

## Naupliar development of *Acanthodiaptomus denticornis* (Wierzejski, 1887) and *Arctodiaptomus alpinus* (Imhof, 1885) (Copepoda: Calanoida) and a comparison with other Diaptomidae

Christian D. Jersabek, Alfred Goldschmid and Robert Schabetsberger  
University of Salzburg, Institute of Zoology, Hellbrunnerstraße 34, A-5020  
Salzburg, Austria

**Abstract.** The six naupliar instars of the two alpine species *Acanthodiaptomus denticornis* and *Arctodiaptomus alpinus* are described and illustrated. Their external morphology is compared with that of all presently known diaptomid nauplii in an attempt to provide useful taxonomic characteristics to identify larval diaptomids. The larval stages of the two species are remarkably similar in size and overall appearance, and show an identical pattern of limb setation throughout the whole development. Diagnostic characters are mainly related to the differentiation of antennules and caudal armature.

### Introduction

The calanoid copepods *Acanthodiaptomus denticornis* and *Arctodiaptomus alpinus* are widely distributed in high-altitude lakes throughout the European Alps. Here they usually show a univoltine life cycle, producing exclusively hibernating resting eggs (Jersabek and Schabetsberger, 1995). Therefore, these diaptomids may be present only as immature stages over a considerable portion of the year and planktologists may face problems with species identification when, as in most cases, larval and juvenile stages are not adequately described in the literature. Therefore, it is increasingly difficult to study stage-dependent ecological phenomena and to explain the dynamics of community composition if more than one diaptomid species co-exist in a lake. Green and Northcote (1982) could readily distinguish co-existing diaptomid nauplii on the basis of body size and differences in caudal armature at the magnification usually used for counting.

Besides species discrimination, post-embryonic morphology can be used as an additional source of characters to trace phylogenetic relationships between species and to identify polarity criteria (i.e. plesiomorphic–apomorphic states) and homologies provided by the ontogenesis of different taxa (Dahms, 1991; Hulsemann, 1991). Thus, as generic and specific limits in diaptomids continue to be vague in several cases (Reddy, 1994), systematics traditionally relying on adult semaphoronts will benefit from the incorporation of other approaches and ontogenetic stages (Dahms and Schminke, 1995).

Yet, only the following of >400 diaptomid species belonging to 50 genera (Dussart and Defaye, 1983) have been studied concerning their naupliar development: Europe: *Diaptomus castor* (Jurine) (Gurney, 1931), *Eudiaptomus gracilis* (Sars) (Wuthrich, 1948), *E. vulgaris* (Schmeil) (Grandori, 1912; Dietrich, 1915; Ravera, 1953), *Mixodiaptomus laciniatus* (Lilljeborg) (Wuthrich, 1948; Ravera, 1953); North America: *Agladiaptomus leptopus* Forbes (Pinel-Alloul and Lamoureaux, 1988), *Hesperodiaptomus kenai* Wilson (Green and Northcote, 1982), *Leptodiaptomus siciloides* Lilljeborg (Ewers, 1930; Comita and Tommerdahl,

1960); *Skistodiptomus oregonensis* Lilljeborg (Comita and McNett, 1976); South America: '*Diptomus*' *proximus* Kiefer (González, 1968), *Notodiptomus conifer* (Sars) (De Gouvea, 1980), *Notodiptomus coniferooides* (Wright) (Cicchino, 1972), *Notodiptomus corderoi* Wright (Cipólli, 1973); Asia: *Allodiptomus raoi* Kiefer (Devi and Reddy, 1989a), *Heliodyptomus cinctus* (Gurney) (Reddy and Devi, 1990a), *H.contortus* (Gurney) (Reddy and Devi, 1989), *Megadyptomus hebes* Kiefer (Reddy and Devi, 1985), *Neodyptomus lindbergi* Brehm (Devi and Reddy, 1990a), *Paradyptomus greeni* (Gurney) (Devi and Reddy, 1989a), *Phylloidyptomus annae* (Apstein) (Dahms and Fernando, 1993), *P.blanci* (Guerne & Richard) (Reddy and Devi, 1990b), *Tropodyptomus informis* Kiefer (Devi and Reddy, 1990b).

The present paper provides a detailed description and character analysis of the naupliar stages of *Ac.denticornis* and *Ar.alpinus*, comparing their morphology with that of other larval diptomids, as described in the literature (op. cit.). In the case of *M.laciniatus*, it was possible to include and compare the authors' field results from an alpine lake. It is our intention to enable a valid comparison of naupliar stages belonging to the two species in future studies. In a following publication (C.D.Jersabek, in preparation), this study will be continued by describing the copepodite development of the two species.

## Method

First naupliar stages were obtained from resting eggs produced by lake-caught females during spawning experiments in the laboratory (cf. Jersabek and Schabetsberger, 1995). Eggs were stored in the dark at temperatures of 0–2°C. After a diapausing period of 7–8 months, the temperature was raised and thus hatching stimulated. Nauplii were isolated and transferred in groups of 5–10 animals to 50 ml beakers containing 30 µm filtered eutrophic pond water, where development proceeded at room temperatures (18–20°C) without any artificial food being added.

Nauplii were dissected using microneedles and a stereomicroscope. Drawings were made at 250× magnification (habitus of nauplii) and 500× (dissected appendages), using a Leitz-Laborlux microscope equipped with a camera lucida. Body lengths were measured from the anterior to the posterior end of the nauplius, excluding caudal armature; body width is given as the widest part of the animal. Measurements are given for the animals figured (anaesthetized in MS 222) and for up to 20 field specimens from Lake Dreibrüdersee (preserved in 4% formalin). They are accurate to the nearest 2 µm. Finer details, such as setae, hairs, spines, aesthetascs and sutures, were checked using oil-immersion (1250×), phase- and interference-contrast optics. Water was the preferred mounting medium over glycerine or polyvinylalcohol, as these media reduce the contrast of fine structures. The details depicted were checked with the opposite appendage and 2–4 additional specimens per stage for variability. Since no asymmetry of segmentation or setation was noticed between paired appendages, only one of each pair is shown. Moreover, morphological results were compared with developmental instars from the original habitat, Lake Dreibrüdersee (for

habitat description, see Jersabek and Schabetsberger, 1996). Illustrations of entire animals were obtained after anaesthetizing them in strongly diluted MS 222, which gave better results than using carbonized water. Copepods usually recovered quickly after the addition of fresh water.

A data base was compiled for minimum variance cluster analysis by recording the setation patterns of appendages, caudal armature, symmetry of caudal lobes or lack thereof. All six naupliar stages from adequately described species were checked for a total of 80 characters. We used the MVSP 2.1 statistical package for classifying larval diaptomids according to the expression of larval character states.

Abbreviations used in the text and figures are: NI–NVI, first to sixth nauplius; A1, antennula; A2, antenna; Md, mandible; Mx1, maxillule; Mx2, maxilla; Mxp, maxilliped; P1–P2, first and second swimming leg. Morphological terminology follows that of Huys and Boxshall (1991).

### The naupliar instars

The larval development of the two species is strikingly similar throughout all stages, but minor morphological differences exist, mainly related to details of limb setation, posture of particular setae or spines, caudal armature, and symmetry of the posterior end, allowing differentiation between species.

The nauplii are oval, becoming more elongate during the course of development, when the hind body gradually protrudes caudally from the naupliar dorsal shield from NII onwards. The uniramous antennules remain 3-segmented throughout all six stages. They are strongly reflexed to serve as active oars in the lecithotrophic first nauplius, but extend almost directly forward when swimming or at rest in all feeding stages. The main developmental changes in the biramous antennae are an increase of setae and the number of exopodal segments. They are inserted parorally and generally produce locomotory and feeding currents, and assist in mastication with two or three modified protopodal setae. The biramous mandibles retain the same number of segments throughout the six instars, but there is a gnathobasal process present on the coxa from NIV onwards and the number of setae progressively increases after each moulting. All other post-mandibular appendages, i.e. maxillules, maxillae, maxillipeds, first and second swimming legs, are successively indicated as a single seta (Mx1 in NIII) or functionless limb buds in the metanaupliar stages NIV–NVI. The labrum is a simple muscular lobe that overlies the mouth opening and can be slightly moved in the anteroposterior plane. It is bare in the first nauplius, but ornamented with spinule rows and hairs in the later stages, as is the ventral body wall. The nauplius eye sits dorsally to the anterior end of the labrum and is tripartite, comprising a pair of dorsal ocelli and a median ventral ocellus. First indications of caudal asymmetry are shown from NII onwards, whereas the rounded hind body is symmetrical at the first stage. There is no conspicuous segmentation of the body throughout the naupliar phase.

All ontogenetic stages of the two species are obvious from bright red carotenoid colouration. Details of limb morphology of all presently known diaptomid larvae are summarized in Table I.

**Table I.** Armature of naupliar limbs and caudal lobes. Each entry refers to the number of setae present. +, r, -: presence, rudiment, absence of an antennular aesthetasc; \*: no information on aesthetase; \*: doubtful observation. Species arranged in order of decreasing number of elements. Species abbreviations and references: Ad, *Acanthodiaptomus denticornis* (this study); Al, *Agladiaptomus leptopus* (Pinel-Alloul and Lamoreux, 1988); Ar, *Allodiaptomus raoi* (Devi and Reddy, 1989b); Aa, *Arctodiaptomus alpinus* (this study); Dp, '*Diaptomus*' *proximus* (González, 1968); Eg, *Eudiaptomus gracilis* (Wuthrich, 1948); Ev, *Eudiaptomus vulgaris* (Grandori, 1912; Ravera, 1953); Hci, *Heliodiaptomus cinctus* (Reddy and Devi, 1990a); Hco, *Heliodiaptomus contortus* (Reddy and Devi, 1989); Hk, *Hesperodiaptomus kenai* (Green and Northcote, 1982); Ls, *Leptodiaptomus siciloides* (Comita and Tommerdahl, 1960); Mh, *Megadiaptomus hebes* (Reddy and Devi, 1985); Ml, *Mixodiaptomus laciniatus* (Wuthrich, 1948; Ravera, 1953); Nl, *Neodiaptomus lindbergi* (Devi and Reddy, 1990a); Nc, *Notodiaptomus conifer* (De Gouvea, 1980); Ncf, *Notodiaptomus coniferoides* (Cicchino, 1972); Ncr, *Notodiaptomus corderoi* (Cipólli, 1973); Pg, *Paradiaptomus greeni* (Devi and Reddy, 1989a); Pa, *Phyllodiaptomus annae* (Dahms and Fernando, 1993); Pb, *Phyllodiaptomus blanci* (Reddy and Devi, 1990b); So, *Skistodiaptomus oregonensis* (Comita and McNett, 1976); Ti, *Tropodiaptomus informis* (Devi and Reddy, 1990b)

Setation	NI	NII	NIII	NIV	NV	NVI	Species
							<b>Antennula</b>
Terminal segment	3-	3-	6-	11-	13-	16+	Al
	-	+	+	10+	+	16+	Aa, Ad, Ev*, Ti
	-	+	+	+	r	-	So
	-	+	+	-	-	-	Eg, Ls, Ml
	-	+	+	9+	+	+	Ncr
	-	+	+	9-	-	-	Pg
			7		11		Dp*
			9	12	12	15	Nc**
	-	+	6+	+	+	+	Ncf*, Pa
	-	+	+	10+	12r	14-	Mh
	-	-	-	+	+	+	Hk
	-	-	+	9-	-	-	Pb
	-	+	+	+	11r	-	Nl
	-	+	+	+	12+	13+	Hco
	-	+	r	-	-	-	Hci
	-	+	+	-	11-	-	Ar
							<b>Antenna</b>
Coxa	3*	2	3	3	3	3	Ev
	2	-	-	-	-	-	Aa, Ad, Eg, Ml, Nc, So, Ti
	1	3	-	-	-	-	Ncr
	-	2	-	-	-	-	Hci, Hk, Ls, Ncf, Pa
	-	1	-	-	-	-	Al
	-	2	2	-	-	-	Ar, Hco, Nl
	2	-	-	2	-	-	Mh
	1	-	-	-	-	-	Pb, Pg
	-	1	1	1	1	-	Dp
Basis	3	3	4	5	5	5	Other species
	2	-	-	-	-	-	Hk
	3	-	-	4	-	-	Ls, Pg, So
	1	1	5	5	-	6	Dp
	2	3	4	4	-	5	Ncr
	-	2	-	-	-	-	Nc
	1	3	-	-	4	-	Al
Endopod	4	5	7	7	9	10	Ar
	-	-	-	-	-	9	Other species
	3	-	-	-	-	-	Ncf, Pa
	4	-	6	-	-	-	Hk, Mh
	3	4	7	-	-	-	Nc
	-	5	6	-	8	-	Ncr
	2	-	-	5	6	8	Dp
Exopod	6	7	9	10	11	12	Other species
	-	-	8	-	-	-	Ncr
	-	-	10	-	10	11	Mh
	-	-	9	-	-	-	Pa, Pg
	5	-	7	-	11	12	Nc

Table 1—continued

Setation	NI	NII	NIII	NIV	NV	NVI	Species
				Antenna			
Exopod	6	—	9	9	10	11	Pb
	—	—	7	8	11	12	Ncf
	—	—	8	9	10	10	Ti
	—	6	—	8	7	8	Dp
Exopod segments	6	6	6	6	6	7	Pa
	5	—	—	—	—	—	Aa, Ad
	6	—	—	—	—	6	Ncf
	5	—	—	—	—	—	Eg, Ev, MI
	—	5	—	—	—	—	Hco, Mh, Nc, NI, So
	—	—	5	—	—	—	Ar, Dp, Ncr
	—	6	6	—	5	5	Hk*, Ls*
	—	5	5	5	6	6	Pb, Pg
	—	6	—	—	5	—	Al*
	—	5	—	—	—	5	Hci
				Mandibula			
Teeth on gnathobase				4	7	5	Ls
				—	6	6	Pg
				—	5	—	Aa, Ad, Eg, Hci, MI, Ti
				—	4	—	Ar, Hco, Mh, NI, Pa
				—	5	5	Al, Ncf
				—	4	—	Hk, Pb, So
Basis	2	3	4	6	6	6	Aa, Ad, Eg, MI, Pa
	—	—	—	5	—	—	Hk
	—	—	3	—	5	5	Ncr
	—	2	—	—	—	—	Hci, Hco, Ls, Mh, NI, So
	—	3	—	4	—	—	Ev*
	—	2	—	—	—	—	Ar, Pb, Pg, Ti
	—	—	—	—	4	—	Al
	—	—	—	—	—	4	Nc
	—	—	—	—	—	—	Ncf
	—	1	—	—	—	—	Dp
Endopod	6	9	10	11	11	11	Aa, Ad, Ev, MI
	—	8	—	—	—	—	Hco
	—	9	9*	—	—	—	Eg
	—	8	—	—	—	—	Hk, NI
	—	—	—	10	10	12	Ti
	—	—	8	11	11	11	Ls
	—	7	9	—	—	—	Al
	—	8	10	10	10	10	Ncf
	—	—	8	—	11	11	So
	—	—	9	9	—	—	Pb
	—	—	8	10	10	—	Mh, Pg
	—	—	9	9	—	—	Ar
	—	—	—	10	—	10	Hci
	—	8	8	—	10	—	Nc
	—	—	—	9	—	—	Pa
	—	6	6	7	7	6*	Dp
Exopod	5	6	6	6	6	6	Other species
	—	5	—	—	—	—	Hk, Ls, So
	—	6	5	—	—	—	Mh
	—	5	—	5	7	7	Dp
	—	—	—	6	6	6	Nc
				Maxillula			
Lacinia coxalis				2	2	2	Ls
				1	—	—	Other species
Lacinia basalis				1	2	3	Pg
				2	—	2	Ls
				1	—	—	Other species

Table 1—continued

Setation	NI	NII	NIII	NIV	NV	NVI	Species
				Maxillula			
Lacinia basalis				—	1	—	Ar
				0	0	1	Pb
				—	—	0	Nc, Ncf, Ncr
Endopod			1	3	6	8	Aa, Ad, Ml, Hk
			—	—	5	—	Eg, Ev, Pg
			—	—	—	7	Nl
	1		2	—	—	5	Nc
			—	—	—	6	Al, Mh, Pa, Ti
			—	4	4	—	Ls
			—	3	5	5	Ncr
			—	—	4	6	So
			—	—	5	5	Ar, Hci, Hco
			—	—	4	—	Pb
			1	—	—	4	Ncf
			—	2	3	3	Dp
Exopod				3	5	7	Pg
				—	5	6	Other species
				2	—	—	Ls
				3	—	5	Dp
				—	4	4	Ar
			Maxilla				
			1	1	2	9	Nc
			—	—	—	?	Ncr
					—	?	Dp
					—	18	Aa, Ad, Hk
					—	15	Eg, Ml
					—	14	Al, Pa
					—	13	Other species
					—	11	Ev*
					1	varias	Ncf
			Maxilliped				
					2	3	Nc
					0	2	Other species
			Swimming leg 1				
Endopod						4	Hci
						3	Other species
Exopod						2	Al, Ls, Ncr
						5	Hci
						4	Ar, Hco, Mh, Pg, Ti
						3	Other species
						2	Ls
			Swimming leg 2				
Endopod						2	Other species
						3	Hci, Hco
Exopod						2	Al
						3	Other species
						4	Hco
						5	Hci
			Caudal armature				
Pairs of appendages	1	2	2	3	3	3	Nc
	—	1	—	2	—	—	Other species
	—	—	—	—	2	—	Eg, Ev, Pa
	—	—	1	—	—	—	Ls

***Acanthodiptomus denticornis* (Wierzejski, 1887) Figures 1–5*****Nauplius I***

**General features** (Figure 1). Body egg-shaped, length 193  $\mu\text{m}$  (field specimens: 176  $\mu\text{m}$ , range 160–194  $\mu\text{m}$ ,  $n = 11$ ), maximum width 109  $\mu\text{m}$  (ratio length/width ( $l/w$ ) = 1.77); rounded caudal region undifferentiated, with two plumose setae of almost equal length subcaudally on ventral side. Labrum and ventral body wall smooth, labrum held close to the body. Only the first three cephalic appendages developed ('orthonauplius'). There is no mouth or anus.

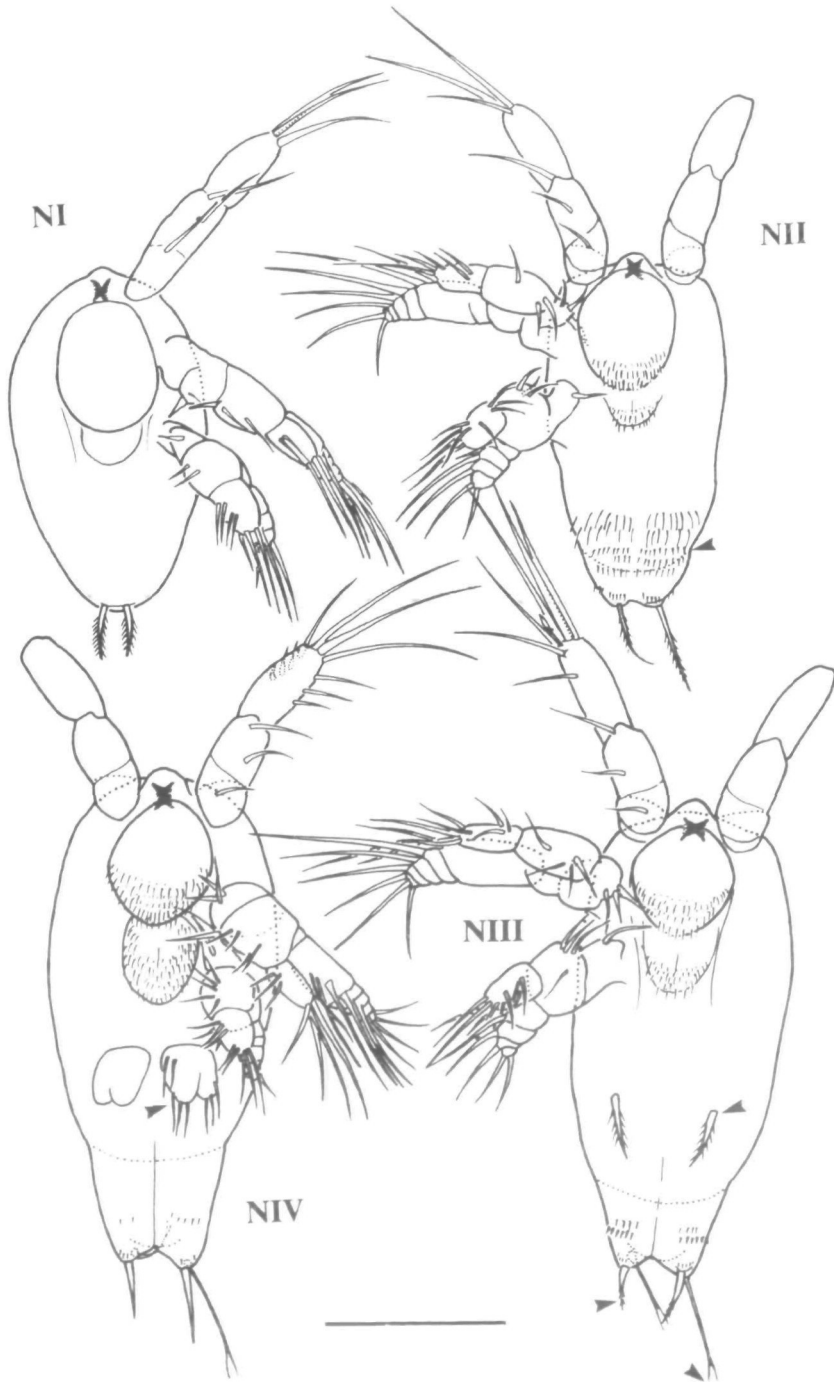
**Antennule** (Figure 2). Uniramous, three-segmented with inconspicuous segmentation between first and second segment. Basal segment with one spinulose seta at distal inner edge, second segment bearing two inner spinulose setae with the distal one being slightly longer than the one at midlength, reaching 1.07 times the length of the terminal segment. Basal and second segment with transverse spinule rows as figured. Flattened terminal segment 1.75 times longer than wide, with convex dorsal and straight or slightly concave ventral margin. Its surface ornamented with five transverse rows of up to seven small spinules. Three plumose setae of almost equal length terminally, reaching 1.7 times the length of the segment. No aesthetasc on distal end of terminal segment.

**Antenna** (Figure 3). Biramous, consisting of a two-segmented protopod, with an indistinct suture between coxa and basis. Coxa with a moderately strong bare masticatory and one bare slender seta. Basal endite weakly bilobed, with one spiniform and one slender seta on proximal lobe, and one slender seta on distal lobe. Endopod consists of one segment with two slender, unequal bare setae laterally and two strong plumose setae terminally. Endopod adorned with a subapical row of six spinules. Exopod 2.2 times longer than endopod, faintly 5-segmented, bearing one plumose seta each at innermost tip of segment plus a second outer bare seta terminally on fifth segment. Sixth basal exopodal segment of later stages not yet recognizable, but later suture indicated by a transverse row of spinules.

**Mandible** (Figure 4). Biramous, with exo- and endopod being almost equal in length. Coxa with single spinulose seta, without masticatory process. Basal endite with two equal bare setae. Unsegmented endopod nearly circular in shape, bearing two pairs of equal bare setae on inner margin and one pair of plumose terminal setae. Two small spinules near base of inner terminal seta. Exopod faintly 4-segmented with 1,1,1 and 1 plumose seta at inner tip of each segment plus a second bare seta on fourth segment.

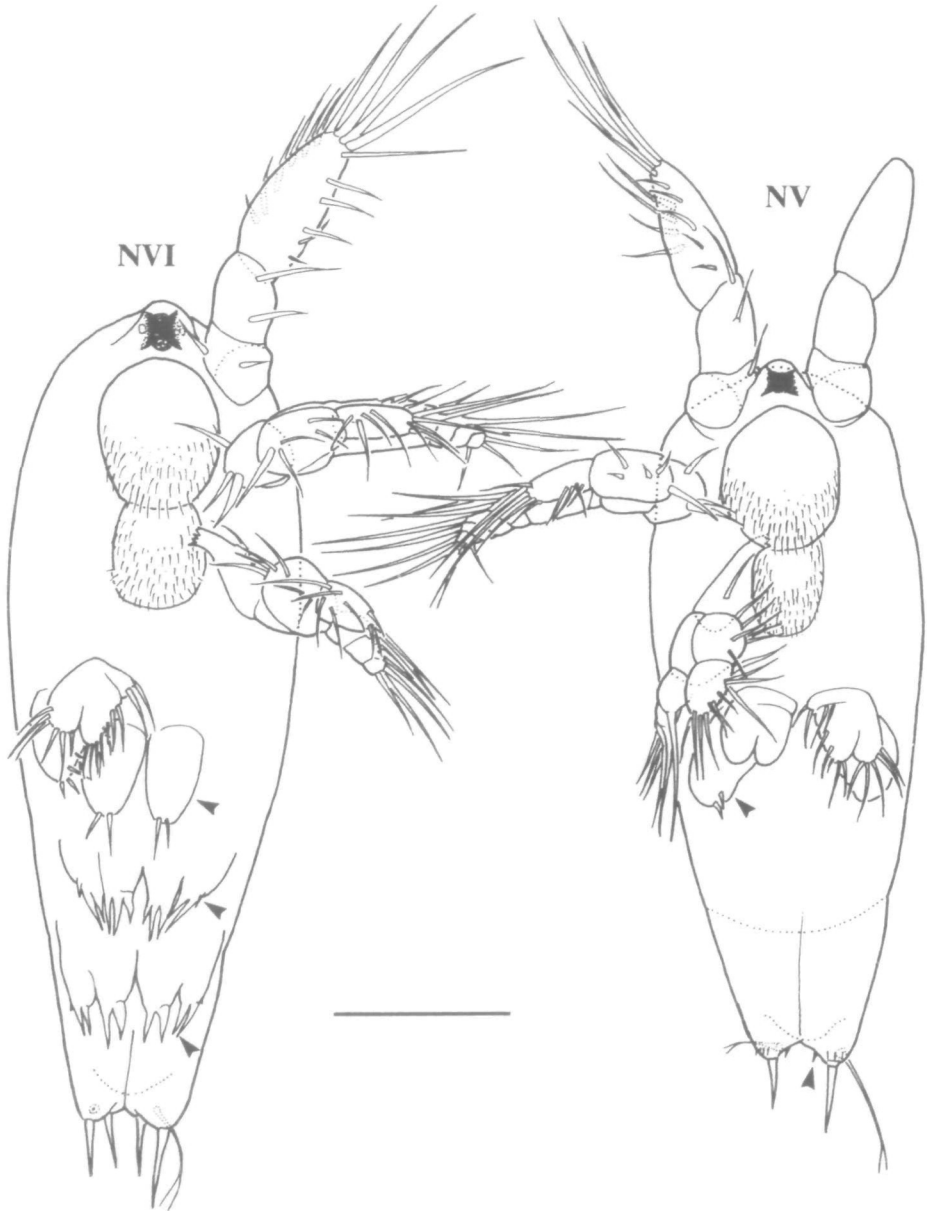
***Nauplius II***

**General features** (Figure 1). In this and all subsequent instars, the body becomes more elongate and pear shaped — length 205  $\mu\text{m}$  (field specimens: 211  $\mu\text{m}$ , range 202–225  $\mu\text{m}$ ,  $n = 13$ ), maximum width 103  $\mu\text{m}$ ;  $l/w = 1.99$  — with more prominent rostrum and bilobed hind body emerging caudally under the naupliar shield. As



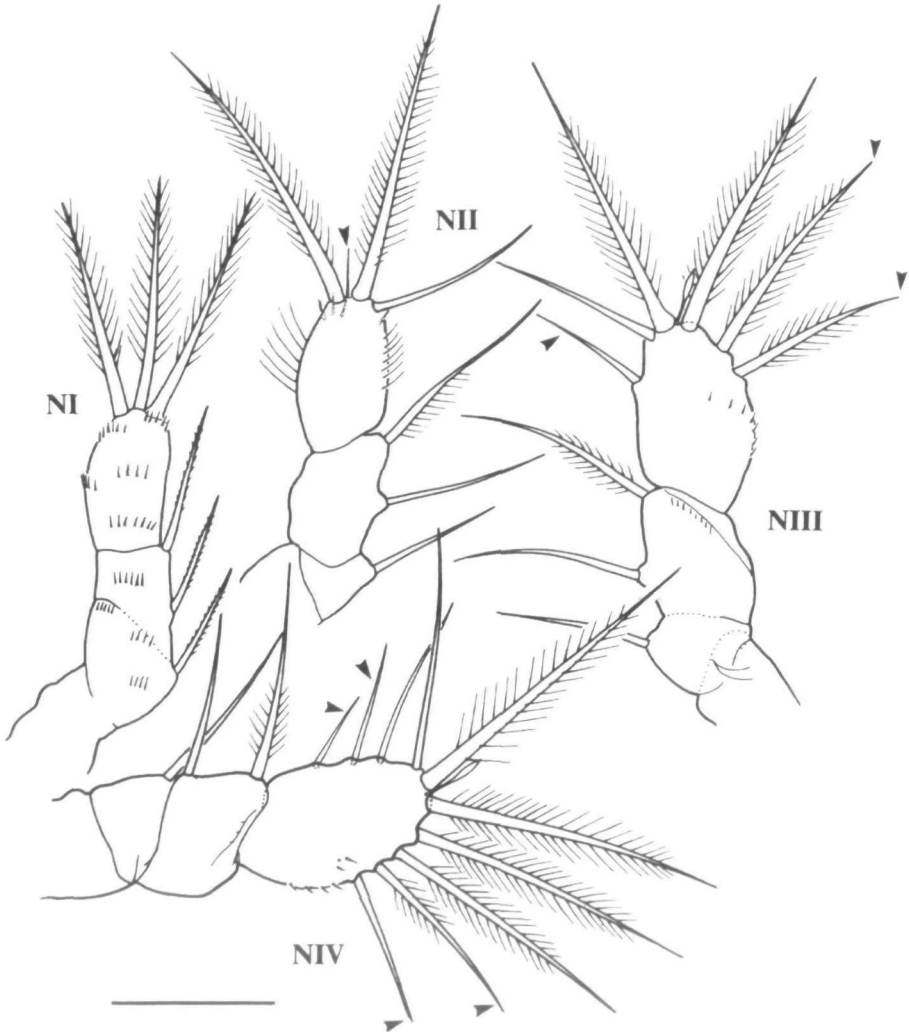
**Fig. 1.** *Acanthodiptomus denticornis*. Naupliar stages NI–NVI, ventral view. Arrows indicate newly added structures as compared with the preceding stage. Scale bar = 100  $\mu\text{m}$ .





**Fig. 1.** continued.

in all following stages, the left caudal lobe is more strongly developed than the right one. Two plumose setae of almost equal length (up to 25% of body length) are inserted terminally on caudal lobes, the right one being bent upwards. Labrum and ventral body wall ornamented with hairs all over caudal third. Ventro-posterior part of body with irregular transverse rows of delicate hairs and small spines as illustrated.



**Fig. 2.** *Acanthodiptomus denticornis*. Naupliar antennules NI–NVI, lateral view. Arrows indicate newly added structures as compared with the preceding stage. Scale bar = 50  $\mu\text{m}$ .

**Antennule** (Figure 2). Overall size and setation as in NI, but differs as follows: seta on first segment and proximal seta on second segment bare, distal seta on second segment with long hairs on one side and distinctly longer than terminal segment (1.48:1). Ventro-terminal seta slender, bare and only somewhat longer than segment. Terminal segment 1.72 times longer than wide, fringed with 6–7 long hairs along lateral margins. With the exception of four subapical spines on third segment, no further ornamentation of segment surfaces. Aesthetasc represented by a bristle situated on a knob between terminal setae.

**Antenna** (Figure 3). Differs from NI as follows. Coxa with a strong lanceolate

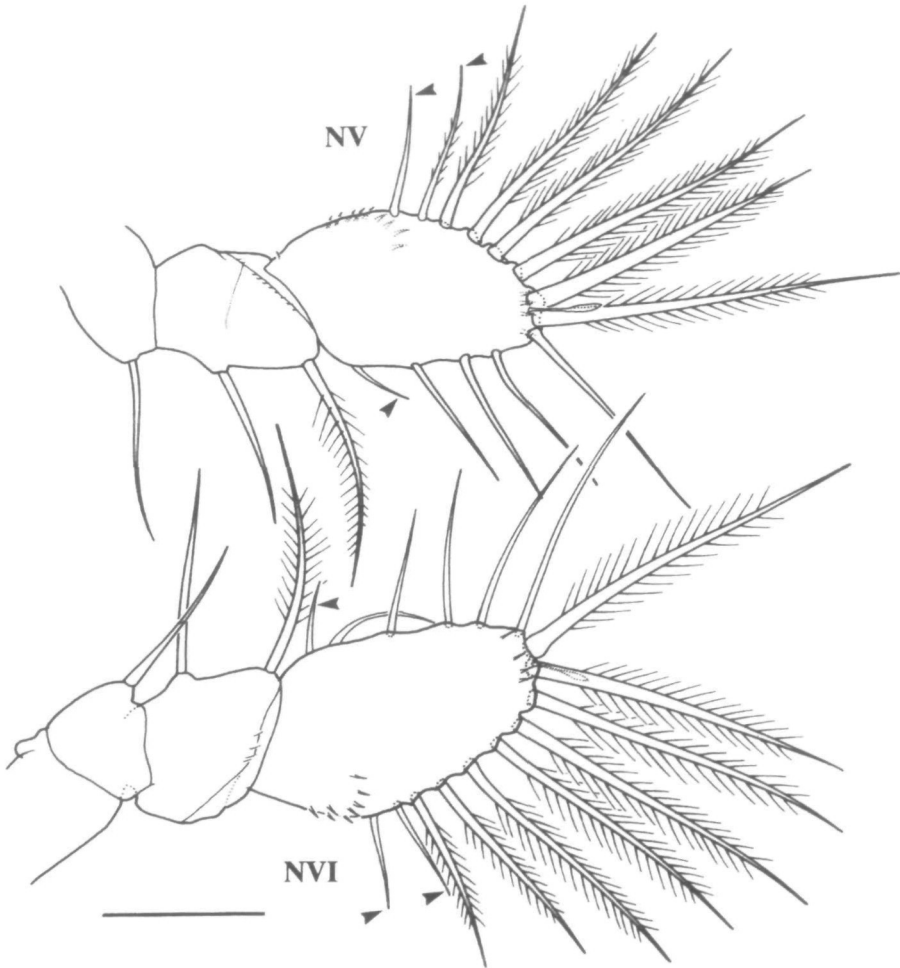
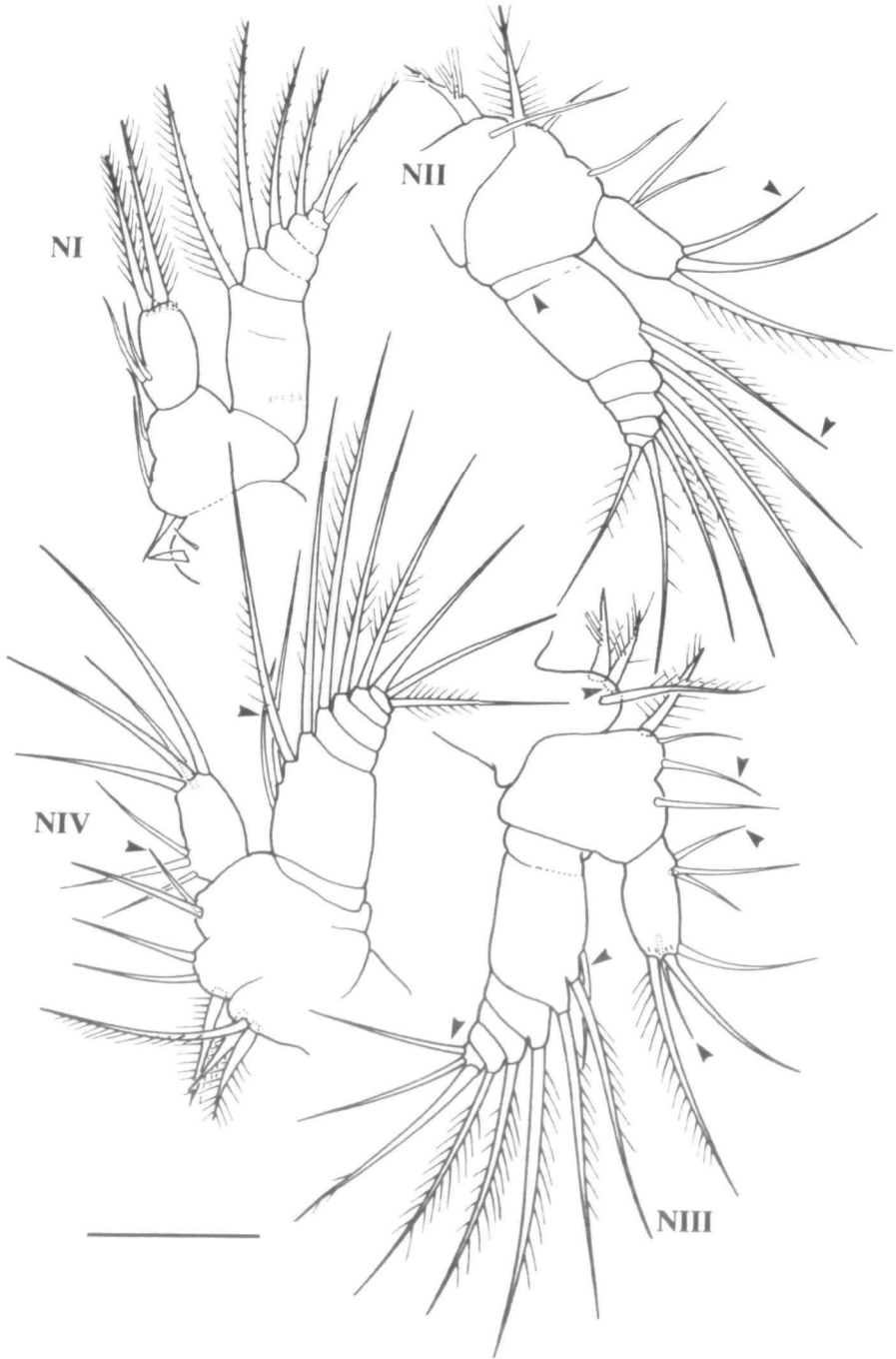


Fig. 2. continued.

masticatory seta with characteristically arranged stiff hairs and an additional slender bare seta. Proximal seta on basis strong and equipped with stiff hairs, probably also with masticatory function. Endopod with a third terminal seta, only outer terminal seta with hairs on one side, others bare. Exopod 2.1 times longer than endopod, 6-segmented, with an indistinct suture between small, unarmed first segment and second segment, which is considerably longer than wide; segments with 0,2,1,1,1,2 sparsely feathered setae. Setae longer than in NI.

**Mandible** (Figure 4). Similar to NI, with the following alterations: basis with two plumose and one bare seta, proximal seta dagger-shaped. Endopod with three groups of 4,2, and 3 setae, with one bare seta in each group, and a row of very



**Fig. 3.** *Acanthodiptomus denticornis*. Naupliar antennae NI–NVI, posterior (NI–NIV, NVI) and anterior (NV) views. Arrows indicate newly added structures as compared with the preceding stage. Scale bar = 50  $\mu\text{m}$ .

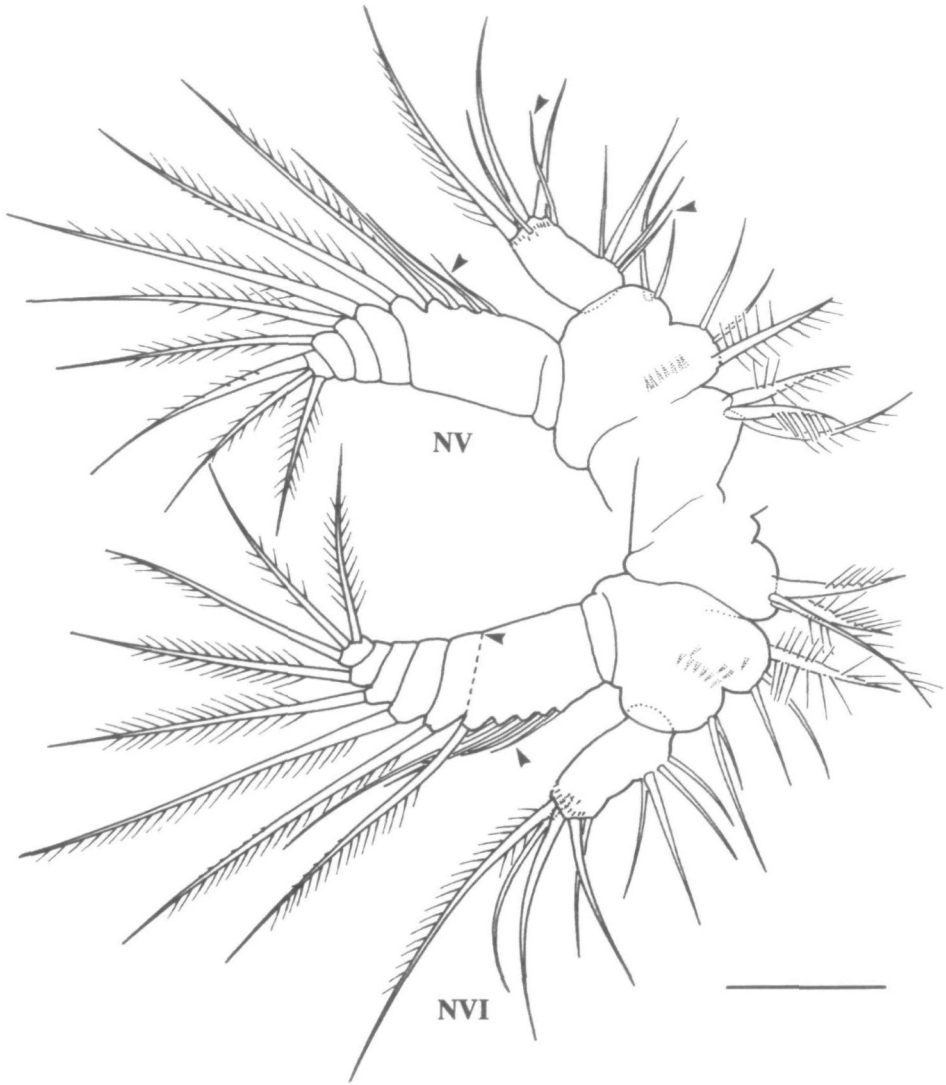
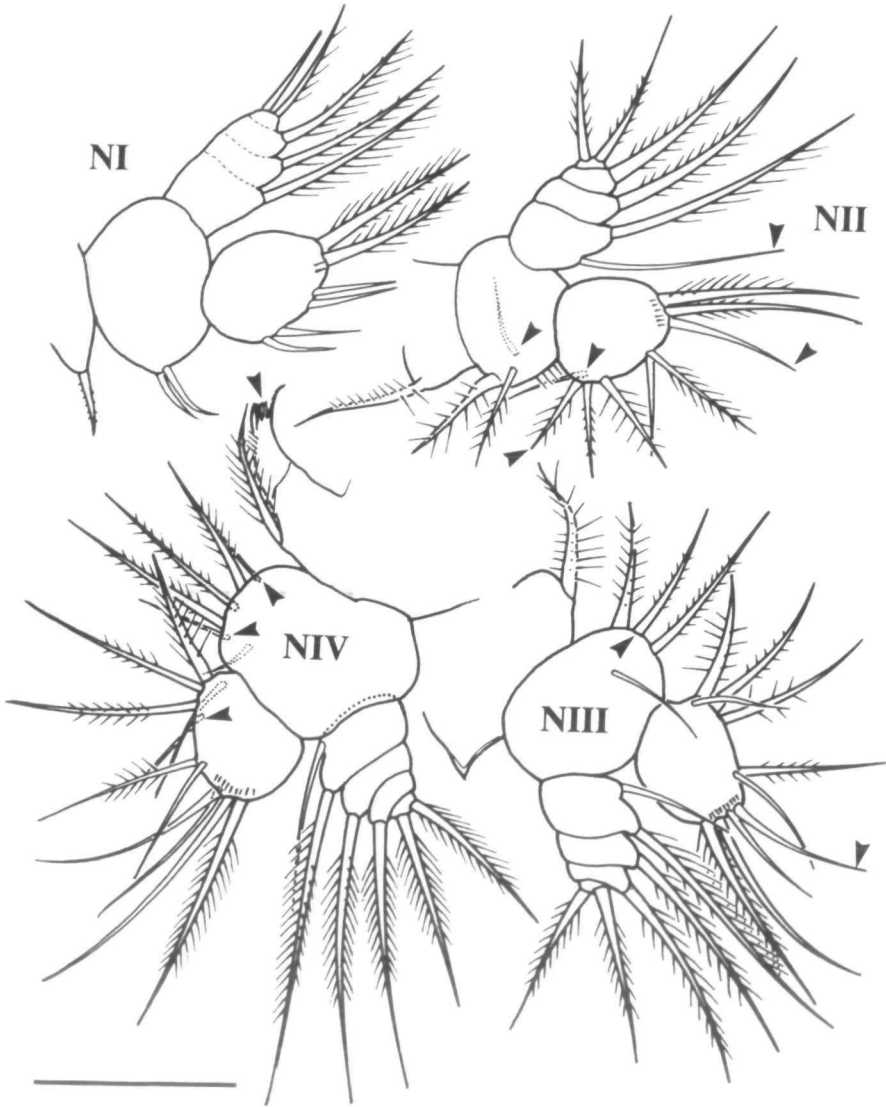


Fig. 3. continued.

delicate spinules subapically. Exopod with one additional bare seta on first segment, reaching final setation of 2,1,1, and 2 setae.

### *Nauplius III*

**General features** (Figure 1). Body length 265  $\mu\text{m}$  (field specimens: 250  $\mu\text{m}$ , range 240–268,  $n = 18$ ), maximum width 121  $\mu\text{m}$ ,  $l/w = 2.21$ . In this and all following instars, the caudal lobes bear two long dorsally reflexed setae with bifurcated ends.



**Fig. 4.** *Acanthodiptomus denticornis*. Naupliar mandibles NI–NVI, posterior (NIII, NV) and anterior (NI, II, IV, VI) views. Arrows indicate newly added structures as compared with the preceding stage. Scale bar = 50  $\mu\text{m}$ .

The right seta is increasingly reflexed and may be carried almost parallel to dorsal body surface. Caudal asymmetry becomes more pronounced by a dorsal shift of the former terminal right seta and the appearance of two stout caudal spines, the left one being longer and inserted subterminally on the caudal lobe. Ventro-posterior body bi-merous by longitudinal suture and its surface with transverse rows of delicate spinules rather than hairs, interrupted medially. First appearance of other than the first three pairs of limbs ('metanauplius').

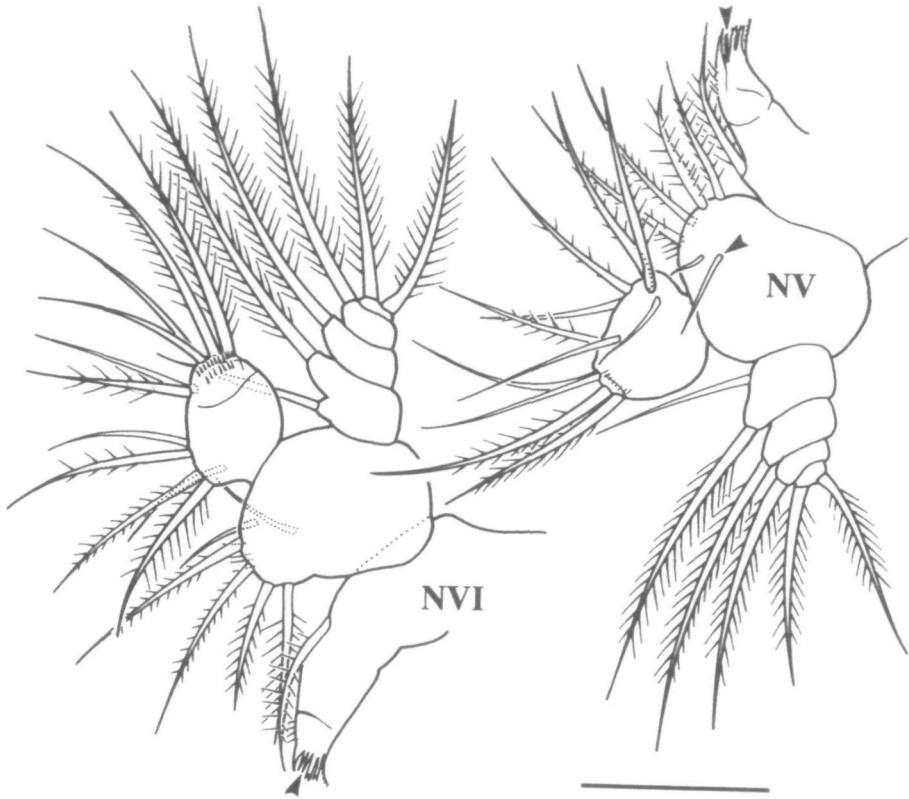
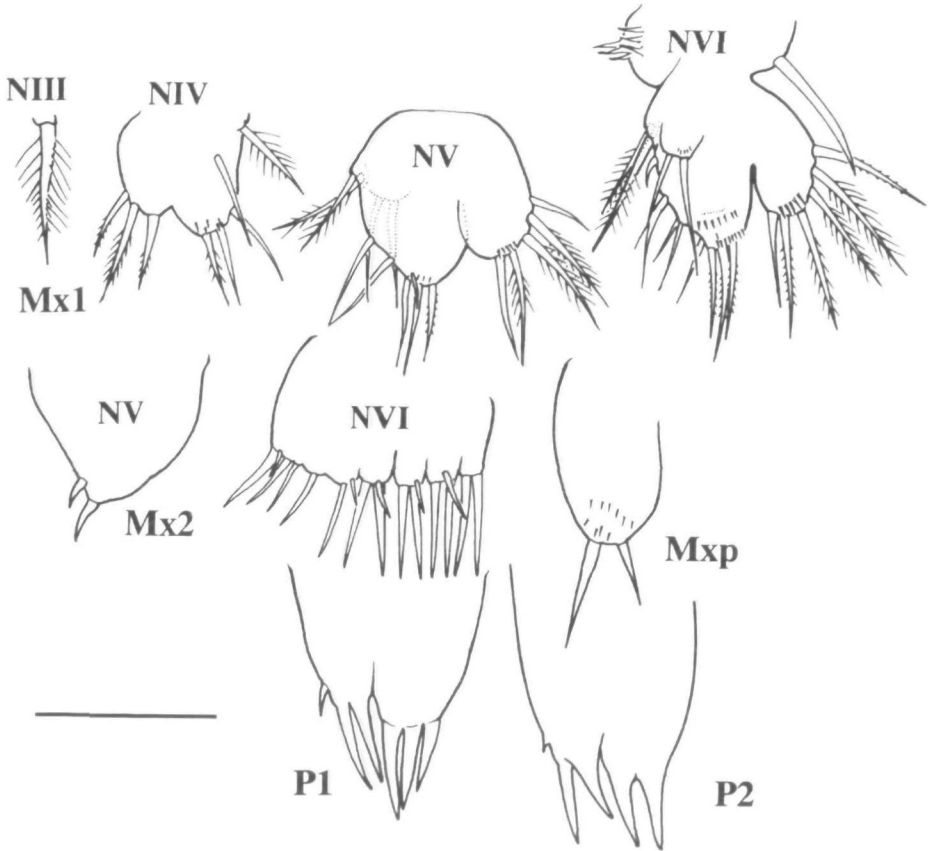


Fig. 4. continued.

**Antennule** (Figure 2). Seta on first segment longer than second segment. Crease-like structure accompanied by delicate spinules anteriorly on second segment. Terminal segment now with six setae, with one additional bare seta on ventral margin and two additional plumose setae on dorsal margin. One oar-shaped aesthasc between plumose terminal setae as in all succeeding stages. Terminal segment 1.70 times longer than wide, devoid of marginal hairs, but with a curved row of spinules extending from the medial to the dorsal surface.

**Antenna** (Figure 3). Coxa with two equal masticatory hooks and with one plumose seta. Basis as in preceding stage, but with one additional bare seta on proximal lobe. Endopod with a third proximal and a fourth subterminal seta. Four to five delicate spinules near the base of terminal setae. Exopod 2.4 times longer than endopod, 6-segmented, with 0,3,1,1,1,3 setae. As in all succeeding naupliar instars, newly added seta on second exopodal segment bare and lying close to inner margin of exopod.



**Fig. 5.** *Acanthodiptomus denticornis*. Naupliar maxillules (Mx1) NIII–NVI, anterior (NIII, IV, VI) and posterior (NV) views; maxillae (Mx2), anterior (NV) and posterior (NVI) views; maxilliped (Mxp), first (P1) and second (P2) swimming leg (NVI), anterior views. Scale bar = 50  $\mu\text{m}$ .

**Mandible** (Figure 4). As in preceding stage, with the following changes: basal endite with a third plumose seta laterally, endopod with one further seta added terminally.

**Maxillule** (Figure 5). Appears as a plumose seta which is stout at its base and quickly tapers off to a slender tip. This seta has been assigned to the future endopod of the Mx1 by Comita and McNett (1976).

#### *Nauplius IV*

**General features** (Figure 1). Body length 282  $\mu\text{m}$  (field specimens: 308  $\mu\text{m}$ , range 279–338,  $n = 19$ ), maximum width 127  $\mu\text{m}$ ;  $l/w = 2.22$ . Caudal asymmetry even stronger with left caudal spine reaching 15% of body length. Both caudal setae originating dorsally. Ornamentation of ventro-posterior body surface similar to preceding stage, but more sparsely.



**Antennule** (Figure 2). No further changes on first two segments. Terminal segment now bearing 10 setae, with two additional bare setae on ventral margin and two additional setae, one plumose, one bare, on dorsal margin. Terminal segment oar-shaped with almost straight ventral margin and convex dorsal margin, 1.63 times longer than wide. Surface ornamentation as in preceding stage.

**Antenna** (Figure 3). Coxa almost unchanged, basis with one additional bare seta on its distal lobe. Endopod with seven setae as in NIII, all bare and relatively longer as in previous stage. Exopod 2.1 times the length of the endopod, 6-segmented with a fourth seta added proximally on its second segment, now bearing 0,4,1,1,1,3 setae.

**Mandible** (Figure 4). Coxal endite transformed into medially directed gnathobasal process with teeth along its distomedial margin and one dorsal seta. Cutting edge with three teeth, one sharply pointed with a comb of stout hairs along its proximal margin, other two teeth indented. Gnathobase with a large plumose seta at its base. The basal endite bears three plumose and three bare setae. Endopod with three groups of 5,2,4 setae, one newly added to the proximal group. Exopod unchanged.

**Maxillule** (Figure 5). Bilobed, with prospective endo- and exopod represented by one lobe each. Inner lobe distinctly larger than outer one, bearing one plumose and one bare seta proximally (probably the first Anlage of coxal and basal lacinia, respectively), and two bare and one spinulose setae distally, plus some spinules subapically. Outer lobe with three spinulose terminal setae, middle one longest.

### *Nauplius V*

**General features** (Figure 1). More strongly elongate, with body length 392  $\mu\text{m}$  (field specimens: 348  $\mu\text{m}$ , range 323–361,  $n = 12$ ), maximum width 152  $\mu\text{m}$ ;  $l/w = 2.58$ . Two minute medial spines have been added to the asymmetrical caudal armature. Longest spine relatively shorter (10% of body length) than in NIV. No ornamentation of ventro-posterior body surface. First appearance of the last cephalic appendage as a maxillary bud.

**Antennule** (Figure 2). No further changes on first two segments. Terminal segment now bearing 13 setae, with one additional bare seta proximally on ventral margin and two additional setae, one plumose, one bare, proximally on dorsal margin. Proximal-most ventral seta bent anteriorly. Oar-shaped terminal segment 1.70 times longer than wide, with surface ornamentation as in preceding stage, plus a row of four subapical spinules.

**Antenna** (Figure 3). Apart from a spinule row on the basal surface, coxa and basis are almost unchanged. Endopod with one additional bare seta in proximal as well as in terminal group of setae, now bearing nine setae in total. Endopod surface ornamented with small spines at base of terminal setae. Exopod 2.1 times longer than endopod, 6-segmented with a fifth seta added proximally on its second segment, now bearing 0,5,1,1,1,3 setae.

*Mandible* (Figure 4). Cutting blade of gnathobase now with four teeth and a hair-like seta, two teeth are sharply pointed, two indented. Basal endite with four plumose setae and a row of 3–4 hairs marginally, and two bare setae on the segment's surface. Endo- and exopod as previously, but exopod slightly longer than endopod (1.1:1).

*Maxillule* (Figure 5). Represented as a four-lobed process. The two larger lobes are the exo- and the endopod, with the former bearing three plumose and two bare setae, the latter bearing one spinulose and five bare setae. The two smaller lobes are regarded as being the laciniae of the coxa and the basis. The coxal and the basal laciniae bear two plumose and two bare setae, respectively. Exo- and endopod with a sparse row of subapical spinules each.

*Maxilla* (Figure 5). Simple lobe tipped with two unequal, slightly curved spiniform setae.

#### *Nauplius VI*

*General features* (Figure 1). Further elongated, with body length 456  $\mu\text{m}$  (field specimens: 401  $\mu\text{m}$ , range 385–415,  $n = 10$ ), maximum width 162  $\mu\text{m}$ ;  $l/w = 2.82$ . Four well-developed caudal spines, those on left lobus longer, left terminal caudal spine reaching 10% of body length as in NV. First three thoracic limbs (maxilliped, first and second swimming leg) present as buds.

*Antennule* (Figure 2). No further changes on first two segments. Terminal segment now with 16 setae in total, with one additional bare seta proximally on ventral margin and two new bare setae proximally on dorsal margin. Second proximal seta on ventral margin characteristically curved. Terminal segment 1.76 times longer than wide, with surface ornamentation similar to preceding stage.

*Antenna* (Figure 3). Coxa, basis and endopod almost unchanged, except for some further spinules on surface of basis. Exopod 2.1 times longer than endopod, 7-segmented with an indistinct suture dividing former second segment up into second and third segment. Second segment with an additional bare seta. Exopod now bearing 12 (0,5,1,1,1,1,3) setae.

*Mandible* (Figure 4). Cutting blade of gnathobase now with three pointed and two indented teeth and one hair-like seta. Otherwise as previously, except for a second subapical spinule row and a distinct, but non-continuous suture in distal half of endopod.

*Maxillule* (Figure 5). Exo- and endopod bearing six and eight setae, respectively, with one and three bare setae added on the inner margin each. Subapical armature of both rami more distinct, with two rows of 6–7 and 8–9 spinules

observed on endopod, and five larger spinules observed on exopod. Endopod with a delicate, hook-like process, rather than a seta, at its inner proximal margin. Coxal and basal laciniae as previously, with some delicate spinules detected on basal lacinia. Coxa with one bare epipodal seta. Precoxa with a group of finger-like projections, probably prospective setae of the precoxal arthrite, arranged in two rows.

**Maxilla** (Figure 5). Four distinct lobes anteriorly and three faintly developed lobes posteriorly, carrying 2,3,3,3,2,1 and 4 incipient bare setae. All are rather delicate structures, especially the short subterminal setae on lobes 2,3,4,5, and 7, which may be easily overlooked.

**Maxilliped** (Figure 5). Thumb-shaped lobe tipped with two unequal elongate spines, the inner one being distinctly longer. Surface armed with two rows of tiny spinules distally.

**Swimming leg 1** (Figure 5). Bilobed bud, with the longer prospective endopod bearing three spiniform projections terminally, and the prospective exopod bearing one short spiniform projection subapically and two equal spiniform projections terminally.

**Swimming leg 2** (Figure 5). Bilobed bud, with prospective endopod being slightly longer than prospective exopod, bearing two terminal spiniform projections of almost equal length. Exopod with two of these plus an outer acutiform protuberance.

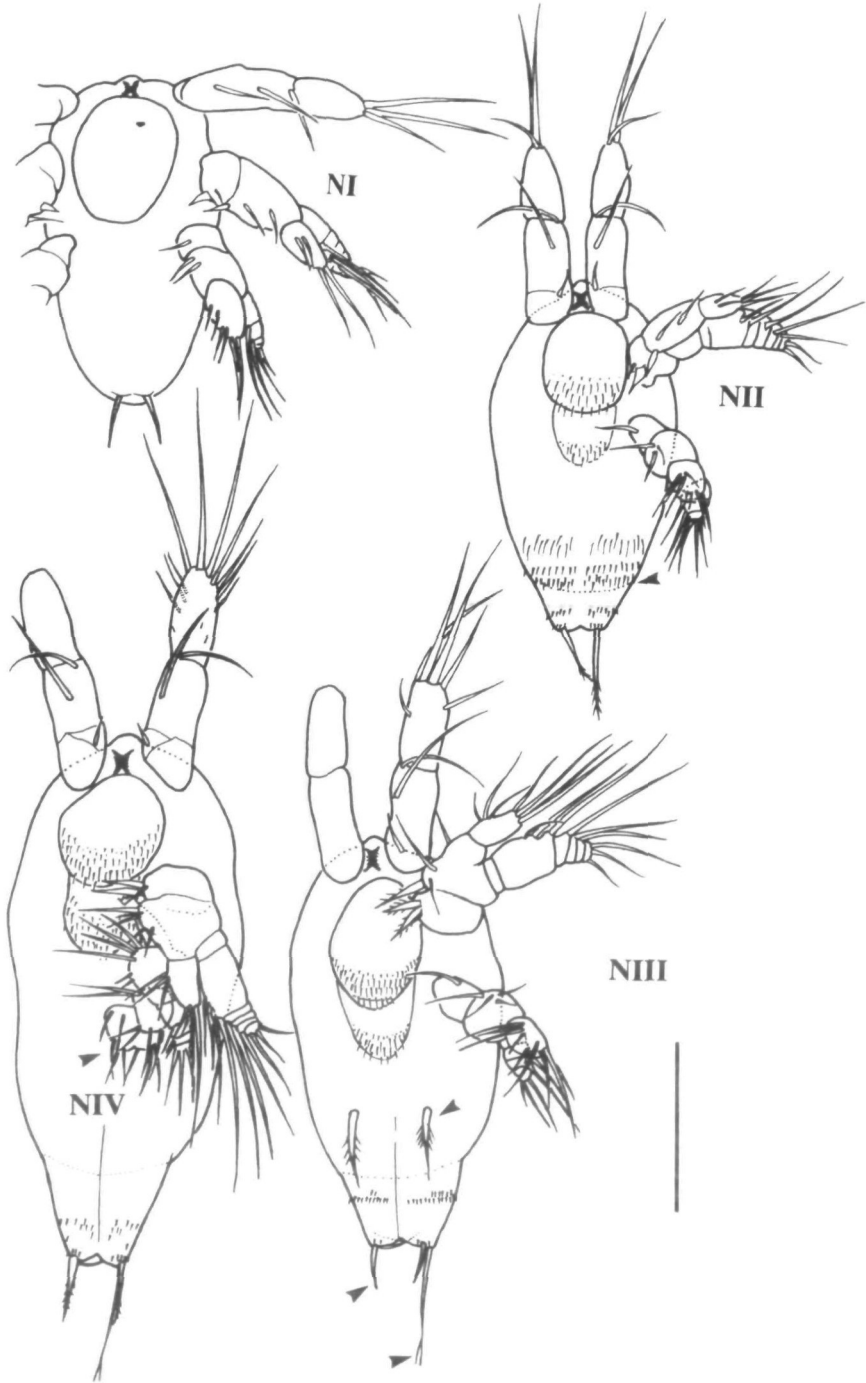
### ***Arctodiaptomus alpinus* (Imhof, 1885) Figures 6–10**

The nauplii of this species are strikingly similar to those of *Ac.denticornis*. The two species show an absolute identical pattern of limb setation throughout all instars. Hence, only measurements and differential characters are described here. Differences related to the feathering of setae are figured, but not explicitly mentioned in the text.

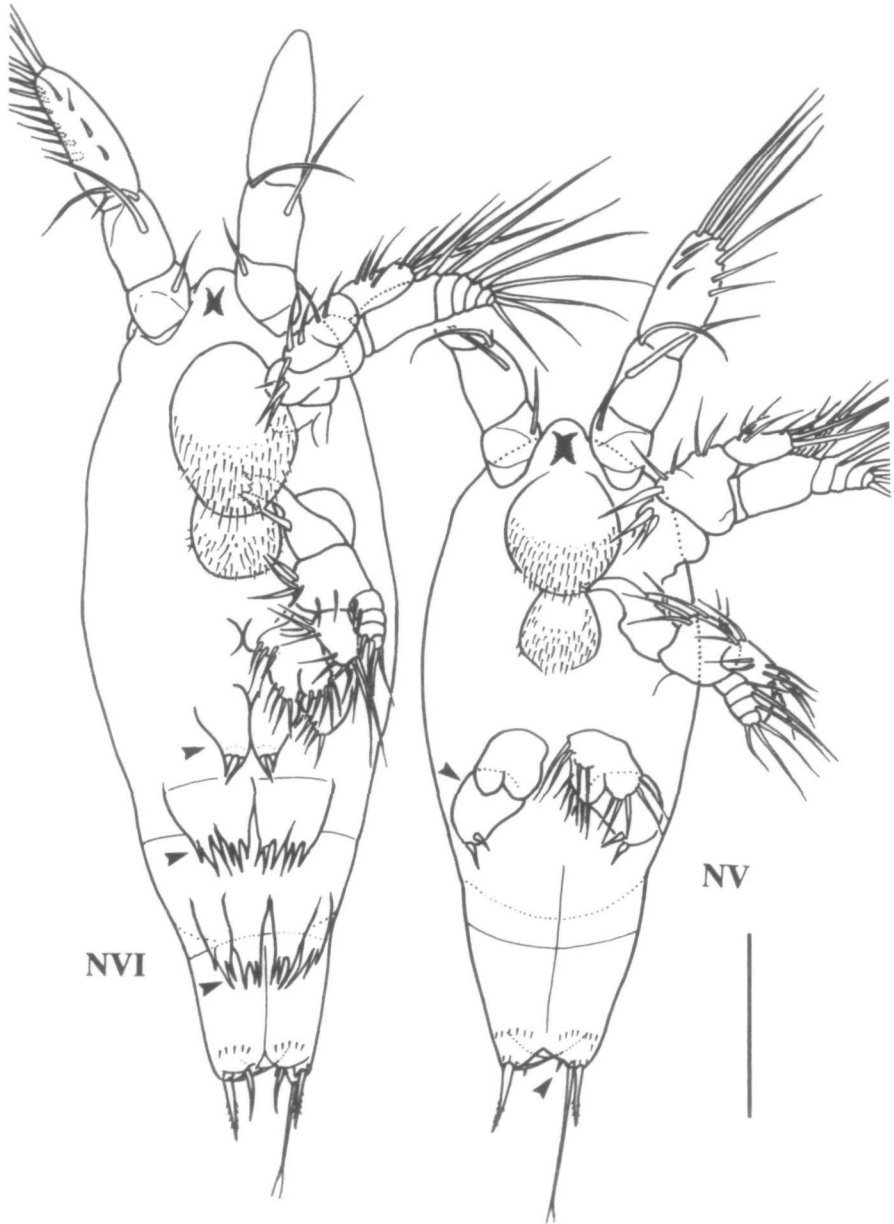
#### ***Nauplius I***

**General features** (Figure 6). Body length 194  $\mu\text{m}$  (field specimens: 181  $\mu\text{m}$ , range 170–197  $\mu\text{m}$ ,  $n = 20$ ), maximum width 103  $\mu\text{m}$  (ratio l/w = 1.88).

**Antennule** (Figure 7). The distal seta on the penultimate segment is distinctly longer than the one at midlength, reaching 1.38 times the length of the terminal segment. Terminal segment 1.70 times longer than wide. Its surface ornamented with groups of small spinules and a subapical row of fine hairs. Terminal setae reach 1.8 times the length of the segment.



**Fig. 6.** *Arctodiaptomus alpinus*. Naupliar stages NI–NVI, ventral view. Arrows indicate newly added structures as compared with the preceding stage. Scale bar = 100  $\mu\text{m}$ .

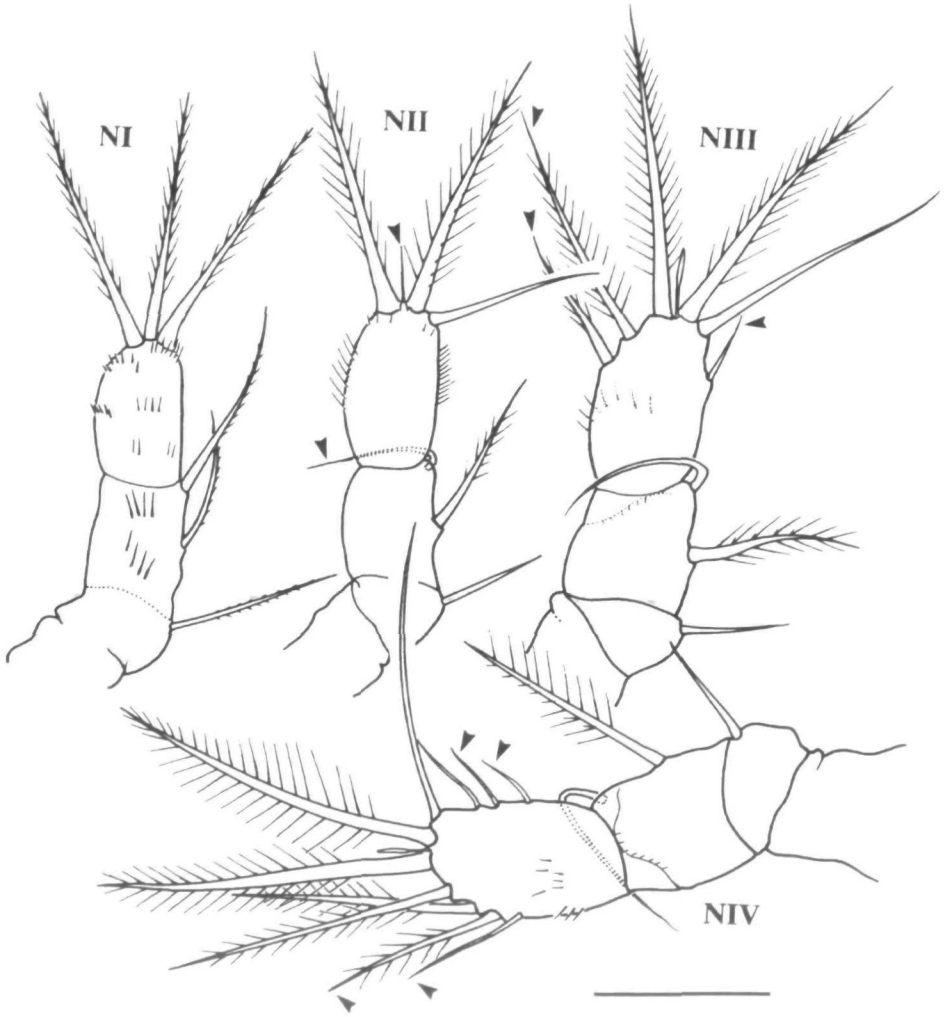


**Fig. 6.** continued.

*Antenna* (Figure 8) and *mandible* (Figure 9) as in *Ac.denticornis*.

### *Nauplius II*

*General features* (Figure 6). Body length 209  $\mu\text{m}$  (field specimens: 216  $\mu\text{m}$ , range 203–232  $\mu\text{m}$ ,  $n = 22$ ), maximum width 109  $\mu\text{m}$ ;  $l/w = 1.92$ .



**Fig. 7.** *Arctodiaptomus alpinus*. Naupliar antennules NI–NVI, lateral view. The terminal segment of another specimen from Lake Dreibrüdersee (preserved in formalin) is also shown. Arrows indicate newly added structures as compared with the preceding stage. Scale bar = 50  $\mu\text{m}$ .

**Antennule** (Figure 7). Proximal seta on penultimate segment plumose, distal seta bare and characteristically curved towards the dorsal side, as in all succeeding stages. Seta on proximal segment distinctly shorter than proximal seta on penultimate segment.

**Antenna** (Figure 8). Exopod 1.8 times longer than endopod.

**Mandible** (Figure 9). As in *Ac.denticornis*.

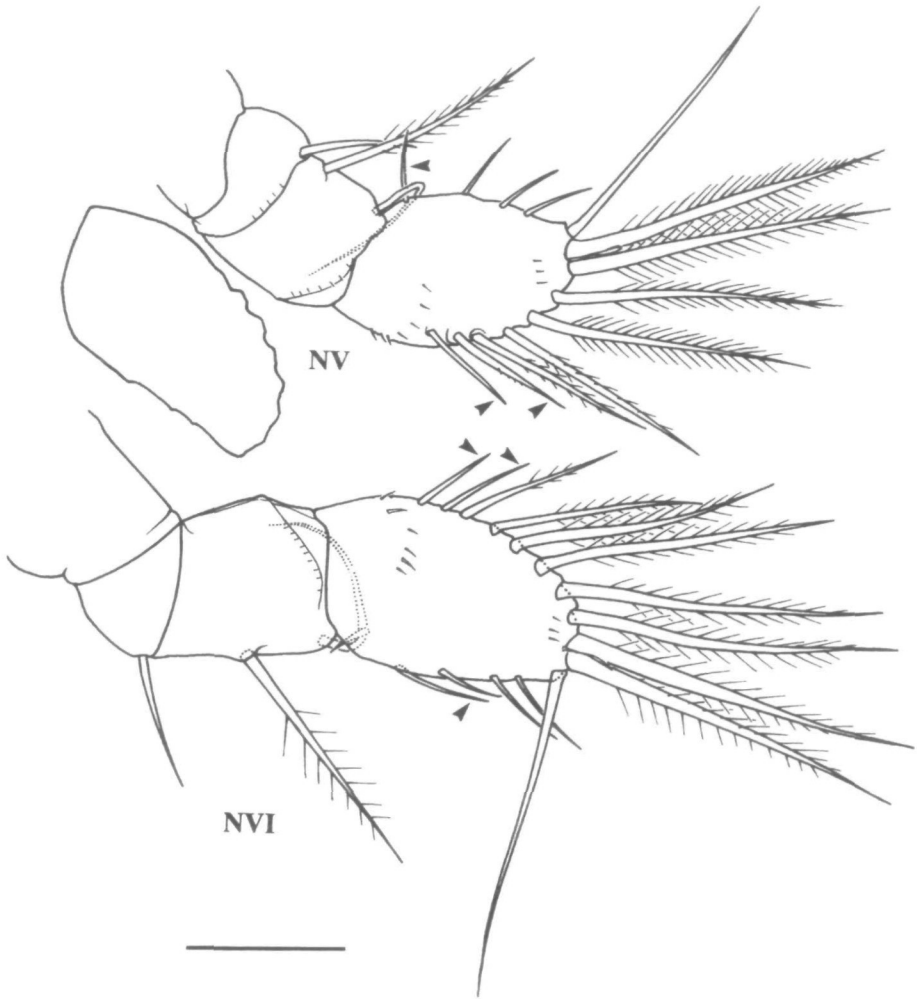
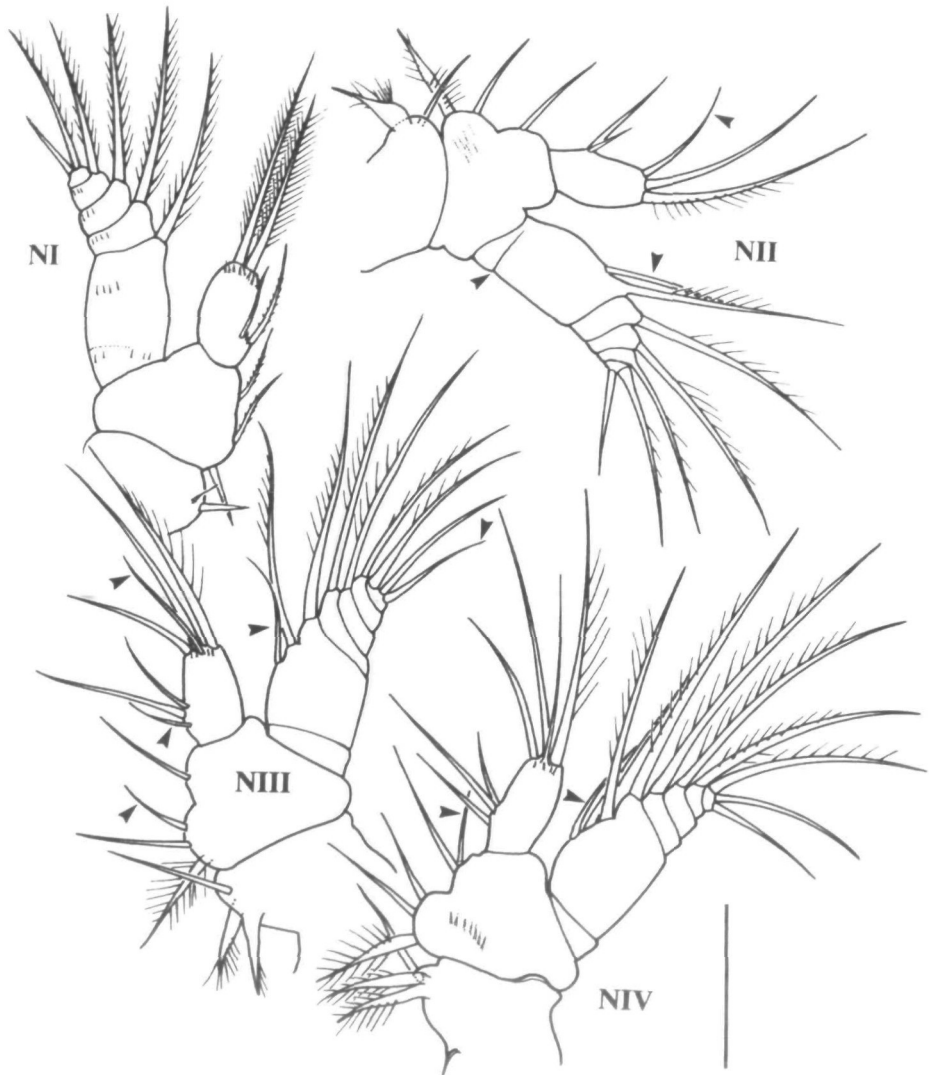


Fig. 7. continued.

### *Nauplius III*

**General features** (Figure 6). Body length 246  $\mu\text{m}$  (field specimens: 245  $\mu\text{m}$ , range 233–261,  $n = 21$ ), maximum width 126  $\mu\text{m}$ ;  $l/w = 1.96$ . Caudal lobes almost symmetrical, asymmetry indicated by a slightly stronger right spine.

**Antennule** (Figure 7). Seta on first segment distinctly shorter than proximal seta on penultimate segment. Newly added seta on ventral margin distinctly shorter than width of segment, and bare terminal seta distinctly longer ( $1.5\times$ ) than terminal segment. Surface ornamentation on terminal segment reduced to a curved row of stout hairs extending from medially to dorsally.



**Fig. 8.** *Arctodiaptomus alpinus*. Naupliar antennae NI–NVI, posterior (NI, III, V, VI) and anterior (NII, IV) views. Arrows indicate newly added structures as compared with the preceding stage. Scale bar = 50  $\mu\text{m}$ .

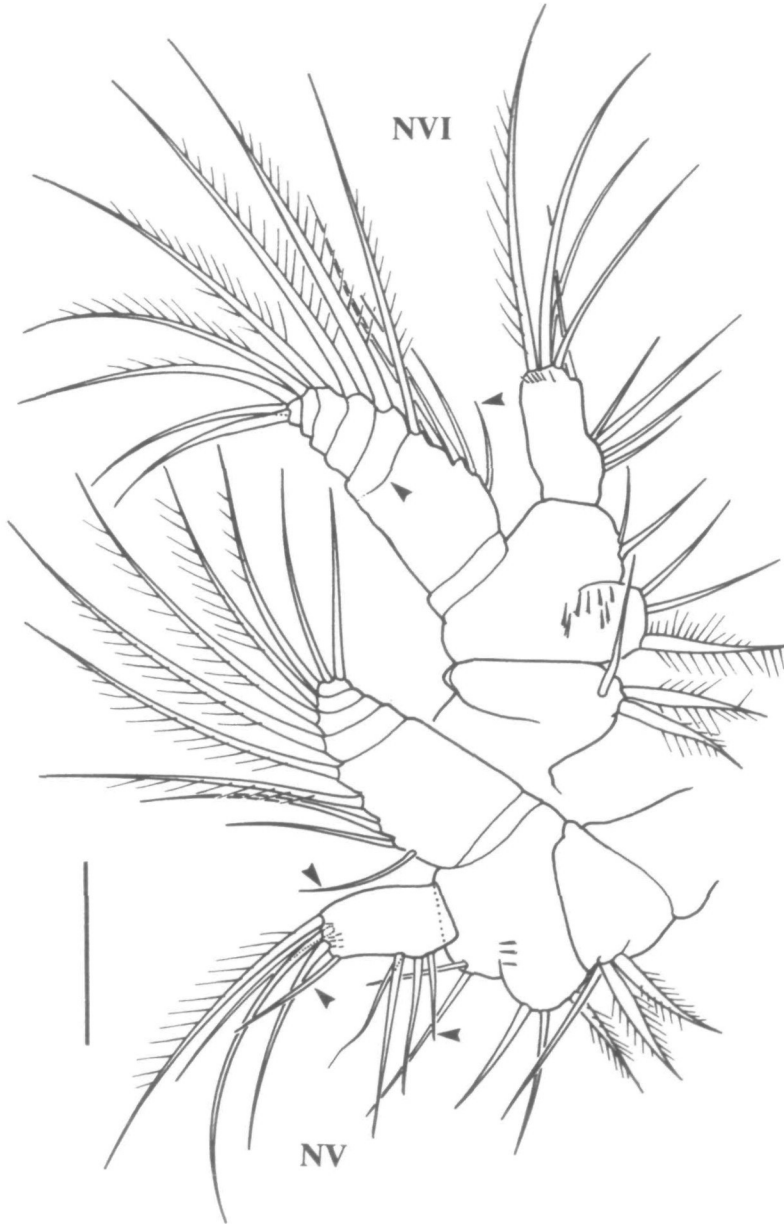
**Antenna** (Figure 8). Exopod 2.0 times longer than endopod.

**Mandible** (Figure 9) and **maxillule** (Figure 10) as in *Ac.denticornis*.

#### *Nauplius IV*

**General features** (Figure 6). Body length 308  $\mu\text{m}$  (field specimens: 285  $\mu\text{m}$ , range 2050

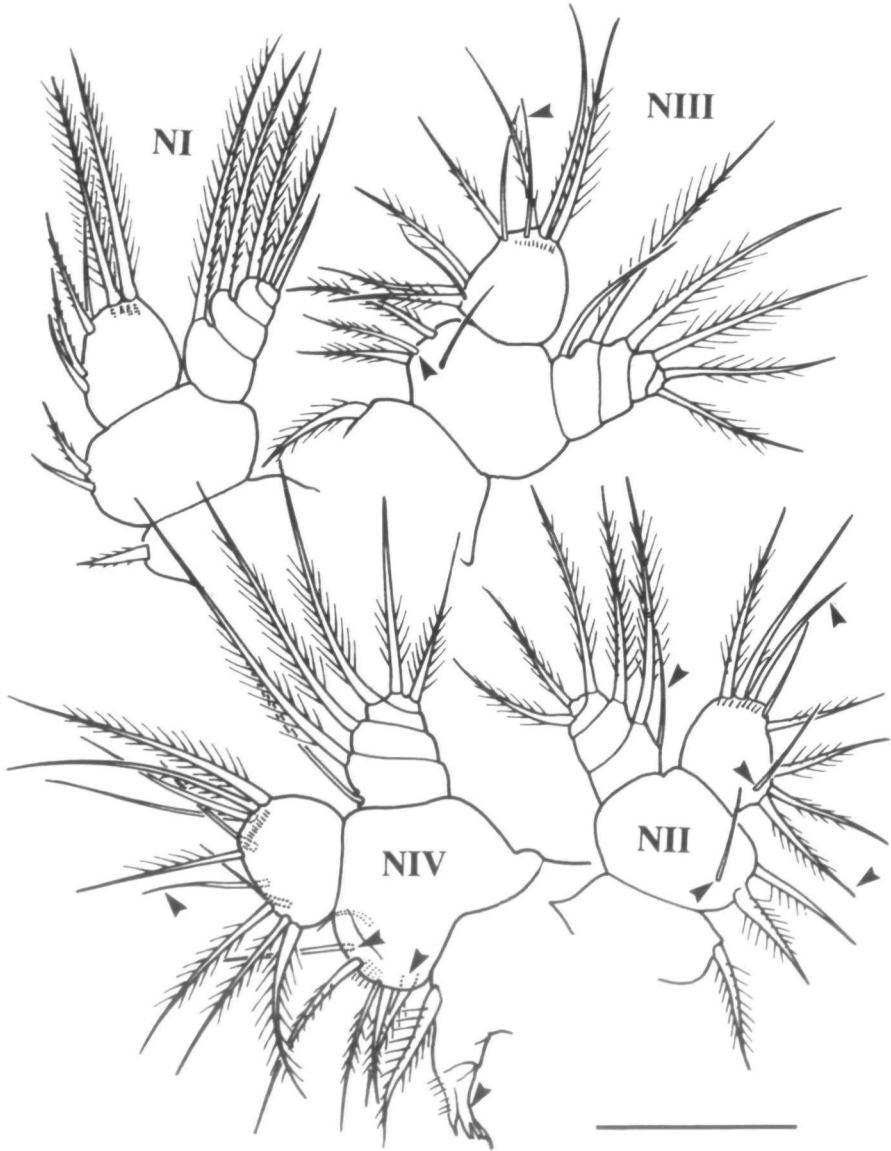




**Fig. 8.** continued.

263–304  $\mu\text{m}$ ,  $n = 20$ ), maximum width 136  $\mu\text{m}$ ;  $l/w = 2.26$ . Right caudal spine stronger than left one, reaching 12% of body length.

*Antennule* (Figure 7). Newly added setae on dorsal and ventral margin relatively shorter than in *Ac.denticornis*. Terminal segment 1.63 (but up to 1.93 in preserved



**Fig. 9.** *Arctodiaptomus alpinus*. Naupliar mandibles NI–NVI, posterior (NI–III, V, VI) and anterior (NIV) views. Arrows indicate newly added structures as compared with the preceding stage. Scale bar = 50  $\mu\text{m}$ .

field specimens) times longer than wide. Seta on first segment reaches only half the length of the proximal seta on the penultimate second segment, as in all following instars.

**Antenna** (Figure 8). Exopod 2.0 times longer than endopod.

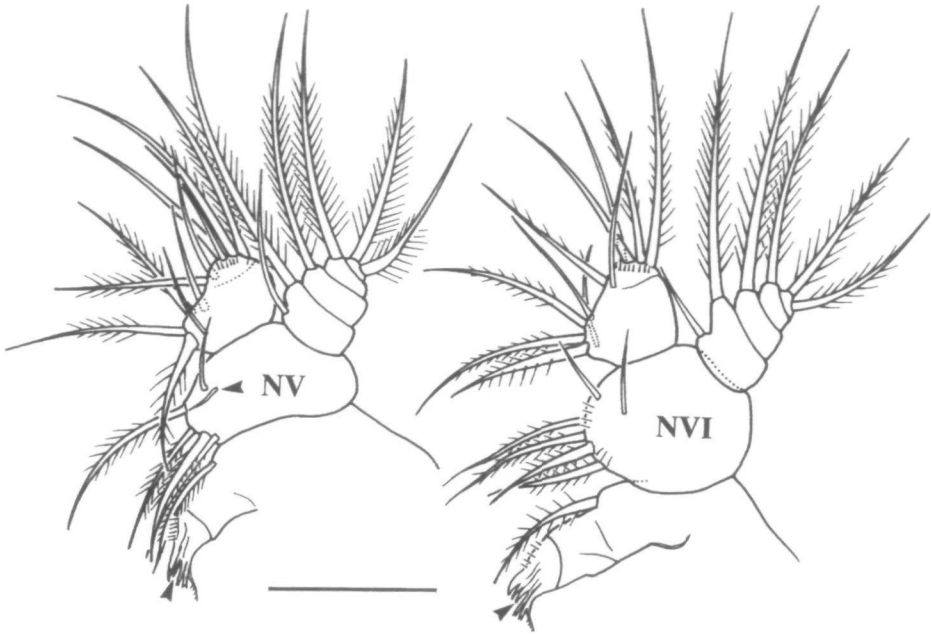


Fig. 9. continued.

*Mandible* (Figure 9) and *maxillule* (Figure 10) as in *Ac.denticornis*.

#### *Nauplius V*

*General features* (Figure 6). Body length 340  $\mu\text{m}$  (field specimens: 339  $\mu\text{m}$ , range 304–375,  $n = 20$ ), maximum width 144  $\mu\text{m}$ ;  $l/w = 2.36$ . Indications of caudal asymmetry with stronger left portion, but more pronounced right caudal spine, reaching 11% of body length.

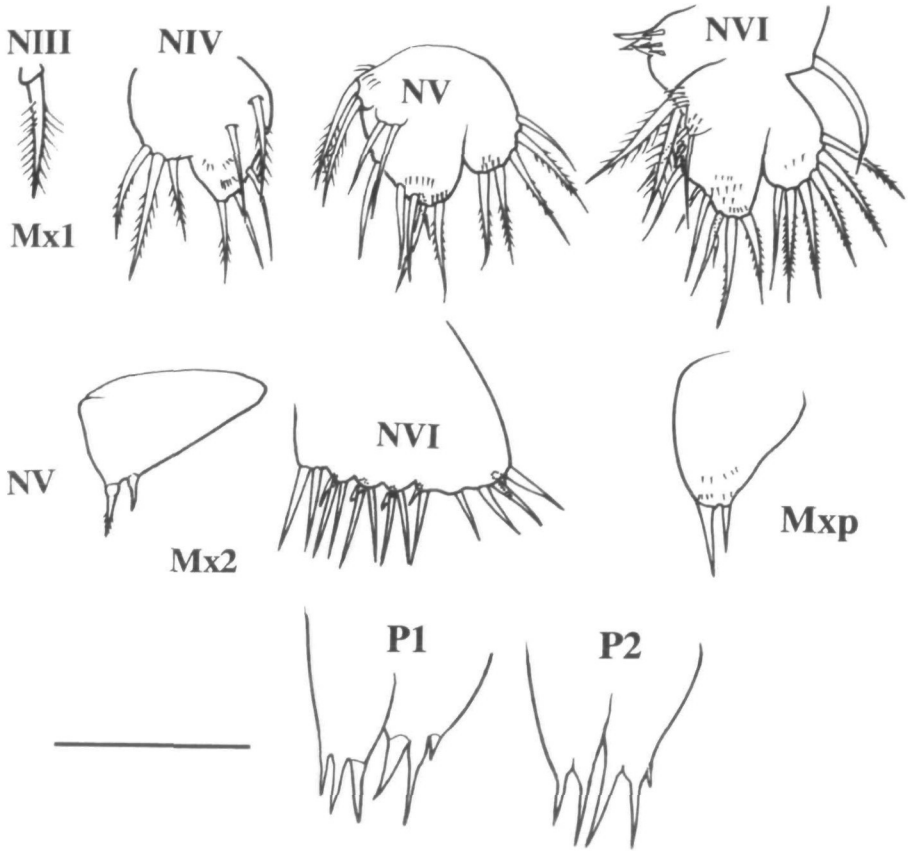
*Antennule* (Figure 7). Ventral setae on terminal segment very short (less than half the width of the segment). Proximal-most ventral seta points backwards to be encircled by the distal seta from the penultimate segment. Terminal segment 1.51 (but up to 1.74 in preserved field specimens) times longer than wide.

*Antenna* (Figure 8). Exopod 1.9 times longer than endopod.

*Mandible* (Figure 9), *maxillule* and *maxilla* (Figure 10) as in *Ac.denticornis*.

#### *Nauplius VI*

*General features* (Figure 6). Body length 442  $\mu\text{m}$  (field specimens: 388  $\mu\text{m}$ , range 367–423,  $n = 20$ ), maximum width 170  $\mu\text{m}$ ;  $l/w = 2.60$ . Four well-developed caudal



**Fig. 10.** *Arctodiaptomus alpinus*. Naupliar maxillules (Mx1) NIII–NVI, anterior view; maxillae (Mx2), anterior view; maxilliped (Mxp), first (P1) and second (P2) swimming leg (NVI), anterior views. Scale bar = 50  $\mu$ m.

spines, those on the right lobus slightly longer, right terminal caudal spine reaching 8% of body length.

**Antennule** (Figure 7). Proximal-most ventral seta on terminal segment as in preceding stage. Terminal segment 1.65 times longer than wide.

**Antenna** (Figure 8). Exopod 1.8 times longer than endopod.

**Mandible** (Figure 9), **maxillule**, **maxilla**, **maxilliped**, **swimming leg 1** and **2** (Figure 10) very much like in *Ac.denticornis*, but setae generally shorter.

#### *Larval characters of the Diaptomidae*

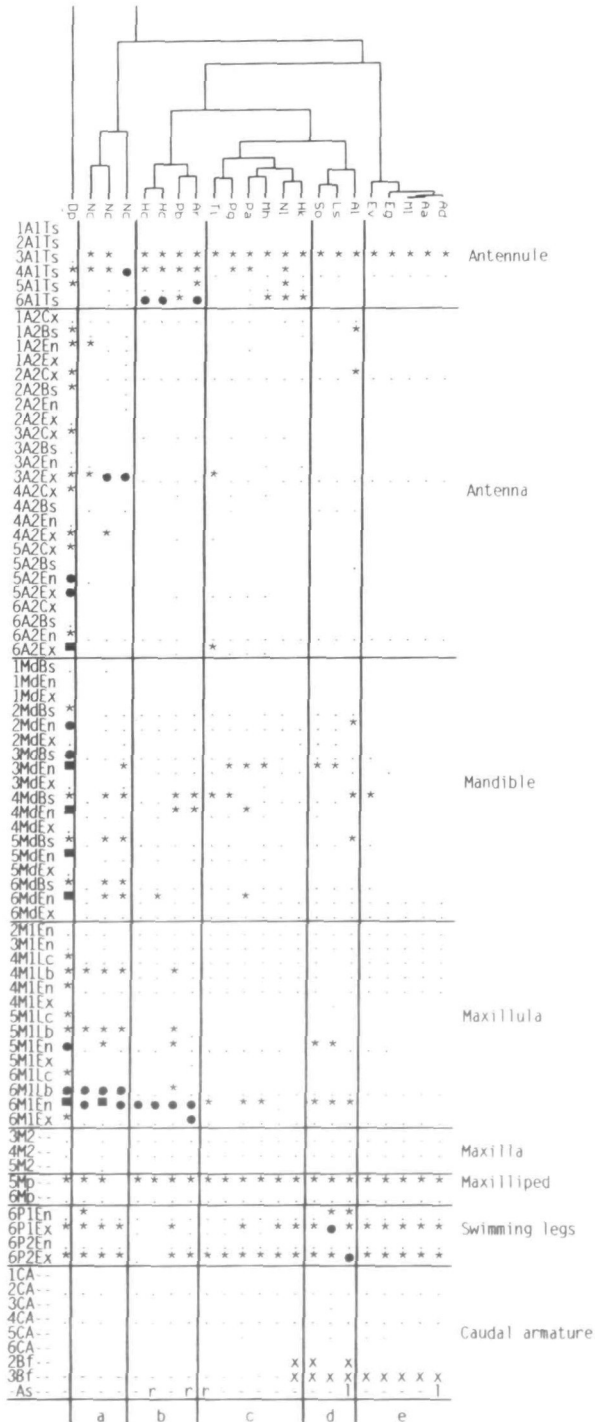
Table I gives an overview of meristic and stage-dependent characters which are of relevance to the study and comparison of diaptomid nauplii. For the classification

procedure, only characters were used which are described for all species and are not particularly prone to subjective errors (e.g. number of exopodal segments on A2 and Md due to indistinct sutures, setation of the premetamorphic Mx2 due to minute transparent incipient setae, number of teeth on mandibular gnathobase, presence or absence of an antennular aesthetasc).

In order to facilitate comparisons, an attempt was made to group the diaptomid larvae on the basis of similarities in their external morphology by using the minimum variance clustering procedure. According to the branching pattern of the dendrogram generated by agglomerative clustering, the species can be divided into five clear-cut groups that may be described in terms of their geographical distribution as follows. The 'neotropical' group, comprising species from the South American genus *Notodiaptomus* (a), two 'oriental' groups (b, c) with species from India and Sri Lanka, and, surprisingly, one species from North America. Accordingly, (d) and (e) may be termed the 'nearctic' and the 'palaearctic' groups, comprising three North American and five European species, respectively (Figure 11). The latter display a close affinity to each other in the following aspects: maximum setation on all limbs in the first orthonauplius, highest number of 16 setae developed on the terminal antennular segment and of eight setae developed on the maxillular endopod in the premetamorphic sixth stage, and a pair of bifid caudal setae in all metanauplii. North American and European species share, among other characters, the highest number of antennular setae in NV and NVI (except *Hesperodiaptomus kenai*), and bifid caudal setae in metanauplii. However, the former are quite distinct from the latter as they have an increased tendency towards a reduction of the setal number on the mandibular base in all but the first nauplius, only six setae developed on the maxillular endopod (except *H.kenai*), and bifid setae appear as early as the second stage (except *Leptodiaptomus siciloides*). Important differences between *H.kenai* and the other North American species include: reduced number of setae on the terminal antennular segment in NV and NVI, maximum number of setae on the mandibular base and the maxillular endopod in NV and NVI. The most conspicuous characters of the Indian species grouped together in subcluster (b) are that there are only 13–14 setae on the terminal antennular segment, as well as only five setae on the endopod of the maxillule in NVI. A sparse setation of the maxillule in late metanauplii also seems to be characteristic in the neotropical genus *Notodiaptomus* (a). An outlying position is achieved by '*Diaptomus*' *proximus*, which has been reported to have the lowest numbers of setae on A2, Md and Mx1.

## Discussion

About 25 studies, including this article, describing the naupliar development of 23 diaptomid species, belonging to 17 genera, have been published so far worldwide. From these, 20 provide sufficient information to allow adequate comparisons of the larval character states between 22 species. Despite comparatively small morphological differences between diaptomid nauplii, it seems possible to recognize species-specific characters provided by naupliar morphology. However, given the lack of comparative information on naupliar character states (between different species and populations), and the fact that in most genera only one species has



been studied thoroughly, the data are not numerous enough to permit generalizations or to evaluate given characters from a phylogenetic point of view as yet. Nevertheless, by grouping meristic (countable) larval characters, intergeneric relationships similar to that reflected by the geographical distribution of diaptomids are revealed, suggesting that known phylogenetic lineages may be traced even in early developmental stages.

### *Naupliar development of Arctodiaptomus and Acanthodiaptomus*

In spite of overall similarities, the larvae of *Ac.denticornis* are quite distinct from those of *Ar.alpinus* in the following respects: the left caudal portion is distinctly larger than the right in metanauplii of *Ac.denticornis*, while there are only indications of caudal asymmetry with the right caudal spine being more pronounced in *Ar.alpinus*. In *Ac.denticornis*, the plumose distal seta on the penultimate antennular segment is directed ventrally, while it is bare and typically curved dorsally in all but the first nauplius in *Ar.alpinus*. Here, the proximal seta on this segment is plumose, but bare in *Ac.denticornis*. The first orthonauplius of diaptomid copepods is quite simple in appendage structure and armature, like lecithotrophic nauplii in general, and it is difficult to separate the NI stage of the two species on the basis of differences in the relative length of setae on the ventral margin of the terminal antennular segment. The two species share an identical pattern of limb setation in all naupliar stages.

### *Comparison with the larval development of other Diaptomidae*

The naupliar stages of *Ac.denticornis* and *Ar.alpinus* resemble closely those known in other European diaptomids in their morphological and developmental details, but are clearly separated from other species. All European species studied as yet share the same pattern of stage-dependent appearance of setae on the antennule, with the setal number on the distal segment reaching the maximum of 16 in the premetamorphic stage. On the other hand, the relative and absolute length, as well as the posture of particular setae, may provide valuable characteristics attributable to distinct species. For instance, the characteristically curved distal seta on the penultimate antennular segment in NII–NVI is a most peculiar character of *Ar.alpinus* and *M.laciniatus* [not figured by Wuthrich (1948) and Ravera (1953), but well developed in an Austrian population]. While the extraordinarily long seta on the first antennular segment, projecting beyond the antennular tip, seems to be diagnostic of metanauplii in *M.laciniatus*. Unfortunately,

**Fig. 11.** Dendrogram from minimum-variance clustering of naupliar character states for 22 diaptomid species. Key to character states: 1–6, naupliar stages I–VI; A1, antennule; A2, antenna; Md, mandible; M1, maxillula; M2, maxilla; Mp, maxilliped; P1, P2, first and second swimming leg; Ts, terminal segment; Cx, Bs, En, Ex, coxa, basis, endo- and exopod; Lc, Lb, lacinia coxalis and basalis, respectively; CA, caudal appendages; Bf, bifid (x) or non-bifid (–) caudal setae; As, caudal asymmetry with stronger right (r) or left (l) caudal portion, no or only indication of asymmetry (–). Symbols represent numbers of reduced setae as compared with the maximum number: 1 (.), 2 (\*), 3 (•), 4–6 (■). For species abbreviations and references see Table I.

there is reason to suspect that several authors did not pay attention to such details. The shape and ornamentation of the distal segment of the antennule may contribute to additional characteristics in other species (cf. Devi and Reddy, 1990b), but have been observed to vary slightly between generations and populations in *Ar.alpinus*.

While caudal asymmetry (i.e. caudal lobe size and/or size of caudal spines) is a striking feature in the vast majority of marine Calanoida (Björnberg, 1972), it is much less pronounced in larval Diaptomidae; only six out of 27 species have been reported to show a conspicuous caudal asymmetry. The left portion is more strongly developed in *Ac.denticornis* (this study), *Aglaodiaptomus leptopus* (Green and Northcote, 1982; Pinel-Alloul and Lamoreux, 1988) and in *Leptodiaptomus minutus* (Czaika, 1982), while the right part is stronger in *Allo-diaptomus raoi* (Devi and Reddy, 1989b), *Heliodiaptomus cinctus* (Reddy and Devi, 1990a) and *Tropodiaptomus informis* (Devi and Reddy, 1990b). However, indications of a caudal asymmetry are probably present in most if not all calanoid species, in contrast to the symmetry of the other groups of freshwater Copepoda, such as Cyclopoida and Harpacticoida (cf. Dahms and Fernando, 1993), which is considered to be a derived feature (Björnberg, 1972).

As a unique character found only in the Diaptomidae, a pair of caudal setae with bifurcated tips has been reported for all 14 European and North American species studied as yet, but for none from Asia and South America (13 species). While in European species bifid setae were hitherto observed only in metanaupliar stages (NIII–NVI), they have been described for the second orthonauplius as well in three North American species (*A.leptopus*, *H.kenai* and *Skistodiaptomus oregonensis*). However, while Comita and McNett (1976) and Green and Northcote (1982) figure bifid caudal setae also in NII of the latter species, Czaika (1982) explicitly mentions their presence only for NIII–NVI in *S.oregonensis*. Whether this is a case of intraspecific variation or simply an observational error is not clear, although the latter may easily occur due to the high transparency of these delicate structures.

Further differences between the European species have been reported for the setation of the basis and endopod of the mandible in metanauplii NIII–NVI, as well as for the endopod of the maxillule in the fifth larval instar of *Eudiaptomus* species. However, these differences, if real, are so minor that it seems unlikely that they are functionally significant. As we have failed to find evidence confirming differences in the external morphology in *M.laciniatus*, as figured by Wuthrich (1948) and Ravera (1953) (only five endopodal setae on Mx1 and only two pairs of caudal appendages in NV), we regard these differences as observational errors due to difficulty in resolving these minute structures.

Contrary to *Eudiaptomus gracilis*, for which an aesthetasc on the terminal antennular segment has been described only in the second and third stage (Wuthrich, 1948), a well-developed aesthetasc is retained throughout the whole metanaupliar development in *Ar.alpinus* and *Ac.denticornis*. Wuthrich's (1948) figures for *M.laciniatus* (aesthetasc figured only in NII and NIII) do not fit our findings of a well-developed aesthetasc in all stages. Thus, it is likely that this structure has also been overlooked in *E.gracilis* by the same author. No evidence of



this character is provided for *Eudiaptomus vulgaris* by the descriptions of Grandori (1912), Dietrich (1915) and Ravera (1953). However, this complete absence of an aesthetasc is probably due to a lack of observational detail in these early studies. Reduction events from a well-developed to a vestigial aesthetasc in the fifth (*S.oregonensis*, *Megadiaptomus hebes*, *Neodiaptomus lindbergi*) or even the third (*Heliodiaptomus cinctus*) nauplius have been observed (Comita and McNett, 1976; Reddy and Devi, 1985, 1990a; Devi and Reddy, 1990a). Apart from *Ar.alpinus*, *Ac.denticornis* and *M.laciniatus*, only *Diaptomus castor* (Gurney, 1931), *Heliodiaptomus contortus* (Reddy and Devi, 1989), *Notodiaptomus corderoi* (Cipólli, 1973), *Phyllodiaptomus annae* (Dahms and Fernando, 1993) and *Tropodiaptomus informis* (Devi and Reddy, 1990b) are hitherto known to retain a well-developed aesthetasc throughout naupliar development. Thus, as exemplified by the otherwise closely related congeners *H.cinctus/contortus*, the development of this chemosensory receptor seems to be highly variable, even within a single genus, and there seems to be a tendency towards the reduction of this structure in diaptomid larvae. However, in cyclopoid nauplii, an antennular aesthetasc has hitherto been mentioned only exceptionally. Dahms and Fernando (1992) cast doubt about the complete absence of chemosensory receptors in copepod nauplii, and presumed its presence for Cyclopoida as well.

Exceptional cases of a stage-dependent character development have been described for the South American species *Notodiaptomus conifer* (De Gouvea, 1980) and *N.corderoi* (Cipólli, 1973), which show a somewhat premature appearance of postmandibular appendages. In the second stage of *N.conifer*, the maxillule is already developed as a single seta and a second pair of caudal setae is present, as it is usual not before the first metanauplius in other species. Together with the presence of a maxillipedal bud and a third pair of caudal appendages as early as the fourth stage, these characters are rare phenomena among diaptomid nauplii which are not shared by any other species so far studied. The two species share, among other characters, the following larval features which at our present state of knowledge are unique within the Diaptomidae: in NIII, the maxillule is represented as a lobus with two setae and the maxilla is already developed as a single seta in NIII and NIV. The maxillule consists of two segments in NV with a single seta on the proximal segment, and limb buds are foreshadowed by spinule rows in the respective preceding stage. It may be of interest to note that none of these characteristics have been mentioned for the third *Notodiaptomus* species studied as yet (Cicchino, 1983).

In view of the superficial drawings and the poor description of the naupliar development of the Venezuelan '*Diaptomus*' *proximus* by González (1968), we did not dare to interpret the reported differences. Whether these differences are real or merely reflect a lack of detail will have to be clarified in future studies.

Summarizing our own studies and a perusal of the existing literature on diaptomid larvae, we conclude that the most valuable characters to differentiate between diaptomid species from the viewpoint of larval characters are the number, arrangement and length of antennular setae, the form of the terminal segment of the antennule, differences in caudal armature, as well as the setation of the maxillary buds. Further characters of taxonomic significance may be

contributed by differences in the stage-dependent appearance of post-mandibular limbs, body size and ornamentation. It seems beyond doubt that fitting together larval, juvenile and adult characters could be a valuable step towards the clarification of some puzzling problems in diaptomid systematics and to provide a firm basis for the discussion of phylogenetic relationships.

## Acknowledgements

We are grateful to Dr Hans-Uwe Dahms, University of Oldenburg, Germany and Prof. Dr Takea K.S.Björnberg, Saõ Sebastiaõ, Brazil, for providing literature and improving the manuscript by several constructive suggestions. Thanks are also due to Nicola Smith for correcting the English language. We dedicate this publication to the late Prof. Dr Hans Adam, University of Salzburg.

## References

- Björnberg, T.K.S. (1972) Developmental stages of some tropical and subtropical planktonic marine copepods. *Stud. Fauna Curacao*, **136**, 1–185.
- Cicchino, G. (1972) Desarrollo post-embrionario de *Notodiaptomus coniferoides* (Wright, 1927) (Crustacea, Copepoda). *Physis*, **31**, 585–596.
- Cipólli, M.N. (1973) Morfologia externa das fases de desenvolvimento de *Diaptomus corderoi* Wright, 1936 (Crustacea, Copepoda, Calanoida). *Bol. Zool. Biol. Mar. N.S.*, **30**, 567–612.
- Comita, G.W. and McNett, S.J. (1976) The postembryonic developmental instars of *Diaptomus oregonensis* Lilljeborg, 1889 (Copepoda). *Crustaceana*, **30**, 123–163.
- Comita, G.W. and Tommerdahl, D.M. (1960) The postembryonic developmental instars of *Diaptomus siciloides* Lilljeborg. *J. Morphol.*, **107**, 297–355.
- Czaika, S.C. (1982) Identification of nauplii N1–N6 and copepodids C1–C6 of the Great Lakes calanoid and cyclopoid copepods (Calanoida, Copepoda). *J. Great Lakes Res.*, **88**, 439–469.
- Dahms, H.-U. (1991) Usefulness of postembryonic characters for phylogenetic reconstruction in Harpacticoida (Crustacea, Copepoda). *Proceedings of the Fourth International Conference on Copepoda. Bull. Plankton Soc. Jpn Spec. Vol.*, **87**–104.
- Dahms, H.-U. and Fernando, C.H. (1992) Naupliar development of *Mesocyclops aequatorialis similis* and *Thermocyclops consimilis* (Copepoda: Cyclopoida) from Lake Awasa, a tropical rift valley lake in Ethiopia. *Can. J. Zool.*, **70**, 2283–2297.
- Dahms, H.-U. and Fernando, C.H. (1993) Naupliar development of *Phyllodiaptomus annae* (Apstein, 1907) (Copepoda: Calanoida) from Sri Lanka. *Zool. J. Linn. Soc.*, **108**, 197–208.
- Dahms, H.-U. and Schminke, H.K. (1995) A multidisciplinary approach to the fine-systematics within *Tisbe*—an evaluation of morphological and molecular methods. *Hydrobiologia*, **308**, 45–50.
- De Gouvea, E.P. (1980) Estágios do desenvolvimento naupliar de *Notodiaptomus conifer* (Sars, 1901) (Copepoda, Calanoida). *Cienc. Cult.*, **32**, 1047–1059.
- Devi, C.R. and Reddy, Y.R. (1989a) The complete postembryonic development of *Paradiaptomus greeni* (Gurney, 1906) (Copepoda, Calanoida) reared in the laboratory. *Crustaceana*, **56**, 141–161.
- Devi, R.C. and Reddy, Y.R. (1989b) The complete postembryonic development of *Allodiaptomus raoi* Kiefer, 1936 (Copepoda, Calanoida) reared in the laboratory. *Crustaceana*, **56**, 246–266.
- Devi, R.D. and Reddy, Y.R. (1990a) Larval stages of *Neodiaptomus lindbergi* Brehm, 1953 (Copepoda, Calanoida). *Hydrobiologia*, **206**, 99–114.
- Devi, R.D. and Reddy, Y.R. (1990b) The complete postembryonic development of *Tropodiaptomus informis* Kiefer, 1936 (Copepoda: Calanoida) reared in the laboratory. *J. Plankton Res.*, **12**, 55–75.
- Dietrich, W. (1915) Die Metamorphose der freilebenden Süßwassercopepoden. I. Die Nauplien und das erste Copepodidstadium. *Z. Wiss. Zool.*, **113**, 252–324.
- Dussart, B. and Defaye, D. (1983) *Répertoire mondial des Crustacés Copépodes des eaux intérieures. I. Calanoides*. CNRS, Paris, 224 pp.
- Ewers, L.A. (1930) The larval development of fresh-water Copepoda. *Contrib. Franz Theodore Stone Lab.*, **3**, 1–43.
- González, A.S. (1968) Desarrollo larvario de *Diaptomus proximus* Kiefer (Copepoda, Calanoida). *Hydrobiologia*, **82**, 528–544.

- Grandori, R. (1912) Studi sullo sviluppo larvale dei copepodi pelagici. *Redia*, **8**, 360–456.
- Green, J.D. and Northcote, T.G. (1982) The naupliar instars of *Diatomus kenai* (Copepoda, Calanoida) and their distinction from those of four other diatomids. *Can. J. Zool.*, **60**, 2162–2172.
- Gurney, R. (1931) *British Fresh-water Copepoda I*. The Ray Society, London, 238 pp.
- Hulsemann, K. (1991) Tracing homologies in appendages during ontogenetic development of calanoid copepods. *Bull. Plankton Soc. Jpn Spec. Vol.*, 105–114.
- Huys, R. and Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468 pp.
- Jersabek, C.D. and Schabetsberger, R. (1995) Resting egg production and oviducal cycling in two sympatric species of alpine diatomids (Copepoda: Calanoida) in relation to temperature and food availability. *J. Plankton Res.*, **17**, 2049–2078.
- Jersabek, C.D. and Schabetsberger, R. (1996) Limnological aspects of an alpine karst lake with extreme changes in water level. *Limnologica*, **26**, 1–13.
- Pinel-Alloul, B. and Lamoureux, J. (1988) Développement post-embryonnaire du copepode calanoïde *Diatomus (Aglaodiatomus) leptopus* S.A. Forbes, 1882. I. Phase nauplienne. *Crustaceana*, **54**, 69–84.
- Ravera, O. (1953) Gli stadi di sviluppo dei copepodi pelagici del Lago Maggiore. *Mem. Ist. Ital. Idrobiol.*, **7**, 129–151.
- Reddy, R.Y. (1994) Copepoda: Calanoida: Diatomidae. Key to the genera *Heliodiatomus*, *Allodiatomus*, *Neodiatomus*, *Phyllodiatomus*, *Eodiatomus*, *Arctodiatomus* and *Sinodiatomus*. *Guides to the Identification of the Microinvertebrates of the Continental Waters of the World*, **5**, SPB Academic Publishing, 221 pp.
- Reddy, R.Y. and Devi, C.R. (1985) The complete postembryonic development of *Megadiatomus hebes* Kiefer, 1936 (Copepoda, Calanoida) reared in the laboratory. *Crustaceana*, **48**, 40–63.
- Reddy, R.Y. and Devi, C.R. (1989) The complete postembryonic development of *Heliodiatomus conortus* (Gurney, 1907) (Copepoda, Calanoida) reared in the laboratory. *Crustaceana*, **57**, 113–133.
- Reddy, R.Y. and Devi, C.R. (1990a) The complete postembryonic development of *Heliodiatomus cinctus* (Gurney, 1907) (Copepoda, Calanoida), reared in the laboratory. *Crustaceana*, **58**, 45–66.
- Reddy, R.Y. and Devi, C.R. (1990b) Postembryonic development of *Phyllodiatomus blanci* (Guerne and Richard, 1896) (Copepoda, Calanoida). *Hydrobiologia*, **190**, 155–170.
- Wuthrich, M. (1948) Etude du développement des nauplii de *Diatomus gracilis*, O. Sars, et *Diatomus laciniatus*, Lilljeborg. *Rev. Suisse Zool.*, **55**, 427–445.

Received on April 4, 1996; accepted on July 3, 1996