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Patterns of setal numbers conserved during early development of swimming legs of Copepoda (Crustacea)

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Abstract

During swimming leg development, the number of setae present on the exopod and endopod of the bilobed bud, the transformed swimming leg with 1-segmented rami and the swimming leg with 2-segmented rami of copepods is analysed. For swimming leg 1, the most frequent number of setae on the presumptive rami of the bilobed bud is found at a higher percentage among copepod species than the most frequent number of setae for either the transformed swimming leg with 1-segmented rami or the swimming leg with 2-segmented rami. However, for swimming legs 2–4 the most frequent number of setae for the the transformed swimming leg with 1-segmented rami is found at a higher percentage of species than that on either the bilobed bud or the swimming leg with 2-segmented rami. Thus, in the cases of swimming legs 2–4, species with different numbers of setae on the presumptive exopod and endopod of the bud bilobed bud develop the same number of setae on the rami of the transformed swimming leg with 1-segmented rami. Increasing the number of species analysed is expected to make more robust the hypothesis that the number of setae on the transformed swimming leg with 1-segmented rami is conserved relative to the number of setae on the bilobed bud.

Introduction

Development of swimming legs 1–4 of copepods takes place from the last naupliar stage through the copepodid phase of development (Ferrari, 1988; Ferrari & Benforado, 1998). The number and kinds of changes which may take place in these appendages varies among different copepod species. For the species studied here, each pair of swimming legs begins development as a contralateral pair of bilobed buds armed with setae on the fourth (swimming leg 1) or third (swimming legs 2–4) somite from the posterior somite (bearing the caudal ramus) on the copepod body (Ferrari, 1988, 1993). The lobes of the bud are the presumptive exopod, lateral or dorsal and presumptive endopod, medial or ventral. Each bud is transformed during the following molt into a recognizable swimming leg united to its contralateral twin by a coupler attached to their coxa. The rami of the transformed swimming leg appear 1-segmented. During the following molt, an arthrodial membrane usually separates a proximal and a distal segment on both the exopod and the endopod. This paper examines the different numbers of setae found on the rami during each of these three early steps in swimming leg development.

Methods

Data presented here are from an ongoing study of the appendage development in copepods; the initial focus of the study was on the Cyclopidae (Ferrari, 1998) and therefore the data are heavily weighted for that family (27 of 64 species in Tables 1 and 2). Development of swimming legs 1 and 2 begins at the last naupliar stage when the bilobed bud of these appendages initially appears. Information about the last naupliar stage were studied for 29 copepod species (Table 1). Subsequent development of swimming legs 1 and 2 and the complete development of swimming legs 3 and 4, takes place during the six stages of the copepodid phase of development. Descriptions of these stages were studied for 35 species more (see Table 2), giving a total of

Table 1. Species for which the complete development of all swimming legs is known

Order	Family	Genus	Species
ca	Clausocalanidae	*Pseudocalanus*	*elongatus*
ca	Paracalanidae	*Acrocalanus*	*gibber*
ca	Pseudodiaptomidae	*Pseudodiaptomus*	*forbesi*
ca	Temoridae	*Temora*	*longicornis*
ca	Tortanidae	*Tortanus*	*dextrilobatus*
cy	Cyclopidae	*Acanthocyclops*	*carolinianus*
cy	Cyclopidae	*Acanthocyclops*	*robustus*
cy	Cyclopidae	*Apocyclops*	*dimorphus*
cy	Cyclopidae	*Apocyclops*	*panamensis*
cy	Cyclopidae	*Cyclops*	*scutifer*
cy	Cyclopidae	*Diacyclops*	*navus*
cy	Cyclopidae	*Diacyclops*	*thomasi*
cy	Cyclopidae	*Eucyclops*	*agilis*
cy	Cyclopidae	*Macrocyclops*	*albidus*
cy	Cyclopidae	*Megacyclops*	*latipes*
cy	Cyclopidae	*Mesocyclops*	*edax*
cy	Cyclopidae	*Mesocyclops*	*longisetus*
cy	Cyclopidae	*Microcyclops*	*rubellus*
cy	Cyclopidae	*Thermocyclops*	*decipiens*
cy	Cyclopidae	*Tropocyclops*	*jamaicensis*
cy	Cyclopidae	*Tropocyclops*	*prasinus*
cy	Notodelphyidae	*Dorpygus*	*seclusus*
cy	Notodelphyidae	*Notodelphys*	*affinis*
cy	Oithonidae	*Dioithona*	*oculata*
cy	Oithonidae	*Limnoithona*	*tetraspina*
h	Canuellidae	*Coullana*	*canadensis*
h	Longipediidae	*Longipedia*	*americana*
h	Miraciidae	*Macrosetella*	*gracilis*
s	Asterocheridae	*Scottomyzon*	*gibberum*

ca = Calanoida, cy = Cyclopoida, h = Harpacticoida, s = Siphonostomatoida.

Table 2. Species for which data about the bilobed bud of swimming legs 1 and 2 on nauplius 6 is unknown; only the copepodid phase of development is known

Order	Family	Genus	Species
ca	Acartiidae	*Acartia*	*spinata*
ca	Aetideidae	*Euchirella*	*messinensis*
ca	Centropagidae	*Boeckella*	*poopoensis*
ca	Diaptomidae	*Skistodiaptomus*	*pygmaeus*
ca	Euchaetidae	*Euchaeta*	*media*
ca	Lucicutiidae	*Lucicutia*	*grandis*
ca	Metridinidae	*Pleuromamma*	*xiphias*
ca	Phyllopidae	*Phyllopus*	*helgae*
ca	Ridgewayiidae	*Ridgewayia*	*klausruetzleri*
cy	Cyclopidae	*Allocyclops*	*silvaticus*
cy	Cyclopidae	*Allocyclops*	sp.
cy	Cyclopidae	*Bryocyclops*	*caroli*
cy	Cyclopidae	*Diacyclops*	*dispinosus*
cy	Cyclopidae	*Diacyclops*	*eulitoralis*
cy	Cyclopidae	*Graeteriella*	*brehmi*
cy	Cyclopidae	*Halicyclops*	*aberrans*
cy	Cyclopidae	*Mesocyclops*	*rutneri*
cy	Cyclopidae	*Muscocyclops*	*operculatus*
cy	Cyclopidae	*Neocyclops*	*vicinus*
cy	Cyclopidae	*Paracyclops*	*chiltoni*
cy	Cyclopidae	*Speocyclops*	*racovitzai*
cy	Cyclopidae	*Stolonicyclops*	*heggiensis*
cy	Cyclopidae	*Troglocyclops*	*jaustocki*
cy	Cyclopinidae	*Cyclopina*	*caroli*
cy	Cyclopinidae	*Procyclopina*	*feiticeira*
cy	Notodelphyidae	*Scolecodes*	*huntsmani*
cy	Oithonidae	*Oithona*	*similis*
cy	Oithonidae	*Oithona*	*simplex*
h	Metiidae	*Metis*	sp.
p	Clausidiidae	*Conchyliurus*	*quintus*
p	Clausidiidae	*Heroicyclops*	*adherens*
p	Clausidiidae	*Leptinogaster*	*major*
p	Corycaeidae	*Corycaeus*	*angelicus*
p	Myicolidae	*Midicola*	*spinosus*

ca = Calanoida, cy = Cyclopoida, h = Harpacticoida, p = Poecilostomatoida.

64 species for these stages. The results for swimming legs 2–4 are presented first; the results for swimming leg 1 are presented last because swimming leg 1 differs significantly from swimming legs 2–4 in the early setation of the leg bud and the setation of the transformed leg (Ferrari & Benforado, 1998).

Results

Twenty-two of 29 species (76%) bear three setae on the presumptive exopod and two setae on the presumptive endopod of the bilobed bud of swimming leg 2 which is present at last naupliar stage. Three other combinations are expressed among the eight other species studied here (Table 3). Fifty-six of 64 species (88%) bear seven setae on the exopod and six setae on the endopod of the transformed swimming leg 2 with 1-segmented rami, which is present at copepodid 1. Eight species express three other combinations of setae on the exopod and the endopod (Table 3). For 36 of 64 species (56%), swimming leg 2 has a 2-segmented exopod with one seta on the proximal segment and seven on the distal segment and a 2-segmented endopod with one seta on the proximal segment and six on the distal. The species express-

Table 3. Infrequent combinations of setal numbers for bilobed bud, 1-segmented ramus and 2-segmented ramus stages of swimming leg 2

	Presumptive Re & Presumptive Ri (most frequent is 3 and 2)
3 & 1:	*Apocyclops dimorphus, A. panamensis, Microcyclops rubellus*
2 & 2:	*Acrocalanus gibber, Pseudocalanus elongatus, Pseudodiaptomus forbsi*
1 & 0:	*Macrosetella gracilis*
	1-segmented Re & 1-segmented Ri (most frequent is 7 and 6)
7 & 5:	*Coullana canadensis, Bryocyclops caroli, Speocyclops racovitzai*
7 & 4:	*Corycaeus angelicus*
6 & 5:	*Longipedia americana*
6 & 4:	*Macrosetella gracilis*
5 & 3:	*Metis* sp.
4 & 6:	*Acartia spinata*
	2-segmented Re & 2-segmented Ri (most frequent is 7 distal and 1 proximal, and 6 distal and 1 proximal)
7, 1 & 7, 1:	*Pseudodiaptomus forbsi, Ridgewayia klausruetzleri, Tortanus dextrilobatus*
7, 1 & 5, 1:	*Graeteriella breluni, Muscocyclops operculatus, Procyclopina feiticeira, Diacyclops eulitoralis, Stolonicyclops heggieusis*
7, 1 & 4, 1:	*Bryocyclops caroli, Speocyclops racovitzai, Corycaeus angelicus*
7, 1 & 5, 0:	*Scolecodes luutsuani*
6, 1 & 7, 1:	*Skistodiaptomus pygmaeus*
6, 1 & 6, 1:	*Cyclopina caroli, Oithona similis*
6, 1 & 4, 1:	*Coullana canadensis*
6, 1 & 4, 0:	*Macrosetella gracilis*
5, 1 & 5, 1:	*Longipedia americana*
5, 1 & 4, 0:	*Metis* sp.
7, 1 & 8 -:	*Phyllopus helgae, Pleuromamma xiphias, Boeckella poopoensis*
7, 1 & 7 -:	*Lucicutia grandis, Temora longicornis*
7, 1 & 6 -:	*Pseudocalanus elongatus, Euchirella messinensis*
8 - & 6 -:	*Euchaeta media*
6 - & 6 -:	*Acartia spinata*

Re = exopod; *Ri* = endopod; a dash indicates that the arthrodial membrane is not formed between proximal and distal segment.

ing the fifteen other combinations are listed in Table 3. These include five species in which the endopod remains 1-segmented and the exopod of two of the five also remains 1-segmented.

Thirty-three of 64 species (52%) bear three setae on the presumptive exopod and two setae on the presumptive endopod of the bilobed bud of swimming leg 3; this bilobed bud is present at copepodid I. The remaining species express six other combinations of setae on this bilobed bud (Table 4). Fifty-two of 64 species (81%) bear seven setae on the exopod and six setae on the endopod of the transformed swimming leg 3 with 1-segmented rami which is present at copepodid II. Twelve species express seven other combinations of setae (Table 4). For 38 of 64 species (59%), swimming leg 3 with 2-segmented rami has an exopod with one seta on the proximal segment and seven on the distal segment and an endopod with one seta on the proximal segment and six on the distal segment. Species expressing the 14 other combinations of numbers are listed in Table 4. These species include eight in which the endopod remains 1-segmented and for two of these latter eight species the exopod also remains 1-segmented. Examples of swimming leg 3 are shown in Figures 1–3.

Twenty-nine of 64 species (45%) bear three setae on the presumptive exopod and two setae on the presumptive endopod of the bilobed bud of swimming leg 4; this bilobed bud is present at copepodid II. The remaining species express six other combinations of setae (Table 5). Forty-six of 64 species (72%) bear seven setae on the exopod and six setae on the endopod

Table 4. Infrequent combinations of setal numbers for bilobed bud, 1-segmented ramus and 2-segmented ramus stages of swimming leg 3

	Presumptive Re & Presumptive Ri (most frequent is 3 and 2)
3 & 1:	*Tropocyclops jamaicensis, T. prasinus, Apocyclops panamensis, A. dimorphus, Graeteriella brehmi, Corycaeus angelicus*
3 & 0:	*Paracyclops chiltoni, Speocyclops racovitzai, Diacyclops eulitoralis, Stolonicyclops heggiensis, Metis* sp.
2 & 2:	*Acrocalanus gibber, Pseudocalanus elongatus, Pseudodiaptomus forbsi*
2 & 1:	*Allocyclops* sp., *Midicola spinosus*
2 & 0:	*Allocyclops silvaticus, Bryocyclops caroli, Muscocyclops operculatus, Eucyclops agilis, Neocyclops vicinus, Conchyliurus quintus, Leptinogaster major, Scottomyzon gibberum, Hemicyclops adherens*
1 & 0:	*Cyclopina caroli, Halicyclops aberrans, Troglocyclops janstocki, Herrmannella saxidoni*
	1-segmented Re & 1-segmented Ri (most frequent is 7 and 6)
7 & 5:	*Speocyclops racovitzai, Scolecodes huntsmani, Herrmannella saxidoni, Scottomyzon gibberum*
7 & 2:	*Corycaeus angelicus*
6 & 6:	*Skistodiaptomus pygmaeus, Oithona similis*
6 & 5:	*Longipedia americana*
6 & 4:	*Macrosetella gracilis, Metis* sp.
5 & 4:	*Coullana canadensis*
4 & 6:	*Acartia spinata*
	2-segmented Re & 2-segmented Ri (most frequent is 7 distal and 1 proximal, and 6 distal and 1 proximal)
7, 1 & 7, 1:	*Boeckella poopoensis, Ridgewayia klausruetzleri, Pseudodiaptomus forbsi*
7, 1 & 5, 1:	*Bryocyclops caroli* female, *Diacyclops eulitoralis, Stolonicyclops heggiensis, Muscocyclops operculatus, Procyclopina feiticeira, Macrosetella gracilis, Herrmannella saxidoni, Scottomyzon gibberum*
7, 1 & 4, 1:	*Speocyclops racovitzai*
7, 1 & 2, 1:	*Corycaeus angelicus*
6, 1 & 7, 1:	*Skistodiaptomus pygmaeus*
6, 1 & 6, 1:	*Oithona similis*
5, 1 & 5, 1:	*Longipedia americana*
5, 1 & 4, 1:	*Metis* sp.
4, 1 & 3, 1:	*Coullana canadensis*
7, 1 & 8 - :	*Phyllopus helgae, Pleuromamma xiphias, Tortanus dextrilobatus*
7, 1 & 7 - :	*Lucicutia grandis, Euchaeta media*
8 - & 7 - :	*Temora longicornis*
6 - & 4 - :	*Scolecodes huntsmani*
5 - & 7 - :	*Acartia spinata*

Legend as for Table 3.

of the transformed swimming leg 4 with 1-segmented rami, which is present at copepodid III. Eighteen species express twelve other combinations of setae (Table 5). For 32 of 64 species (50%), swimming leg 4 with 2-segmented rami has an exopod with one seta on the proximal segment and nine on the distal segment and an endopod with one seta on the proximal segment and six on the distal. The remaining species expressing combinations are listed in Table 5. These include seven species in which the endopod remains 1-segmented and three of these seven species have a 1-segmented exopod.

Twenty-two of 29 species (76%) bear four setae on the presumptive exopod and two setae on the presumptive endopod of the biolobed bud of swimming leg 1. This bilobed bud is present at the last naupliar stage. The remaining species express five other combinations of setae (Table 6). Forty-one of 64 species

Table 5. Infrequent combinations of setal numbers for bilobed bud, 1-segmented ramus and 2-segmented ramus stages of swimming leg 4

	Presumptive Re & Presumptive Ri (most frequent is 3 and 2)
3 & 1:	*Tropocyclops jamaicensis, T. prasinus, Encyclops agilis, Microcyclops rubellus, Apocyclops dimorphus, A. panamensis, Graeteriella brehmi*
3 & 0:	*Paracyclops chiltoni, Bryocyclops caroli, Diacyclops enlitoralis, Speocyclops racovitzai, Stolonicyclops heggiensis, Metis* sp.
2 & 2:	*Acrocalanus gibber, Pseudocalanus elongatus, Pseudodiaptomus forbsi*
2 & 1:	*Allocyclops* sp., *Midicola spinosus, Scottomyzon gibberum*
2 & 0:	*Neocyclops vicinus, Allocyclops silvaticus Muscocyclops operculatus, Conchylinrus quintus, Hemicyclops adherens, Leptinogaster major, Coullana canadensis*
1 & 0:	*Cyclopina caroli, Troglocyclops jaustocki, Halicyclops aberrans, Notodelphys affinis, Scolecodes lumstmani, Doropygus seclusus, Herrmannella saxidomi, Corycaeus angelicus*
	1-segmented Re & 1-segmented Ri (most frequent is 7 and 6)
7 & 5:	*Bryocyclops caroli, Speocyclops racovitzai*
7 & 4:	*Macrosetella gracilis, Scottomyzon gibberum*
7 & 3:	*Herrmannella saxidomi*
6 & 6:	*Neocyclops vicinus, Leptinogaster major, Skistodiaptomus pygmaeus*
6 & 5:	*Allocyclops silvaticus, Muscocyclops operculatus*
6 & 4:	*Metis* sp.
6 & 1:	*Corycaeus angelicus*
5 & 6:	*Oithona similis*
5 & 5:	*Doropygus seclusus*
5 & 4:	*Coullana canadensis, Longipedia americana*
4 & 6:	*Acartia spinata*
1 & 0:	*Scolecodes lumstmani*
	2-segmented Re & 2-segmented Ri (most frequent is 9 distal and 1 proximal, and 6 distal and 1 proximal)
9, 1 & 7, 1:	*Acrocalanus gibber, Boeckella poopoensis, Phyllopus helgae, Ridgewayia klausruetzleri, Pseudodiaptomus forbsi*
9, 1 & 5, 1:	*Diacyclops enlitoralis*
9, 1 & 4, 1:	*Scottomyzon gibberum*
9, 1 & 3, 1:	*Herrmannella saxidomi*
8, 1 & 7, 1:	*Skistodiaptomus pygmaeus*
8, 1 & 6, 1:	*Apocyclops dimorphus, A. panamensis, Graeteriella brehmi, Microcyclops rubellus, Leptinogaster major, Macrosetella gracilis*
7, 1 & 5, 1:	*Allocyclops* sp., *A. silvaticus*
7, 1 & 4, 1:	*Bryocyclops caroli* male, *Metis* sp.
6, 1 & 4, 1:	*Muscocyclops operculatus, Speocyclops racovitzai*
6, 1 & 5, 1:	*Longipedia americana*
6, 0 & 6, 1:	*Oithona similis*
5, 1 & 4, 1:	*Coullana canadensis*
9, 1 & 8 - :	*Pleuromamma xiphias*
9, 1 & 7 - :	*Halicyclops aberrans*
9, 1 & 5 - :	*Bryocyclops caroli* female
9, 1 & 2 - :	*Corycaeus angelicus*
7, 1 & 6 - :	*Stolonicyclops heggiensis*
10 - & 7 -:	*Temora longicornis, Scolecodes lumstmani*
6 - & 7 -:	*Acartia spinata*

Legend as for Table 3.

Table 6. Infrequent combinations of setal numbers for bilobed bud, 1-segmented ramus and 2-segmented ramus stages of swimming leg 1

	Presumptive Re & Presumptive Ri (most frequent is 4 and 2)
4 & 3:	*Tortanus dextrilobatus, Temora longicornis*
3 & 2:	*Coullana canadensis*
2 & 3:	*Acrocalanus gibber, Pseudocalanus elongatus, Pseudodiaptomus forbsi*
0 & 0:	*Macrosetella gracilis*
	1-segmented Re & 1-segmented Ri (most frequent is 8 and 7)
8 & 6:	*Allocyclops* sp., *A. silvaticus, Graeteriella brehmi, Procyclopina feiticeira, Coullana canadensis, Phyllopus helgae, Lucicutia grandis, Corycaeus angelicus*
8 & 5:	*Bryocyclops caroli, Speocyclops racovitzai, Scolecodes lumstmani*
7 & 7:	*Pseudodiaptomus forbsi*
7 & 6:	*Stolonicyclops heggiensis*
7 & 5:	*Euchirella messinensis, Muscocyclops operculatus, Longipedia americana, Pseudocalanus elongatus*
6 & 7:	*Skistodiaptomus pygmaeus, Tortanus dextrilobatus*
6 & 6:	*Acrocalanus gibber*
6 & 5:	*Euchaeta media*
6 & 2:	*Metis* sp.
4 & 3:	*Macrosetella gracilis*
	2-segmented Re & 2-segmented Ri (most frequent is 8 distal and 1 proximal, and 7 distal and 1 proximal)
8, 1 & 6, 1:	*Apocyclops dimorphus, A. panamensis, Halicyclops aberrans, Neocyclops vicinus Paracyclops chiltoni, Microcyclops rubellus, Diacyclops eulitoralis, Dioithona oculata, Oithona similis, O. simplex, Limnoithona tetraspina, Notodelphys affinis, Doropygus seclusus, Cyclopina caroli, Conchyliurus quintus, Herrmannella saxidoni, Leptinogaster major, Midicola spinosus, Coullana canadensis, Boeckella poopoensis, Pseudiaptomus forbsi, Acartia spinata*
8, 1 & 5, 1:	*Allocyclops* sp., *A. silvaticus, Graeteriella brehmi, Procyclopina feiticeira, Corycaeus angelicus*
8, 1 & 4, 1:	*Bryocyclops caroli*
7, 1 & 4, 1:	*Muscocyclops operculatus, Speocyclops racovitzai, Longipedia americana*
7, 1 & 5, 1:	*Stolonicyclops heggiensis*
7, 0 & 5, 1:	*Acrocalanus gibber*
6, 1 & 6, 1:	*Skistodiaptomus pygmaeus*
5, 1 & 2, 0:	*Metis* sp.
4, 0 & 2, 1:	*Macrosetella gracilis*
8, 1 & 7 - :	*Phyllopus helgae, Temora longicornis*
8, 1 & 6 - :	*Lucicutia grandis*
7, 1 & 5 - :	*Scolecodes lumtsmani, Pseudocalanus elongatus*
7, 0 & 8 - :	*Tortanus dextrilobatus*
8 - & 5 - :	*Euchirella messinensis*
7 - & 5 - :	*Euchaeta media*

Legend as for Table 3.

(64%) bear eight setae on the exopod and seven setae on the endopod of the transformed swimming leg 1 with 1-segmented rami, which is present at copepodid I. Twenty-three species express five other combinations of setae (Table 6). For 20 of 64 species (31%), swimming leg 1 with 2-segmented rami has an exopod with one seta on the proximal segment and eight on the distal segment and an endopod with one seta on the proximal segment and seven on the distal. Species expressing fifteen other combinations are listed in Table 6. Among these are eight in which the endopod remains 1-segmented and one of these also has a 1-

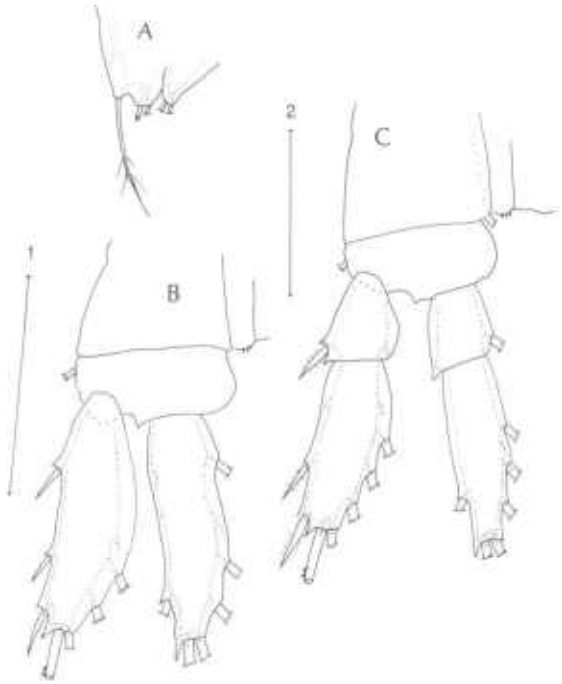

Figure 1. Thermocyclops decipiens leg 3. (A) bilobed bud at copepodid I; (B) transformed swimming leg with 1-segmented rami at copepodid II; (C) swimming leg with 2-segmented rami at copepodid III. Line 1 for A, B and line 2 for C are 0.05 mm. External setae of the exopod complete; terminal seta of the exopod with oval cutoff; all other setae with wavy line cutoff. Dotted outline within rami indicates exoskeleton of the following developmental stage.

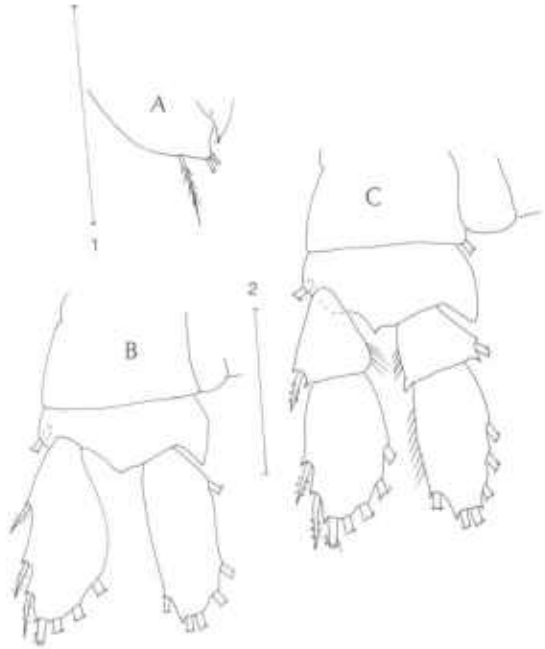

Figure 2. Encyclops agilis leg 3. (A) bilobed bud at copepodid I [presumptive endopodal lobe with one seta]; (B) transformed swimming leg with 1-segmented rami at copepodid II; (C) swimming leg with 2-segmented rami at copepodid III. Line 1 for A, B and line 2 for C are 0.05 mm. External setae of the exopod complete; terminal seta of the exopod with oval cutoff; all other setae with wavy line cutoff.

segmented exopod. Examples of swimming leg 1 are shown in Figures 4–6.

Discussion

The most frequent combination of setal numbers on the bilobed bud (3 on the exopod and 2 on the endopod), the transformed swimming leg with 1-segmented rami (7 on the exopod and 6 on the endopod) and the swimming leg with 2-segmented rami (1 proximal and 7 distal on the exopod and 1 proximal and 6 distal on the endopod), are identical for swimming legs 2 and 3. However the most frequent combination for swimming leg 4 with 2-segmented rami (1 proximal and 9 distal on the exopod and 1 proximal and 6 distal on the endopod) differs from swimming legs 2 and 3. Ferrari & Benforado (1998) suggest that the 2-segmented exopod of swimming leg 4 represents two contiguous steps in development of swimming legs 2 and 3. Combining these two steps results in the early allocation to the distal segment of the two setae which will arm the middle segment of the exopod of the adult.

For swimming leg 1, the bilobed bud, the transformed swimming leg with 1-segmented rami and the 2-segmented rami are quite different from the other swimming legs. Swimming leg 1 of copepods differs from swimming legs 2–4 because as many as four setae may be present on the presumptive exopod of the bilobed bud and as many as three setae may be present on the presumptive endopod (the latter restricted to Calanoida). The transformed swimming leg 1 with 1-segmented rami differs from swimming legs 2–4 because as many as eight setae may be present on the exopod and as many as seven setae may be present on the endopod. Ferrari & Benforado (1998) suggest that the extra setae, the eighth on the exopod and the seventh on the endopod of the transformed swimming leg 1 with 1-segmented rami, will be allocated to the middle segment of each ramus on the adult. Setae serially homologous to those allocated to the middle segment of each ramus on the adult appear later in development of swimming legs 2–4.

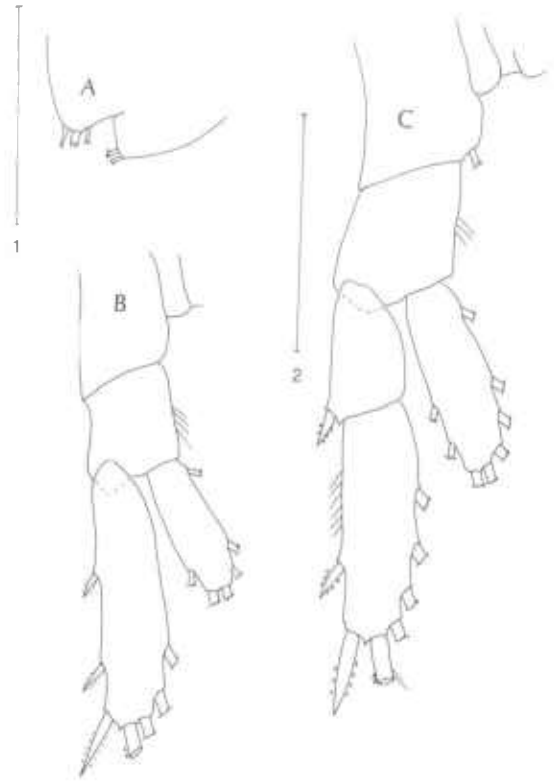

Figure 3. Tortanus dextrilobatus leg 3. (A) bilobed bud at copepodid I; (B) transformed swimming leg with 1-segmented rami at copepodid II; (C) swimming leg with 2-segmented rami at copepodid III [endopod remains 1-segmented]. Line 1 for A, B is 0.05 mm; line 2 for C is 0.1 mm. Remaining legend as for Figure 2.

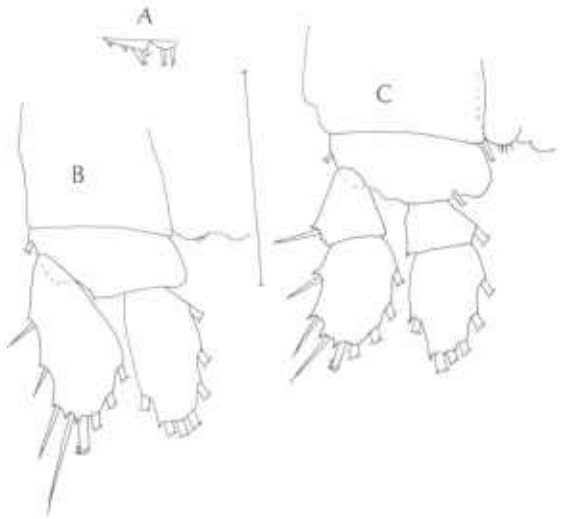

Figure 4. Apocyclops panamensis leg 1. (A) bilobed bud at nauplius 6; (B) transformed swimming leg with 1-segmented rami at copepodid I; (C) swimming leg with 2-segmented rami at copepodid II. Line 1 for (A) (B) (C) is 0.05 mm. Remaining legend as for Figure 2.

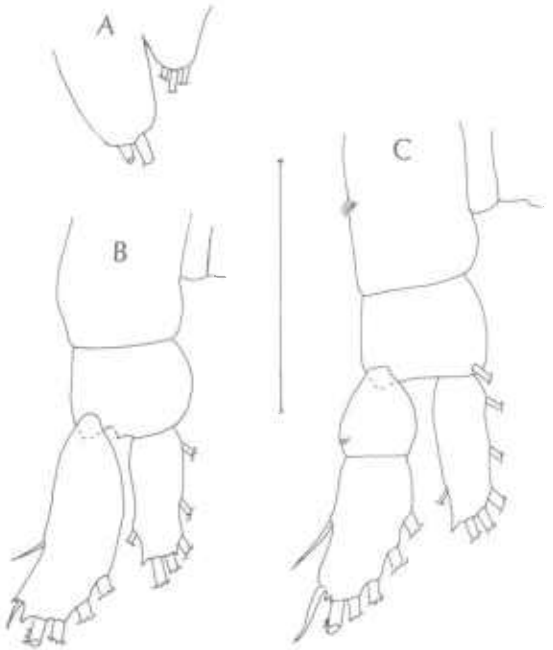

Figure 5. Acrocalanus gibber leg 1. (A) bilobed bud at nauplius 6 I [presumptive exopodal lobe with two seta]; (B) transformed swimming leg with 1-segmented rami at copepodid I; (C) swimming leg with 2-segmented rami at copepodid II [endopod remains 1-segmented]. Line 1 for (A) (B) and line 2 for (C) are 0.05 mm. Remaining legend as for Figure 2.

Table 7. The percentage of the most frequent combinations of setal numbers among all species studied for the three early stages in development of swimming legs 1–4

Leg	Bud	1-segmented rami	2-segmented rami
1	76	64	31
2	76	88	56
3	52	81	59
4	45	72	50

For swimming leg 1, the most frequent combination of setal numbers for the exopod and endopod of the bilobed bud is found in a higher percentage of species than the progressively decreasing percentages for the most frequent combination on the transformed swimming leg with 1-segmented rami or the swimming leg with 2-segmented rami (Table 7). This sequence appears logical because the larger number of setae present in the later two steps of development (up to 15 for the 1-segmented leg 1 and up to 19 setae for the 2-segmented leg 1, or up to 13 for the 1-segmented leg 2 and up to 15 setae for the 2-segmented leg 2) should provide more opportunity for variation than the

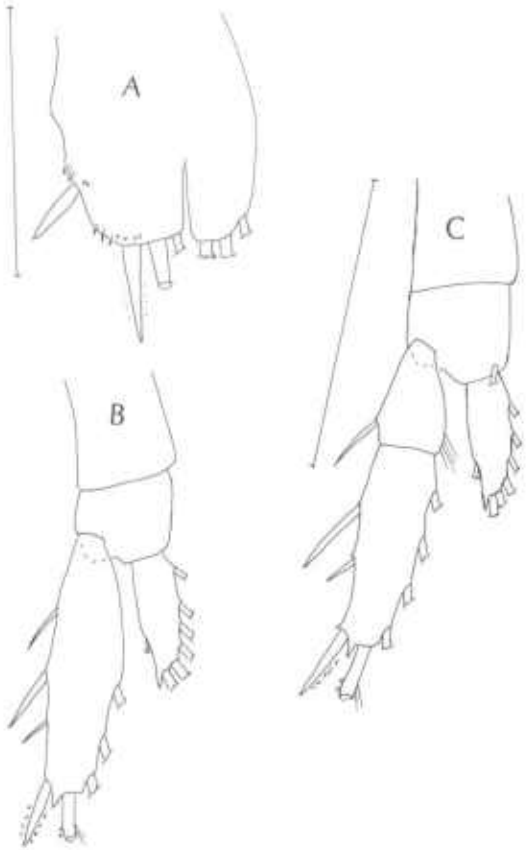

Figure 6. Temora longicornis leg 1. (A) bilobed bud at nauplius 6; (B) transformed swimming leg with 1-segmented rami at copepodid I; (C) swimming leg with 2-segmented rami at copepodid II [endopod remains 1-segmented]. Line 1 for (A) (B) and line 2 for (C) are 0.05 mm. Remaining legend as for Figure 2.

six or seven setae present on the bilobed bud of leg 1, or the five setae present on the bilobed bud of leg 2.

However, this sequence of decreasing percentages as development progresses is not expressed for swimming legs 2–4. For these three legs, the most frequent combination of setal numbers on the exopod and endopod of the transformed swimming leg with 1-segmented rami occurs in a higher percentage of species than the most frequent combination for either the bilobed bud or the swimming leg with 2-segmented rami (Table 7). That is, several species each with a different combination of setal numbers on the bilobed bud have the same combination of setae on the transformed swimming leg with 1-segmented rami. For example, *Eucyclops agilis*, *Tropocyclops jamaicensis* and *T. prasinus* with 3 setae on the presumptive exopod and 1 seta on the presumptive endopod of the bilobed bud of swimming leg 3, *Paracyclops chiltoni* with 3 setae on the presumptive exopod but without a seta on the presumptive endopod of the bilobed bud of that leg and *Hemicyclops adherens* and *Coullana canadensis* with 2 and no setae respectively (Table 5) are transformed into a swimming leg 3 with 7 exopodal and 6 endopodal setae on the 1-segmented rami. This is the most frequent combination for that step of development. So for swimming legs 2–4, the transformed swimming leg with 1-segmented rami, rather than the bilobed bud, has setal numbers better conserved among these copepods.

As noted earlier, the data analysed here are heavily weighted for species of Cyclopidae. It is reasonable to expect that the above results might change as data for more copepods are analysed. The addition of more copepods from two orders may result in significant changes. The harpacticoid species presented here, *Macrosetella gracilis*, *Coullana canadensis*, and *Longipedia americana*, usually have a lower number of setae on any ramus than the most frequent combination found in this study. Including more harpacticoids may be expected to increase the number of different combinations for both rami so that the percentage of the most frequent combination among all included copepods will decline. Inclusion of more calanoids will differentially reduce the most frequent combination for the bilobed bud of leg 1 because most calanoids can be expected to have four setae on the presumptive exopod and three seta on the presumptive endopod of the bilobed bud of swimming leg 1. These calanoid bilobed buds are expected to be transformed into swimming legs 1 with 8 exopodal and 7 endopodal setae, which is the most frequent combination found for that transformed swimming leg with 1-segmented rami.

Homologies of the setae present in these various combinations will be addressed in a forthcoming study. For combinations of relatively large numbers of setae on the exopod plus endopod (3 and 2, 7 and 6, or 7 distal and 1 proximal and 6 distal and 1 proximal on swimming legs 2–3; 3 and 2, 7 and 6, or 4 distal and 1 proximal and 6 distal and 1 proximal on swimming leg 4; 4 and 2–3, 8 and 7, or 8 distal and 1 proximal and 7 distal and 1 proximal on swimming leg 1), setae are homologous among species expressing the same combination. Problems with homology exist for some combinations of relatively smaller numbers of setae. The resolution of setal homologies should increase the number of combinations with relatively fewer setae and reduce the percentage of each combination. The addition of more species and the resolution of setal

homologies should make more robust the hypothesis that the combination of setal numbers for the transformed swimming leg with 1-segmented rami is better conserved among copepods than the combination for the bilobed bud.

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References

Ferrari, F. D., 1988. Developmental patterns in numbers of ramal segments of copepod post-maxillipedal legs. Crustaceana 54: 256–293.

Ferrari, F. D., 1993. Exceptions to the rule of development that anterior is older among serially homologous segments of post-maxillipedal legs in copepods. J. Crust. Biol. 13: 763–768.

Ferrari, F. D., 1998. Setal developmental patterns of the thoracopods of cyclopid copepods (Cyclopoida) and their use in phylogenetic inference. J. Crust. Biol. 18: 471–489.

Ferrari, F. D. & A. Benforado, 1998. Relationships between arthrodial membrane formation and addition of setae to swimming legs 1–4 of *Dioithona oculata*, *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Temora longicornis* (Crustacea: Copepoda). Crustaceana 71: 545–564.