homonomous postmandibular limbs (with multisegmented exopods), while all ostracode limb pairs are morphologically differentiated to serve different functions. In addition, *Hesslandona* (but not Ostracoda) has a 2nd antenna with basal endites and a multisegmented mandibular exopod.

That the earliest known instar of *Hesslandona* has four, not three, limbs doesn't necessarily indicate that it is not a crustacean *s.s.* (Hou *et al.* 1996) but only that an earlier instar may simply not yet have been discovered, or that, as in most Ostracoda, the instars are not released until the embryo has developed more than three limbs.

Interestingly, the medial eye of Myodocopida is similar to the three anteromedial structures of *Hesslandona*, and thus we favor Müller's (1982; Müller & Walossek 1985b) interpretation that the structure in *Hesslandona* represents three medial eye cups or possibly two cups and a ventral Bellonci organ. In particular, the appearance of the two probable dorsal cups in *Hesslandona* (Müller 1982, Pl. 2:2a–4) resembles that of the two greatly enlarged eye cups of the medial eye of the extant myodocopid *Gigantocypris* (Land 1978, 1984), an ostracode with many rather primitive myodocopid character states (Torres *et al.*, in press), as well as specializations (which may include the enlarged medial eye and loss of compound eyes) for its bathypelagic habitat. The anteromedial 'lobes of probable compound eye' of the Orsten crustacean fossil *Bredocaris* (Müller & Walossek 1988, Pl. 7:2, 4–6) are similar also and may be medial eye cups rather than compound eyes.

Manawa

We are unable to include a comparison with that interesting and undoubtedly rather primitive ostracode, *Manawa* (Swanson 1989), because we have no material and are unable to make clear comparisons with the published figures. *Manawa*, discovered only about a decade ago, is the only ostracode known to have univalved early instars (in common with the Cambrian *Kunmingella*, early stages of which are known only from shells) and has posterodorsal trunk segmentation. None of the illustrated limbs of *Manawa* (Swanson 1989) appear to be as unambiguously biramous as those of the Myodocopa we have chosen to discuss (except the 2nd antennae, which are also clearly biramous in most Ostracoda); they also appear more like the limbs of podocopids than those of myodocopids.

Conclusion: Holocene Ostracoda with primitive character states

Thus, it seems clear to us that a search for taxa with plesiomorphic character states among Holocene ostracodes should focus on the Myodocopa, rather than, or at least in addition to, the Podocopa. As noted above, no podocopids have as unambiguously primitive biramous limbs as do some primitive Myodocopids. Therefore, it is difficult to homologize the parts of podocopid limbs with those of myodocopid ostracodes, other crustaceans, and fossil arthropods with preserved limbs.

Our selection of material

For this paper we selected and examined (some specimens only examined by Cohen and/or Kornicker) the following recent Holocene Ostracoda with probably primitive character states. An asterisk (*) denotes taxa with dorsal trunk segmentation. This material is deposited in the National Museum of Natural History (USNM), Smithsonian Institution, or is in the Belize study collection of A. Cohen (AC).

Myodocopa (Halocyprida) ostracodes with clearly unambiguously biramous 2nd maxilla or 1st trunk limbs (5th and 6th limbs), some also with dorsal trunk segmentation

Cladocopina: *Metapolycope duplex* Kornicker & Iliffe (Kornicker & Iliffe 1989a) (USNM 193320, 193330), *M. ?duplex*, males and females (AC).

Halocypridina (Thaumatocypridoidea): *Thaumatoconcha radiata* Kornicker & Sohn (Kornicker & Sohn 1976), males and females (USNM 143754), *T. polythrix* Kor-

nicker & Sohn (Kornicker & Sohn 1976), male (USNM 143792), *Danielopolina bahamensis* Kornicker & Iliffe (Kornicker & Iliffe 1989b), male (USNM 193286); Halocypridina (Halocypridoidea): *Spelaeoecia capax* Kornicker (Kornicker *et al.* 1990) (USNM 194267), *S. sagax* Kornicker (Kornicker *et al.* 1990), male (USNM 193690), *S. bermudensis* Angel & Iliffe (Angel & Iliffe 1987), female (USNM 193405), *Deeveya medix* Kornicker (Kornicker *et al.* 1990), female and male (USNM 193602), *D. spiralis* Kornicker & Iliffe (Kornicker & Iliffe 1985), (USNM 193117), *D. styrax* Kornicker (Kornicker *et al.* 1990), male (USNM 193482).

Podocopa ostracodes with dorsal trunk segmentation:

*Platycopida: *Cytherella kornickeri* Maddocks & Iliffe (Maddocks & Iliffe 1986), male (USNM 216419), *C. bermudensis* Maddocks & Iliffe (Maddocks & Iliffe 1986), male (USNM 216414), ?*C.* sp. (AC).

Podocopida (Sigillocopina): *Saipanetta bensoni* Maddocks (Maddocks 1972), three males (USNM 181852).

Dissections and scanning electron micrography were performed as described by Cohen & Morin (1997).

Names of ostracode limbs

Hou *et al.* (1996) used standard crustacean terms to refer to each limb, as we do herein, to provide clear comparison with other Crustacea. In this paper, we assume that the 4th and 5th limbs are head limbs, because in Ostracoda the maxillary excretory gland, if present, is always associated with the 5th limb (e.g., Cannon 1931, pp. 476–469; Maddocks 1992, p. 431 [and references]). Thus, the 4th limb is termed the 1st maxilla and the 5th limb the 2nd maxilla (because of varying past usage of ostracodologists, we prefer this nomenclature to the more ambiguous maxillule and maxilla, respectively).

An alternative view of some merit is that in some or all podocopid ostracodes the 5th limb is instead a trunk limb. Several arguments have been advanced to support this interpretation and are well explained by Smith & Martens (in press): (1) The 5th limb is not attached to the ventral head plate ('sternum') in *Saipanetta*, Bairdiocopina and Cytherocopina (e.g., Schulz 1976, p. 101; Martens 1990, p. 473); (2) in many podocopids (Bairdiocopina and Cytherocopina and the cypridocope *Macrocypris*), the podocopid 5th–7th limbs are clearly homologous walking legs with homologous segments and chaetotaxy (Meisch 1996); and (3) during the larval development of *Eucypris* and *Herpetocypris* (Cypridocopina, Cypridoidea) the 5th limbs change from walking legs (homologous to the 6th and 7th limbs) in the A-4 (adult

minus four) instar to feeding appendages in the A-3 instar (Smith & Martens, in press). This raises the question of whether Ostracoda, or at least Podocopa, are Crustacea *s.s.*; Walossek & Müller (1998) reiterated the criteria of five head limbs for Crustacea. On the other hand, the differentiation of the 5th head limb as a 2nd maxilla distinct from trunk limbs may have occurred several times within the Crustacea; the 5th limb of both the Cephalocarida and of the Cambrian crustacean *Bredocaris* resembles the trunk limbs but also originates anterior to a separation between the head and trunk; *Bredocaris* also has delayed development of limbs from anlagen (Müller & Walossek 1988; Walossek & Müller 1992; Walossek 1995).

Embryology is poorly known in the Myodocopa; most release a 1st instar with at least five or six limbs (e.g., Poulsen 1962, pp. 35–56, Figs. 11, 12 of wrinkled late embryo; Cohen 1983; Hiruta 1983; Kornicker 1981, pp. 36–38, 1989b, pp. 58–66, 1992, pp. 54, 123, 204–219). The earliest instar of both *Thaumatoconcha* (Kornicker & Sohn 1976) and *Metapolycope* (Kornicker & Iliffe 1989a), Halocyprida with relatively primitive character states (see below), have five limbs. Only the 1st instar of *Euconchoecia* (a halocyprid with more derived character states) has been described with three limbs; in each subsequent instar one additional limb appears until all but the copulatory (8th) limbs are present (Tseng 1975; see also Ikeda 1992). We refer readers to Smith & Martens (in press) for further discussion. If, in the future, a maxillary gland is identified with a particular limb, that limb, whatever its position, will be known to be the 2nd maxilla; similarly, if ontogenetic research clearly demonstrates embryological loss of the 1st or 2nd maxillae, the 5th limb would accordingly be a trunk limb.

For the convenience of clarity we will refer to the 5th limb in all Ostracoda as the 2nd maxilla; unfortunately the lack of a universal standard terminology employed in published descriptions of ostracode limbs has resulted in some confusion for other crustacean systematists and even among ostracode taxonomists working with different groups (Maddocks 1982, p. 223; Cohen 1982, p. 181). In the past, for example, the crustacean 4th limb (i.e. crustacean 4th head limb, maxillule or 1st maxilla) unfortunately has been termed, in the ostracodes, variously the maxilla (e.g., Müller 1894, p. 53; Skogsberg 1920, p. 31; Kesling 1951, p. 31; Howe *et al.* 1961, p. Q6; Maddocks 1972, Fig. 3C; Kornicker & Sohn 1976, Figs. 20A, 28C; Kornicker & van Morkhoven 1976, Fig. 4F; Kaesler 1987, Fig. 13.31) and (more correctly) 4th limb (e.g., Cohen & Morin 1997) or maxillule (e.g., Cannon 1931, Fig. 1; Maddocks & Iliffe 1986, Fig. 3A, F; Athersuch *et al.* 1989, Fig. 8). In Ostracoda the crustacean 5th limb (i.e. 5th head limb or 2nd maxilla) has been called the 1st thoracic leg (e.g., Kesling 1951, p. 36; Maddocks 1972, Fig. 4B, D; Howe *et al.* 1961, p. Q7) or maxilliped (e.g., Müller 1894, p. 61), 1st walking leg (e.g., Athersuch *et al.* 1989, Fig. 8),

and perhaps more correctly the maxilla (Cannon 1931; Hartmann 1966, p. 23), 5th limb (e.g., Skogsberg 1920, p. 37; Kornicker & Sohn 1976, Figs. 20A, 29; Kornicker & van Morkhoven 1976, Fig. 4G; Maddocks & Iliffe 1986, Figs. 3I, J, 5B; Abe & Vannier 1993; Cohen & Morin 1997) or 5th cephalic appendage (e.g., Kaesler 1987, Fig. 13.31), but more rarely the 2nd maxilla (e.g., Müller 1894, p. 63; Maddocks 1982, p. 223; Kaesler 1987, p. 243) as it is now more generally considered to be, because the maxillary excretory gland, if present, is always associated with the 5th limb in ostracodes (Cannon 1931, pp. 476–479).

Homology of ostracode limb parts

In determining homologies of the parts of ostracode limbs, it seems best to start by applying general crustacean terms to some myodocopid ostracode limbs that are unambiguously biramous (that is, bear a clearly defined endopod and exopod terminal on a basis, as well as an epipod on a coxa). Once this is done, the homologies of limbs with fewer and less clearly identifiable limb articles and rami, such as those of the podocopid *Zabythocypris* used by Hou *et al.* for comparison with *Kunmingella*, can be attempted by comparing the shapes and positions of limb extensions to those on a more primitive biramous limb.

Hessler & Newman (1975) provided a figure of a hypothetical primitive crustacean limb, based on shared features exhibited by several 'phyllopodous' groups (Fig. 1A). Although perhaps not universally accepted as a primitive limb from which all crustacean appendages can be derived (as noted above), this hypothetical limb conveniently offers the basic crustacean biramous features for comparison with those of extant ostracodes. The Hessler & Newman limb (Fig. 1A) has a clearly defined endopod, exopod, and epipod arising from a protopod (representing the combined coxa and basis) that bears several endites along the medial border (the hypothetical ancestral crustacean 1st maxilla of Boxshall 1998 is appropriate also but lacks an epipod; furthermore, it was published after submission of this paper).

From this limb, it is easy to derive what Hartmann (1966) referred to as the ostracode 'ground plan' limb, bearing essentially the same features but with the protopod divided into a recognizable precoxa, coxa, and basis, and with the exopod now subdivided (Fig. 1B). Why he chose to depict two epipods is unclear. Among extant ostracodes, we see limbs very similar to this in several species in the Myodocopa (but not the Podocopa). We have chosen to illustrate first the 1st trunk limb of *Spelaeoecia* (Fig. 1C). In this genus, not only are the endopod, exopod, and epipod clearly recognizable, but the basis and coxa are clear, and the protopod bears a weak suture that would appear to demarcate the precoxa from the coxa.
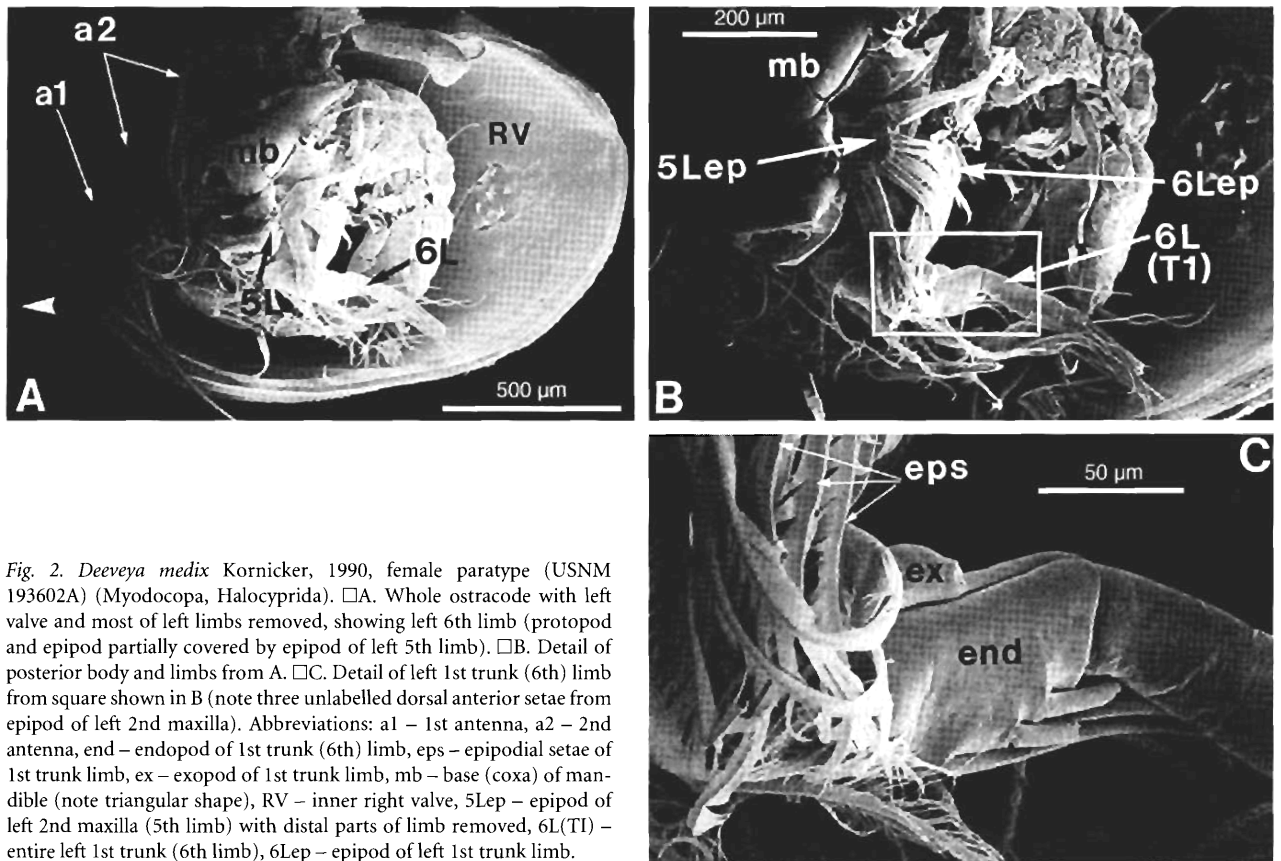
Fig. 2. Deeveya medix Kornicker, 1990, female paratype (USNM 193602A) (Myodocopa, Halocyprida). □A. Whole ostracode with left valve and most of left limbs removed, showing left 6th limb (protopod and epipod partially covered by epipod of left 5th limb). □B. Detail of posterior body and limbs from A. □C. Detail of left 1st trunk (6th) limb from square shown in B (note three unlabelled dorsal anterior setae from epipod of left 2nd maxilla). Abbreviations: a1 – 1st antenna, a2 – 2nd antenna, end – endopod of 1st trunk (6th) limb, eps – epipodial setae of 1st trunk limb, ex – exopod of 1st trunk limb, mb – base (coxa) of mandible (note triangular shape), RV – inner right valve, 5Lep – epipod of left 2nd maxilla (5th limb) with distal parts of limb removed, 6L(TI) – entire left 1st trunk (6th limb), 6Lep – epipod of left 1st trunk limb.

This, then, is a relatively primitive and unambiguously biramous limb among the Holocene ostracodes. The epipod is a flat, very setose plate, which in myodocopids has been shown to aid in water circulation within the carapace (e.g., Cannon 1931, p. 438; Vannier & Abe 1993, p. 66). The short lobe-like exopod has a single article bearing five setae, while the longer (in ostracode terminology, more palp-like) endopod has some setae on each of the three articles. Internal muscles extend from the body to the base of the epipod, to the precoxa, and to the precoxa–coxa boundary. Muscles extend from within the precoxa to the distal epipodial edge, and to the coxa (some from the precoxa–coxa boundary). Additional muscles extend from the epipodial area to the base of the exopod and endopod, and muscles extend from the basis to the exopod and into the endopod.

The 1st trunk (6th) limbs are similar in *Spelaeoecia* (Fig. 1C) and its sister genus, *Deeveya* (Figs. 2, 3A). In these genera, both the 2nd maxilla (5th limb) and 1st trunk limbs have a very proximal plate-like and setose epipod.

In the SEM of *Deeveya* (Fig. 2), the setae of the 2nd maxillary epipod lie over the insertion of the adjacent epipod of the 1st trunk limb, and both are very basal on the limb, at the point of its insertion on the body (the distal part of the left 2nd maxilla was removed to expose the lateral view of the entire left 1st trunk limb). The 1st trunk limb, but not the 2nd maxilla, has both a distinct distal exopod and endopod attached terminally to the basis, and a distinct proximal epipod attached close to the body (Figs. 2, 3A). Other figures of the primitive biramous 1st trunk (6th) limbs of several species belonging to these two genera can be found in a number of publications (Kornicker & Palmer 1987, Fig. 3C of *D. bransoni*; Kornicker 1989a, Fig. 2F of *S. bermudensis*; Kornicker, *et al.* 1990, Fig. 5 of *S. styx*, Fig. 11g of *S. sagax*, Fig. 19b of *D. styrax*, Fig. 26b of *D. hirpex*; Kornicker & Iliffe 1992, Fig. 5h of *S. jamaicensis*; Kornicker & Yager 1996, Fig. 6e of *S. cubensis*; Kornicker & Barr 1997, Fig. 4c, d of *S. barri*; some of these figures with designation of endopod and exopod reversed).

Other myodocopid primitive and unambiguously biramous limbs: 2nd maxilla (5th limb) and 1st trunk limb (6th limb)

The 1st trunk limb in Halocypridina

The 1st trunk limb is also clearly primitive and biramous in the myodocopid family Thaumatocyprididae (Halocyprida), belonging to a superfamily, the Thaumatocypridoidea, which is represented as early as the Permian by the fossil valves, but not limbs, of an extinct genus, *Thaumatomma* (Kornicker & Sohn 1976, p. 107). At least one species of the Holocene genus *Thaumatocypris* (*T. polythrix*) shows definite traces of posterodorsal segmentation (at least seven segments, Fig. 3B). The thaumatocyprid 1st trunk limb (Fig. 3C) is similar to that of the Deeveyinae, with epipod (a setose plate) arising from the coxa next to the limb attachment to the body, and with an endopod (three articles) and exopod (one article) arising terminally from the basis; the basis and coxa are separated by a suture (also Kornicker & Sohn 1976, Figs. 43J, 61D, 70F, 77I of *Danielopolina carolynae*; Kornicker & Iliffe 1989c, Fig. 12D of *D. styx*; Kornicker & Iliffe 1995, Fig. 7B of *D. phalanx*). The 1st trunk limb of *Thaumatoconcha* first appears in the A-4 or possibly A-5 instar and is fully developed in the A-3 instar (Kornicker & Sohn 1976, p. 15).

The 2nd maxilla in Cladocopina

A primitive and biramous 2nd maxilla is present in *Metapolycope* (Fig. 3D), a Holocene genus of Cladocopida (Myodocopa), and one of the few myodocopid genera (all cladocopids) with well-defined posterodorsal trunk segmentation, having at least four such segments (Cohen, unpublished SEM; also Kornicker & van Morkhoven, Fig. 4J; Kornicker & Iliffe 1989a, Fig. 30J–L). Müller (1894, p. 62) designated the epipod, exopod and endopod for the three rami of the 5th limb of another cladocopid (but termed the 5th limb a maxilliped). Trunk segmentation is probably a primitive characteristic, and fossil cladocopid valves occurred as early as the Permian (Kornicker & Sohn 1976, p. 6). The 2nd maxilla of *Metapolycope* has a biramous morphology similar to that of the primitive halocyprid 1st trunk limbs described above, and it has apparently similar insertions of four or five muscles (Figs. 1C, 3D) (also Kornicker & van Morkhoven 1976, Fig. 4G of *Metapolycope hartmanni*; Kornicker & Iliffe 1989a, Figs. 31F, 33E–H, 34I, J of *M. duplex*). All three rami of the 2nd maxilla appear with the first instar of *M. duplex* (Kornicker & Iliffe 1989a, Fig. 34I, J). While Boxshall's (1998, p. 163) statement that the 2nd maxilla of 'myodocopidan ostracods' has traditionally (but not herein) been described as having three exopodial articles (traditionally

usually three in Halocypridina and five in Myodocopida; see below) is mostly correct, that limb is basically uniramous in Halocypridina and Myodocopida, and in Cladocopina it has traditionally been described with one endopodial and one exopodial article (references above). Boxshall appears to include halocyprids with the myodocopid *Azygocypridina* in a single order (Boxshall 1998, p. 163); the halocyprids are usually (Table 1; Kornicker & Sohn 1976; Cohen 1982; Morin & Cohen 1991) considered to include not only *Spelaeoecia*, but the cladocopid *Metapolycope*, which has a much more clearly biramous 2nd maxilla.

Cladocopids do not have the same primitive and biramous limbs with an epipod as do halocyprids, so a more direct comparison is not possible. First, no halocyprids have clearly biramous 2nd maxillae. Second, the 1st and 2nd trunk limbs are lacking in all living cladocopids. In males of both halocyprids and cladocopids, the most posterior limb is an unpaired copulatory limb located on the left and just anterior to the furca. The reduced number of limbs in living cladocopids is probably a derived loss of two trunk limbs correlated with the small size of these interstitial ostracodes, although many other equally small ostracodes have more limbs.

Triadocypris, a Triassic fossil (Myodocopida) with preserved epipod

An ostracode limb with basal epipod in the form of a setose plate has been present in ostracodes at least since the Triassic. Weitschat's (1983a, b) fine description of *Triadocypris spitzbergensis* is important in presenting the oldest fossil myodocopid (and at least one of the few such early ostracodes) with some preserved body parts that are clearly homologous with those of some living ostracodes; these include both a very flexible worm-shaped 2nd trunk (7th) limb with multiple external annulation (a synapomorphy of the order Myodocopida) and a separate flat setose plate-like epipod apparently closely attached to the body (Fig. 4 herein; compare to Morin & Cohen 1988, Fig. 1B). In all living Myodocopida the worm-like 2nd trunk limb also is inserted laterally on the body, just posterior to and under a single similar setose plate; that plate is attached very basally to the 2nd maxilla (5th limb). The basal setose plate of the 2nd maxilla of *Triadocypris* and other Myodocopida is similar in position and form, and clearly homologous to the epipod of the cladocopid 2nd maxilla and halocyprid 1st trunk limb, limbs which additionally bear a distal exopod and endopod (described above). Distally in Myodocopida, the 2nd maxilla is so compressed that, as discussed above, there is no obvious division into exopod and endopod. Setae are found on the myodocopid 7th limbs only in adults (A) and the penultimate instar (A-1). These setae are untapered in adults, but
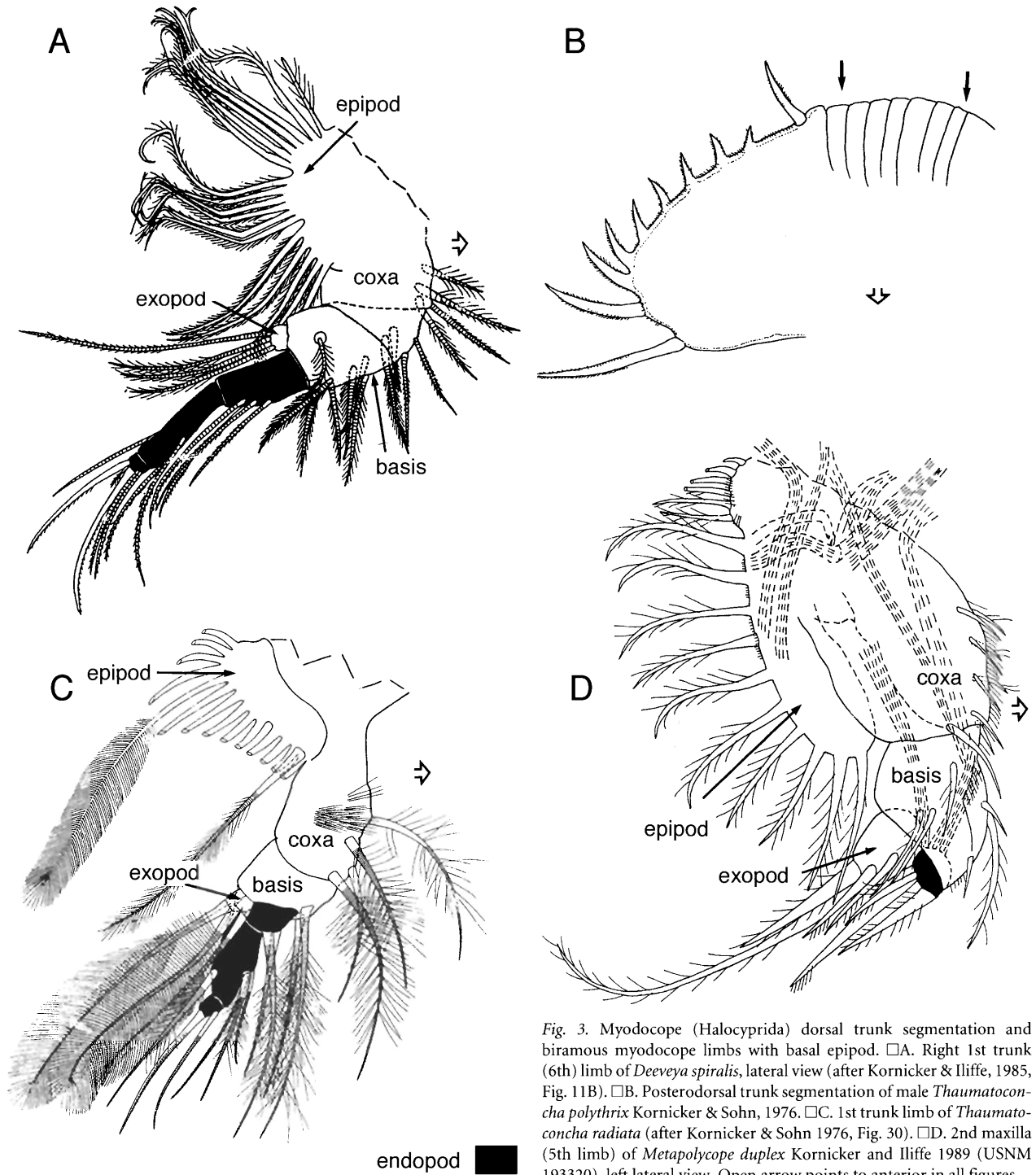
Fig. 3. Myodocope (Halocyprida) dorsal trunk segmentation and biramous myodocope limbs with basal epipod. □A. Right 1st trunk (6th) limb of *Deeveya spiralis*, lateral view (after Kornicker & Iliffe, 1985, Fig. 11B). □B. Posterodorsal trunk segmentation of male *Thaumatoconcha polythrix* Kornicker & Sohn, 1976. □C. 1st trunk limb of *Thaumatoconcha radiata* (after Kornicker & Sohn 1976, Fig. 30). □D. 2nd maxilla (5th limb) of *Metapolycope duplex* Kornicker and Iliffe 1989 (USNM 193320), left lateral view. Open arrow points to anterior in all figures.

tapered in late juvenile instars (e.g., Kornicker 1981), and apparently tapered in figured specimens of *Triadocypris*, suggesting that those are A-1 juveniles (Weitschat 1983b, Pl. 134). In Myodocopida the flattened and reduced 1st trunk (6th) limbs are inserted ventromedially on the body.

The three very lateral posterior sac-like lobes of *Triadocypris*, as well as an unusual perhaps anterolateral orifice (Weitschat 1983a, Fig. 10), are found in no living Myodocopida (or other Ostracoda), and the fossil subfamily Triadocypridininae Weitschat (Weitschat 1983a, b) should be raised to familial status within the Myodocopida. The Triadocyprididae shares some characters (but none diagnostic) with and may be related to the Cypridinidae, Cylindroleberididae (Asteropteroninae), and Philomedi-
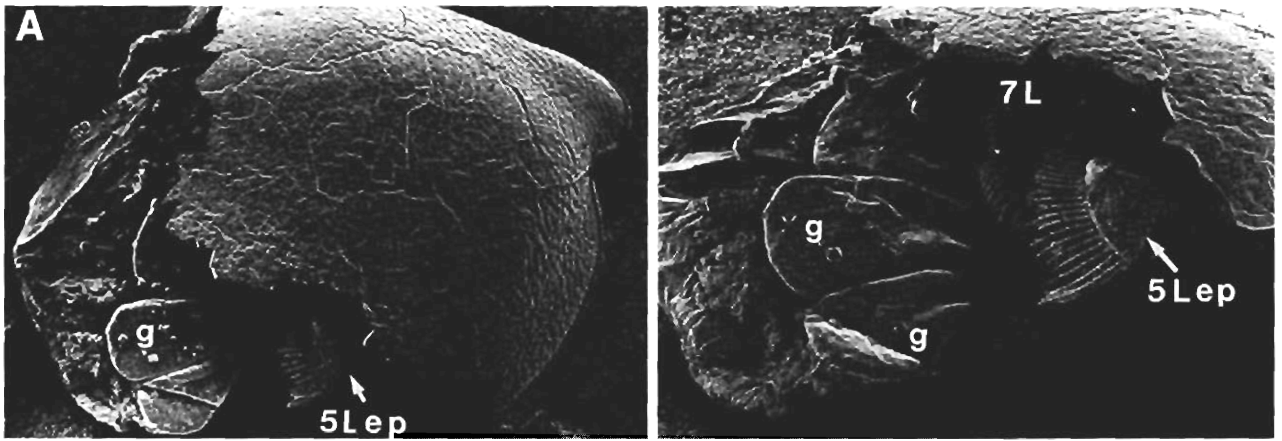
Fig. 4. Triadocypris spitzbergensis Weitschat 1983a, b (Myodocopa, Myodocopida) (photos by W. Weitschat). □A. Whole fossil from right side with posterior right valve removed revealing the epipod of the 2nd maxilla (5th limb), base of the 2nd trunk (7th) limb and three lobes (gills?). □B. Enlargement of revealed posterior limbs from A. Abbreviations: ep – epipod, g – ?gills, 7 – 2nd trunk (7th) limb.

dae; the central adductor muscle scars most closely resemble cypridinid scars. As Weitschat (1983a, b) pointed out, the lateral 'gill-like' lobes of *Triadocypris* show at least slight similarity to lobes or gills found much more dorsally (on the posterodorsal median) in various other myodocopids, i.e. the flat book-gills (e.g., Vannier *et al.* 1996) of the Cylindroleberididae and rounded lobes (possibly used in respiration) in some Cypridinidae (only males and only some genera or species, and not including the most primitive living Cypridinidae). In all of these taxa, the gills and/or lobes may indicate remnants of trunk segmentation but are not necessarily homologous and seem to have rearisen many times, at least in the Cypridinidae.

Myodocopida: comparison of some interpretations of the 2nd maxilla

In the Myodocopida (see our classification in Table 1), the trunk limbs are highly modified and appear uniramous, and the 2nd maxilla is distally so compressed that there is no obvious division into exopod and endopod; this ambiguity explains a continued general acceptance of the traditional labelling of the distal limb as a multisegmented exopod with up to five articles, but no endopod. We have not illustrated these limbs of the Myodocopina because they are very difficult to interpret, but we have added some comments on an interpretation published since submission of this paper (Boxshall 1998). We agree with Boxshall (1998, p.166) that appendage characters are important in understanding phylogenetic relationships. In all Myodocopida (see our classification in Table 1) the 2nd maxilla exhibits many complex derived character states, because it is a highly modified

and compacted feeding limb. The limb is so compacted that a definite interpretation of crustacean homologies is impossible for us. We favor either (1) Poulsen's well-illustrated speculation that in Myodocopida the five articles traditionally all labelled as exopodial could perhaps best be interpreted instead as three exopodial and two endopodial articles (Poulsen 1965, p. 456, Fig. 152, with summary of previous interpretations) or (2) Skogsberg's second interpretation as five endopodial and no exopodial articles (1920, Fig. VI; see also his Fig. V), and reject the interpretation of *Azygocypridina* shown in Boxshall's figure (Boxshall 1998, Fig. 13.6a). Boxshall's interpretation overlooked the fact that the small outer lobe, which he labelled the entire exopod, actually extends much further in *Azygocypridina* and all other Myodocopida and lies between the protopod and what Boxshall labelled as the distal endopodial articles (separated from each by sutures); this elongate u-shaped lobe is proposed as the first (of three) exopodial articles by Poulsen. This elongate lobe includes (without suture or other interruption) both Boxshall's exopod and part of what he labels as basis and as endopod (i.e. his most proximal and medial endopodial article is part of the lobe he labels as exopod). This is shown in previous illustrations of *Azygocypridina* and other Myodocopida (e.g., Skogsberg 1920, Figs. IV and V; Poulsen 1965, p. 456; Cohen & Morin 1989, Fig. 9G; 1993, Fig. 14). This elongate article is itself separated basally by a suture from what Boxshall calls the protopodal basis; it is traditionally called the 3rd exopodial article, but in Poulsen's (1965, p. 456) speculative interpretation it is called the 1st exopodial article. We realize that Poulsen's interpretation requires a jointed exopod which is separated by sutures in part from the basis and in part from the 2nd article of the endopod, and interpret the

position as being due to the extreme reduction and compaction of the myodocopid 2nd maxilla.

Boxshall (1998) also failed to discuss (or clearly label) another unusual aspect implied by his interpretation of the 2nd maxilla of *Azygocypridina*, i.e. that his interpretation requires two precoxal, one coxal, and two basal endites. Both the traditional and speculative myodocopid interpretations attribute Boxshall's two most distal protopodal endites (unlabelled on Boxshall's basis) to the feeding armature of the compacted 1st and 2nd endopodial (traditionally exopodial) articles. These two articles are not protopodal endites, but are separated by a suture (shown in Boxshall's figure) which divides the entire protopod (with very setose epipod homologous to that of *Metapolycope*) from the entire rest of the limb. Furthermore, the 1st and 2nd endopodial (traditionally exopodial) articles are completely separated from each other by sutures (in Boxshall's interpretation the basis would be completely divided into two parts and incorporate part of the basal exopod).

Boxshall's statement that the compacted 2nd maxilla of *Azygocypridina* 'is the most fully expressed maxillary exopod in the myodocopid Ostracoda' appears inappropriate. The number of exopodial articles is speculative in *Azygocypridina*. Boxshall appears to include halocyprids with *Azygocypridina* in a single order, and the cladocopid *Metapolycope* has a much more clearly biramous 2nd maxilla (Fig. 3D; discussed above). Similarly, we are not sure what Boxshall meant in stating that the 1st maxilla of *Azygocypridina* is 'the most complex maxillule found in the Myodocopida' (Boxshall 1998, p. 156). In the cladocopid *Metapolycope* the 1st maxilla has a protopod divided into precoxa, coxa, and basis and with three setose endites, an unsegmented exopod, and a three-segmented endopod (Kornicker & Van Morkhoven 1976, Fig. 4f; Kornicker & Iliffe 1989a, Fig. 33d); *Metapolycope* is likely the 'myodocopid' meant by Boxshall as having a plesiomorphic three-segmented endopod. Muscles extrinsic to the limb do not appear to insert on the two rami of *Metapolycope*, which is thus in accordance with the coxa–basis plane signature proposed by Boxshall (1998, p. 156) (Kornicker, unpublished drawing).

Interpretations of the coxa, epipod, and exopod in the Podocopa and possible homologies with Myodocopa and other Crustacea

Antennae

Homologies between the uniramous 1st (with up to eight articles) and biramous 2nd antennae of the two ostracode subclasses, Myodocopa and Podocopa, are clear.

The reduced exopod of the 2nd antenna (e.g., Fig. 5B) is probably a synapomorphy for the Podocopa, because in most Crustacea, as well as in all Myodocopa ostracodes, the exopod has more articles (up to nine in Myodocopa) and is usually larger than the endopod (e.g., Kornicker & Sohn 1976, Fig. 27A; Kornicker, 1981, Fig. 73C, 92B; Kornicker & Iliffe 1989a, Fig. 30E; to compare to a more primitive podocope 2nd antenna, e.g., of a Platycopida, Maddocks & Iliffe 1986, Fig. 3G). Podocopa also share some perhaps unique characters of sperm morphology, which probably constitute an additional synapomorphy (Wingstrand 1988). *Manawa* shares the probable antennal synapomorphy with Podocopa (Table 1; Swanson 1989, Text-fig. 3A).

Mandible, 1st and 2nd maxillae: the coxa

The protopodal coxa (or precoxa if subdivision present, or proximal part of undivided protopods) is the most basal limb segment in Crustacea, i.e. the article attached to the body, and the coxa is apparently mislabelled on the Hou *et al.* (1996) figures of the mandible and both maxillae (compare our Fig. 5C–F to Hou *et al.* 1996, Fig. 8C–E). As noted earlier, the black color used by Hou *et al.* (1996) to indicate the 'coxa' is unfortunately almost an imperceptibly darker black than the black used to indicate the 'exopodite' (Hou *et al.* 1996, Fig. 8C–E).

In their mandibular figure the coxal endite, a huge basal molar-like tooth, is apparently labelled as the coxa (blackened in Hou *et al.* 1996, Fig. 8C). However, the basal triangular portion (protopod) of the mandible to which that tooth is attached in *Zabythocypris* and most other Podocopa (e.g., Maddocks 1969, Fig. 58A of *Z. heterodoxa*) is omitted from Hou *et al.*'s figure (they do not show the entire most basal area of the limb). The molar-like tooth is actually the endite of a protopod, which is not shown. Interestingly, in most Myodocopa the most proximal article of the mandible, the coxa, has a similar rather triangular basal attachment area and a large endite. Furthermore, in most cladocopids and halocyprids, the coxal endite is a strong basal molar-like tooth similar to that shown for *Zabythocypris*, but the endite is clearly distal to the limb attachment to the body; i.e. the tooth is a distal coxal endite, not the entire coxa alone (e.g., Kornicker & Sohn 1976, Fig. 2A; Kornicker & van Morkhoven 1976, Fig. 4E; Kornicker & Iliffe 1989a, Fig. 30F–H). Very possibly, this ostracode coxal endite is homologous to the large 'proximal endite' (proposed as the genesis of the crustacean coxa by Walossek & Müller 1998) of the Orsten fossils, *Bredocaris* (Müller & Walossek 1988, Fig. 3C) and *Skara* (Müller & Walossek 1985a, Fig. 7C) and is thus a symplesiomorphic crustacean, as well as ostracode, character.

In the maxillary figures of Hou *et al.* (Hou *et al.* 1996, Fig. 8D, E; compare to our Fig. 5D, E), only distal parts of the basal articles of the 1st and 2nd maxilla are blackened;
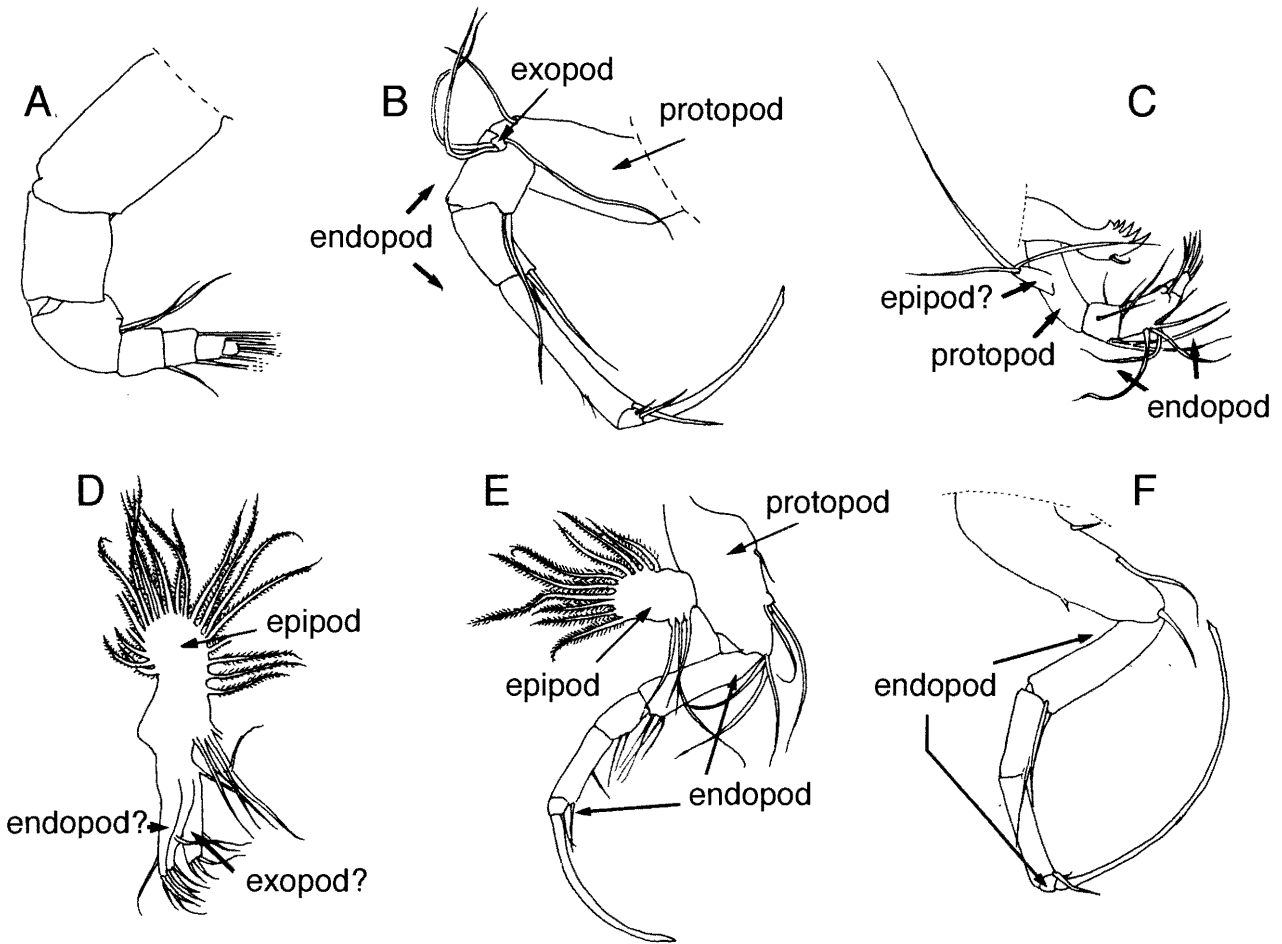
Fig. 5. First six limbs of *Zabythocypris redunca* Athersuch & Gooday, 1979 (Podocopa, Podocopida, Bairdiocopina, Bythocyprididae) (after Hou *et al.* 1996, Fig. 8) □A. 1st antenna. □B. 2nd antenna. □C. Mandible (proximal part not shown). □D. 1st maxilla (4th limb) (one lobe not shown). □E. 2nd maxilla (5th limb). □F. 1st trunk (6th) limb.

the coxa is mislabelled for those limbs, because by definition the coxa is the most proximal part of the limb and not an attached setal lobe. We only wish to point out that something more distal on a limb should not by definition be labelled a coxa without an explanation of how it was transformed to a more distal position on the limb. Hou *et al.* did not explain why a distal part of the limb is homologous with the coxa.

Mandible, 1st and 2nd maxillae: the epipod and/ or exopod

In the podocopid mandible, the slightly setose and less plate-like protopodal lobe (Fig. 5C) may represent an exopod; it is similar in shape (though only partially in position) to the myodocopid mandibular exopod (e.g., Kornicker & Sohn 1976, Fig. 28A; Kornicker 1981, Fig.

74A; Kornicker & Iliffe 1989a, Fig. 30G). Most myodocopid mandibles have both an exopod and endopod inserted terminally on the basis, but no proximal epipod.

The homology of the more setose protopodal ramus present on the 1st and 2nd maxillae of *Zabythocypris* (Hou *et al.* 1996, Fig. 8 D, E) is more ambiguous, because in shape that ramus resembles an epipod-like setose plate (Fig. 5D, E), but such podocopid plates are sometimes in a position that is neither basal nor terminal on the protopod (i.e. not clearly that of an epipod or exopod). Note that the 1st maxilla of *Zabythocypris* as figured by Hou *et al.* (Hou *et al.* 1996, Fig. 8D) shows only three elongate distal lobes. The podocopid 1st maxilla actually has four such lobes (e.g., Maddocks 1969, Fig. 54C of *Z. helicina*). One distal lobe was probably underneath the others when drawn and thus omitted. One of these elongate lobes (the 'palp' in ostracode terminology) is probably homologous to an endopod. In the Platycopida and many Podocopida

(including *Saipanetta*), the most distal of those four lobes is jointed with two or three articles (Maddocks 1972, Fig. 3C of *Saipanetta*; Maddocks & Iliffe 1986, Fig. 3F of a Platycopida; Martens 1990, Fig. 13H of a Cytherocopina; Wouters & Martens 1994, Pl. 1:8 of a Cypridoidea), but the three more proximal adjacent lobes are unjointed and may represent endites (unless the two more proximal lobes represent endites and the two more terminal lobes are exopod and endopod).

By comparison of form, the rather proximal setose plates ('branchial' or 'vibratory plates' in ostracode terminology) of the podocopid 1st and 2nd maxillae are homologous to the epipod of the cladocopid (Myodocopa) 2nd maxilla; as described above, the cladocopid setose plate cannot be an exopod, because the cladocopid limb also has a more distal and differently formed exopod (as well as an endopod) located terminally on the basis (Fig. 3C). Interestingly, the 2nd maxilla of the probably more primitive podocopid *Cytherella* (Platycopida) appears perhaps to have both a setose plate-like epipod, as well as a setose exopod and a jointed clasper-shaped endopod (e.g., Maddocks 1982, p. 225; Maddocks & Iliffe 1986, Figs. 3I, J, 5B), but the possible exopod is ambiguously positioned and unusually setose. Similar problems exist in determining the homologies of the less setose and more distal unjointed protopodal extensions of the trunk limbs of *Saipanetta* (Sigillocopina, Podocopida) (Maddocks 1972, Fig. 4A, C; Maddocks 1973, Pls. 4-15, 5-7); those may represent an exopod rather than an epipod.

We are certainly not the first to consider these homologies (e.g., Hartmann 1966, pp. 189–204), and hope that we will not be the last.

The number of extant ostracode species

A minor correction we would like to make is that there are very roughly 8,000 described Holocene ostracode species (7,000 podocopids + 600 myodocopids, Morin & Cohen 1991, p. 2), not 13,000 (7,000 + 6,000), as erroneously cited (Hou *et al.* 1996, p. 1131). New taxa are being discovered each year, and there may be 25,000 (or more) living species including those ostracodes still unknown. Many more fossil taxa have been named.

Conclusions

1 The Myodocopa and Podocopa probably form a monophyletic group, the Ostracoda, but no living taxa exhibit only primitive morphology. Primitive attributes probably include dorsal trunk segmentation and biramous limbs with a basal epipod. A few Podocopa have dorsal trunk segmentation. A few Halocyprida (Myodocopa) have both dorsal trunk seg-

mentation and an unambiguously biramous limb with basal epipod.

2 The 2nd maxilla and the 1st trunk limb of several probably primitive living Ostracoda of the order Halocyprida (Myodocopa) are unambiguously biramous appendages with a proximal precoxa, coxa, and basis, setose plate-like epipod originating on the precoxa, as well as both an endopod and exopod attached to the terminal end of the basis. These limbs are proposed as the best choice for comparison of ostracode limbs with those of other crustaceans and fossil arthropods.

3 A molar-like tooth that is present proximally on the mandibular protopod of many ostracodes (many Podocopa and primitive halocyprid Myodocopa) is the coxal endite and is attached to the coxa (or basal protopod when the protopod is undivided).

4 A setose plate-like epipod, as identified on the biramous limbs of some primitive Holocene halocyprids, was present in myodocopid ostracodes at least as early as the Triassic, as demonstrated by the fossil *Triadocypris*.

5 The proximal setose plate present basally on the 2nd maxilla and 1st trunk limb of many podocopids may be homologous to the myodocopid epipod.

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