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Metamorphosis between naupliar and copepodid phases in the Harpacticoida

HANS-UWE DAHMS

Universität Oldenburg, Postfach 2503, Fachbereich 7, Arbeitsgruppe Zoomorphologie, D-2900 Oldenburg, Germany

SUMMARY

It has been argued that, among Crustacea, copepods show 'the most complete example of metamorphosis': from nauplius to copepodid. In groups with either specialized nauplii or copepodids of a particular shape, body form changes markedly from nauplius VI to copepodid I. During post-embryonic development, one pair of appendages is formed at each successive stage, even in cases where some of these precursors are not developed externally. The same holds for the copepodid phase in which one somite is added per moult from a proliferation zone anterior to the anal somite. Of the appendages, the antennules continue to acquire further segments, setae and spines in the course of post-embryonic development, whereas the antennae and mandibles change drastically by losing their naupliar masticatory parts and, in the case of the mandibles, by developing completely different replacement structures. The antennae lose their masticatory function and migrate pre-orally from their naupliar paroral position. Even more striking are the changes affecting the post-mandibular mouthparts. From functionless naupliar limb-buds, these achieve almost the adult state as early as C I without any precursors in previous stages, whereas precursors of swimming legs 1 and 2 are indicated at N VI in most cases but, together with legs 3–6, differentiate in each successive instar from C I onwards. The caudal rami change in shape and in the number and structure of their setae. Sexual dimorphism becomes apparent only in the copepodid phase (as early as in C I in one case). Intermoult stages are important for tracing the origin and homology of larval and juvenile structures. Although 'metamorphosis' from nauplius to copepodid is in many cases accompanied by remarkable changes, there also are examples of continuity in morphological and behavioural features.

1. INTRODUCTION

Gurney (1942) argued that the Copepoda is the crustacean taxon which shows 'the most complete example of metamorphosis': from nauplius to copepodid. There are a few studies already focusing on the changes from naupliar to copepodid phase in Copepoda (Chappuis 1916; Dietrich 1915; Ziegelmayer 1925). However, there is a lack of detail in these attempts, and intermoult stages have not been used for the investigation. Change in body form is not extreme in many free-living copepods. In groups with either specialized nauplii or copepodids of particular shape, however, body form changes markedly during the moult from the sixth stage nauplius to the first copepodid. Striking changes also occur in the appendages. The copepodid antenna has a mainly locomotory function and is not directly involved in mastication. This led Lauterbach (1980) to suggest that the antennae were originally oral appendages of the nauplius larva, and as such 'larvale Sonderbildungen' (structures peculiar to the larval state) which have been taken over by the adult organization.

Legs 1 and 2 are already bilobed at N VI in most cases, and have a two-segmented protopodite and one-segmented rami at C I. The biarticulated caudal seta appearing as early as N III is certainly homologous with the biarticulated dorsal seta of the copepodid caudal ramus. During the copepodid phase, differentiation of appendages is restricted mainly to the antennules and to the natatory legs. The antennae, oral appendages, maxillipeds and caudal rami undergo only minor structural alterations, if any.

2. MATERIAL AND METHODS

Post-embryonic stages were obtained from the sites listed in the appendix and treated as described by Dahms (1990*a*).

Specimens were fixed in 4% (by volume) formalin and transferred to W 15 (embedding medium of C. Zeiss Company) for microscopical investigation. Structures were studied using an oil-immersion phase contrast objective (× 100) and figured with the aid of a *camera lucida*.

Abbreviations used are: N I–VI, first to sixth naupliar stage; C I–VI, first to sixth copepodid stage; enp, endopodite; A 1, 2, antennule, antenna; Md, mandible; Mx 1, 2, maxillule, maxilla; Mxp, maxilliped; P 1–6, legs 1–6; char., character; Cu.r., caudal ramus; cu.set., caudal setae; bra., branched caudal seta of C I giving rise to the two major setae of a copepodid caudal ramus; prot., protuberance; I–III, the three setae of the second segment of an oligoarth-

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ran naupliar three-segmented antennule, being homologous with the corresponding segment of copepodid antennules, as a rule bearing one seta.

3. METAMORPHOSIS BETWEEN NAUPLIAR AND COPEPODID PHASES

(*a*) *Body shape and life habits*

See figure 1. In some harpacticoid taxa the body form changes markedly during metamorphosis, particularly in families with globular (Metidae) or foreshortened (Diosaccidae, Thalestridae) nauplii but elongate copepodids, or dorsoventrally flattened nauplii but laterally compressed copepodids (Tegastidae). In *Tegastes clausi* (figure 1*b*), C I is laterally compressed as in the adults, and C I of *Alteutha interrupta* (figure 1*d*) is dorsoventrally flattened. Also, the copepodids of Tegastidae and Peltidiidae are arched anteriofrontally throughout this phase. Tegastidae and Peltidiidae (regarded as phylogenetically

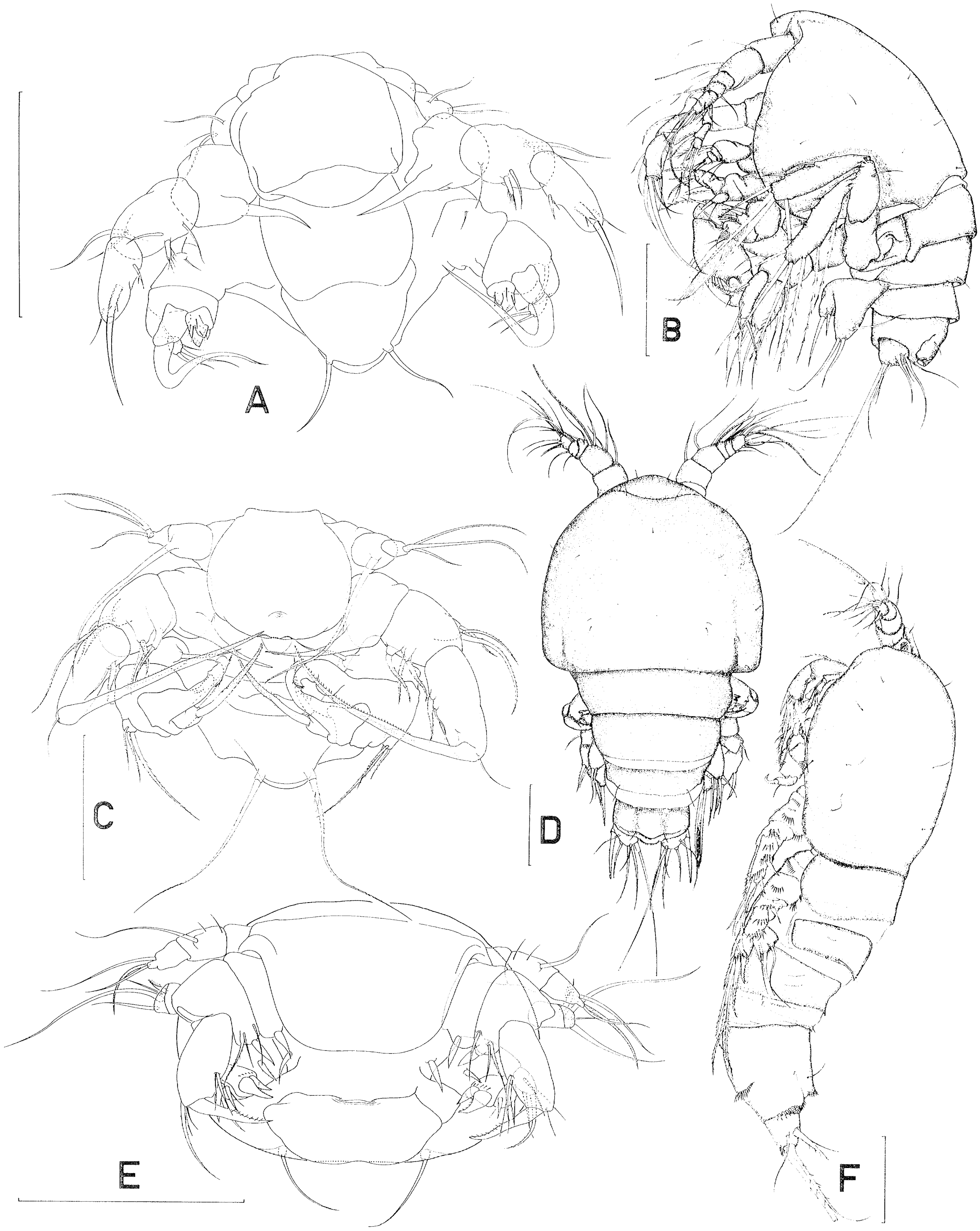

Figure 1. Transformation from nauplius (A, C, E) to copepodid (B, D, F) among Tegastidae, Peltidiidae and Diosaccidae: *Parategastes sphaericus*, N I (A) – *Tegastes clausi*, C I (B); *Alteutha oblonga*, N I (C) – *Alteutha interrupta*, C I (D); *Paramphiascella fulvofasciata*, N I (E) – C I (F). First naupliar stages are shown in ventral view; first copepodids in lateral view except *Alteutha interrupta* (D) which is in dorsal view. Scale bars 50 μm.

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closely allied by Lang (1948)) are characterized by a behavioural peculiarity of their naupliar and copepodid instars. Harpacticoid nauplii and copepodids are usually similar in behaviour and lifestyle. Among tegastids and peltidiids, however, the nauplii are clumsy creepers, not able to swim, whereas the copepodids are excellent swimmers from stage 1 onwards.

During the post-embryonic development, one additional pair of appendages is developed at each consecutive stage, even in species in which some of these precursors are not developed externally. From the first stage orthonauplius, the maxillule precursors develop at N II, the maxillae at N III, and one further appendage pair at each stage, until legs 2 are indicated at N VI. Therefore the leg 3 Anlagen are not developed before the first copepodid. In the copepodid phase, one somite is added per moult from a proliferation zone in front of the anal somite. In contrast to the nauplii, the somites following the

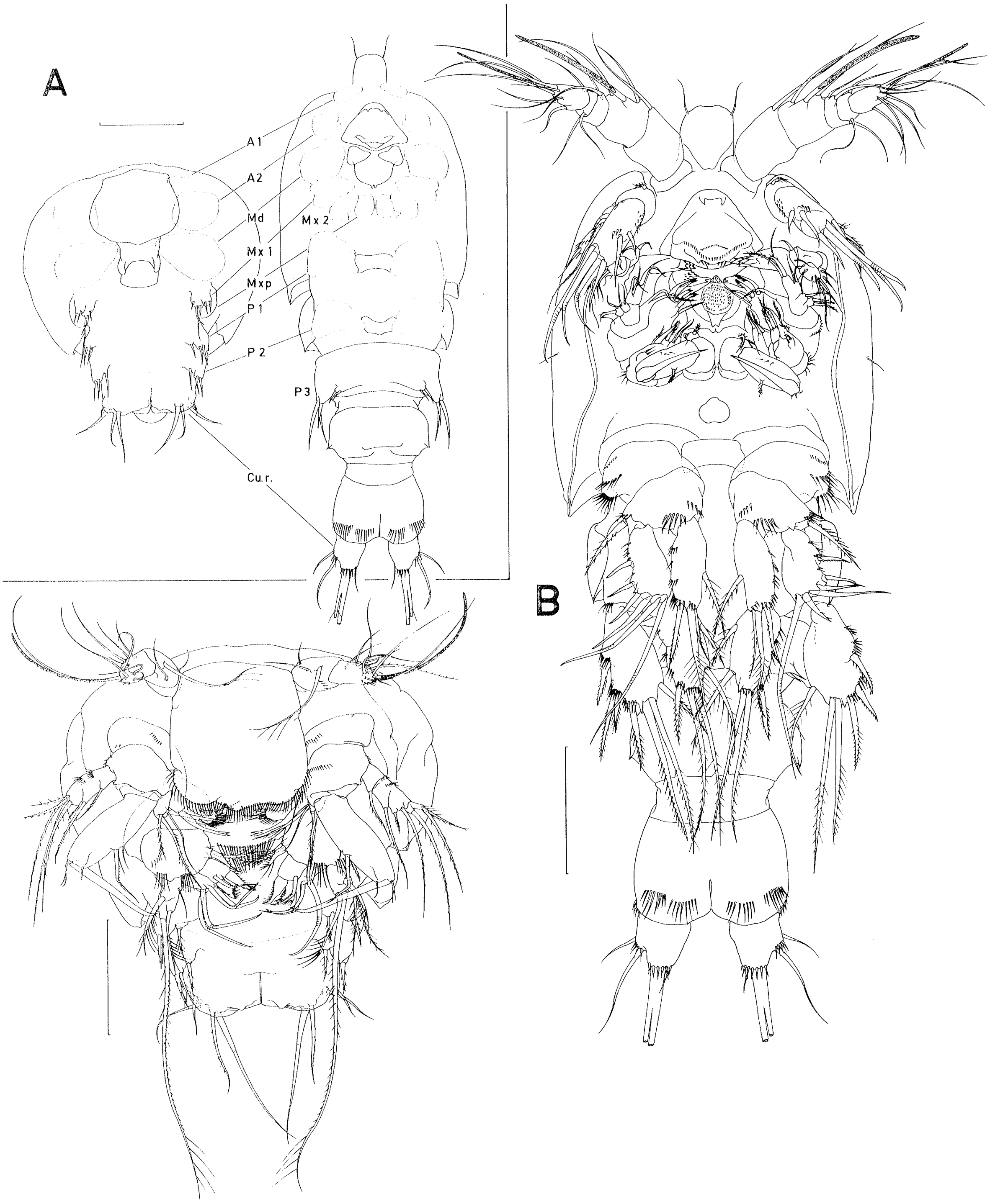

Figure 2. Nauplius VI and copepodid I of *Amonardia normani*. Semischematic illustrations of ventral side, insertion planes of appendages indicated (A). Habitus in ventral view (B) (A 1, antennule, A 2, antenna, Md, mandible, Mx 1, maxillule, Mx 2, maxilla, Mxp, maxilliped, P 1–3, legs 1–3; Cu.r., caudal ramus). Scale bars 50 µm.

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cephalosome are well separated. In families with the second thoracic somite separate from the cephalosome (Canuellidae and some families of Maxillipedasphalea *sensu* Lang 1948), the first free segment bears leg 1, the second leg 2 and the third leg 3 at C I stage. The fourth thoracic segment lacks any appendage except in Ectinosomatidae, where it bears a bilobed appendage precursor. The anal somite bears an operculum and anus dorsomediocaudally and two caudal rami at its distal edge (Dahms 1993).

Representatives of all other families have four free segments at C I, as the leg 1-bearing second thoracic segment is fused with the cephalosome. Here, the first free thoracic segment is the third, which bears leg 2.

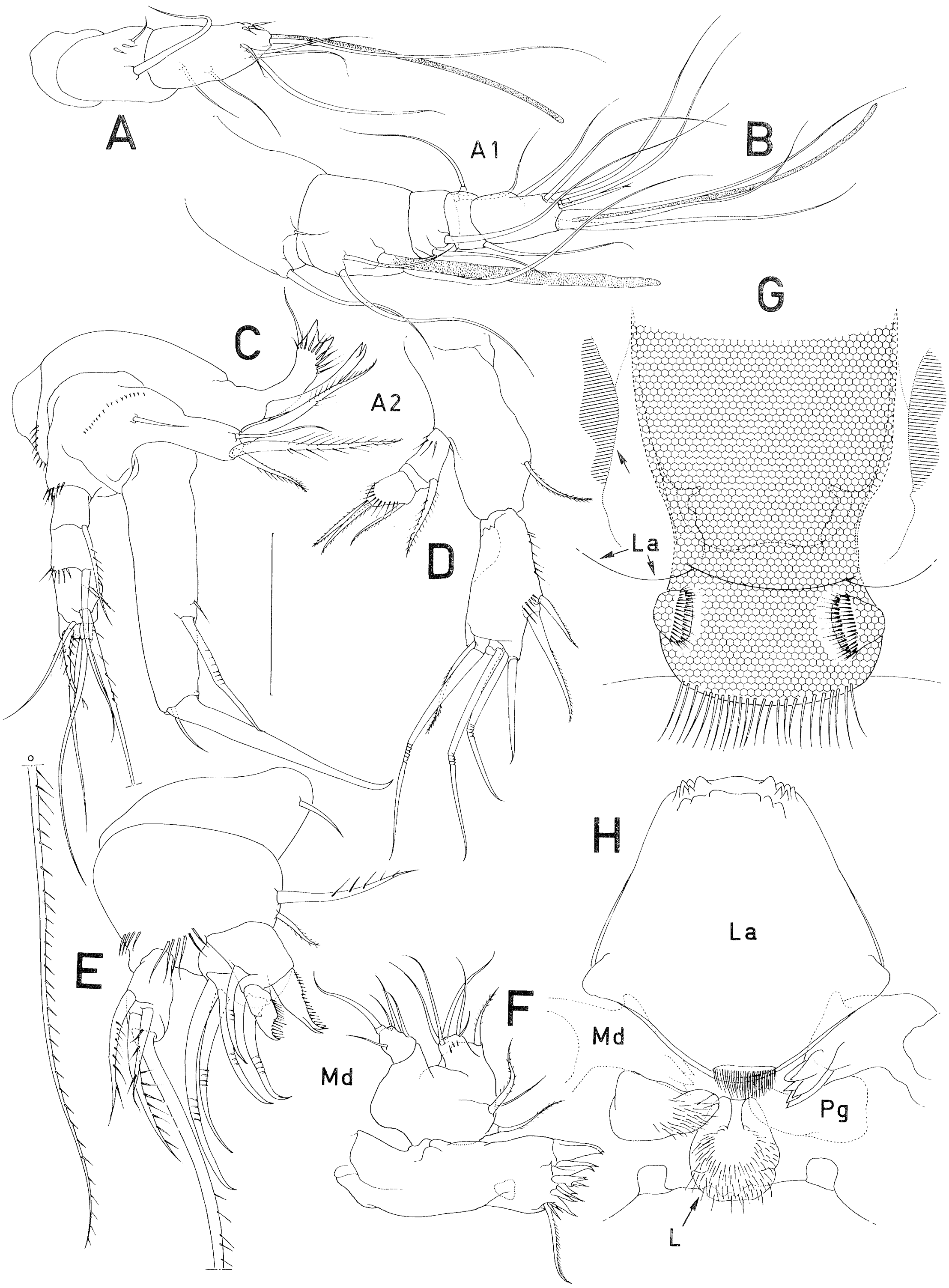

Figure 3. Metamorphosis of antennules (A 1; A, B), antennae (A 2; C, D), mandibles (Md; E, F), naupliar circumoral structures (G) – ventral body wall indicated by a pattern of netting – and copepodid lingua and paragnaths (H) of *Amonardia normani* from nauplius VI (A, C, E, G) to copepodid I (B, D, F, H). (La, labrum; Li, lingua; Pg, paragnath). Scale bar 50 μm.

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The articulation between thorax and abdomen is not developed before C III. At this stage, with the appearance of the fifth leg as a limb-bud, the division between 'prosome' and 'urosome' can clearly be located as in the adult.

(*b*) *A case-model: metamorphosis in Amonardia normani*

See figures 2–4. Morphological changes from naupliar to copepodid organization were studied in detail in the diosaccid *Amonardia normani*, because it was possible to obtain several intermoult N VI instars of this species by experimental manipulation. As figure 2 shows, there is a remarkable increase in size from N VI to C I (the body length is nearly doubled). The semischematic figure 2*a* also shows the addition of the Anlage of leg 3 in the copepodid and of the maxilla. It is not possible to trace the latter in the nauplius. The first copepodid also has four free somites besides the cephalosome, the caudalmost being the anal somite. Also, the caudal rami become distinctly separated. A ventral view (figure 2*a*) shows best the overall dissimilarity of these successive stages. Here, I point especially to the prominent naupliar labrum which becomes, both allometrically and in absolute size, much reduced in the copepodids.

As for the appendages, it is the second segment of the three-segmented naupliar antennule which is homologous with the first visible segment of the copepodid (figure 3*a*,*b*). This is made evident by the two

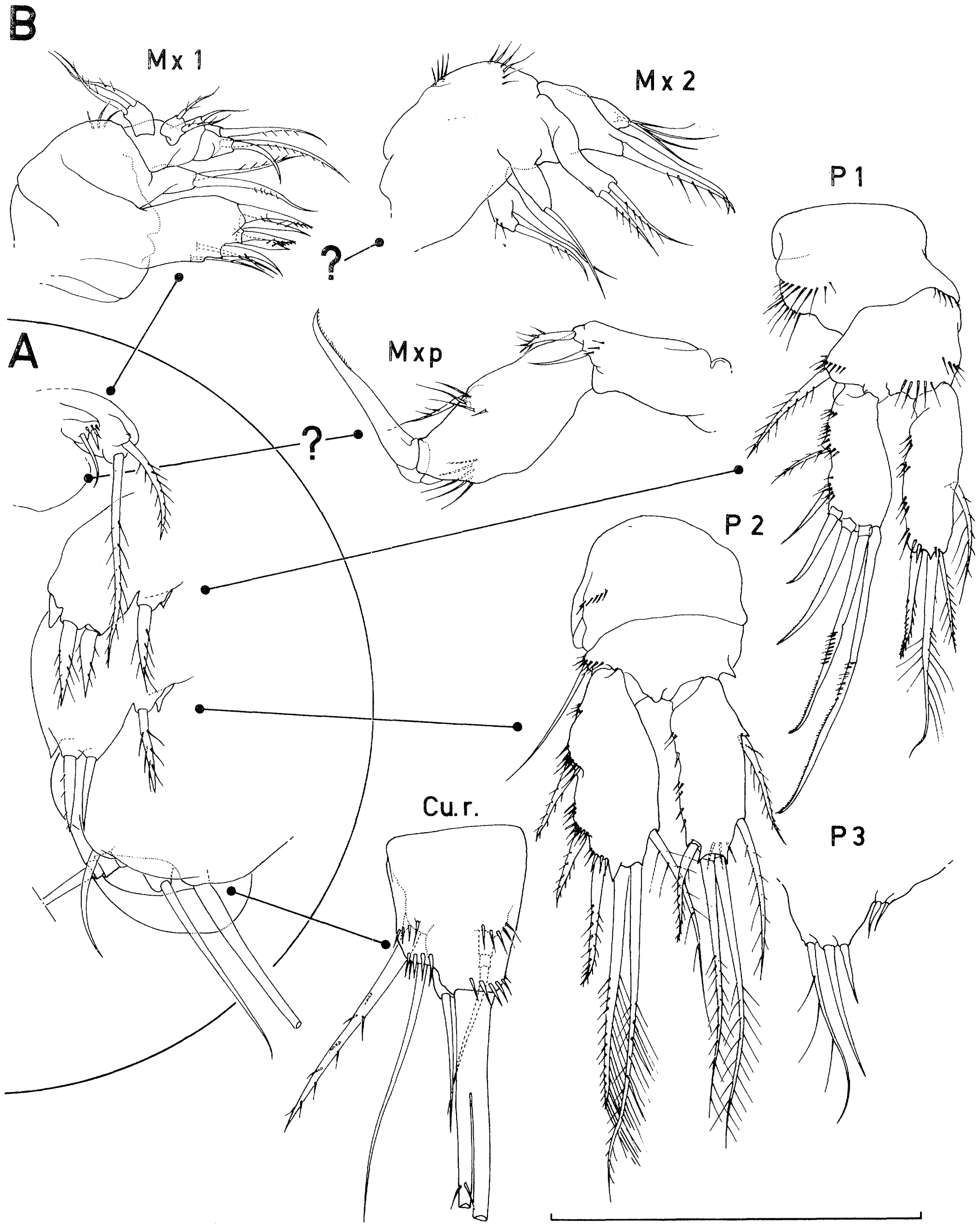

Figure 4. Metamorphosis of post-mandibular appendages and caudal rami of *Amonardia normani* from nauplius VI (A, right ventral side) to copepodid I (B)(Mx 1, 2, maxillule, maxilla; Mxp, maxilliped; P 1–3, legs 1–3; Cu.r., caudal ramus). Scale bar 50 μm.

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homologous setae which are similar in structure and length in both segments (cf. Dahms 1991). The first naupliar segment must have been either fused or lost, to leave the former second naupliar segment as the first segment of the copepodids. The second to fourth antennular segments of copepodids are developed *de novo*, whereas the distal fifth segment represents the tip of the naupliar antennule. Already from the first copepodid onwards, the terminal aesthetasc is joined basally to the two accompanying setae to form a 'tritheca-complex'. In the nauplius it originates, together with a seta, from a common protuberance, but both are not fused basally.

The antennae are remarkably transformed (figure 3*c*,*d*). The naupliar coxa with its prominent masticatory gnathobase is lost altogether. Even the naupliar basis – following the current opinion of many researchers – must have been fused with the first endopodal segment and lost all its inner armature, namely four setae, two of which are large. However, because the naupliar antennal endopodites among Oligoarthra are always one-segmented (Dahms 1990*a*), it may be that the so-called allobasis of copepodids represents merely the basis (the inner subdistal seta being the remnant of the inner armed process). If so, the single endopodite segment of the

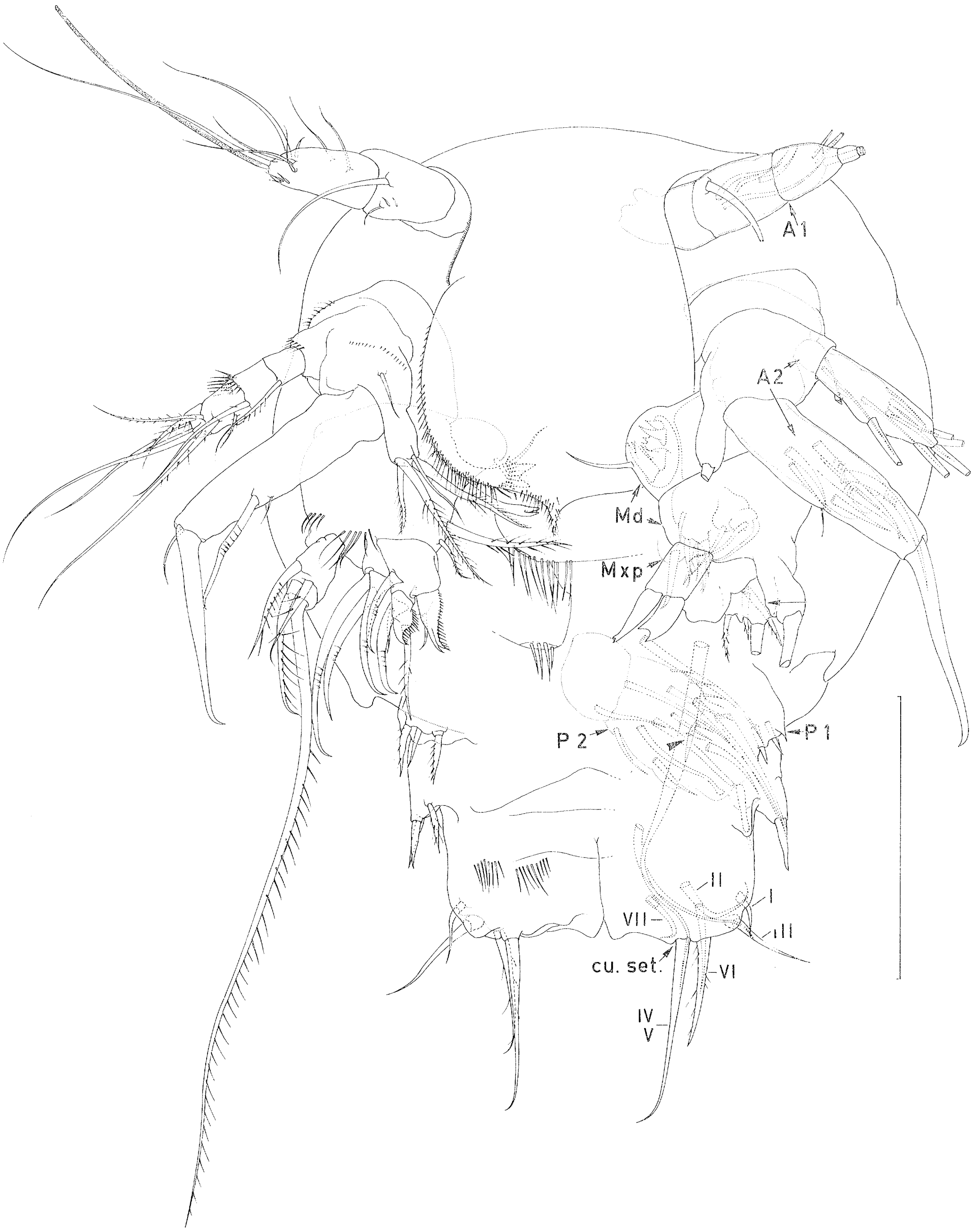

Figure 5. Intermoult nauplius VI stage of *Amonardia normani* in ventral view. Prospective appendages of copepodid I are indicated by dashed lines on left side; naupliar structures are given in detail and full line on right side (A 1, antennule; A 2, antenna; Md, mandible; Mx 1, maxillule; Mxp, maxilliped; P 1–2, swimming legs 1–2; cu.set., caudal setae). Scale bar 50 µm.

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copepodid antenna must be homologous with the corresponding segment of the nauplius. The four-segmented exopodite of the nauplius is transformed to a three-segmented ramus in the copepodid with remarkable reduction of its setal armature.

The mandibular coxa of the nauplius gives rise to the copepodid coxa (figure 3*e*, *f*; see discussion below). The single coxal seta which is always present in oligoarthran nauplii (Dahms 1990*a*) may well give rise to the masticatory seta at the inner corner of the copepodid cutting edge. The armature of the inner medial bulge of the basis increases from two setae in the nauplius to three in the copepodids. The exopodite is one-segmented in both phases, but acquires a new fifth seta at C I. The endopodite is not yet distinctly separated at C I, and has lost one of its setae. In both rami, individual elements of the armature undergo considerable changes in form at this moult. Whereas the copepodid antennule is gaining in size, the antenna and mandible show remarkable negative allometric growth.

In the nauplius of *Amonardia normani* there is a tongue-like flap of the ventral body wall which forms the floor of the antennal precoxal cavity and ventral plate (figures 2, 3*g* and 5). Such a structure is distinctly developed in most harpacticoid nauplii (Dahms 1990*a*). Whereas it may be retained as the copepodid lingua (or hypopharynx?: see discussion below) the paragnaths are formed anew during the moult to C I (figure 3*h*).

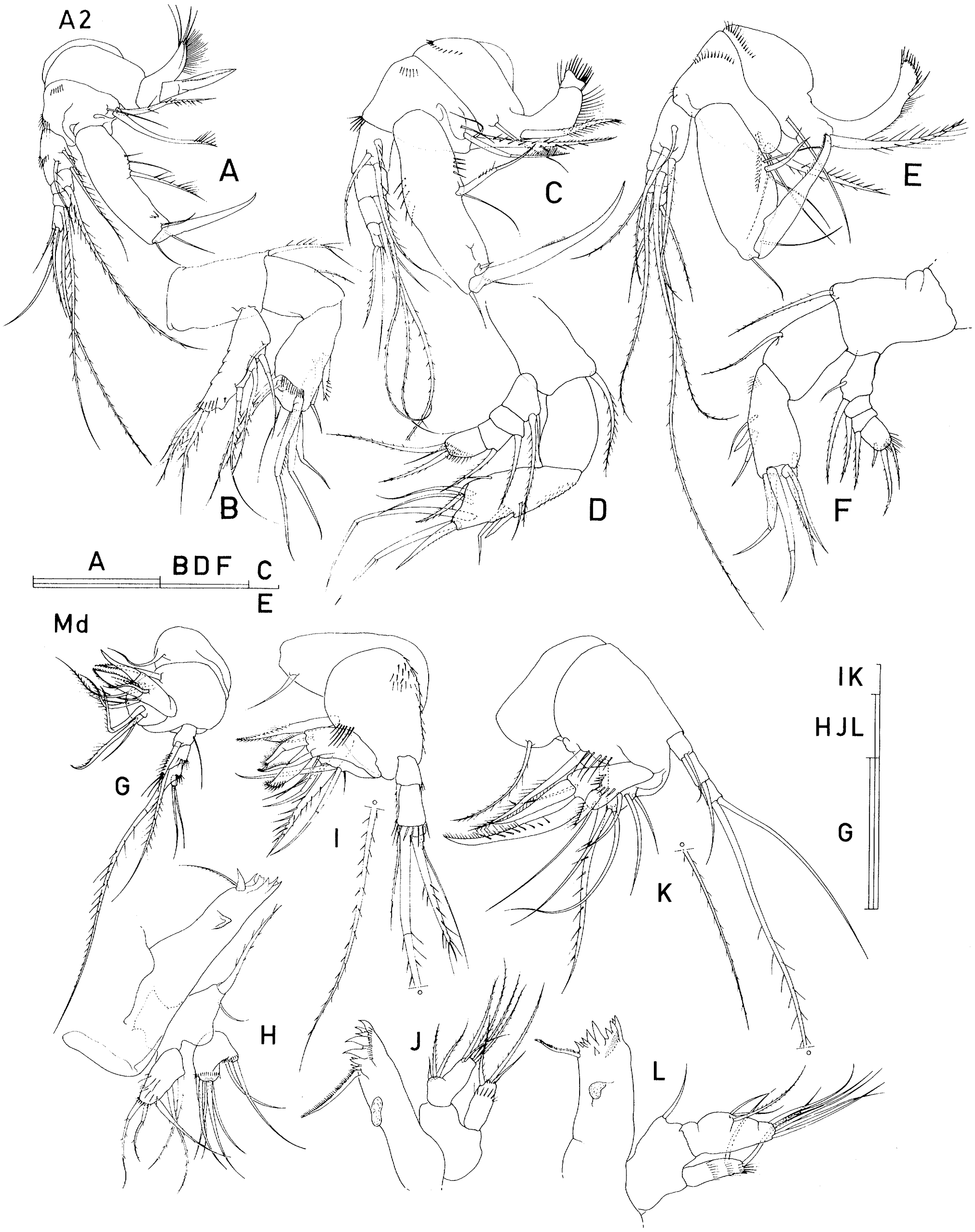

Figure 6. Metamorphosis of antennules from nauplius VI (A, C, E, G, I, K) to copepodid I (B, D, F, H, J, L): *Longipedia minor* (A, B); *Ectinosoma melaniceps* (C, D); *Parathalestris harpactoides* (E, F); *Scutellidium hippolytes* (G, H); *Zaus spinatus* (I, J); *Heterolaophonte minuta* (K, L). Scale bars 50 μm.

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The maxillule emerges from a sparsely armed bilobed naupliar bud, becoming almost adult-shaped at C I (figure 4*b*). The same holds for the maxilla (which could not even be traced in the nauplius) and maxilliped. From slightly bilobed Anlagen – the inner lobe with one seta, the outer with two setae and a spine – biramous natatory legs 1 and 2 develop, showing coxa and basis already and indicating the future development of the two-segmented state by an indentation. Leg 3 is developed anew, being slightly bilobed already with two setules and three setae on the prospective endopodite and exopodite respectively.

The caudal ramus emerges from a rather undifferentiated hind-portion of the nauplii, but is almost adult-shaped in C I. Precursors of all adult setae are present. However, the major seta is branched at this stage and will give rise to the two major setae of harpacticoid caudal rami at C II (Dahms 1993). Individual setae will be homologized with evidence from intermoult instars.

(*c*) *Use of intermoult stages*

See figure 5. Intermoult stages, where structures of the subsequent stage are already visible through the cuticle, are always important for tracing the origin and homology of structures within a series of post-embryonic stages. For example, the sixth nauplius of

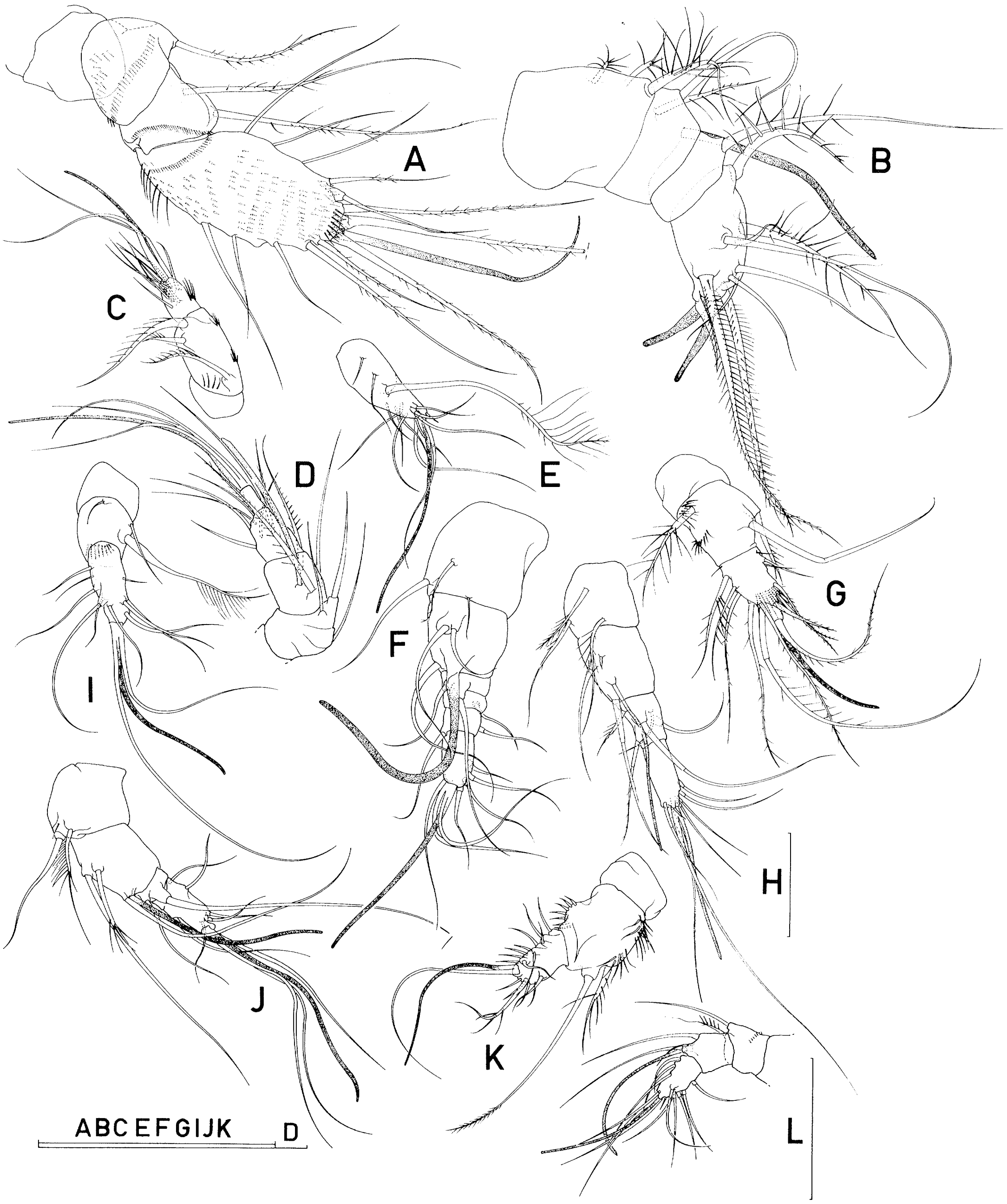

Figure 7. Metamorphosis of antennae (A–F) and mandibles (G–L) of *Scutellidium hippolytes* (A, B, G, H), *Tisbe gracilis* (C, D, I, J) and *Drescheriella glacialis* (E, F, K, L) (A 2, antenna; Md, mandible; N VI, nauplius VI; C I, copepodid I). Scale bars 50 μm.

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Amonardia normani shows the site of formation of the copepodid appendages (figure 5). Clearly the antennule, antenna, mandible, maxillule, leg 1, leg 2 and the caudal ramus are derived from naupliar precursors. The setae of the antennal endopodite and exopodite of the copepodid are visible within the sheaths of the naupliar endopodite. The mandibular 'syncoxa' (see discussion below) is derived from the naupliar coxa, whereas its endopodite is formed, not within the endopodal process, but in the outer lateral field of the naupliar endopodite. The prospective copepodite legs 1 and 2 are largely superimposed; however, leg 2 situated dorsally to leg 1 has its caudal setae emerging from the caudalmost bud of the nauplii.

Of the major caudal setae, the largest is clearly derived from the large innermost seta of the nauplii (cf. figures 5 and 9). Also, the three outermost naupliar setae clearly give rise to copepodid successors. If

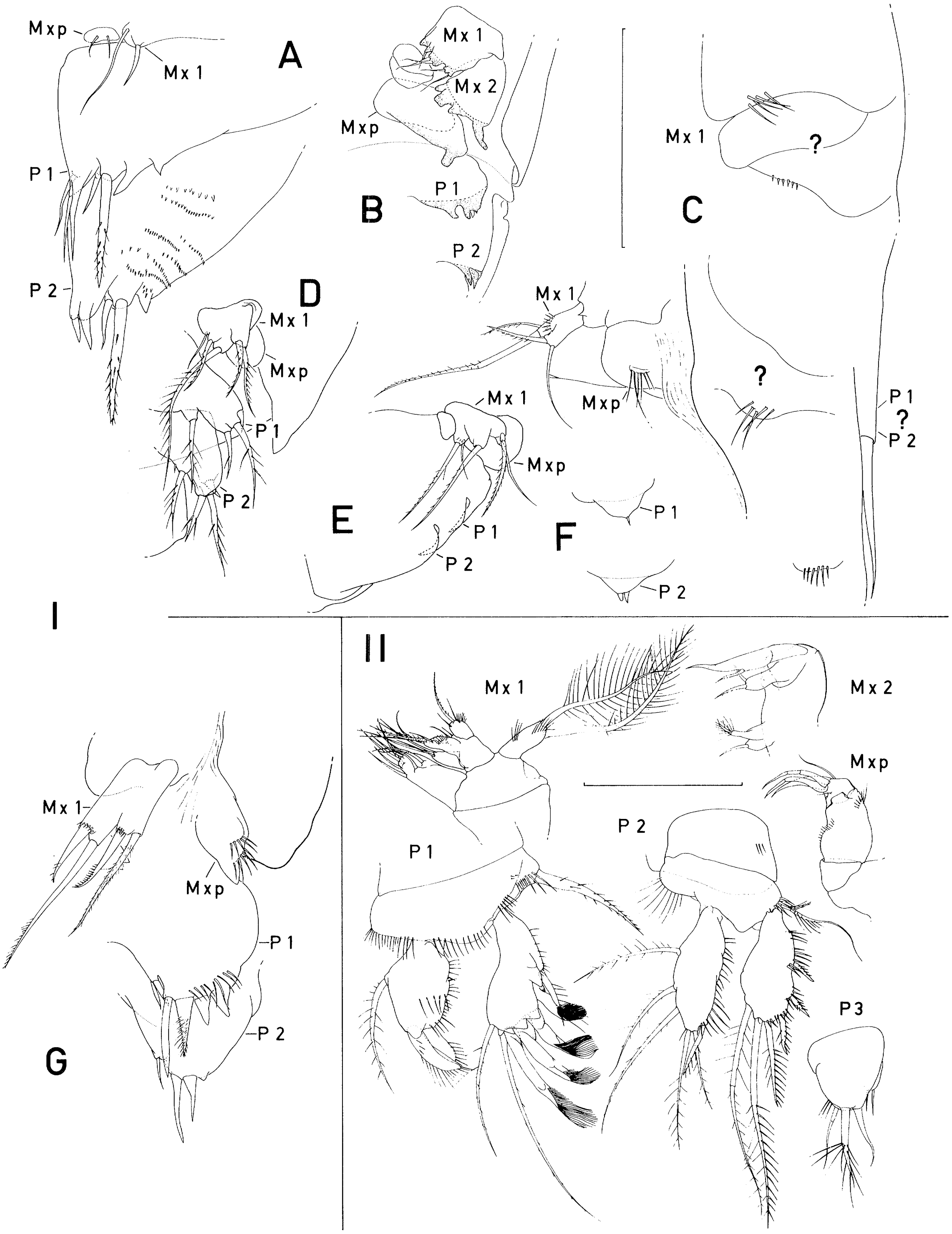

Figure 8. Metamorphosis of post-mandibular appendages in Harpacticoida (maxillule to leg 2). I. Morphology at nauplius VI of *Longipedia minor* (A); *Paraleptastacus brevicaudatus* (B); *Macrosetella gracilis* (C); *Amphiascopsis* sp. (D); *Amphiascus propinquus* (E); *Tisbe gracilis* (F); *Scutellidium hippolytes* (G). II. Morphology at copepodid I of *Scutellidium hippolytes* (Mx 1, 2, maxillule, maxilla; Mxp, maxilliped; P 1–3, legs 1–3). Scale bars 50 μm.

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the major seta of C I gives rise to setae IV and V, the adjacent to seta VI, and the outermost to seta I, there must be two copepodid setae developed *de novo*: seta VII on the inner side of the major branched seta, and seta II dorsal to seta VI.

(*d*) *Metamorphosis of the antennules*

See figure 6. The five- to six-segmented naupliar antennules of polyarthran harpacticoids (Longipediidae, Canuellidae) become four-segmented at C I as is shown by *Longipedia minor* (figure 6*a*,*b*). The mode of segment formation is described by Dahms (1991). Among Oligoarthra, the number of naupliar segments never exceeds three. In Exanechentera (Tisbidimorpha) and in Podogennonta (Thalestridimorpha, Metidae) it is reduced. Peltidiidae bear two-segmented and Tegastidae one-segmented antennules. Among Thalestridae, both one-segmented (as demonstrated by *Parathalestris harpactoides*, figure 6*e*) and three-segmented antennules are common, whereas in Miracidae they are one-segmented and in Metidae two-segmented. For the homologization of antennular segments, see Dahms (1990*a*). From a one- to three-segmented (Oligoarthra) naupliar antennule, a three- to six-segmented copepodid antennule may develop, as shown in figure 6 for various species and in table 1 for 21 representatives belonging to 14 oligoarthran families. The proximal aesthetasc is always situated on the second segment. Whatever the segment number of the naupliar antennule (except in Longipediidae), it remains constant throughout the naupliar phase, whereas in the copepodid phase there is an increase in segments.

There is remarkable similarity in antennular formation in Harpacticidae and Thalestridae (figure 6) not reported by Dahms (1989, 1990*a*). All harpacticid genera of which descriptions are available, and all free-living thalestrids, have six-segmented antennules with the aesthetasc on the second segment at C I (figure 6*e*,*f*,*i*,*j*; table 1) becoming seven-segmented at C II. Harpacticoid antennules of six segments at C I are restricted to these two families.

(*e*) *Metamorphosis of antennae and mandibles*

See figure 7. The structural transformation of antennae and mandibles is basically the same in most harpacticoids as described for *Amonardia normani*. Peculiar exceptions are those taxa (*Tisbe holothuriae* group; Tachidiidimorpha, cf. Dahms 1990*a*) where most of the masticatory parts of these limbs are already reduced at N VI. As further examples, the naupliar and copepodid antennae and mandibles of *Scutellidium hippolytes*, *Tisbe gracilis* and *Drescheriella glacialis* are shown in figure 7.

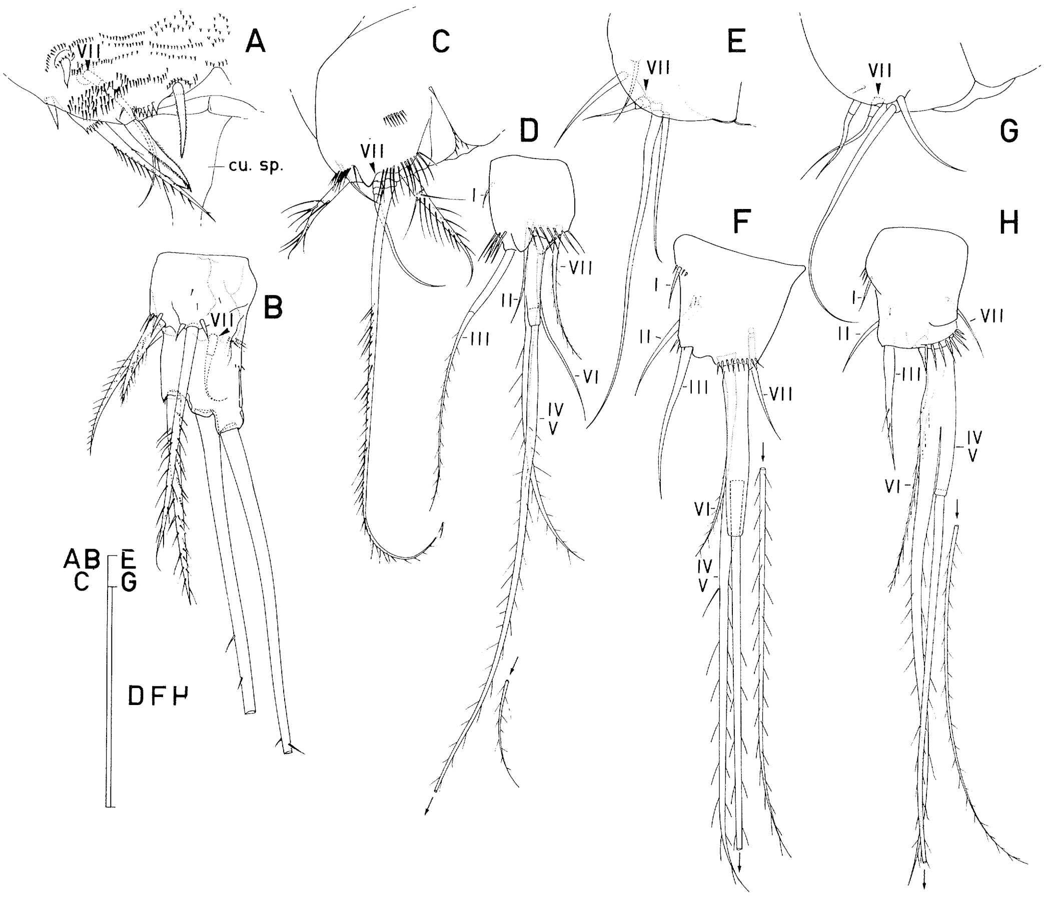

Figure 9. Metamorphosis of caudal rami from nauplius VI (A, C, E, G) to copepodid I (B, D, F, H) in *Longipedia minor* (A, B); *Scutellidium hippolytes* (C, D); *Tisbe gracilis* (E, F); *Drescheriella glacialis* (G, H)(I–VII, caudal setae 1–7, cf. Huys 1988; VII, biarticulated dorsal seta). Scale bars 50 μm.

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(*f*) *Metamorphosis of post-mandibular appendages*

See figure 8. The morphology, development and position of the post-mandibular appendages is remarkably variable. Therefore precise identification is often difficult, especially in species where several post-mandibular Anlagen are not developed or are not visible above the cuticle. However, all copepodid oral appendages have almost the adult structure.

In the Polyarthra the maxillule has two rami but the prospective endopodite is fused to the basis. This is shown for *Longipedia minor* (figure 8*a*). Among Ectinosomatidae there is one lobe with one spinulose and one naked seta from N IV to N VI (Dahms 1990*a*). In the remaining oligoarthran sections the setae do not exceed five at N VI, whether the maxillule Anlage be unilobed or bilobed.

There is no trace of the maxilla during naupliar

Table 1. *Metamorphosis of antennules and hind-body from nauplius VI to copepodid I*

(E.g. ((2)4/*2*: (number of setae plus aesthetasc on preterminal segment) number of segments/segment bearing proximal aesthetasc in copepodids). Abbreviations used: char., character; cu.set., number of caudal setae; bra., branched caudal seta of C I giving rise to setae IV + V; prot., protuberance.)

	N VI		C I	
Family and species	A1-char.	cu.set.	A1-char.	cu.set.
LONGIPEDIIDAE	(1)6(NI)			
Longipedia minor	5(NII–VI)	6	(3)5/*2*	7
CANUELLIDAE				
Canuella perplexa	(1)5	6	(2)4/*2*	7
PHYLLOGNATHOPODIDAE				
Phyllognathopus viguieri	(3)3	6	(1)5/*2*	6
ECTINOSOMATIDAE				
Ectinosoma melaniceps	(3)3	5	(3)3/*2*	6(bra.)
Halectinosoma gothiceps	(3)3	5	(3)3/*2*	6(bra.)
TISBIDAE				
Tisbe spp.	(3)3	5	(3)4/*2*	6(bra.)
Drescheriella glacialis	(3)3	5	(1)4/*2*	6(bra.)
Scutellidium hippolytes	(3)3	5	(3)4/*2*	6(bra.)
PELTIDIIDAE				
Alteutha oblonga (NI)	(1)2	—		
A. interrupta (CI)			(1)5/*2*	6(bra.)
TEGASTIDAE				
Parategastes sphaericus (NI)	(3)1	—		
Tegastes clausi (CI)			(1)5/*2*	7
TACHIDIIDAE				
Tachidius discipes	(3)3	4	(0)4/*2*	6(bra.)
Euterpina acutifrons	(1)3	3	(0)4/*2*	4(bra.)
HARPACTICIDAE				
Tigriopus brevicornis	(3)3	4	(2)6/*2*	6(bra.)
Harpacticus obscurus	(3)3	—	(2)6/*2*	7
Zaus spinatus	(3)3	5	(2)6/*2*	7
THALESTRIDAE				
Thalestris longimana (NI)	(6)1	—	(1)6/*2*	6(bra.)
Parathalestris harpactoides	(14)1	5	(3)6/*2*	6(bra.)
DIOSACCIDAE				
Paramphiascella fulvofasciata	(3)3	5	(1)5/*2*	5(bra.)
MIRACIDAE				
Macrosetella gracilis	(7)1	4	(1)5/*2*	6(bra.)
AMEIRIDAE				
Nitokra spinipes	(3)3	5	(2)5/*2*	5(bra.)
CANTHOCAMPTIDAE				
Bryocamptus pygmaeus	(3)3	5	(1)3/*2*	5(bra.)
CYLINDROPSYLLIDAE				
Paraleptastacus brevicaudatus (N VI)	(3)3	2 + 3 prot.		
P. espinulatus (C I)	—	—	(2)3/*2*	5(bra.)
LAOPHONTIDAE				
Heterolaophonte minuta	(3)3	4 + 1 prot.	(3)3/*2*	6(bra.)

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development of the Polyarthra. In the Oligoarthra, it is often difficult to decide whether a structure at N VI is the maxilla or the maxilliped. *Paraleptastacus brevicaudatus* (figure 8*b*) provides a rare case of a harpacticoid in which all post-mandibular appendages to leg 2 are present in sequence. In *Macrosetella gracilis*, however, there are only a few folds and spinules at N VI which are difficult to trace (figure 8*c*).

The maxilliped appears as a lobe with two or three setae already at N V of Polyarthra, as shown for *Londipedia minor* in figure 8*a*. Among Oligoarthra, the maxilliped Anlage is never bilobed and is not always present. In most investigated taxa it is a bulging flap, sometimes ornamented with spinules as in *Tisbe gracilis* (figure 8*f*) or *Scutellidium hippolytes* (figure 8*g*).

The first copepodid already bears the limb-bud of the third natatory leg either as one lobe (with two or three setae) or bilobed (with two setae on the inner and three setae on the outer lobule, as in *Scutellidium hippolytes* (figure 8 II)).

In harpacticoids whose adults have swimming legs with three-segmented rami, the development of the segment number is as follows (cf. Dahms 1993). In C I, legs 1 and 2 show coxa, basis and one-segmented rami, and the limb-bud of leg 3 is a single lobe or slightly bilobed. The coxa is without armature throughout the copepodid phase except in Polyarthra. The basis always bears one seta at the outer distal corner. The seta at the inner distal corner of the basis of leg 1 develops exclusively from C II onwards. The one-segmented rami of leg 1 and leg 2 bear a variable number of setae, at C I never exceeding seven in all (Hamond 1987). The endopodite usually has the same number of setae as the exopodite, or fewer.

(*g*) *Metamorphosis of caudal rami*

See figure 9. The naupliar hind-body bears six setae at N VI in Polyarthra (e.g. *Longipedia minor*, figure 9*a*). In Oligoarthra, three to six setae are present at this stage. The caudal armature is remarkably varied, even among lower-ranked taxa. The biarticulated seta (homologous to seta 3 of the copepodids according to Hamond (1987) or seta VII according to Huys (1988)) appears at N III even in species with only two setae at this instar (e.g. *Tisbe gracilis*, cf. Dahms *et al.* 1992). This is the only seta which can be traced with certainty from the naupliar to the copepodid phase without additional evidence from intermoult stages. However, findings from intermoult specimens of *Amonardia normani* (see above) may be applied by analogy to other harpacticoids, e.g. the major seta of the naupliar hind-body probably gives rise to copepodid setae IV and V of other harpacticoids as well (cf. figure 9).

Among harpacticoids, the caudal rami at C II are armed at most with seven setae each (exception: e.g. *Amonardia normani* with six setae, see above). At stage C I, however, two types of rami can be distinguished with respect to the morphology of the principal seta(e). The most common (table 1) is characterized by a branched seta complex as in *S. hippolytes* (figure 9*d*), *T. gracilis* (figure 9*f*) and *D. glacialis* (figure 9*h*). In *Bryocamptus pygmaeus* and *Alteutha interrupta* both branches are deeply cleft with a common basal plate at C I and do not become separated before C II stage (Dahms 1993).

The second type is less common among Harpacticoida. Here there is no branched seta complex from stage C I onwards. Both principal setae are separate from the first copepodid instar as shown by *Longipedia minor* (figure 9*b*). It is also the only type known from Polyarthra (Vincx & Heip 1979; Onbé 1984) and the primitive Phyllognathopodidae (Dahms 1993). This type has been found also in *Tegastes clausi* and the harpacticids *Harpacticus obscurus*, *H. uniremis* and *Zaus spinatus*, whereas in another harpacticid taxon, *Tigriopus brevicornis*, there is one branched principal seta at C I.

4. DISCUSSION

(*a*) *General morphology*

Asymmetry seems to be restricted to spinular ornamentations of the body and appendages of harpacticoid nauplii (Dahms 1987*c*). In calanoids, asymmetry applies also to the hind-body and its setation (cf. McKinnon & Arnott 1985), the antennules, and legs 5. Gibson & Grice (1977) even showed that an unusually long spine termed a masticatory hook is present on the basipodal segment exclusively of the left antenna of the calanoid *Labidocera aestiva*. In harpacticoid copepodids, asymmetry is rare and, to the author's knowledge restricted to leg 5 (e.g. among Ambunguipedidae, Huys 1990).

Antennules

The antennular segment number can be one to three among oligoarthran nauplii (Dahms 1990*a*). Where it is three-segmented, the first segment is always unarmed and the second bears three setae in most cases. Homologues of these 3 setae are assumed in the Polyarthra. Thus segments 2 and 3 of *Longipedia minor* correspond to segment 2 in the Oligoarthra, and the distal segments of *L. minor* are homologous to the third in the Oligoarthra. These three proximal setae are retained on the first segment of C I in *L. minor*, whereas the first segment of the nauplius either becomes totally reduced or fused to the former second segment. The same holds for oligoarthran antennules: the naupliar first segment is lost and the second gives rise to the first segment in the copepodid. This is especially evident when the first segment of C I still bears three setae, as shown here for *Amonardia normani*, *Longipedia minor*, *Ectinosoma melaniceps*, *Parathalestris harpactoides*, *Scutellidium hippolytes*, *Zaus spinatus* and *Heterolaophonte minuta*.

These findings, however, contradict what is known from other copepod orders. Oberg (1906) showed that the first naupliar segment is homologous with the first copepodid segment for Calanoida and Cyclopoida. This was later confirmed by Gurney (1931) and Hulsemann (1991). In the Calanoida, the first, second and third segments of the antennule in the nauplius are homologous with segments 1, 2–3, and 4–9 of the first copepodid and then give rise to segments I–V,

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VI–XX and XXI–XXVIII of the adult, respectively (numbering system of Huys & Boxshall 1991).

Paragnaths–Lingua

A ventral mouth wall, described here as a tongue-like flap, is the floor of the antennal precoxal cavity and ventral plate. This structure might be retained as the copepodid lingua, and is functionally similar to the hypopharynx of insects. Whereas Manton (1977) denied the presence of a hypopharynx in Crustacea, paragnaths are said to be present. She described the latter from adults of the harpacticoids *Amphiascus* and *Tisbe* (syn. *Idya*).

Apart from this study, the subcuticular formation of paragnaths in the Harpacticoida has otherwise been demonstrated only for a nauplius VI intermoult stage of *Amphiascus minutus* (Rosenfield 1967).

Precoxae

Hansen (1893) was the first to recognize a three-jointed protopodite for the postantennular limbs of Crustacea. He was generally criticized for recognizing a precoxa, but Lang (1947) confirmed – although without a figure – that a naupliar precoxal segment is present in the antenna and the mandible of copepod nauplii from the second naupliar stage onwards. The present study, however, shows that a distinctly three-segmented protopodite is present in the antenna as early as N I of at least some harpacticoid species. In other species an antennal precoxa has not been seen, but this may be a result of an unfavourable position of the limb obscuring observation. However, a mandibular precoxa as proposed by Hansen has not been found in any harpacticoid nauplius. The antennal precoxa cannot be found in the copepodite phase. Here, the expression of this segment is restricted to other appendages (e.g. the natatory legs).

Postmandibular appendages

At N VI, precursors of the maxillule, maxilla, maxilliped, and legs 1 and 2 may all be present and can then be identified according to their position from front to rear (e.g. Dahms 1990*b*). However, if one or more of these should be lacking, it is difficult to identify the remaining ones for they are often not easy to distinguish by their shape or armature. This is the reason for much of the confusion existing in the literature on harpacticoid naupliar post-mandibular appendage development. Even in nauplii with similar Anlagen, their interpretation differ between authors (cf. the discussion on *Canuella perplexa*, Dahms (1990a)).

According to Barnett (1966), describing the laophontids *Platychelipus littoralis* and *P. laophontoides*, the leg 2 endopodite of C I is vestigial and leg 3 is absent, which is the only observation yet of legs 3 lacking at C I among Harpacticoida.

Hind-body

There are six caudal setae in N VI in the Polyarthra and in the primitive oligoarthran *Phyllognathopus viguieri* (table 1). At C I the number is seven in both taxa. Six setae at N VI is the maximum number present in Cyclopoida. In contrast to Izawa (1987), I therefore regard six caudal setae as plesiomorphic relative to a lower number.

Nauplii of some planktonic longipediids and ectinosomatids have a naupliar caudal spine. As shown by Onbé (1984) for *Longipedia americana*, this spine is reduced in length during the naupliar phase and is not present at C I and C II. However, at C III a dorsal spine reappears in the midline of the distal edge of the anal operculum. In the following stages it increases in size and is flanked by two smaller spines in the adult. However, future investigations will have to elucidate whether the dorsal spine of C III to C VI is homologous with the caudal spine of the nauplii. If it is not homologous it will serve as a good example for the parallel development of a structure within the naupliar and copepodid phases. In this context, Björnberg's (1972) drawing of the ventral side of *Microsetella rosea* has to be mentioned. It shows a spine originating from halfway along the ventral (!) face of the anal segment. Such a spine has not been described for *M. norvegica*, which is in agreement with my own inspection of the C I stage of this species. Thus this observation has to be reinvestigated.

(*b*) *Ontogenetic transformations and tracing homology*

Within the Harpacticoida, the post-mandibular appendages differ greatly in the time of their appearance, in the number of Anlagen present at N VI, and in their shape and armature. Even within one genus the expression of an appendage is variable, as shown by the presence of the maxilliped in *Bryocamptus zschokkei* and its absence in *B. pygmaeus* and *B. echinatus* (Dahms 1987*c*).

Labelling the exuvial rudiments as they appear in the developmental sequence as maxillulae, maxillae, etc. should not be considered reliable, because a suppression of Anlagen can occur within this series (e.g. the maxilla in *Longipedia minor*, *Canuella perplexa* and *Zaus spinatus* (Dahms 1990*a*)).

All evidence from the Harpacticoida suggests that chitinous structures can be modified only through moults. This is not necessarily the case in other arthropods, as is most strikingly shown by the life cycle of Tantulocarida (Boxshall & Lincoln 1987). In Copepoda, the underlying tissue forms the Anlagen of both modified and unmodified structures before each moult. It is not always easy to homologize outer chitinous structures with their potential precursors formed under the cuticle because the same tissue may form different cuticular structures. Sometimes anatomical changes under the cuticle (formation of segments, buds of appendages) remain hidden there without any obvious external indications. Therefore Walker (1981) suggested that superficial subexuvial structures should be correlated with the exuvial Anlagen – if present – to verify their identity. This, however, may require histological studies in most cases.

Intermoult stages can provide important evidence for the homologies of limbs or limb portions during

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ontogeny. This is the case when that part of the newly developed limb under consideration is developed within the homologous parts of the former exoskeleton, or when its new armature at least is still within the sheaths of the former.

However, there are problems involved in tracing homologous elements. Often, tiny chitinous parts are too delicate to be seen under the old exoskeleton, hidden by the outer appendages and the armature of the instar, or superimposed and scrambled, and are therefore difficult to make out. In such instances guesswork may lead to misinterpretations. Also, portions of the new limbs may shift from their site of origin during the premoult phase. For example, the copepodid mandibular exopodite of *Amonardia normani* (figure 5) is withdrawn from its place of formation to the mandibular basis of N VI. Certain evidence about homologous structures, therefore, can be obtained only when new elements are still in the sheaths of their precursors. However, the present study revealed some findings which, although previously hypothesized in part, remained unproven. These are: the limb portions called naupliar and copepodid antennal endopodites are actually homologous; the so-called mandibular syncoxa of the copepodids is formed within the naupliar coxa; the mandibular endopodite is derived from the outer lateral field of the naupliar endopodite; and the maxilliped, which cannot be traced externally in the nauplii, is developed in fact without any naupliar precursor. As for the copepodid pre- or syncoxa, it has to be asked whether this term is justified at all, because the relevant part of the mandibular protopodite is clearly derived from the naupliar coxal precursor, and there is no mandibular precoxa to be detected among copepod nauplii, at least among those of the Harpacticoida (Dahms 1990*a*).

(*c*) *Sexual dimorphism*

This has never been observed among nauplii, but may become apparent in the first copepodid, as shown for *Zaus robustus* (Ito 1976). In this particular case, sexual dimorphism is a result of metamorphosis from the naupliar to the juvenile organization. However, more commonly, it is not possible to distinguish the sexes earlier than at C III or IV, on the basis of antennular segmentation and armature and the shape and armature of legs 5 and 6.

(*d*) *Similarities between nauplii and copepodids*

Even though the 'metamorphosis' from nauplius to copepodid is accompanied by remarkable changes, there are also examples of striking continuity in morphological and behavioural features between both phases. For example, nauplii of Longipediidae are characterized by a caudal process, and a similar structure is also present in later copepodids. The nauplii of *Zaus spinatus* bear a spinule fan, both on the antennal endopodite claw and on the mandibular endopodite spine. Such a fan also exists on the endopodite of leg 1 in the copepodids. The nauplius shield of *Rhizothrix minuta* is covered with cuticular denticles characteristic also for the cephalothorax and free segments of its copepodids. Björnberg (1965) reported two eye-spat lenses surrounded by dark pigment already present in the nauplii of *M. efferata*, like those long known as characteristic of the copepodids and adult. Nauplii and copepodids of *Euterpina acutifrons* both have stout, blade-like caudal setae (Tesch 1915).

There is also pronounced continuity of locomotory behaviour and habitat preference between nauplii and copepodids throughout the Harpacticoida. Nauplii that can swim well usually belong to taxa with strongly swimming copepodids (e.g. Phyllognathopodidae, Tisbidae, Canthocamptidae). Among inbenthic taxa, both nauplii and copepodids are skilful crawlers but unable to swim (e.g. Cylindropsyllidae). The same can be observed in the mode of feeding. Already Storch (1928) noted in a study of naupliar feeding among Copepoda: '. . . daher ist es von Interesse, daß eine gewisse Parallelität besteht zwischen der Form des Nahrungserwerbes der Nauplien und der erwachsenen Formen, indem der allgemeine Typus bei Larve und Copepoden im wesentlichen übereinstimmt . . .'. In Polyarthra where the nauplii are suspension feeders, the copepodids are also able to filter-feed (Vincx & Heip 1979), whereas in Oligoarthra, both nauplii and copepodids feed on larger particles (Dahms 1990*a*). Also, nauplii and copepodids usually show few differences in behaviour or habitat preference (except Tegastidae and Peltidiidae); if the nauplius is a good swimmer, so too is the copepodid.

5. CONCLUSION

Within the Harpacticoida, both post-embryonic phases are well adapted to an inbenthic, epibenthic, phytal, associated or pelagic lifestyle and display a variety of specializations within each of these. Thus convergent evolution is as common in the naupliar phase as in the copepodid phase. Also, the degree of evolutionary transformation may be different in these phases. A relatively apomorphic adult or copepodid, therefore, may develop from a relatively plesiomorphic nauplius.

Although new structures and additional meristic characters are acquired by successive naupliar instars which accumulate until N VI, even the 1st stage nauplius usually bears species-diagnostic characters (Dahms 1990*a*). Besides qualitative and quantitative structural additions, reductions or functional transformations take place in the sequence of naupliar ontogeny (Dahms 1991). However, in most cases there is little morphological change within the naupliar phase.

Metamorphic transformations from naupliar to copepodid organization affect size, body shape, segmentation and appendages. Whereas the general structure of the antennules is kept, antennae and mandibles change shape and function most drastically. The post-mandibular appendages are transformed from undifferentiated naupliar Anlagen (except the natatory legs) to almost the adult condi-

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tion. Leg 3 Anlage is not developed before the first copepodid.

The copepodids foreshadow the adult organization from the first stage onwards, and the first copepodid can be distinguished from others almost at the species level. Therefore those ontogenetic features of the copepodid which do not already belong to the adult organization are phylogenetically useful. These characters may exhibit marked stage-specific changes or are reminiscent of ancestral copepodid states. Intermoult stages provide information on the homology of naupliar and copepodid structures.

The extent of transformation during metamorphosis may hide an often underlying continuity. The larva may already show precursors of adult characters, whereas the copepodids and adults may still exhibit vestiges of larval structures. Therefore nauplii and copepodids often develop not so much successively but more in a parallel mode. In each phase of the life cycle, one set of structures is realized, another latent. The persistence of larval characters throughout life (e.g. the naupliar caudal spine) makes much more readily understandable the phenomena of the return of naupliar characters in the copepodids. It is perhaps generally the case that what changes in metamorphosis is only the balance of gene activity. Genes that are most active in the early stages are perhaps never turned off entirely but remain effective at depressed levels throughout the lifetime of the individual.

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APPENDIX 1. SOURCES OF MATERIAL

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Parategastes sphaericus (Claus, 1863). Nauplii reared from a female collected from *Laminaria digitata* holdfast. Helgoland – 8 May 1986.

Alteutha interrupta (Goodsir, 1845). Copepodids from *Flustra foliacea*. Helgoland – 22 July 1986.

Alteutha oblonga (Goodsir, 1845). Nauplii reared from a female from *Flustra foliacea*. Helgoland – 1986.

Zaus spinatus Goodsir, 1845. Reared from females from *Laminaria hyperborea*. Helgoland – 23 July 1986.

Parathalestris harpactoides (Claus, 1863). From macroalgae, intertidal zone. Helgoland – 8 May 1986.

Macrosetella gracilis (Dana, 1848). Instars from plankton, Red Sea (R. Böttger-Schnack) – 4 November 1980.

Amonardia normani (Brady, 1872). Reared from littoral sediment. Baltic Sea near Kungshamn. Sweden – 12 August 1985.

Paramphiascella fulvofasciata Rosenfield & Coull, 1974. Reared from *Laminaria hyperborea* holdfasts. Helgoland – 20 July 1983 (Dahms 1987*b*).

Amphiascus propinquus Sars, 1906. Helgoland – 24 May 1986.

Amphiascopsis sp. Gurney, 1927. Mediterranean, Villefranche-Sur-Mer – 1986.

Heterolaophonte minuta (Boeck, 1872). Reared from gravid females from intertidal zone. Mellum Island. North Sea – 12 July 1985.

Paraleptastacus brevicaudatus Wilson, 1932. Reared from gravid females from sandy beach. Helgoland-Düne – 28 May 1986.

Bryocamptus pygmaeus (Sars, 1862). Collected from *Sphagnum* spp. Lengener Meer, NW-Germany – 12 June 1984.

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