

Exopodites, Epipodites and Gills in Crustaceans

GEOFF A. BOXSHALL¹ & DAMIÀ JAUME²

¹ Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom [g.boxshall@nhm.ac.uk]

² IMEDEA (CSIC-UIB), Instituto Mediterráneo de Estudios Avanzados, c/Miquel Marqués, 21, 07190 Esporles (Illes Balears), Spain [d.jaume@uib.es]

Received 01.iii.2009, accepted 22.v.2009.

Published online at www.arthropod-systematics.de on 25.viii.2009.

> Abstract

The structure of the outer parts of the maxillae and post-maxillary limbs is compared across the major crustacean groups. New anatomical observations are presented on the musculature of selected limbs of key taxa and general patterns in limb structure for the Crustacea are discussed. Exopodites vary in form but are typically provided with musculature, whereas epipodites and other exites lack musculature in all post-maxillary limbs. Within the Crustacea, only the *Myodocopa* possesses an epipodite on the maxilla. New evidence from developmental genetics, from embryology, and from new Palaeozoic fossils is integrated into a wider consideration of the homology of exites (outer lobes). This evidence supports the homology of the distal epipodite of anostracan branchiopods with the epipodite-podobranch complex of malacostracans. The evidence for the homology of pre-epipodites across the Crustacea is less robust, as is the evidence that the possession of a proximal pre-epipodite and a distal epipodite is the ancestral malacostracan condition. The widely assumed homology of the peracaridan oostegite with the pre-epipodite is questioned: little supporting evidence exists and possible differences in underlying control mechanisms need further exploration.

> Key words

Comparative anatomy, limb structure, musculature, Crustacea.

1. Introduction

The main axis of crustacean post-antennular limbs originally comprises a proximal protopodal part plus two distal rami, an outer exopodite and an inner endopodite or telopodite (see BOXSHALL 2004 for review). The medial (inner) surface of a trunk limb can be produced to form a series of endites, including the proximal gnathobase. Similarly, the lateral (outer) surface of a trunk limb may be produced to form one or more exites, or outer lobes. In this paper we focus on the lateral compartment of the limb, i.e. on the exopodite and the exites of all kinds, and we compare the amazing diversity of lateral limb structures expressed throughout the Crustacea. We also focus primarily on the maxilla and post-maxillary trunk limbs because, as indicated by the cephalocaridan condition (SANDERS 1963; HESSLER 1964), the limbs posterior to the maxillule are derived from a common pattern. However, where relevant we will include information on

maxillary structure. In addition we consider crustacean gills since many of the structures referred to as gills, a functionally based but anatomically imprecise term, are modified exites carried on the limbs. Other gills are modifications of the body wall adjacent to limb bases.

The main aims of this paper are to explore the structure of the lateral compartment of limbs and to re-examine the evidence supporting the identification of homologous structures in different crustacean groups. The evidence base comprises some new anatomical observations on selected crustaceans, integrated with the new data emerging from morphological studies on fossil arthropods, particularly those from the Palaeozoic, from gene expression patterns as revealed by recent evolutionary-development studies, and from embryological studies. In addition, we seek to address some of the terminology problems by identifying new

criteria that might serve to strengthen the standard definitions.

2. Materials and methods

2.1. Material studied

Amphionides reynaudi (H. Milne Edwards, 1833) material from collections of NHM, London: Reg. No. 1984.403.

Anaspides tasmaniae (Thomson, 1893) material from collections of NHM, London: Reg. Nos. 1953.12.4.3–16.

Andaniotes linearis K.H. Barnard, 1932 material from collections of NHM, London: Reg. Nos. 1936.11.2.649–656.

Argulus foliaceus (Linnaeus, 1758) adult female serial sectioned (transverse sections) at 8 µm, stained with Mallory's trichrome.

Argulus japonicus Thiele, 1900 unregistered material from collections of NHM, London.

Bentheuphausia amblyops G.O. Sars, 1885 material from collections of NHM, London: Reg. Nos. 1940.VIII.5.1–4.

Nebalia pugettensis Clark, 1932 ovigerous female from collections of NHM, London: Reg. No. 1983.91.21.

Phreatogammarus fragilis (Chilton, 1882) material from collections of NHM, London: Reg. Nos. 1928.12.1.2282–2285.

Proasellus banyulensis (Racovitza, 1919) collected at Son Regalat, Bellpuig, Artà, Mallorca (Balearic Islands) by D. Jaume.

Pseudericthrus larva of *Pseudosquilla* sp. from collections of NHM, London: Reg. No. 1967.11.4.5.

Polycope sp. material from collection of NHM, London: Reg. No. 1986.46.

Spelaeomysis bottazzii Caroli, 1924 material collected from Zinzulusa Cave, Lecce, Italy by D. Jaume, G. Boxshall & G. Belmonte.

Sphaeromides raymondi Dollfus, 1897 males from collections of NHM, London: Reg. Nos. 1948.3.9.7–9.

Tulumella sp. material collected from the Exuma Cays, Bahamas, by T.M. Iliffe, G.A. Boxshall and D. Jaume.

2.2. Methods

Dissected appendages were observed as temporary mounts in lactophenol on a Leitz Diaplan microscope equipped with differential interference optics. Anatomical drawings were made with the aid of a camera lucida. Material for SEM was washed in distilled water, dehydrated through graded acetone series, critical point dried using liquid carbon dioxide as the exchange medium, mounted on aluminium stubs and sputter coated with palladium. Coated material was examined on a Phillips XL30 Field Emission Scanning Electron microscope operated at 5 kV.

When describing limb axes we used proximal-distal to describe the axis from the origin on the body

to its tip, anterior-posterior for the axis parallel to the longitudinal anterior-posterior axis of the body, and lateral-medial (and outer-inner) to describe parts of limbs lying away from or closer to the vertical plane on the longitudinal anterior-posterior axis. Dorsal and ventral are used topologically, with reference to the ventral nerve cord.

3. The exopodite

The exopodite is the outer ramus of the biramous arthropodan leg and has traditionally been defined by its origin on the distal part of the protopodite (the basis), lateral to the endopodite. The exopodite has been distinguished from other outer structures (exites of various kinds) on limbs by the possession of musculature inserting within it: such musculature is typically lacking in exites. Exopodites are divided into segments in some arthropods and the presence of intrinsic musculature allows segments to move relative to one another. Recently, the developmental approach employed by WOLFF & SCHOLTZ (2008) has generated a new criterion – the exopodite and endopodite are formed by a secondary subdivision of the growth zone of the main limb axis whereas lateral outgrowths, such as exites, result from the establishment of new axes. The earliest expression of the *Distal-less* gene in the tips of biramous limb buds is irrespective of the form of the adult limb, i.e. whether it is stenopodial or phyllopodial (OLESEN et al. 2001). As noted by WOLFF & SCHOLTZ (2008), the process of exopodite and endopodite formation by subdivision of the primary limb axis is reflected by the transformation of the initially undivided *Distal-less* expression into two separate domains representing the tips of the two rami (WILLIAMS 2004). The mechanism producing this split is currently unknown but suggested likely scenarios are the suppression of *Distal-less* expression in the area between the exopodal and endopodal domains, or apoptosis (WOLFF & SCHOLTZ 2008).

3.1. Exopodites in non-crustacean Arthropoda

Comparison of the form of the exopodite across key fossil and Recent arthropod taxa led BOXSHALL (2004) to suggest that the ancestral state of the arthropodan exopodite was probably two-segmented. In early Palaeozoic arthropods, such as trilobites, the trunk limbs are typically biramous, with a well developed inner walking branch (the endopodite) and a well-developed, more-lamellate outer branch (the exopodite)

(EDGECOMBE & RAMSKÖLD 1996). Marrellomorphs, such as the Cambrian *Marrella* and the Silurian *Xylorkorys*, also retain biramous post-antennular limbs (WHITTINGTON 1971; SIVETER et al. 2007a) and their exopodites are well developed and apparently multi-segmented. The basal arachnomorphan *Sanctacaris* from the Cambrian has slender but not conspicuously segmented exopodites on its prosomal limbs (BRIGGS & COLLINS 1988; and see also BOXSHALL 2004).

In chelicerates, exopodites are rarely retained. Among extant chelicerates the Xiphosura retain exopodites on the flap-like, opisthosomal limbs (see BOXSHALL 2004: fig. 4C). The study of *Limulus* development by MITTMANN & SCHOLTZ (2001) revealed the presence of transient, laterally-located, points of *Distal-less* expression on the developing prosomal limbs buds. This expression pattern was interpreted by MITTMANN & SCHOLTZ (2001) and by WOLFF & SCHOLTZ (2008) as evidence of the vestiges of epipodites but by BOXSHALL (2004) as vestiges of exopodites. We favour the latter interpretation because it is congruent with data on fossil chelicerates, in particular on the recently discovered *Offacolus*, from the Silurian Herefordshire Lagerstätte. The prosoma of *Offacolus* carries a pair of small uniramous chelicerae followed by six pairs of limbs, the first five of which each carry a large exopodite in addition to the walking limb branch (the endopodite); the sixth being uniramous (SUTTON et al. 2002). It is the exact correspondence of the *Distal-less* expression pattern in *Limulus* (absent on chelicerae, present on pedipalps and walking legs 1 to 4, absent in chilaria) with the exopodite expression pattern in *Offacolus* (absent on chelicerae, present on limbs 2 to 6, absent in limb 7) that we find compelling.

Extrapolating from their study on the clonal composition of amphipod trunk limbs, WOLFF & SCHOLTZ (2008) stated that it was “more reasonable to interpret the two branches in many Cambrian arthropod limbs as a uniramous limb with an exite”, going on to conclude that a “true biramous limb” comprising an endopodite and an exopodite “evolved as a result of a split of the initial limb bud within euarthropods, probably either in the lineage of the Mandibulata or that of the Tetraconata”. This challenges the view of the biramous limb as a euarthropodan apomorphy. One implication of this re-interpretation is that the structures identified as exopodites on the prosomal limbs of *Offacolus*, for example, represent epipodites (a special type of exite, see below). Given their large size, cylindrical construction and the changes of angle between adjacent podomeres, which indicate an apparent segmented state, we consider this highly unlikely. The segmented state of the exopodite is especially significant since the ‘segments’ (podomeres) do not resemble the annulations of annulate structures in arthropods, such as malacostracan antennules.

WOLFF & SCHOLTZ’s (2008) suggestion is partly based on their interpretation of the development of the flabellum on the fourth walking leg of *Limulus polyphemus*, in which *Distal-less* expression in the pedipalps to fourth walking legs inclusive is concentrated in a large inner group of cells that gives rise to the endopodite and a small outer group of cells where it is only transient, except in walking leg 4 where the group of cells gives rise to the flabellum of the adult (MITTMANN & SCHOLTZ 2001). WOLFF & SCHOLTZ (2008) infer from the timing of development of the flabellum, after the normal limb axis has been established, that it represents a secondary axis rather than a subdivision of the primary limb bud (which helps to define a ramus). We do not share this interpretation and we hypothesise that the late expression of *Distal-less* on the flabellum (and its serial homologues on the more anterior limbs), relative to that on the endopodite is secondary – a result of heterochrony. We consider it likely, given the absence of an expressed exopodite on the pedipalps and walking limbs 1 to 3, that the expression of *Distal-less* marking the exopodal bud, as well as being weak and transient, is also secondarily delayed in all the post-chelicerate prosomal limbs. The flabellum thus represents the delayed exopodal bud of walking leg 4, its ancestral adult condition being indicated by the equivalent walking limb of *Offacolus*.

3.2. Branchiopoda

In the Crustacea the form of the exopodite is variable. Within the Branchiopoda the exopodite of trunk limbs is unsegmented and lamella-like both in fossils such as *Rehbachella* (WALOSSEK 1993) and in extant Anostraca and Notostraca (OLESEN 2007). The presence of muscles originating in the undivided protopodal part of the limb and inserting proximally within the exopodite as, for example, in the anostracan *Thamnocephalus* (WILLIAMS 2008) helps to define this exopodite as a primary ramus. When considering the development of limbs in crustaceans, WILLIAMS (2007) wrote “Although the exopod and, much more rarely, the endopod can be lost in certain taxa ... apparent fusions or splitting of these branches do not occur.” However, just in the Branchiopoda there are several examples of exopodites that are divided into dorsal and ventral lobes. Trunk limbs from species representing three diplostracan taxa, Laevicaudata, Spinicaudata and Cyclotherida, figured in OLESEN (2007: figs. 10D,H,I) all show such exopodites divided into dorsal and ventral lobes. In *Lynceus* the ventrally-extended exopodal lobe appears almost flagellum-like (MARTIN 1992: fig. 38A). In all three taxa the bilobate exopodites have a long outer margin which carries a row of well-developed, closely-set, plumose setae extending from the

dorsal to the ventral extremity. This setal array runs continuously along the margin, in close proximity to the inner surface of the carapace valves with which it is functionally linked. Motions of the setose exopodite create flow fields in the volume of water retained within the carapace, enhancing respiratory and/or osmotic exchange across the modified inner surface of the carapace (MARTIN 1992).

In female branchiopods the divided exopodites of the trunk limbs can fulfil an additional reproductive function. In lynceids (Laevicaudata) the dorsal lobes of the exopodites of trunk limbs 9 and 10 are elongate and, in conjunction with lateral flaps on the body wall, function to retain the egg mass in the brood chamber within the carapace (MARTIN 1992). In the Spinicaudata the dorsal exopodal lobes are modified on trunk limbs 9 to 11 and form the so-called dorsal filaments to which the eggs are attached (MARTIN 1992). In female Notostraca the eleventh pair of trunk limbs is modified as an egg-bearing oostegopod, and the undivided exopodite serves as a lid closing off the concave pouch where the eggs are carried (FRYER 1988).

3.3. Branchiura

The anterior trunk limbs of the Branchiura carry structures referred to as flagella, the homology of which has been controversial. WILSON (1902) considered the flagellum to be protopodal in origin although BOUVIER (1898) had correctly demonstrated that it arises at the base of the exopodite. In *Dolops* and in most species of *Argulus* the flagellum is present only on the first two pairs of thoracopods and takes the form of a medially-directed lobe originating on the posterodorsal margin of the laterally-directed exopodite (Fig. 1). Each flagellum originates from the extreme proximal part of the exopodite, close to its articulation with the basis (Fig. 2). Each is reflexed medially, lying over the posterodorsal surface of both coxa and basis, and carries along its free surface a row of well-developed, closely-set, plumose setae. This setal array lies in close proximity to the under surface of the laterally-projecting carapace lobes of *Argulus*. Motions of the swimming legs generate water flow across the modified ventral surface of the carapace, enhancing osmotic exchange through the so-called 'respiratory areas' (HAASE 1975).

The exopodal nature of the flagellum is clearly demonstrated by its origin on the exopodite and by the presence of a short intrinsic muscle inserting within its base (Fig. 3). As in the case of the diplostracan taxa, the subdivided exopodite can be functionally linked with the presence of modified areas on the adjacent surface of the carapace. Flagella are absent in the genus *Chonopeltis*, which is characterised by reduced carapace lobes and exposed swimming legs, and in

some species of *Argulus*, particularly those from the marine environment. It would be interesting to analyse in detail the correlation between the absence of flagella in *Argulus* species and the salinity regime inhabited.

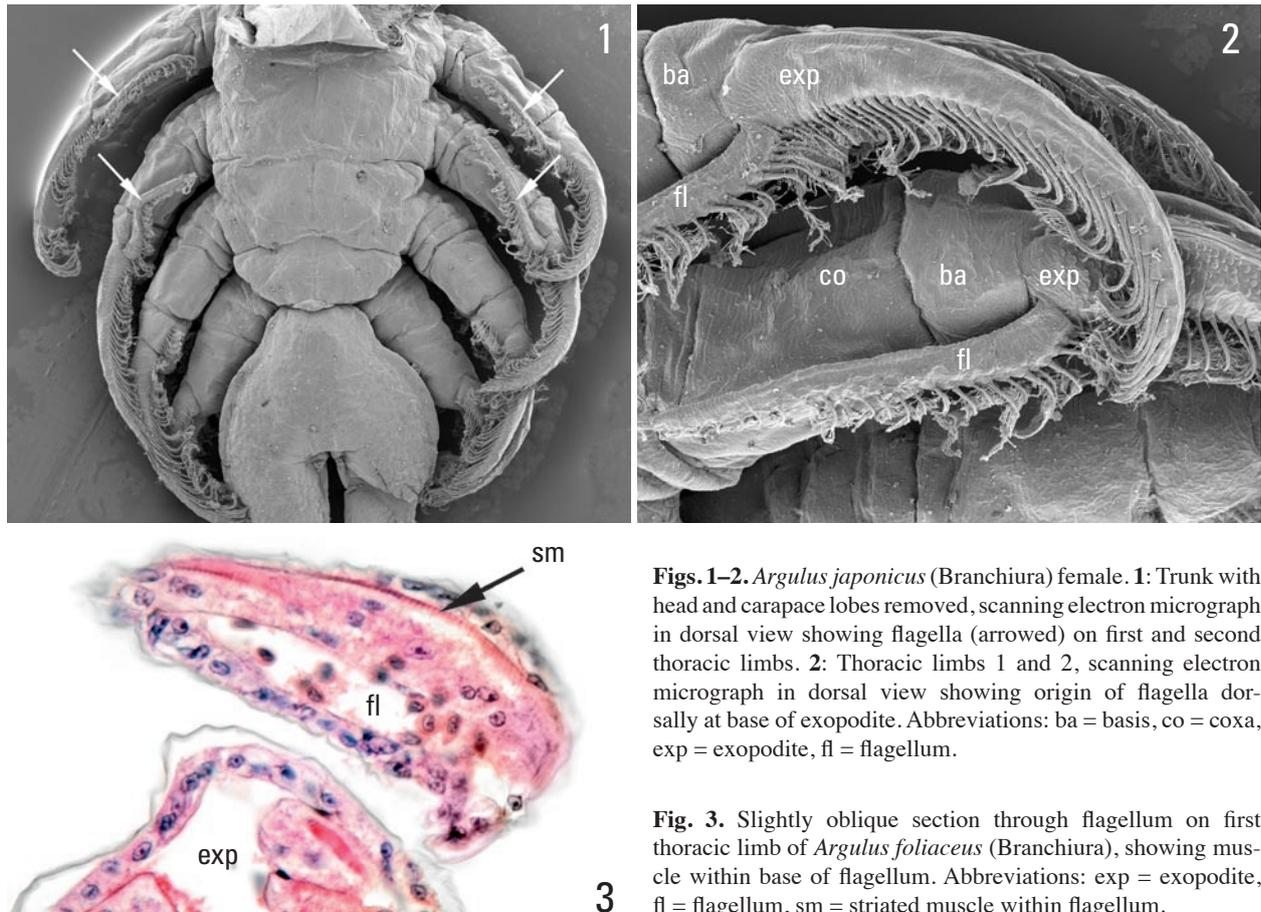
3.4. Cephalocarida

In the trunk limb of the Cephalocarida the structure identified by SANDERS (1963) and HESSLER (1964) as the exopodite is two-segmented and contains five intrinsic muscles within the proximal segment, four of which (HESSLER 1964: fig. 3, ext₁₋₃ and exj) insert around the proximal rim of the distal segment. However, the exopodite carries a flattened outer lobe basally on the margin of the first segment. This leaf-like lobe was referred to as the pseudepipod by SANDERS (1963) because it "inserts on the proximal exopodal segment rather than on the coxa", but other authors have regarded it as an epipodite. RICHTER (2002), for example, considered that the site of origin of the pseudepipod and the presence of setae are not strong enough evidence to reject the possibility of homology with the branchiopod and malacostracan epipodite.

We regard the musculature as an important additional line of evidence. We accept that the pseudepipod represents a subdivision of the exopodite because the presence of muscles (originating within the protopod) inserting within it (HESSLER 1964: fig. 3, psf₁₋₃) confirms its derivation as part of a ramus (typically supplied with musculature) rather than as an epipodite or other outer lobe (typically lacking musculature). The pseudepipod of cephalocaridans resembles the flagellum of the branchiuran fish lice in its location at the base of the exopodite and in the presence of muscles inserting within it.

3.5. Podocopa

The Podocopa and Myodocopa are treated separately here in accord with the emerging evidence that the Ostracoda is not a monophyletic taxon (e.g. REGIER et al. 2008). MCKENZIE et al. (1999) referred to the branchial plates of podocopan mandibles, maxillules and maxillae as epipodial plates. This interpretation has been quite widespread, although there are several others; HANSEN (1925) for example regarded the branchial plate of the mandible as an exopodite, that of the maxillule as an epipodite, and that of the fifth limb as a pre-epipodite. HORNE (2005) pointed out that the so-called 'branchial plate' on the mandible is carried on the basis and is supplied with intrinsic muscles originating in the basis. He reinterpreted it as the exopodite. Given the musculature pattern, we agree and note that no epipodites are known from the mandibles



Figs. 1–2. *Argulus japonicus* (Branchiura) female. **1:** Trunk with head and carapace lobes removed, scanning electron micrograph in dorsal view showing flagella (arrowed) on first and second thoracic limbs. **2:** Thoracic limbs 1 and 2, scanning electron micrograph in dorsal view showing origin of flagella dorsally at base of exopodite. Abbreviations: ba = basis, co = coxa, exp = exopodite, fl = flagellum.

Fig. 3. Slightly oblique section through flagellum on first thoracic limb of *Argulus foliaceus* (Branchiura), showing muscle within base of flagellum. Abbreviations: exp = exopodite, fl = flagellum, sm = striated muscle within flagellum.

of any members of the Podocopa, or from any crustacean. HORNE (2005) also concluded that the ‘branchial plates’ of podocopan maxillules and maxillae (= fifth limbs) are modified exopodites, and showed that they are supplied with muscles originating in the basis, as for example in *Eucypris virens* (see HORNE 2005: fig. 8). We agree that the branchial plates are exopodites.

The podocopan sixth limb is primitively biramous but the exopodite is reduced. It is represented by an elongate segment in the sigilloidean *Saipanetta*, by a small setose lobe in the bairdioidean *Neonesidea*, by one or two setae in some other taxa, or is lacking (HORNE 2005).

The exopodites on the maxillules and maxillae of podocopans sometimes show subdivision into a posterior lobe bearing many plumose setae and an anterior lobe bearing a few anteriorly-directed setae (often referred to as “reflexed setae”) that lack setules (HORNE 2005). Only the posterior lobe of the exopodite appears to be involved in generating water flow.

3.6. Mydocopa

Mydocopans carry a reflexed lobe on the basis of the mandibular palp and, although sometimes re-

ferred to as an epipod or epipodial plate, this is the exopodite (HORNE 2005). The maxillule carries a one-segmented setose exopodite in mydocopans such as *Azygocypridina* (BOXSHALL 1997: fig. 13.2b) and in the cladocopine *Metapolycope duplex* the maxillary exopodite is apparently divided into two segments by a weak diagonal suture during the first instar only, although subsequent instars have a one-segmented exopodite (KORNICKER & ILIFFE 1989). HORNE (2005) suggested that the two-segmented state may be regarded as a plesiomorphic character state within the Crustacea and commented that this may be taken as evidence that “the Mydocopa are a very early offshoot of the crown-group Crustacea”.

The maxillae and sixth limbs in mydocopans are biramous, each with a small setose, one-segmented exopodite (BOXSHALL 1997; COHEN et al. 1998; KORNICKER 2000).

3.7. Malacostraca

The exopodite on the pereopods of both leptostracan and archaeostracan Phyllocarida is unsegmented and lamellate (SARS 1896; BRIGGS et al. 2004). Internally the exopodite has conspicuous afferent and efferent

channels, typical of the haemolymph circulation system of such respiratory structures, as in *Nebalia* (VAN NIER et al. 1996) and *Dahlella* (SHU et al. 1999), and there may be traces of such structures preserved in the Silurian fossil *Cinerocaris* (see below). The exopodite is muscular, with short muscles that originate in the protopodal part of the limb passing into and inserting within the exopodite (Fig. 4).

In stomatopods (Hoplocarida) the pereopodal exopodites are missing on the anterior five pairs (the maxillipeds) and, according to CLAUS (1871), they are apparently represented by the slender, two-segmented, inner, stenopodial ramus on pereopods 6 to 8, which undergoes rotation during development.

In the pereopods of eumalacostracans the fundamentally two-segmented exopodite is commonly flagellate with an annulated distal segment (Fig. 5). There are intrinsic muscles present in the proximal segment and these insert on or close to the telescoped proximal rim of the distal segment. Typically no musculature extends much beyond the proximal rim towards the flagellate tip of the distal segment (cf. BOXSHALL 2004: fig. 5F). A well-developed, multi-annulate exopodal flagellum is retained at least in some of the pereopods in many malacostracan groups, including the Anaspidacea, a few genera of Bathynellacea (for example *Paraiberobathynella*, *Sinobathynella* and *Billibathynella*), the dendrobranchiate Decapoda, the Lophogastrida, Cumacea, Tanaidacea and Mysida. In other malacostracan taxa the distal segment of the two-segmented exopodite is undivided, as for example in the pereopods of most of the Bathynellacea (family Parabathynellidae), the Euphausiacea and the Thermosbaenacea (HESSLER 1982; WAGNER 1994; CAMACHO 2004). Rarely the entire exopodite is lamellate, as in the maxilliped of mysids such as *Spelaeomysis* (Fig. 6) and *Stygiomysis* (WAGNER 1992), and in some Bathynellacea (the family Bathynellidae) the exopodite is unsegmented. In the Spelaeogriphacea the exopodites of the posterior pereopods are transformed into gill-like structures (GRINDLEY & HESSLER 1971). The exopodite of pereopods 2 to 8 of the Carboniferous syncarid *Palaeocaris secretanae* has an undivided distal segment (PERRIER et al. 2006), indicating that its annulate state in Recent syncarids might be secondarily derived within the group. However, we consider it

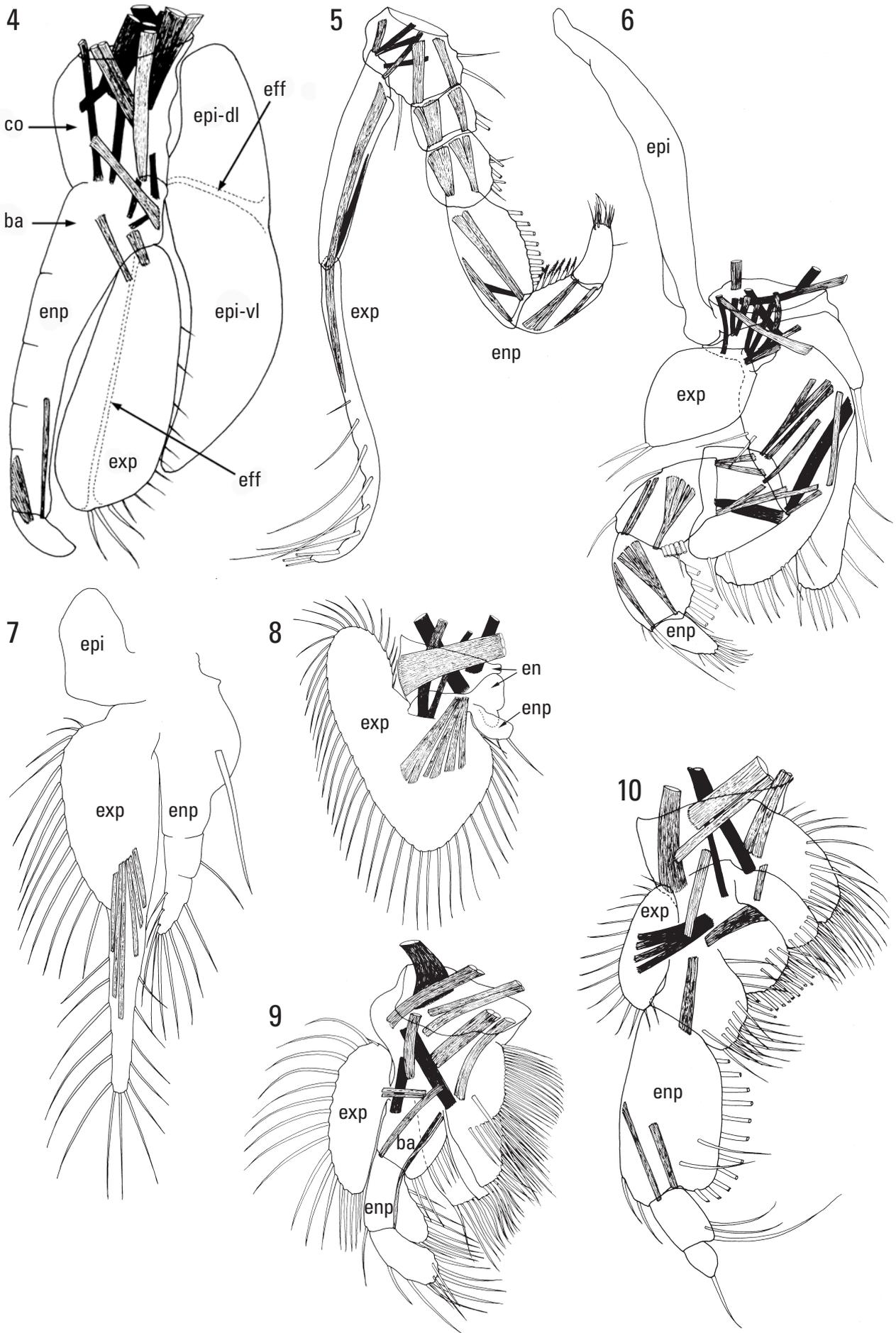
probable that the distal exopodal segment was annulate in the ancestral stock of the Eumalacostraca.

Interpreting the status of reduced exopodites in some eumalacostracans remains problematic, partly because of changes in muscle signature patterns. In the highly derived maxilliped of *Amphionides*, for example, the exopodite is flattened, lamellate and unsegmented but is bipartite with a broad proximal section and a slender, tapering distal section (Fig. 7). Unusually, the intrinsic musculature is located somewhat distally within the exopodite, forming a broad fan spanning the transition region where the broad base and slender tip merge. We infer that this region represents the plane of the original articulation between proximal and distal segments of a two-segmented exopodite.

The exopodite of the maxilla in decapod malacostracans typically forms a well developed lamellate outer lobe, known as the scaphognathite or 'bailer' (SCHRAM 1986). It has setose margins and typically functions to create water flow across the gills. The maxilla of *Amphionides* shows extreme development of the scaphognathite: it dominates the limb and the endopod and endites are all profoundly atrophied (Fig. 8). All the musculature serves to move the scaphognathite, with the extrinsic muscles moving the entire limb and the intrinsic muscles moving just the scaphognathite. A lamellate exopodal lobe is also found in the Mysida, Euphausiacea (Figs. 9–10) and the Lophogastrida (MANTON 1928), but is usually considerably smaller than in the decapods. In most other eumalacostracans, including syncarids, the exopodite of the maxilla is reduced or absent. In the stomatopods HANSEN (1925) identified a small sub-triangular protruding plate on the outer margin of the third maxillary segment as representing the exopodite. After examination of both larval and adult stomatopod maxillae, we find no evidence to substantiate this suggestion. In the Phyllocarida the exopodite is absent in the archaeostracan *Cinerocaris magnifica* (BRIGGS et al. 2004) but in the Leptostraca a slender exopodite is present (SARS 1896).

The exopodite of the maxilla in malacostracans has on occasion been misinterpreted as an epipodite or referred to as an exite, but no malacostracans, fossil or extant, are known to possess an epipodite on the maxilla (HANSEN 1925).

Figs. 4–10. Malacostraca. **4:** Second pereopod of ovigerous female of *Nebalia pugettensis* (Leptostraca), showing limb-intrinsic musculature supplying exopodite but no muscles entering epipodite. **5:** First pereopod of *Spelaeomysis bottazzii* (Mysida) showing intrinsic musculature. **6:** Maxilliped of *Spelaeomysis bottazzii* showing reduced, lamellate exopodite, well developed epipodite and intrinsic musculature. **7:** Maxilliped of *Amphionides reynaudi* (Amphionidacea) showing intrinsic musculature in foliaceous exopodite only. **8:** Maxilla of *Amphionides reynaudi* showing intrinsic musculature. **9:** Maxilla of *Spelaeomysis bottazzii* showing intrinsic musculature. **10:** Maxilla of *Bentheuphausia amblyops* (Euphausiacea) showing intrinsic musculature. Abbreviations: ba = basis, co = coxa, eff = major efferent channel of haemolymph system, en = endite, enp = endopodite, epi = epipodite, epi-dl = dorsal lobe of epipodite, epi-vl = ventral lobe of epipodite, exp = exopodite.



3.8. Loss of the exopodite

All post-antennular limbs are primitively biramous, expressing both exopodite and endopodite, in at least some taxa within the Crustacea (BOXSHALL 2004). However, the exopodite is not expressed in many limbs in particular crustacean groups and in extant hexapods and myriapods the post-antennular limbs are also uniramous. OLESEN et al. (2001) noted that the absence of the exopodite in the thoracopods of the haplopodan branchiopod *Leptodora kindtii* was the result of the suppressed bifurcation of the early limb bud. The development of the uniramous pereopods in which the exopodite is not expressed, was compared with that of the biramous pleopods in the amphipod *Orchestia cavimana* by WOLFF & SCHOLTZ (2008). They showed that uniramous pereopods are formed by the suppression of the split into exopodite and endopodite of the primary growth zone of the main limb axis. Comparing the clonal composition of the embryonic pereopods and pleopods, WOLFF & SCHOLTZ (2008) showed that the same population of cells (identical genealogical background) which forms the exopodite in the biramous pleopods contributes to the outer part of the endopodite of the uniramous pereopods along most of the proximo-distal axis but not to the tip. The failure of expression of the exopodite in development results in the 'exopodal' cell columns being conscripted to contribute to the endopodite.

We consider the single expressed ramus to be the endopodite because it externally resembles a typical malacostracan pereopodal endopodite, comprising ischium, merus, carpus, propodus and dactylus, and, internally, amphipod pereopods show the musculature pattern typical of the endopodite of biramous pereopods in other peracaridans (cf. HESSLER 1982). In terms of its basic organization the ramus is an endopodite. Presumably, the failure of development of the exopodite resulted in the population of cells that would have formed the exopodite becoming an unexploited resource that was subsequently recruited to contribute to the endopodite. We interpret this simply as efficient use of resources.

Amphipods are traditionally regarded as lacking pereopodal exopodites (e.g. RICHTER & SCHOLTZ 2001), but STEELE & STEELE (1991) noted that the seventh pereopod (eighth thoracic limb) of some amphipods carries a gill-like exopodite on the basis – not an epipodite on the coxa. This suggested homology requires further exploration: it was not addressed by WOLFF & SCHOLTZ (2008) since the seventh pereopods of *Orchestia* lack 'gills'.

In addition to amphipods, isopods are traditionally regarded as not expressing exopodites on any thoracic limbs (Tab. 1), although JAUME (2001) noted the presence of a small setose lobe on the basis of the fifth per-

Tab. 1. Maximum expression of the presence of exopodites on thoracic limbs of different malacostracan taxa. * based on Dendrobranchiata (data from PEREZ-FARFANTE & KENSLEY 1997); v = possible vestige of exopodite in *Atlantasellus* (data from JAUME 2001); +¹ in manca stage only of certain Apseudomorpha (data from BĂCESCU & PETRESCU 1999); +² data from STEELE & STEELE (1991).

Taxon	Th1 mxp	Th2	Th3	Th4	Th5	Th6	Th7	Th8
Leptostraca	+	+	+	+	+	+	+	+
Hoplocarida	-	-	-	-	-	+	+	+
Anaspidacea	+	+	+	+	+	+	+	-
Bathynellacea	+	+	+	+	+	+	+	+
Decapoda*	+	+	+	+	+	+	+	+
Amphionidacea	+	+	+	+	+	+	+	-
Euphausiacea	+	+	+	+	+	+	+	+
Thermosbaenacea	+	+	+	+	+	+	+	+
Lophogastrida	+	+	+	+	+	+	+	+
Mysidacea	+	+	+	+	+	+	+	+
Amphipoda	-	-	-	-	-	-	-	+ ²
Isopoda	-	-	-	-	v	-	-	-
Bochusacea	-	+	+	+	+	+	+	-
Mictacea	-	+	+	+	+	+	+	-
Tanaidacea	-	+	+	-	-	+ ¹	+ ¹	-
Cumacea	-	-	+	+	+	+	+	-
Spelaeogriphacea	-	+	+	+	+	+	+	-

epods in *Atlantasellus* which he interpreted as possibly representing the exopodite. Tanaidaceans retain an exopodite on the second and third thoracic limbs (chelipeds and first pereopods) but an exopodite is also expressed transiently on the sixth and seventh thoracic limbs during the manca stage of certain apseudomorph tanaidaceans (GUTU & SIEG 1999).

4. Exites – outer lobes

Exite is employed here as a general term for any outer lobe originating on the protopodal part of a limb. It encompasses a variety of lobate structures for which a plethora of terms has been used, including epipodite, podobranch gill, coxal plate, pre-epipodite, mastigobranch, exognath, epipodial plate, pseudoexopod and branchial plate. Some of these terms are no longer in use, others are synonyms. We seek below to identify positional, structural, genetic and developmental criteria that allow the most useful of these terms to be defined unambiguously. We consider that positional and developmental criteria provide the strongest evidence of homology, and are, therefore, of the greatest utility. Although using the expression pattern of certain

genes, such as *Distal-less*, is problematic, we find the restricted but congruent patterns of expression of other genes, for example, *nubbin* and *apterous*, or *trachealess* and *ventral veinless*, to be highly informative. In the case of *Distal-less* it is sometimes the absence of expression at a particular stage of development that is informative, rather than its presence.

4.1. Epipodites and pre-epipodites

4.1.1. Branchiopoda

Anostracans alone among the Branchiopoda carry more than a single exite on the post-cephalic trunk limbs. Fossil branchiopods, such as the Cambrian *Rehbachella* and the Devonian *Lepidocaris* lack any exites at all on any limbs of any known growth stages (WALOSSEK 1993; SCOURFIELD 1926). Recent anostracans, however, may have either two or three exites on the trunk limbs, of which the proximal two are often referred to as pre-epipodites. The distalmost is referred to here as the epipodite of the Branchiopoda.

The epipodite in branchiopods is a flattened, lamellate lobe which is typically carried distally on the outer margin of the protopodal part of the trunk limb, adjacent to the origin of the exopodite. It lacks setation along its free outer margin and lacks musculature. The epipodite also exhibits distinctive gene expression patterns: it strongly expresses *nubbin*, *apterous* (AVEROF & COHEN 1997), *trachealess* (MITCHELL & CREWS 2002) and *ventral veinless* (FRANCH-MARRO et al. 2006), but only weakly expresses *Distal-less* (WILLIAMS et al. 2002; WILLIAMS 1998). In *Triops longicaudatus*, a notostracan, *Distal-less* is never strongly expressed in the epipodite (WILLIAMS 1998). Similarly in the cyclestheridan *Cyclestheria hislopi* the epipodite shows no *Distal-less* expression (OLESEN et al. 2001). However, in the anostracan *Thamnocephalus platyurus* there is some *Distal-less* expression in the epipodite early in development, although this is subsequently down-regulated (WILLIAMS et al. 2002). This is the single epipodite found in non-anostracan branchiopods.

In addition to the epipodite, two pre-epipodites are found in members of one anostracan family, the Chirocephalidae. In other anostracan families, such as the Artemiidae, Thamnocephalidae and Streptocephalidae, only a single pre-epipodite is found but morphogenetic data indicate that it always develops from paired rudiments (WILLIAMS 2007). On the basis of parsimony, WILLIAMS (2007) inferred that the ancestral state for the Anostraca was for paired rudiments to form a single pre-epipodite in the adult, and that the state of having two separate pre-epipodites was autapomorphic to the derived family Chirocephalidae. We consider that the embryological evidence of the

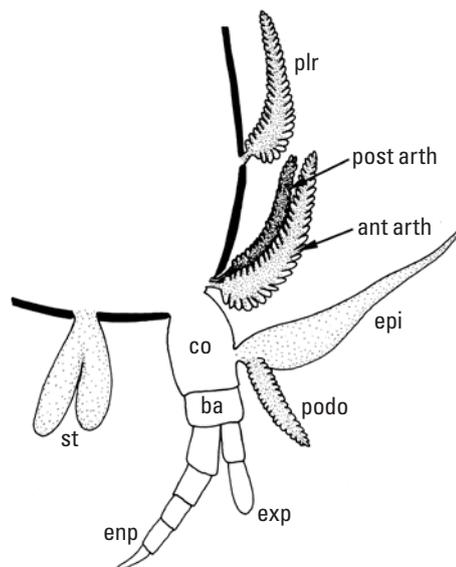


Fig. 11. Schematic showing origins of gills in Malacostraca (adapted from HONG 1988). Abbreviations: ant arth = anterior arthrobranch, ba = basis, co = coxa, enp = endopodite, epi = epipodite, exp = exopodite, plr = pleurobranch, podo = podobranch, post arth = posterior arthrobranch, st = sternal gill.

double origin of the pre-epipodite strongly supports the inference that two pre-epipodites were present in the shared ancestor of the Recent Anostraca, although this is not necessarily indicative of the ancestral state of the crown-group Crustacea.

The anostracan pre-epipodite can be identified morphologically by its double origin. It does not express the genes *nubbin*, *apterous*, *trachealess* and *ventral veinless*, but it maintains its *Distal-less* expression, unlike the true epipodite (WILLIAMS et al. 2002).

In the Branchiopoda, the epipodite and pre-epipodites appear first as the transverse ridge which constitutes the horizontally organised limb bud (with the distal part located laterally) is differentiating into endite lobes and rami (see MØLLER et al. 2004). In the chirocephalid *Eubbranchipus grubii* the epipodite and both pre-epipodites are already expressed in the form of distinct, somewhat flattened lobes by the time the trunk limbs swing into their vertical adult orientation (MØLLER et al. 2004).

4.1.2. Malacostraca

In decapods the podobranch gill and the epipodite typically share a common base (Fig. 11) arising from the lateral compartment of the coxa in post-maxillary limbs (HONG 1988; HAUPT & RICHTER 2008). This epipodite-podobranch complex provides a distinctive and highly recognisable morphological signature that is valuable for comparative studies, although the closeness of the association between podobranch and epipodite varies

Tab. 2. Maximum expression of the presence of the epipodite-podobranch complex on thoracic limbs of different malacostracan taxa. * based on Dendrobranchiata (data from PEREZ-FARFANTE & KENSLEY 1997).

Taxon	Th1 mxp	Th2	Th3	Th4	Th5	Th6	Th7	Th8
Leptostraca	+	+	+	+	+	+	+	+
Hoplocarida	+	+	+	+	+	-	-	-
Anaspidacea	+	+	+	+	+	+	+	-
Bathynellacea	+	+	+	+	+	+	+	+
Decapoda*	+	+	+	+	+	+	+	-
Amphionidacea	+	-	-	-	-	-	-	-
Euphausiacea	+	+	+	+	+	+	+	+
Thermosbaenacea	+	-	-	-	-	-	-	-
Lophogastrida	+	+	+	+	+	+	+	+
Mysidacea	+	-	-	-	-	-	-	-
Amphipoda	-	-	+	+	+	+	+	-
Isopoda	+	-	-	-	-	-	-	-
Tanaidacea	+	-	-	-	-	-	-	-
Cumacea	+	-	-	-	-	-	-	-
Spelaeogriphacea	+	-	-	-	-	-	-	-
Bochusacea	-	-	-	-	-	-	-	-
Mictacea	-	-	-	-	-	-	-	-

with taxon within the Decapoda (TAYLOR & TAYLOR 1989). In brachyurans the epipodite first appears as a rounded bud on the outer surface of coxa of the limb (HONG 1988), typically during the zoeal phase. It elongates during successive moults within the zoeal phase and the podobranch appears at a subsequent moult, as a simple bud, located basally on the epipodite. The epipodites of the various limbs do not necessarily appear at the same stage, so in brachyurans, for example, the appearance of the epipodite bud on the second maxilliped is commonly delayed relative to the first and third maxillipeds. In decapods the epipodite forms as a bud-like outgrowth on the lateral surface of the coxa, at each subsequent moult it lengthens, and, finally, setae are added distally and the podobranch bud appears proximally (HONG 1988).

In the decapod *Pacifastacus leniusculus* the epipodite-podobranch complex is bilobed early in development. DAMEN et al. (2002) apparently found strong expression of the gene *pdm/nubbin* "throughout the epipod/gill". However, using the same model decapod species, FRANCH-MARRO et al. (2006) found expression of *pdm/nubbin* only in the posterior lobe, which corresponds to the epipodite of the adult. The epipodite lobe also expresses *engrailed*, but only in the posterior half (FRANCH-MARRO et al. 2006). The epipodite, like both rami, spans the antero-posterior compartment boundary and *engrailed*-expressing cells are found posterior to the boundary only. The anterior lobe, which cor-

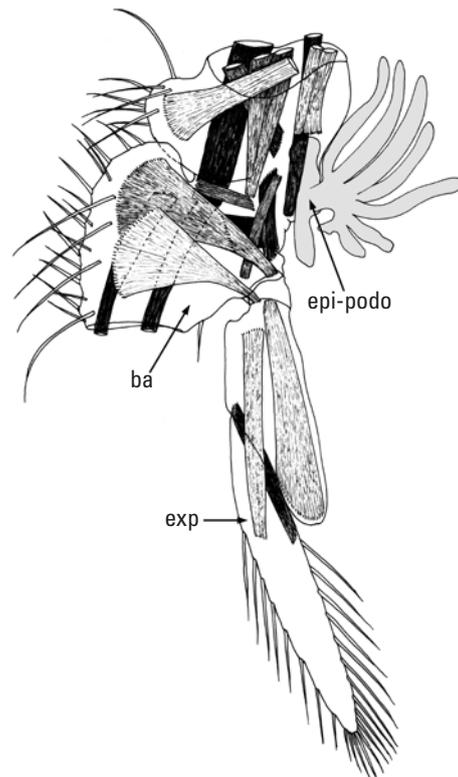


Fig. 12. *Bentheuphausia amblyops* (Euphausiacea). First pereopod with endopod not drawn, showing epipodite-podobranch complex and intrinsic musculature within exopodite. Abbreviations: ba = basis, epi-podo = epipodite-podobranch complex, exp = exopodite.

responds to the podobranch, lacks any *engrailed*-expressing cells and, at least according to FRANCH-MARRO et al. (2006), does not express *pdm/nubbin*.

Euphausiaceans have gills on their pereopods (Figs. 12–13). The gills of the more posterior pereopods tend to be larger and more complex than those on the anterior limbs, but all originate as outgrowths from the epipodite (SARS 1896). The origin of the gill as an outgrowth from the coxal epipodite is robust evidence that the euphausiacean gill is the homologue of the decapod epipodite-podobranch complex. Similarly, in lophogastrids such as *Gnathophausia*, the complex branched coxal gills arise from a common base with the epipodite (SARS 1896). Again, we infer from the shared base originating on the pereopodal coxa, that the gills of the Lophogastrida are homologues of the decapod epipodite-podobranch complex.

Amphipods also have pereopodal gills (Tab. 2). In a perceptive review of gill structure in gammaridean amphipods, STEELE & STEELE (1991) noted that the gill on the last thoracic limb, pereopod 7, originates on the basis and concluded that it represents a modified exopodite rather than an epipodite. We note here that the exopodites on the posterior pereopods of spelaeogriphaceans are also gill-like. STEELE & STEELE (1991) also noted that some amphipods have bilobed coxal

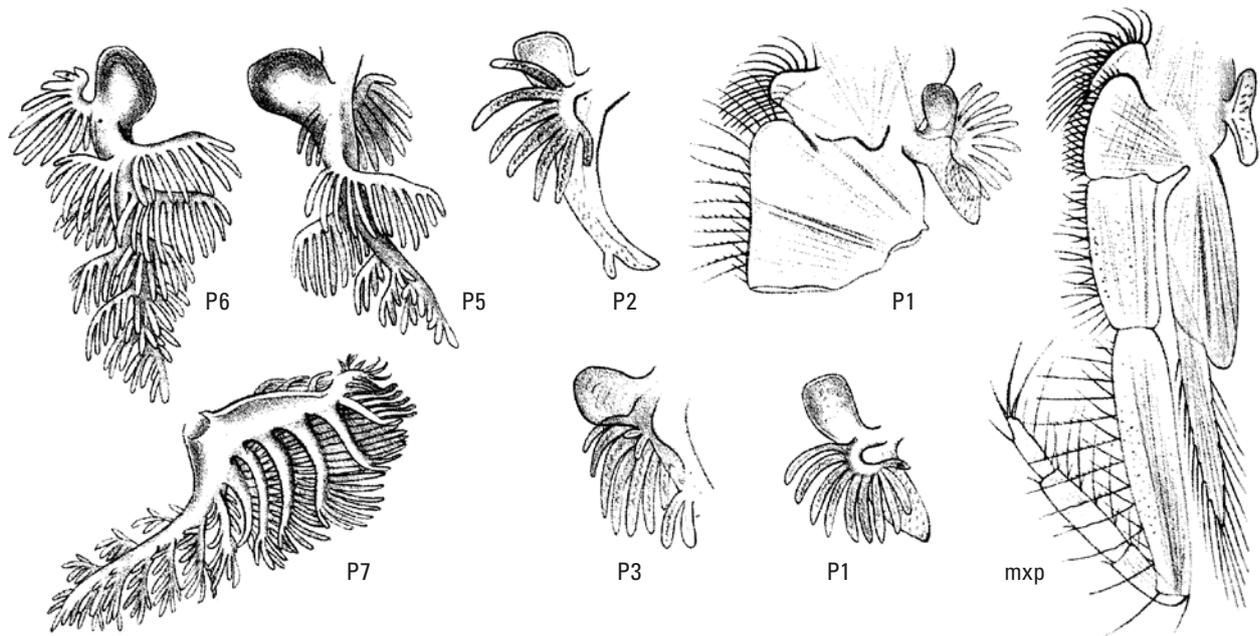


Fig. 13. Gills along pereopod series of *Bentheuphausia amblyops* (Euphausiacea) showing increasing complexity of podobranch in more posterior legs (from Sars 1896). Abbreviations: mxp = maxilliped, P1–7 = pereopods 1–7 (P4 not figured).

gills comprising a small, outer accessory lobe and a large, lamellate gill lobe. It is possible that the bilobed structure represents the epipodite-podobranch complex. The distribution of bilobed gills within the Amphipoda led STEELE & STEELE (1991) to suggest that this was the primitive state and that in most amphipods the outer lobe was lost. We note that vestiges of an apparently bilobed structure can be found in many other amphipods, such as the Sebidae (JAUME et al. 2009). In some female caprellids the epipodite can be expressed, together with the oostegite, even though the pereopod itself is lacking apart from the coxal part which is largely incorporated into the body wall. In the model amphipod *Parhyale hawaiiensis*, the epipodite strongly expresses the genes *tracheless* and *ventral veinless* (FRANCH-MARRO et al. 2006). It also shows the typical expression pattern of *engrailed*, in the posterior compartment of the epipodite only (BROWNE et al. 2005).

Isopods lack pereopodal epipodites but typically retain a well developed epipodite on the maxilliped (Tab. 2). In the cirrolanid *Sphaeromides raymondi* the maxilliped is described as possessing three well developed outer lobes in ovigerous females (RACOVITZA 1912: fig. V). In males (Fig. 14) and immature females the coxa of the maxilliped is produced into a triangular outer lobe but the other lobes are lacking. In the immature female, the triangular coxal lobe was interpreted as representing the epipodite by RACOVITZA (1912: labelled 'ep' in his fig. VI). However, we consider this lobe to be an extension of the coxa rather than an epipodite, because a muscle originating in the trunk

inserts within it and it is not delimited from the coxa, so the surface ornamentation of cuticular crescents is continuous over the surface of both the coxa and the lobe. No ovigerous females of *Sphaeromides* were available for study but we consider that the distal outer coxal lobe represents the epipodite and that the third outer lobe, which is carried on the basis, represents a lateral expansion of the segment margin, rather than a vestigial exopodite. It is interesting to note that both the lateral expansion of the basis and the true epipodite are found only in ovigerous females. A similar lateral expansion of the maxilliped basis is found also in the asellid *Proasellus* (Fig. 15, lat), but in both sexes.

There are reports of an oostegite on the maxilliped of ovigerous females in some isopods (e.g. STOCH et al. 1996). This would be remarkable since oostegites are unknown on the maxilliped for any other peracaridan taxa (Tab. 3). In *Proasellus banyulensis* the maxilliped of the ovigerous female carries a large foliaceous epipodite on the outer margin of the coxa (Fig. 15, epi). This epipodite has a setose distal margin and is identical in both sexes. There is, however, an additional lobate structure on the coxa of the maxilliped of the female in *Proasellus*. A slender, gnathobase-like lobe originates on the medial side of the coxa (Fig. 15) and extends posteriorly so that its setose tip can pass dorsal to the anteriormost of the true oostegites and penetrate the anterior part of the marsupium. This lobe is muscular (MAGNIEZ 1974; present account) and it was referred to as the 'Wasserstrudelapparat' by MAGNIEZ (1974), in clear reference to its presumed function (= water-vortex-apparatus). This lobe is absent in males

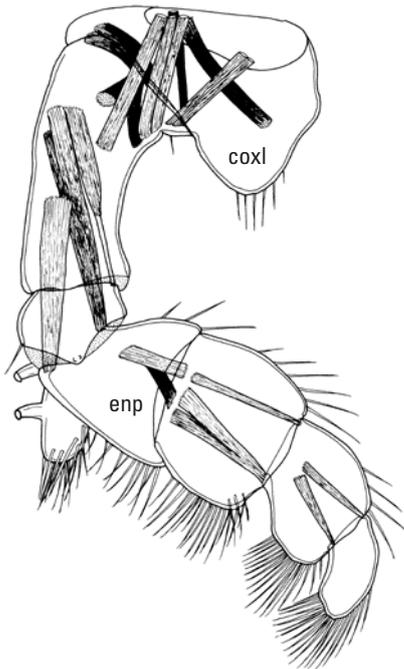


Fig. 14. Maxilliped of male *Sphaeromides raymondi* (Isopoda) showing muscle inserting within triangular lobe on coxa. Abbreviations: coxl = coxal lobe, enp = endopodite.

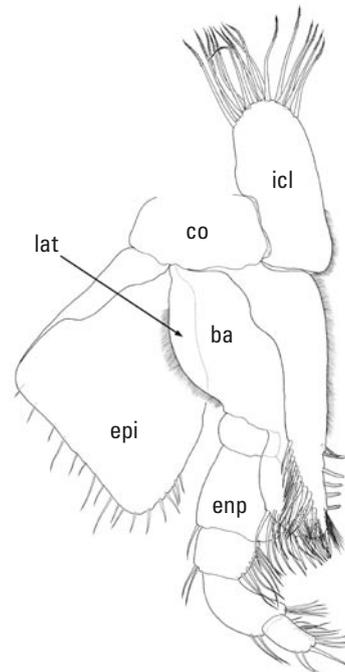


Fig. 15. Right maxilliped of ovigerous female of *Proasellus banyulensis* (Isopoda) anterior (= dorsal) view in anatomical position, showing foliaceous epipodite, inner coxal lobe with setose tip, and expanded lateral margin of basis. Abbreviations: ba = basis, co = coxa, enp = endopodite, epi = epipodite, icl = inner coxal lobe, lat = lateral expansion on basis.

and non-ovigerous females – a pattern of expression similar to that of true oostegites. Influenced by this expression pattern, some authors refer to this lobe as an oostegite, particularly in members of the Stenasellidae where the inner lobe is greatly expanded and foliaceous in form and lacks setae (MAGNIEZ 1974: fig. 2B, o), as is typical for isopod oostegites.

Isopods are unique among the peracaridans in showing this sexually dimorphic, inner coxal lobe on the maxilliped in Asellidae and Stenasellidae. Interestingly, in the Cirolanidae, Aegidae and Cymothoidae the epipodite of the maxilliped is also sexually dimorphic, being “apparently reduced or absent in all life stages except brooding females” (BRUSCA & WILSON 1991). Finally, the lateral expansion on the basis is also sexually dimorphic in *Sphaeromides* (RACOVITZA 1912) [although it is not dimorphic in *Proasellus* (Fig. 15, lat)]. In all of these taxa, aspects of the expressed form of the maxilliped fluctuate in concert with the reproductive cycle of the adult female and, presumably, the mechanism controlling this is similar to that inferred below for oostegites (see section 5). Despite the similar pattern of expression we do not consider the sexually dimorphic, inner coxal lobes on the maxilliped to be true oostegites (i.e. serial homologues of the oostegites on the pereopod series), because of the presence of intrinsic muscles inserting within them. Oostegites lack musculature.

Thermosbaenaceans, tanaidaceans, spelaeogriphaceans and cumaceans all lack pereopodal epipodites

but typically retain a well developed epipodite on the maxilliped (Tab. 2). In most of these taxa the epipodite is a simple lobe but in cumaceans it can be a complex structure forming a multi-lobate gill which may represent the epipodite-podobranch complex. Functionally it works together with the exopodite, which forms the siphon and maintains respiratory water flow through the branchial chamber (BĂCESCU & PETRESCU 1999).

Recent hoplocarids typically have one epipodite on the coxa of each of the first five thoracic limbs. CLAUS (1883) inferred that these epipodites are respiratory and BURNETT & HESSLER (1973) presented strong experimental evidence based on studies of the circulation system supplying the epipodites in *Hemisquilla ensigera*, indicating that they have a primary respiratory function. From their position on the limb and their structure, we infer that these relatively simple lamellar structures are the homologues of the epipodite-podobranch complex.

Uniquely amongst the Recent Malacostraca, two ‘epipodites’ are found on the pereopods of some Anaspidacea. Published examples of amphipods apparently possessing two coxal gills on some pereopods, such as the second gnathopod of particular *Phreatogammarus* species (cf. CHAPMAN 2003), have been re-interpreted as representing a normal coxal epipodite plus a foliaceous, stalked, sternal gill (Bréhier & Jaume pers. comm.). In anaspidaceans the two ‘epipodites’ origi-

nate close together, but separately, on the outer coxal margin and in life largely overlap, thereby functioning as a double lamella (CANNON & MANTON 1929). Different interpretations are possible: (1) these structures may be subdivisions of a single marginal lobe and both may represent the true crustacean epipodite; (2) the distal lobe is the epipodite and the proximal lobe is a pre-epipodite; (3) the double structure is the result of a duplication event. The second of these, the presence of a distal epipodite and a proximal pre-epipodite, has been widely accepted as the ancestral malacostracan condition (CALMAN 1909; HANSEN 1925; SIEWING 1963; DAHL 1983). Currently we lack unequivocal evidence that would enable us to identify the correct interpretation, although the presence of a single coxal epipodite in the Carboniferous *Palaecaris* and in the bathynellaceans should suggest to us at least the possibility that the presence of two lobes is a secondarily derived state within the Syncarida. There is no strong evidence that the proximal lobe of anaspidacean syncarids is the homologue of the pre-epipodite in anostracan branchiopods. However, information on expression patterns in Recent anaspidaceans of genes such as *engrailed*, *tracheiless* and *apterous* is needed in order to resolve the uncertainty regarding the origin and homology of these lobes.

Leptostracans typically have a single, large, lamellate epipodite on each of the pereopods (Tab. 2). It can be bilobed; the epipodite in *Nebalia* and *Speonebalia*, for example, is produced both dorsally and ventrally into flattened lobes (SARS 1885; BOWMAN et al. 1985). In *Paranebalia*, however, the epipodite is reduced and epipodites are absent in *Nebaliella*. The epipodite in *Nebalia* appears relatively late in development after the limbs have completed the swing down to their vertical, adult-orientation (OLESEN & WALOSSEK 2000). It begins development as a triangular-shaped rudiment but becomes a bilobed lamella in the adult. No muscles enter or insert on the epipodite in leptostracans (Fig. 4), it lacks marginal setation, and no *Distal-less* expression is found in the early anlagen of the epipodites (PABST & SCHOLTZ 2009).

Epipodites have also been described on the pereopods of a Silurian archaeostracan. BRIGGS et al. (2004) described extensive lateral lamellate structures on the pereopods of *Cinerocaris magnifica*. They found three dorsal and two ventral flap-like structures originating laterally on the limb stem (protopod) and all were presumed to be delicate because only the outer rim of each was preserved. BRIGGS et al. (2004) refer to the whole ensemble as presumably representing “some combination of exopod and epipods”. The most posteriorly-located of these dorsal and ventral structures are “joined and share a more proximal attachment to the limb”. We find this structure astonishingly similar to the dorso-ventrally bilobed epipodite on the pereopods

Tab. 3. Maximum expression of presence of oostegites on thoracic limbs in peracaridan taxa. r = rudimentary.

Taxon	Th1 mxp	Th2	Th3	Th4	Th5	Th6	Th7	Th8
Lophogastrida	-	+	+	+	+	+	+	+
Amphipoda	-	-	+	+	+	+	-	-
Isopoda	-	+	+	+	+	+	+	-
Bochusacea	-	-	+	+	+	+	+	-
Mictacea	-	-	+	+	+	+	+	-
Tanaidacea	-	+	+	+	+	+	+	-
Cumacea	-	r	+	+	+	+	-	-
Spelaeogriphacea	-	+	+	+	+	+	-	-
Mysidacea	-	+	+	+	+	+	+	+

of Recent leptostracans such as *Nebalia* and *Dahlella* in which the dorsal and ventral lobes are subdivided horizontally by a marked haemolymph channel (see VANNIER et al. 1996: fig. 7A; SHU et al. 1999: fig. 9A). The lamellate exopodite forms a second ventrally-directed lobe in these genera and may be homologous with the second, ventrally-directed flap-like lobe in *Cinerocaris*. The linear thickening strut in *Cinerocaris* (see BRIGGS et al. 2004) is positioned centrally, similar to the main haemolymph channel in the exopodite of Recent leptostracans. The remaining difference between the pereopods of *Cinerocaris* and *Dahlella* is the apparent presence of two additional dorsal, flap-like structures. These may be additional, overlapping epipodite-like structures (pre-epipodites), or duplicated epipodites, or they may be preservational artefacts since only the rims are preserved and it is possible that these rims represent the defining margins of the conspicuous afferent and efferent haemolymph channels that are found on these respiratory structures in living phyllocarids (see SHU et al. 1999).

4.1.3. Podocopa

No epipodites were recognised for any limbs of the Podocopa by HORNE (2005) in his review of ostracod limb structure.

4.1.4. Myodocopa

Epipodites have been reported on the maxillae (as fifth limbs) and sixth limbs of some Myodocopa. The maxilla of myodocopans carries a large branchial plate on the outer margin of the protopod which BOXSHALL (1997) interpreted as being precoxal in origin in *Azygocypridina*, but he found the limb highly modified, compact and difficult to interpret. HORNE

(2005) considered the recognition of a precoxa in myodocopan maxilla to be contentious citing COHEN et al. (1998) who interpreted the proximal part of the limb as an undivided coxa. This obviously has implications for elucidating the homology of the branchial plates. HORNE (2005) interpreted the maxillary branchial plate as a coxal epipodite in the cladocopines *Polycope* and *Metapolycope* because it was carried on an undivided coxa, proximal to the coxa-basis joint (Fig. 16).

No extant crustaceans other than myodocopans have an epipodite on the maxilla. Adopting HORNE'S (2005) interpretation of the part of the maxilla proximal to the coxa-basis joint as an undivided (or at least incompletely divided) coxa, we conclude that the outer lobe in *Azygocypridina* (a myodocopidan) is homologous with that in *Polycope* (a cladocopine halocypridan). Interestingly, branchial plates were also described in two Silurian myodocopans, the cylindroleberid *Colymbosathon* (SIVETER et al. 2003) and the nymphatelinid *Nymphatolina graviora* (SIVETER et al. 2007c). In *Nymphatolina* a similar epipodite is carried on both the maxilla and the sixth limb, suggesting serial homology.

4.1.5. Copepoda, Remipedia, Mystacocarida, Branchiura, Thecostraca and Tantulocarida

No epipodites are found on the maxilla or post-maxillary trunk limbs of any of these taxa. The single isolated outer seta found on the lateral margin of the coxa in the maxilla of certain calanoid copepods has been referred to as "probably representing" the epipodite (HUYS & BOXSHALL 1991) but there is no direct evidence in support of this interpretation, only an assumption of serial homology with the setose epipodite of copepod maxillules.

4.1.6. Pleopodal epipodites or exites

There are reports of pleopodal epipodites in some malacostracans. For example, a small setose outer lobe is present on the protopodal part of the first to fifth pleopods in some isopods belonging to the Flabellifera, such as *Bathynomus* (MILNE EDWARDS & BOUVIER 1902: plt. 6, figs. 2, 3, 5), and in the Phreatoicoidea (NICHOLLS 1943). This structure is referred to both as "epipodite-like" and as "an epipodite" in SCHRAM (1986). The pleopods or the uropods of some amphipods, such as *Thalassostygius* and *Metahadzia*, carry a process at the outer distal angle of the protopod immediately adjacent to the base of the exopodite (VONK 1990; NOTENBOOM 1988), but the homology of such processes is unclear. In a new phreatogammarid am-

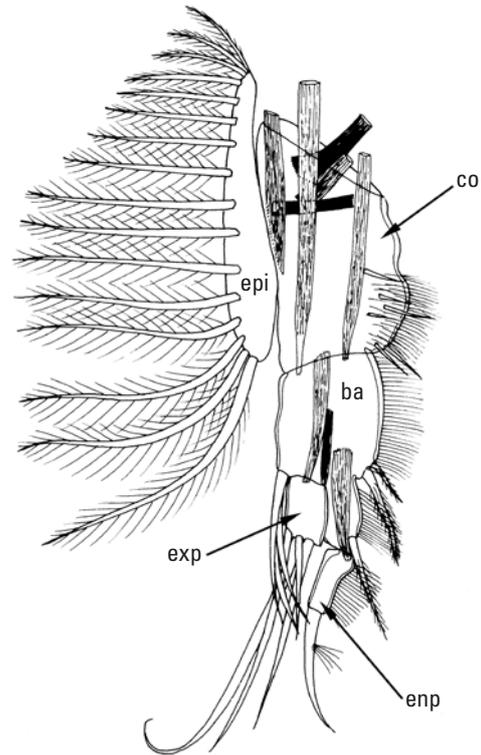


Fig. 16. Maxilla of male *Polycope* sp. (Myodocopa), showing epipodite on lateral margin of protopodal part proximal to coxa-basis joint. Abbreviations: ba = basis, co = coxa, enp = endopodite, epi = epipodite, exp = exopodite.

phipod from Chile, the third pleopod of the adult male displays a conspicuous, finger-like process on the lateral margin of the protopod of the limb (Bréhier & Jaume pers. comm.). This is a secondary sexual character of uncertain homology, but is possibly novel.

In an unidentified species of the leptostracan *Nebalia*, PABST & SCHOLTZ (2009) noted the presence of a tapering process at the outer distal angle of the protopod, immediately adjacent to the base of the exopodite, in the first three pairs of pleopods. This tapering process was not visible on the developing pleopod of *Nebalia pugettensis* at the stage illustrated by WILLIAMS (2004), but the process on the pereopod illustrated by WILLIAMS (2004: fig. 8) is identical to that illustrated on the pleopod by PABST & SCHOLTZ (2009: fig. 3A,C). PABST & SCHOLTZ interpreted these tapering processes on the pleopods as homologues of pereopodal epipodite anlagen and, therefore, as evidence of serial homology in the basal malacostracan lineage, prior to the differentiation of the trunk limbs into pereopods and pleopods. It is noteworthy here that the first pleopod of the archaeostracan *Cinerocaris* apparently possesses at least one flap-like structure (possibly two), in serial homology with the epipodite of the pereopods (BRIGGS et al. 2004).

We accept the suggested homology of these rudimentary processes in the Leptostraca. The presence of

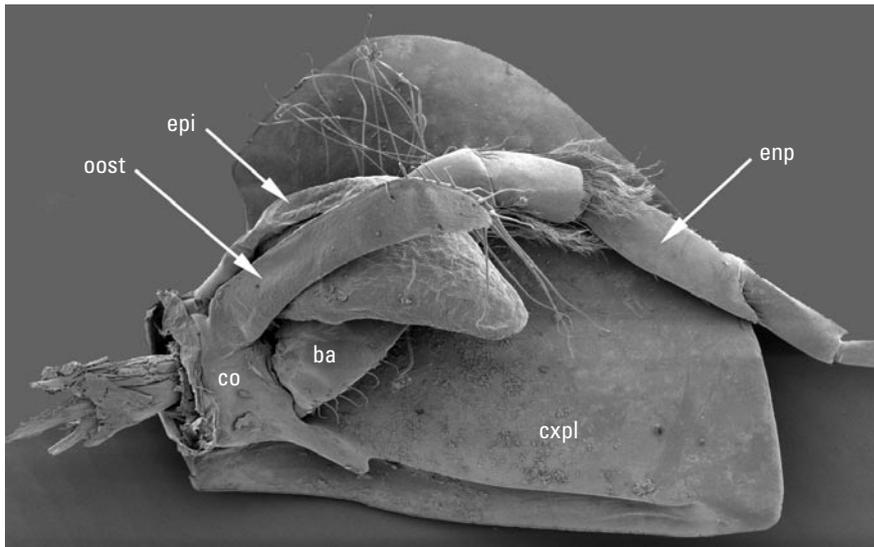


Fig. 17. Scanning electron micrograph of pereopod of *Andaniotes linearis* (Amphipoda; Stegocephaliidae) taken by Jørgen Berge, showing oostegite, epipodite and coxal plate. Abbreviations: ba = basis, co = coxa, cxpl = coxal plate, enp = endopodite, epi = epipodite, oost = oostegite.

a vestige of the epipodite in pleopods is entirely consistent with the occurrence of epipodites on more than just the first eight post-maxillary limbs in anostracan branchiopods. Expression data for genes such as *en-grailed*, *tracheiless* or *apterous* might help to resolve any remaining uncertainty.

4.2. Coxal plates of Amphipoda

Coxal plates are flattened outgrowths of the coxae of the pereopods and are characteristic of amphipods (Fig. 17). Functionally they extend the margins of the pereon ventrolaterally, effectively increasing the lateral compression of the body, shielding an inner channel through which water flows, and affording protection to the gills and oostegites (LINCOLN 1979). In the embryo of the hyalid amphipod *Parhyale hawaiiensis* the nascent coxal plate becomes apparent at stage 21 (120 h: 48% in scheme of BROWNE et al. 2005) arising proximally on the outer surface of the coxa. This is about the same time as the epipodite first appears, located distally on the coxa. In the talitrid *Orchestia cavimana* UNGERER & WOLFF (2005) concluded that the coxal plate and gill (= our epipodite) first appear proximolaterally as a shared anlage (labelled Cxpl+Gi in their figs. 2A and 3A) on pereopods 2 to 7. By the next stage of development the coxal plates and gills (UNGERER & WOLFF 2005: fig. 4C) have separate insertions and the longitudinally-orientated, proximo-laterally originating coxal plate is clearly distinct from the somewhat transversely-orientated, distally-located gill. Just prior to hatching, the coxal plates of pereopods 1 to 7 are described as having developed into broad imbricate shields covering the insertions of the limbs and the gills, which have become 'convoluted' by this stage. Although mislabelled as 'Cpl+Gi' by UNGERER

& WOLFF (2005: fig. 3A), the swelling on pereopod 1 is the anlage of the coxal plate alone because amphipods do not have a gill on the first pereopod (no gill is present on the seventh either).

UNGERER & WOLFF (2005) showed shared anlagen for coxal plate and gill on the very early stage embryonic pereopods 2 to 6 of *Orchestia cavimana*. Additional evidence of this common developmental origin comes from study of the clonal composition of the embryonic limb of *O. cavimana* (WOLFF & SCHOLTZ 2008), which showed that both the coxal plate and the gill are formed by basal clones from the dorsal-most cell columns (descendants of cells abcd7 to abcd9). These columns also contribute to the protopodal segments and the tergites. As pointed out by WOLFF & SCHOLTZ (2008), clonal composition data help to identify the coxal plate as an outer lobe or exite, but currently we lack sufficient comparative clonal data for us to use this information in identifying potential homologues in other malacostracan taxa.

Is the amphipod coxal plate homologous with any other proximally-located, crustacean exite? Its developmental origin as part of a common anlage with the amphipod gill might suggest that the whole coxal plate + gill complex is homologous with the epipodite-podobranch complex described above for decapods, euphausiaceans and lophogastrids. However, it also raises the intriguing possibility that the bilobed 'gill' of amphipods (noted by STEELE & STEELE 1991, see 4.1.2. above) represents the entire epipodite-podobranch complex, in which case, could the amphipod coxal plate be homologue of the anaspidacean proximal epipodite? More evidence is needed to answer these questions.

4.3. Coxal plates of Isopoda

DREYER & WÄGELE (2002) described the coxal plates of isopod pereopods, noting that “the lateral protrusion of the plate with the sharp longitudinal keel that separates the dorsal from the ventral surface of the plate is unique for these [Scutocoxifera] isopods”. The sclerotised coxal plates of isopods such as *Idothea* extend medially, to meet in the ventral midline, however coxal plates are absent in asellotes and phreatoicids. The coxal origin of the plate during embryogenesis was demonstrated by GRUNER (1954) in *Porcellio*. DREYER & WÄGELE (2002) considered that isopod coxal plates evolved within the Isopoda because they are absent in basal taxa such as the Phreatoicidea and Asellota, although they are present in the Calabozoida (BRUSCA & WILSON 1991), the supposed sister group of the Asellota (after WÄGELE 1989). BRUSCA & WILSON (1991) also considered the coxal plates to be derived within the Isopoda – a phylogenetic scheme that would imply that they cannot be homologues of amphipod coxal plates.

4.4. The epipodites of *Tanazios*

Tanazios is a Silurian arthropod interpreted as “a probable stem-lineage crustacean” by SIVETER et al. (2007b) although BOXSHALL (2007) considered that it should be classified as a member of the Labrophora, and its position could shed light on deep mandibulatan phylogeny. All its post-mandibular limbs are similarly patterned, with an endopodite and exopodite plus two exites on the outer margin of the protopodal part of the limb. These exites, although slender and rather pointed in form, are identified as epipodites by SIVETER et al. (2007b), but their narrow shape and relatively small size suggest that these exites are not primarily respiratory in function. The presence of two epipodites in this labrophoran contributes to the body of evidence suggesting that the presence of both an epipodite and a pre-epipodite on the trunk limbs was a more widely distributed character state in the Palaeozoic than previously realised. It could be interpreted as evidence that such a state was basic to the groundplan of the crown group Crustacea.

4.5. The epipodites of *Yicaris*

ZHANG et al. (2007) reported ‘epipodites’ on the trunk limbs of the Cambrian arthropod *Yicaris*, which they classified as a crown-group crustacean. Three of these exite structures are arrayed proximo-distally along the lateral margin of the protopodal part (the basipod of ZHANG et al.) of the post-mandibular trunk limbs. They

were homologised with the epipodite plus pre-epipodite of anostracan Branchiopoda, and a groundplan of three epipodites per limb was suggested for the Eucrustacea (ZHANG et al. 2007). The discovery of a series of larval stages revealed the pattern of development of individual epipodites: each commences development as a spine which then expands to form a leaf-like lamella on the lateral margin. These leaf-like structures pass through a stage with an extremely restricted proximal connection with the limb base (ZHANG et al. 2007: fig. 1h), consistent with having developed from a marginal spine. BOXSHALL (2007) considered that this pattern of development was significantly different from that of crustacean epipodites, which first appear in development as unarmed, rounded, tissue-containing lobes, and that this raised serious doubt over the homology of these structures with crustacean epipodites plus pre-epipodites.

We consider that these developmental differences are significant. We recognise that the epipodite vestige found on the anterior pleopods of *Nebalia* by PABST & SCHOLTZ (2009) has the form of a tapering spini-form lobe, but this is a broad-based expansion of the outer distal angle of the protopod and does not articulate with the segment. In addition, we note a difference in timing, with the epipodite and pre-epipodite anlagen appearing simultaneously, and much earlier, in anostracan embryos (MØLLER et al. 2004) than in *Yicaris* where these structures appear to be added sequentially during the post-embryonic, larval development, together with other setal elements. The absence of epipodite-like structures on limbs elsewhere within the Cambrian arthropod fauna also implies a phylogenetic isolation and suggesting to us that the structures in *Yicaris* represent an independently-derived exite series.

4.6. Pleopodal gills

The pleopods of stomatopods are typically broad, biramous flaps and carry tufted branching gills. These pleopodal gills originate on the exopodite, close to its base, as can be seen most readily in late larval stages (Fig. 18). Similar, highly branching, tufted pleopodal gills are present in the isopod *Bathynomus* (Flabellifera), however, these originate along the outer margin and near the base of the endopodite only (MILNE EDWARDS & BOUVIER 1902: plt. 6, figs. 2–7). A respiratory function for these structures can be inferred from the external morphology and from the enhanced endopodal circulation system elucidated by MILNE EDWARDS & BOUVIER (1902). The five pairs of pleopods in aquatic Isopoda are generally involved in respiration and/or osmo-regulation, although in some groups anterior pairs may be more robust and provide some protection

for the delicate, respiratory pleopods located posteriorly (ROMAN & DALENS 1999). The exopodal gills on the pleopods of stomatopods and the endopodal gills on the pleopods of aquatic isopods are independently derived. Their origins on the rami indicate that neither can be inferred to be serially homologous with the malacostracan pereopodal epipodite.

In some terrestrial isopods the respiratory pleopods show a most remarkable adaptation, forming a pleopodal 'lung' which is closed off externally by a spiracle and extends through the pleonal tissues as a mass of branching internal respiratory tubules (FERRARA et al. 1997). This trachea-like system has arisen within the Oniscidea as an adaptation to terrestriation and is independent of the trachea systems found in insects and in myriapods. In insects the tracheal system arises during development from tracheal placodes, cell clusters which invaginate and migrate to form the primary tracheal branches (MANNING & KRASNOW 1993). Homologues of the *Drosophila* tracheal inducer genes, such as the transcription factors *tracheiless* and *ventral veinless*, were shown by FRANCH-MARRO et al. (2006) to be expressed in crustacean epipodites leading them to speculate on the possibility of an evolutionary relationship between insect tracheae and crustacean epipodites.

4.7. Outer lobes on crustacean maxillules

Various outer lobes have been described from crustacean maxillules, some of which were referred to by HANSEN (1925) as pseudexopods.

4.7.1. Pseudexopod on the malacostracan maxillule

The maxillule of mysids and lophogastrids carries a broad, laterally-directed lobe arising from the posterior face of the coxa and referred to as the pseudexopod by HANSEN (1925). This flap-like lobe is described as delicate and its margins are ornamented with fine setules. According to CANNON & MANTON (1927), this pseudexopod functions as a valve controlling water flow during feeding activity.

The outer margin of the protopod of the maxillule of the syncarid *Paranaspides lacustris* is extended as a thin movable plate, also termed the pseudexopod by HANSEN (1925). This plate extends to meet the lateral ridge of the maxilla so as to completely cover the space between the maxilla and the maxillule. According to CANNON & MANTON (1929), the pseudexopod acts as a valve helping to control water flow during feeding. This structure appears to be derived simply as an extension of the lateral margin to form a flap.

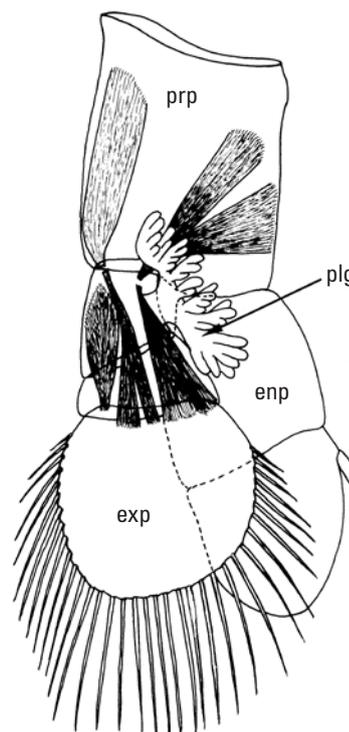
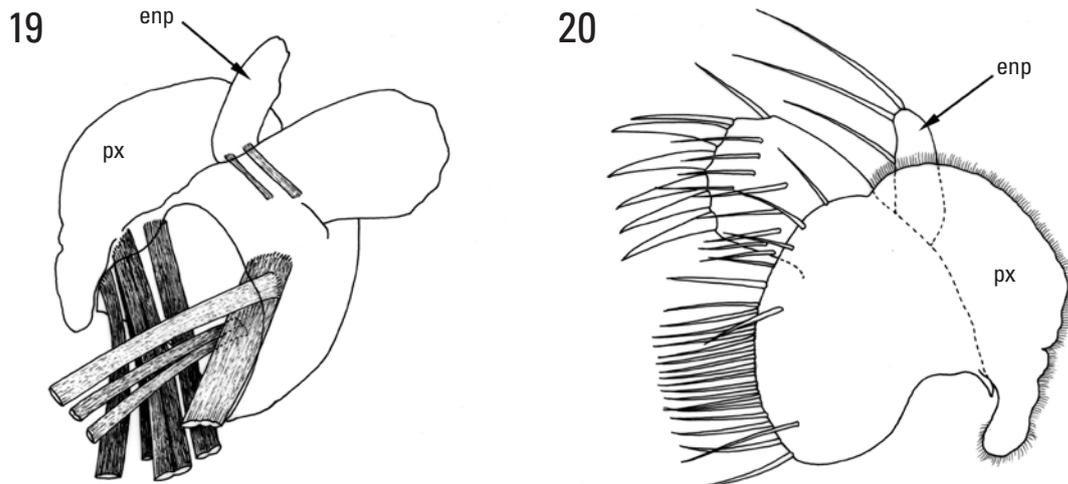


Fig. 18. Second pleopod of pseudosquilla larva of *Pseudosquilla* (Stomatopoda), showing gill on inner margin of first exopodal segment. Abbreviations: enp = endopodite, exp = exopodite, plg = pleopodal gill, prp = protopod.

SARS (1885) and HANSEN (1925) both described a lobe, referred to respectively as the exognath or pseudexopod, on the outer margin of the maxillule in some adult euphausiaceans and, despite HEEGAARD'S (1948) incorrect attempt to reinterpret this as the exopodite, HANSEN'S terminology is still employed by specialists such as MAUCLINE (1967). In *Bentheuphausia amblyops* the pseudexopod forms a fleshy extension of the lateral margin and is produced into a small dorsal lobe (Figs. 19–20). No muscles pass into the pseudexopod and the tissue it contains appears granular with large nuclei and dense cytoplasm, as is typical of highly active cells. In some species the pseudexopod carries setae distally, around its ventral extremity, as well as an ornamentation of fine surface setules. The true exopodite, which is expressed transiently during larval development, is absent in the adult of *Bentheuphausia*. However, *Pseudeuphausia sinica* exhibits a unique condition in which the larval exopodite persists into the adult and is present together with a well-developed pseudexopod (MAUCLINE 1967).

The possession of an exite, referred to as the pseudexopod, on the coxa of maxillule is common to mysidaceans, syncarids and euphausiaceans. Although not referred to as a pseudexopod, atyid decapods of the genus *Typhlatya* possess a very similar outer coxal lobe on the maxillule (JAUME & BRÉHIER 2005: fig. 9A). The pseudexopod appears to have a similar valve-



Figs. 19–20. Pseudexopod on maxillule of *Bentheuphausia amblyops* (Euphausiacea). **19:** Posterior view showing musculature. **20:** Anterior view showing fine setulation on surface of pseudexopod. Abbreviations: enp = endopodite, px = pseudexopod.

like function, controlling water flow in mysidaceans and syncarids, but in euphausiaceans the nature of the pseudexopod tissues suggests to us an osmoregulatory or ionic exchange function. All of these structures appear to be derived as extensions of the lateral coxal margin of the maxillule and are considered here to be exites rather than serial homologues of the epipodite of post-maxillary limbs, although this remains a remote possibility. We have insufficient evidence to determine whether these structures are homologous but their presence in all four taxa supports the inference that they are homologous.

4.7.2. Coxal epipodite and basal exite of the copepod maxillule

Copepods have a setose lobe on the outer margin of the coxa of the maxillule which is referred to as the epipodite (HUYS & BOXSHALL 1991). This is typically prominent in calanoid copepods where it functions to create water flow during feeding, but is reduced (= less prominent and represented by fewer setae) or lost in other orders. Uniquely, the basis also carries a defined outer lobe in the order Platycopioidea, which carries a maximum of two setae (HUYS & BOXSHALL 1991). This exite is represented by just a single seta on the outer margin of the basis in calanoid, misophrioid and basal harpacticoid copepods, and is lost in the remaining orders.

4.7.3. Coxal epipodite of the myodocopan maxillule

BOXSHALL (1997) interpreted the single seta originating near the lateral margin of the coxa of the maxillule in *Azygocypridina* as possibly representing a reduced

epipodite. According to HORNE (2005), more convincing evidence of a coxal epipodite can be found in the cylindroleberidoidean *Cycloleberis squamiger* and the cypridinoid *Skogsbergia squamosa*, both of which have a flattened, but unarmed lobe arising from the maxillulary coxa (KORNICKER 1974, 1975).

5. Oostegites

The Peracarida is traditionally characterised by the possession of a ventral brood pouch, or marsupium, formed by the oostegites in the adult female (SIEWING 1963). Oostegites are medially-directed, lobate outgrowths from the pereopodal coxae. In amphipods they develop gradually in the instars preceding the onset of sexual maturity but in isopods they appear fully formed at the moult into the adult. The oostegites overlap or interlock to provide an enclosure within which eggs and embryos develop, and different numbers of oostegites are expressed in the different peracaridan groups (Tab. 3). In caprellid amphipods two pairs of oostegites can be present in adult females even when the corresponding pereopod is lacking (apart from the coxa, which is largely incorporated into the body wall).

In amphipods, for example *Hyalella azteca*, the oostegites first appear as small lamellae at the sixth stage female, become progressively larger at successive moults, and attain their definitive, marginally setose form in the ninth stage, the adult (GEISLER 1944). We infer that gradual development of the oostegites, as exemplified by the amphipods, is the primitive pattern rather than the sudden appearance model. Oostegite form and development are highly variable and there

are two basic patterns within the Peracarida: oostegites can either retain their adult form through successive broods of an individual female, or oostegites may be lost or significantly reduced between successive broods. In amphipods, mysids and lophogastrids oostegites are retained between broods, although the marginal setation in amphipods may be reduced after each brood. In contrast, isopods, tanaidaceans and cumaceans have oostegites that are almost completely reduced or shed after each brood (SIEWING 1963; WATLING 1983). We agree with RICHTER & SCHOLTZ (2001) that differences in development of oostegites between the peracaridan taxa are not important enough to exclude *a priori* their homology.

In the Bochsacea the oostegites arise in an atypical, posteromedial position on the coxa of the pereopods in the female. SANDERS et al. (1985) interpreted the position of the oostegites in the bochsacean *Hirsutia bathyalis* as a result of a change in alignment of the limb, with the typical linear arrangement of exopodite-endopodite-oostegite being rotated from lateral-medial to anterior-posterior. However, GUTU & ILIFFE (1998) distinguished between the typical peracaridan oostegites as membranous structures devoid of setae (“with few exceptions”), which are temporary and develop to form the marsupium in concert with the egg-laying cycle, and the oostegites of *Thetispelecaris*, which they interpret as permanent structures functioning to retain eggs and also to assist in respiration. GUTU & ILIFFE (1998) and OHTSUKA et al. (2002) both refer to the oostegites of hirsutiids as epipodites. JAUME et al. (2006) concluded that setose lobes present on the pereopods of the bochsacean *Montucaris* which function to retain developing eggs in a ventral marsupium are homologues of the oostegites of other Peracarida. This interpretation is supported by their absence in males, and by their presence in brooding females only (with incomplete development in preparatory females), and their absence from manca stages (JAUME et al. 2006). The hypothesis of SANDERS et al. (1985), that a change in alignment of the limb had occurred, was supported by developmental observations that the exopodite migrates from a lateral origin in manca stage-III to an anterolateral position in manca stage-IV (JAUME et al. 2006).

Oostegites are essentially secondary sexual characters and there is uncertainty over their homology. HANSEN (1925) considered that oostegites were probably “of epipodial nature”. DAHL (1983) stated that “there are good reasons to presume that in the female the proximal epipod on certain thoracic legs has been transformed into an oostegite, the whole proximal epipod series having been lost in the male”. He cited his own unpublished work on *Gammarus pulex*, as showing “a close similarity in the general structural patterns of epipod and oostegite, the main difference consist-

ing in the much richer vascularisation of the epipod.” On the basis that the “mutual positions of oostegite and epipod in *Gammarus* are identical with those of the two epipods in *Anaspides*”, DAHL concluded that the oostegite in female *Gammarus*, “and by inference those of other Peracarida, are transformed epipods of the proximal series”. However DAHL (1983) also commented that “it is not certain that the formation of oostegites was a unique event”. RICHTER & SCHOLTZ (2001) preferred to deal with the two structures separately in their analysis although they considered that “oostegites are probably homologous to epipodites” (citing CLAUS 1885 and SIEWING 1956, as well as DAHL 1983).

We do not find the similarities in “general structural pattern” highlighted by DAHL (1983) to be convincing evidence of the homology of the oostegite with the proximal epipodite (pre-epipodite). In amphipods (Fig. 17), for example, the coxa is highly modified and the relative position of these two structures on the limb does not appear to be a robust character. In peracarids in general the origins on the limb are different: oostegites typically originating as medially-directed lobes while epipodites originate more laterally. Structurally they differ: the thin-walled epipodites being well vascularised for respiratory exchange, while the oostegites are more rigid, less vascularised and have setose margins, at least in amphipods and bochsaceans. Oostegites and epipodites differ in function, size and orientation – none of which constitutes a strong argument against homology [even though it was the “general structural similarity” that was given by DAHL as the argument for homology in the first place]. However, they presumably also differ in their underlying developmental control mechanisms since oostegites are secondary sexual structures, appearing late in development and only in females, and often undergoing cyclical change in concert with the female’s hormonally-controlled, reproductive cycle. This is a stronger argument that leads us to question the traditional assumption of the ‘epipodial nature’ of the peracaridan oostegite.

Reports of the presence of both penile papillae and oostegites in individuals of both gammaridean and corophioid amphipods have been linked to the intersex phenomenon, and serve to reinforce the view that the state of such structures is probably dependent on the hormonal state of the animal.

6. Gills

The term gill has been employed for a variety of structures in aquatic Crustacea and implies a functional involvement in respiratory exchange. The high permeability of gills also predisposes them for ionic and water

exchange, so they may simultaneously contribute to respiratory, osmotic, excretory and acid-base regulation (TAYLOR & TAYLOR 1992).

Most gills are simple lamellate structures but in decapod malacostracans three elaborate gill morphologies are found: trichobranchiate gills (in astacidean crayfish and pagurid hermit crabs), phyllobranchiate gills (in brachyuran crabs, galatheids and carideans) and dendrobranchiate gills (in penaeoid and sergestoid shrimps). Intermediates also occur, as for example in the phylloid trichobranchiate gills of some thalassinids (BATANG et al. 2001). The different gill morphologies are not further considered here.

Up to four gills can be associated with each thoracic limb in the decapods: the podobranch, the anterior and posterior arthrobranchs and the pleurobranch (Fig. 11). However, the theoretical maximum of 32 gills is never present (TAYLOR & TAYLOR 1989). These gills are distinguished by their site of origin. The epipodite-podobranch complex has been considered above; arthrobranchs and pleurobranchs are considered below. The relative timing of appearance of arthrobranchs and pleurobranch can vary so that, as noted by BURKENROAD (1981), the pleurobranch appears after the arthrobranchs in the Dendrobranchiata, while it appears earlier than the arthrobranchs in carideans and stenopodideans. They appear simultaneously in the Reptantia.

6.1. Arthrobranchs of Malacostraca

Arthrobranchs are gills that originate in the arthrodial membrane at the articulation between the body and the thoracic limb. Two different arthrobranchs are found, referred to as anterior and posterior according to position. They begin development as simple rounded buds and can develop into elaborate branching structures in the Decapoda (e.g. HONG 1988). The maximum expression is found in dendrobranchiate decapods where a single arthrobranch is present on maxilliped 1, and two are present on each of the next six pairs of thoracic limbs, with only the final pair lacking any (PEREZ-FARFANTE & KENSLEY 1997). In many decapods the anterior and posterior arthrobranchs are intimately associated, often sharing a common base (HONG 1988). The possibility that anterior and posterior arthrobranchs have a common origin gains some support from the innervation pattern. ISHII et al. (1989) found that both arthrobranchs are innervated by a single branchial nerve that divides into anterior and posterior branches close to their base. In contrast, the podobranch is innervated by a distinct and separate podobranch nerve.

CLAUS (1885) described the arthrobranch buds as originating on the limb base in penaeids and considered that their eventual position in the joint resulted

from the coalescence of the proximal part of the developing limb with the body. This does not represent a dorsal migration, as sometimes stated, and we would simply infer that the arthrobranch Anlagen appear before the limb-body articulation is expressed during development.

Single arthrobranchs are present on thoracopods 3, 4 and 5 of the thermosbaenacean *Tulumella grandis* (CALS & MONOD 1991). In a new species of the genus *Tulumella* that we are currently describing, the arthrobranchs are simple lobate structures arising laterally from the arthrodial membrane at the leg base from thoracopods 2 to 5 (Fig. 21).

6.2. Pleurobranchs of Malacostraca

Pleurobranchs are gills that are located high on the pleuron – the lateral body wall – dorsal to the limb origin. They are found only in the Decapoda and Amphionidacea. The maximum expression can be found in dendrobranchiate decapods where up to six pairs of pleurobranchs can be present, one on each pereon segment from the third to the eighth (PEREZ-FARFANTE & KENSLEY 1997). In penaeids the bud of the pleurobranch appears last, after the buds of the two arthrobranchs were expressed (CLAUS 1885; CALMAN 1909), but in carideans and stenopodideans it appears before the arthrobranchs.

In *Amphionides* pleurobranchs are present only from the third to the seventh pereon segments – the eighth thoracopods being absent in females and modified in males. We infer that the pleurobranchs of *Amphionides* are homologues of those of decapods.

6.3. Book gills of Myodocopa

Cylindroleberids such as *Leuroleberis surugaensis* possess seven pairs of lamellae on the dorso-lateral part of the posterior thorax body wall (VANNIER et al. 1996). The lamellae are broad and flap-like, and their internal anatomy, especially their haemolymph circulation system, is strongly indicative of a respiratory function. The seventh limb of these myodocopans is highly modified and appears to perform a grooming function for the gills (VANNIER et al. 1996). The presence of these gills was also noted in the Silurian cylindroleberid *Colymbosathon* (SIVETER et al. 2003).

VANNIER et al. (1996) proposed that the book gills of cylindroleberids are possible remnants of lost limbs and represent the epipodites. In their schematic VANNIER et al. (1996: fig. 8) attribute the gills to post-cephalic trunk segments 3 to 9, although they noted that this hypothesis was not entirely consistent with developmental data (see KORNIKER 1981) which indi-

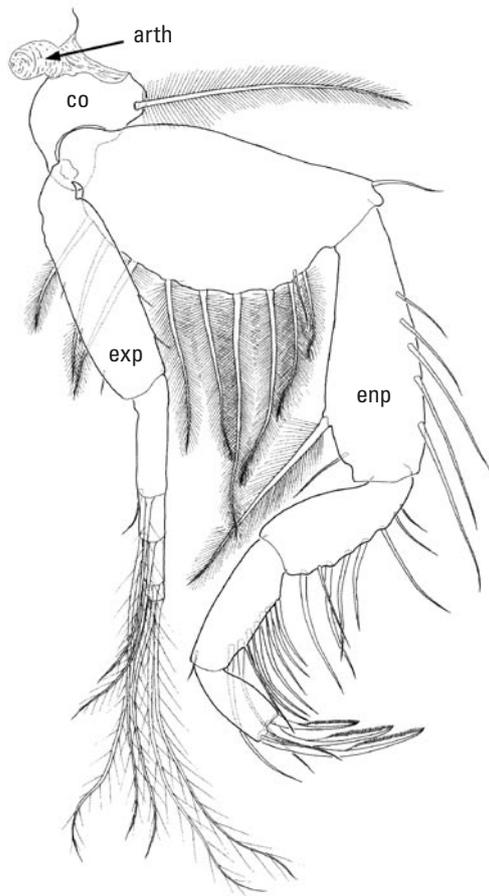


Fig. 21. First pereopod of *Tulumella* sp. (Thermosbaenacea), showing arthrobranch at basal articulation of limb. Abbreviations: arth = arthrobranch, co = coxa, enp = endopodite, exp = exopodite.

cated that the entire set of book gills appears in the first instar, before the seventh limbs appear. An additional problem for this speculative proposal is the variation in number of gill lamellae. While seven is the typical number, up to ten paired lamellae can be found, which might imply that a further three somites were present in the groundplan of this one family. This would suggest a fundamental variability in trunk segmentation that we consider extremely unlikely, given the basic stability found in other short-bodied crustacean taxa.

6.4. Sternal gills of Amphipoda

The sternal gills of gammaridean amphipods are described as “ventral outpouchings of their sterna” by STEELE & STEELE (1991). They are absent in marine amphipods and distributional observations suggest that their presence is correlated with exposure to low-salinity water. As with several other assumed respiratory structures, it appears that they are involved in ionic balance rather than respiratory exchange. Sternal gills are typically paired but some crangonyctids display

a single median gill on the sternites of thoracomeres 3 to 5. The maximum expression of sternal gills on the pereon can be seen in *Phreatogammarus fragilis*, for example, where they are present on thoracomeres 3 to 8. However, several amphipods, such as the melitid *Flagitopisa*, and the crangonyctids *Stygobromus*, *Bactrurus*, *Synurella* and *Crangonyx*, also display sternal gills on the first pleonite (SAWICKI et al. 2005; HOLSINGER 1977).

6.5. Ventral carapace gills in cycloids

Cycloids are Palaeozoic arthropods which survived through almost to the end of the Mesozoic (DZIK 2008). They have widely been classified within the Crustacea: with SCHRAM et al. (1997) for example, regarding them as the sister group of the Copepoda, while DZIK (2008) placed them as a distinct order, the Cyclida, within the Branchiura. We consider cycloids here because of their possession of a gill apparatus and their current treatment within the Crustacea. The gill apparatus, as reconstructed by DZIK (2008) for *Ooplanka decorosa*, resembles book lungs, comprising paired areas of radially-orientated, cuticular infoldings located on the ventral surface of the carapace. The so-called respiratory areas of branchiurans are not book-lungs and their position on the carapace differs: in Branchiura the respiratory areas are laterally located, extending about from the level of the maxilla to the level of thoracopod 3, whereas in cycloids such as *Ooplanka* the book lung occupies a continuous horseshoe-shaped zone on the ventral surface of the almost-circular, univalved carapace, extending from the head region, along the side of the body and across the midline (dorsal to the free abdomen). We consider that cycloid gills are not homologous with branchiuran respiratory areas, or with any of the structures discussed above for the Crustacea. Furthermore, the disposition of the walking limb bases, radiating out from the median sternite, is entirely reminiscent of the chelicerate pattern, not of crustaceans. Despite the crustacean-like antennal reconstructions, we consider the crustacean affinities of cycloids to be doubtful.

7. Conclusions

The exopodite is the outer ramus of the biramous trunk limb and can be defined by its distal origin on the propod, lateral to the endopodite. It is typically muscular, provided at least with muscles originating in the propod and inserting within the ramus itself, and is often two-segmented. In some taxa muscles originate

and insert within the exopodite. The distal segment is originally annulated in the Eumalacostraca. Together with the endopodite, the exopodite is formed by a subdivision of the primary growth zone at the tip of the developing proximal-distal limb axis. This helps to distinguish the exopodite from the epipodite, which results from the secondary establishment of a new, lateral axis.

The crustacean epipodite arises as a lobate outgrowth from the lateral compartment of the coxa of the limb, or of the undivided protopod. It appears first as an unarmed, rounded bud, which is expressed relatively early in development as a lateral outgrowth. During development, in taxa such as the Branchiopoda, where post-maxillary limbs initially appear as transverse ridges in the early embryos, the epipodite primitively appears as a bud just prior to the stage when the limbs begin to swing down to their vertical, adult orientation. In the leptostracans the appearance of the epipodite is delayed until after the swing to vertical is completed. It lacks setae in branchiopods, but in eumalacostracans the epipodite is often setose. The epipodite lacks musculature inserting within it in all post-maxillary limbs. The epipodite is characterised by distinctive gene expression patterns: strongly expressing *nubbin*, *apterous* (AVEROF & COHEN 1997), *tracheiless* (MITCHELL & CREWS 2002) and *ventral veinless* (FRANCH-MARRO et al. 2006), but only weakly expressing *Distal-less* (WILLIAMS 1998; WILLIAMS et al. 2002). RICHTER (2002) regarded the specific expression pattern of *nubbin* and *apterous* genes in the distal epipodite of *Artemia franciscana* and in the epipodite of *Pacifastacus leniusculus* as a strong argument for homology of these two structures. Epipodites are found on the post-maxillary trunk limbs in branchiopods and on the thoracopods (maxillipeds and pereopods) in the Malacostraca. We agree with HANSEN (1925) that no epipodite is found on the maxilla in Malacostraca. Indeed, within the entire Crustacea, only the Myodocopa possess an epipodite on the maxilla.

While the epipodite has several characteristics that facilitate its recognition across taxa, the question remains: How many pre-epipodites are present in the Crustacea? SIEWING (1963) refers to “the restriction of the epipods to one pair” when comparing the peracarids with the anaspidacean syncarids, and attributes two epipodites to the stem form of the Malacostraca. In the Malacostraca DAHL (1983) stated that originally there appear to have been at least two epipodites on each thoracic limb as “still found in the syncarids”. DAHL cited CALMAN (1909) when stating that “there appears to be three epipods in the Decapoda”, but CALMAN (1909: 275–279) clearly indicates that he was including the two arthrobranchs together with the epipodite-podobranch complex in this total. CALMAN was basing his interpretation on CLAUS (1885) who described the

apparent dorsal migration of the arthrobranch and podobranch buds. We consider this apparent migration is a misinterpretation attributable to the relatively late differentiation of the limb-body articulation. DAHL (1983) suggested that the loss of one series (the proximal) of epipodites in the Euphausiacea might be correlated with the proliferation in the remaining (distal) series (cf. SARS 1896: plate XIX). The assumption that the presence of both a distal epipodite and a proximal pre-epipodite was the ancestral malacostracan condition is widespread.

In the Malacostraca, a respiratory pre-epipodite is present only in the Recent Anaspidacea and probably in the Silurian archaeostracan *Cinerocaris*. In both cases the origin of the pre-epipodite is very close to the origin of the epipodite; the two lobes are similar in size, structure and presumed function, are orientated in the same plane and largely overlap. So we need to ask: Is there robust evidence supporting the identification of any other malacostracan exite as the homologue of the pre-epipodite? On the basis of the shared anlage of the coxal plate and the epipodite anlagen in early development, we consider it possible that the coxal plate of the Amphipoda might be the homologue of the pre-epipodite but more evidence is needed. Regarding the widely assumed homology of the peracaridan oostegite with the pre-epipodite, we find the evidence equivocal. Oostegites and pre-epipodites have different sites of origin on the limb protopod, they differ structurally, functionally and in orientation. More importantly, we suggest here that they will differ in their underlying control mechanisms since oostegites are secondary sexual structures, often undergoing cyclical change in concert with the hormonally-controlled, reproductive cycle of the female. We consider that the balance of evidence is currently against the hypothesis that the peracaridan oostegite is the homologue of the proximal epipodite of the Anaspidacea.

On the basis of scant available evidence we are unable to determine whether either of the pre-epipodites of the chirocephalid anostracans is homologous with the pre-epipodite of anaspidacean malacostracans. The pre-epipodite of adult *Anaspides* shows no evidence of a double origin, as shown for the non-chirocephalid anostracan pre-epipodite (WILLIAMS 2007), but good embryological data are not available for anaspidaceans. The only evidence at present derives from the relative position of the pre-epipodite located proximal to the origin of the true epipodite, and this cannot be regarded as definitive. In the case of the pre-epipodite, as for several other structures we have examined in this review, it is clear that many assumptions concerning homology have been made and adopted into the orthodoxy but the supporting evidence is weak or non-existent. We now have a range of powerful new tools to address such questions, including those from

gene expression studies, from cell lineage studies, and from evo-devo. There is an urgent need to exploit such tools to generate the evidence we need to resolve these questions.

8. Acknowledgements

We would like to thank the organisers of the Advances in Crustacean Phylogeny symposium in Rostock for the invitation to participate in the meeting and to contribute to this volume. We would also like to thank all the participants for a great meeting. We are very grateful to Ana Camacho for her advice on the attributes of the Bathynellacea and we acknowledge the improvements to the manuscript suggested by the reviewers and editors. Professor Jørgen Berge (University Centre on Svalbard), kindly allowed us to use his micrograph of *Andaniotes linearis* (Figure 17). This is a contribution to Spanish Ministry of Science and Innovation project CGL2006-01365.

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