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SETAL DEVELOPMENTAL PATTERNS OF THORACOPODS OF THE CYCLOPIDAE (COPEPODA: CYCLOPOIDA) AND THEIR USE IN PHYLOGENETIC INFERENCE

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ABSTRACT

Thoracopod development was analyzed for 25 species from 18 genera among the Cyclopidae. One species from each of 7 genera of presumed older cyclopoids, 5 poecilostomatoid genera, 3 harpacticoid genera, 5 calanoid genera, and a siphonostomatoid were studied to help establish ancestral patterns of thoracopod development. Ancestral character states were inferred from the presence of identical states in species from presumed older families, from the presence of states which show diverse and frequent occurrence among the Copepoda, or from the presence of states shared by serially homologous structures presumed to be determined by the same pleiotropic regulatory process.

Developmental patterns of the 4 swimming legs were assumed to result from the action of 2 different regulatory processes. A pleiotropic process acting early in development determines the morphology of all 8 rami together and results in 3 states among cyclopids, ancestral, and the independently derived delayed and truncated patterns. A second set of up to 8 regulatory processes acts later and one of the 8 determines the morphology of each individual ramus. The ancestral states of the resulting individual rami are, by default, the morphology that results from the pleiotropic regulatory process. Variations in developmental patterns were used to generate a phylogenetic hypothesis. Cyclopids have separated into a lineage of 10 species which has delayed the development of the swimming legs or has modified some individual rami from the delayed condition, and a lineage of 8 species which has truncated the development of the swimming legs or has modified some individual rami from that truncated condition. Four species have retained the ancestral process regulating swimming-leg development and 3 species have modified development of some individual rami from the ancestral condition.

Copepod development is anamorphic. A new somite is added anteriorly from the posterior somite during each stage of development. Thoracomeres 1–4 form during naupliar stages 3–6, respectively, although naupliar somites are not separated from one another. Thoracomeres 5–7, which usually articulate, form during copepodid stages I–III. In general, copepod thoracopods initially appear as setose buds one stage after the formation of their somite. However, the maxilliped of cyclopids is not present as a setose bud during naupliar development and swimming legs 1 and 2 initially are present as setose buds at nauplius 6. During the molt to copepodid I, the maxilliped and buds of the swimming legs 1 and 2 are transformed into complex appendages, which are more similar to their adult morphology. Appendage development during the copepodid phase usually involves the addition of at most one segment and one or more setae at each new copepodid stage.

While there is significant variation among copepods in this general pattern of development, there are only a few studies in which this variation has been used to draw inferences about copepod phylogeny. Distinctions in appendage development have been used to group species (Claus, 1893; Itô, 1984) or higher taxa (Lang, 1948), but only occasionally have characters expressed during development been used to draw phylogenetic inferences (Dahms, 1990; Dahms *et al.*, 1991; Ferrari, 1991). This use of characters expressed during development can be problematical for three reasons. If juvenile and adult characters are analyzed from a simple matrix, an incorrectly robust hypothesis may result if juvenile and adult states are invariably dependent, because they are determined by the same genetic regulatory process. Phylogenetic inferences from analyses which are limited to a specific developmental stage, however, cannot make use of the full expression of developmental variability. Finally, when results from analyses of several stages are compared, inferences may be complicated if stage-specific hypotheses are not concordant.

A method which overcomes many of these

problems involves the use of developmental patterns, i.e., abstracting information from a complete developmental series of morphologies of the same structure in order to define character states (Ferrari, 1988, 1991). The following study determines the setal developmental patterns of thoracopods of 25 species of copepods belonging to 18 genera within the family Cyclopidae, and outlines some of the problems in analyzing these patterns and in using them to create phylogenetic hypotheses.

Materials and Methods

About 660 species of cyclopids are known (Janet Reid, personal communication). These are placed in 57 nominal genera in 4 subfamilies. Twenty-five species in 18 genera from 3 subfamilies are analyzed here (Appendix 1). Choice of these species was determined by availability of cultured or preserved specimens, and not by experimental design.

Specimens usually were fixed and preserved with 4% formaldehyde/96% water or 70% ethanol/30% water. They were cleared in steps through 50% lactic acid/50% water to 100% lactic acid and examined with differential interference optics, or stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% water and examined with bright-field optics.

For convenience here, all developmental stages are designated with Arabic numerals, although in most literature accounts copepodid stages usually are designated with Roman numerals. Thoracopods of cyclopid copepods develop from the last nauplius (stage 6) through the last copepodid (stage 12). The 7 cyclopid thoracopods are abbreviated: maxilliped = mxp; swimming legs 1–4 = P1–4; legs 5 and 6 = P5 and P6. Setae are articulating armament elements of appendage segments.

Because so little information is available about development of copepod thoracopods, a diverse set of noncyclopid copepods (Appendix 1) was also studied in order to provide data from which hypotheses could be formulated about the possible ancestral condition of cyclopid setal developmental patterns. A recent analysis of families of the order Cyclopoida by Ho (1994) suggested including species from the presumed older Notodelphyidae, Oithonidae, and Cyclopinidae. Because relationships of Cyclopoida to other copepod orders remain problematical (Ho, 1990, 1994; Huys and Boxshall, 1991; Stock, 1991), species in presumed older families belonging to the following orders were also included: Clausidiidae, Myicolidae, and Sabelliphilidae of the Poecilostomatoida (for relationships see Ho, 1991); Canuellidae, Longipediidae, and Miraciidae of the Harpacticoida (for relationships see Lang, 1948; Dahms, 1990); Asterocheridae of the Siphonostomatoida (V. Ivanenko, personal communication); Clausocalanidae, Metridinidae, Paracalanidae, Ridgewayiidae, and Temoridae from 5 of 10 superfamilies of the Calanoida (for relationships of superfamilies see Park, 1986).

During appendage development, 2 kinds of variation in setation may be expressed: (1) there may be differences in patterns of change (i.e., the stage in development at which a setal element is gained or lost); and (2) there may be differences in numbers of setal elements, in their morphology, or in their position on a segment (e.g., different numbers may be present at the initial stage of development, or different numbers may be added at a specific stage in development). The analysis here includes only differences in pattern; information of the second kind, which forms the basis of more traditional stage-specific analyses, are not included (although differences in setal numbers are noted in descriptions of thoracopod development).

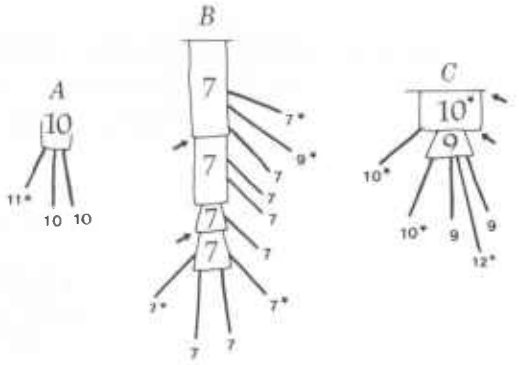

Fig. 1. Stylized representation of cyclopid thoracopods. A, P6; B, mxp; C, P5. Outline of segments in thin lines; setae are thick lines; numbers indicate at which stage a segment or a seta first appears (7 = copepodid I, 12 = copepodid VI); starred structures may not be present; arrows point to arthrodial membranes which may or may not be present.

Ancestral states were determined by the presence of: (1) identical states in species from presumed older families; (2) states which show diverse and frequent occurrence among the monophyletic Copepoda; and (3) states shared by serially homologous structures presumed to be determined by the same pleiotropic regulatory system. For species expressing sexual dimorphism or polymorphisms in appendage development, usually only one of these states is shared with other cyclopids. Here the attributes of sexual dimorphism and polymorphism are defined as character states and the shared individual states are used to determine ancestry and descent during character-state transformations.

Characters and Their States

Setal development of thoracopods is discussed as it relates to each character, beginning with P6, the simplest and least morphologically diverse appendage, and ending with P1–4, the most complex appendages. Initial setal numbers are noted first, followed by a discussion of differences in patterns of setal development.

P6 (Fig. 1A)

P6 initially is present at stage 10 as a simple bud with 2 setae; a seta may be added at stage 11. The only exceptions to this pattern among cyclopids are found in *Muscocyclops operculatus* and in the male of *Allocyclops*

silvaticus; no seta is added at stage 11 (Appendix 2, characters A and B). A similar pattern of no change in setal number is found in *Dioithona oculata* and among noncyclopoids in the female of *Herrmannella saxidomi*. The pattern of a setal addition at stage 11, found in *Notodelphys affinis, Scolecodes huntsmani, Limnoithona tetraspina, Dioithona oculata, Procyclopina feiticeira, Cyclopina caroli,* and among the noncyclopoids in *Midicola spinosus,* the male of *Herrmannella saxidomi, Scottomyzon gibberum, Longipedia americana,* and *Macrosetella gracilis,* is assumed to be ancestral for the cyclopids and assumed to be convergent with the noncyclopoids.

Mxp (Fig. 1B)

Mxp initially is present at stage 7 and consists of a syncoxa with one or two inner setae, a basis, which may be fused to the syncoxa with one or two inner setae, and a 2-segmented endopod (whose segments may be fused); the proximal segment bears onc seta and the distal segment may bear two, three, or four setae. Among cyclopids, the only change during development is the addition of a seta to the syncoxa at stage 9 (Appendix 2, character C), which is shared with *Procyclopina feiticeira, Cyclopina caroli*, and *Ridgewayia klausruetzleri* (Table 1). Failure of this addition in the cyclopids *Bryocyclops caroli, Graeteriella brehmi,* and *Speocyclops racovitzai* results in a pattern shared with the noncyclopoids *Hemicyclops ctenidis, Conchyliurus quintus, Leptinogaster major, Midicola spinosus,* and *Herrmannella saxidomi*. The addition of a seta at stage 9 is assumed to be ancestral, because it is shared with species of Cyclopinidae; the failure of that addition is derived.

P5 (Fig. 1C)

P5 is present at stage 9 as a simple bud with two presumptive exopodal setae distally. A basipod may be added at stage 10 which may articulatc with the exopod and may articulate with the somite; the basipod may bear a lateral seta. One exopodal seta each may be added at stages 10 and 12. The absence of an articulation between thc basipod and exopod (Appendix 2, character D) is shared by *Apocyclops dimorphus, A. panamensis, Allocyclops silvaticus, Bryocyclops caroli,* and *Speocyclops racovitzai*; such an articulation is found only in *Macrosetella gracilis.* The more widespread pattern among cyclopids, an exopod articulating with the basipod at stage 10, is also found in *Scolecodes huntsmani, Limnoithona tetraspina, Procyclopina feiticeira, Cyclopina caroli, Scottomyzon gibberum, Longipedia americana, Hemicyclops ctenidis, Conchyliurus quintus, Leptinogaster major,* and *Herrmannella saxidomi,* and is assumed to be ancestral. The delayed articulation of the basipod, formed at stage 12 (Appendix 2, character E), of *Muscocyclops operculatus* is considered to have been derived independently from the ancestral state.

An articulation between the basipod of P5 and its somite (Appendix 2, character F) is assumed to be ancestral. In most other cyclopids examined, an articulation with the somite is present, although it may become expressed at stage 11 in *Notodelphys affinis, Doropygus seclusus*, and *Dioithona oculata,* rather than at stage 10. Among noncyclopoids, the absencc of this articulation is found only in *Coullana canadensis* and *Macrosetella gracilis.*

Table 1. Changes in numbers of setae on the praecoxa of the maxilliped during copepodid stages 7–12. Character states for cyclopids in Arabic numerals. 0 = hypothesized ancestral state; a = setal addition; l = setal loss; f = female; m = male.

	Copepodid stages					
Taxon	7	8	9	10	11	12
0			a			
l						
Notodelphys				a	a	a
Doropygus				a	a	
Scolecodes				a	a	a
Dioithona				a		
Limnoithona				a		
Cyclopina			a			
Procyclopina			a			
Scottomyzon						
Longipedia		a	a			a
Coullana f		a			a	
Coullana m		a				
Macrosetella						
Hemicyclops						
Leptinogaster						
Conchyliurus						
Midicola						
Herrmannella						
Ridgewayia			a			
Pleuromamma		a	a			
Temora		a				
Acrocalanus f		a	a			
Acrocalanus m		a	a			l
Pseudocalanus f		a	a	a		
Pseudocalanus m		a	a	a		l

Failure to add a basipodal seta to P5 at stage 10 (Appendix 2, character G) is shared by *Eucyclops agilis, Paracyclops chiltoni, Tropocyclops prasinus,* and *T. jamaicensis,* and is not found among the other copepods studied. The more widespread cyclopid condition, the addition of a seta to the basis at stage 10, is shared with *Notodelphys affinis, Scolecodes huntsmani, Doropygus seclusus, Limnoithona tetraspina, Dioithona oculata, Procyclopina feiticeira, Cyclopina caroli, Scottomyzon gibberum, Longipedia americana, Macrosetella gracilis, Hemicyclops ctenidis, Conchyliurus quintus, Leptinogaster major, Midicola spinosus, Herrmannella saxidomi, Ridgewayia klausruetzleri, Pleuromamma xiphias,* and *Temora longicornis,* and is assumed to be ancestral.

The addition of an exopodal seta at stage 10 is shared by *Macrocyclops albidus, Eucyclops agilis, Paracyclops chiltoni, Tropocyclops prasinus,* and *Diacyclops dispinosus.* Among other cyclopoids, it is found in *Limnoithona tetraspina, Procyclopina feiticeira* female, *Cyclopina caroli* female, and in *Scottomyzon gibberum, Macrosetella gracilis* male, *Conchyliurus quintus, Leptinogaster major,* and *Midicola spinosus* (Table 2) among noncyclopoids. This state is assumed to be ancestral. The addition of an exopodal seta at stage 12 of males of *Neocyclops vicinus* and *Halicyclops aberrans* is a transformation of this ancestral state (Appendix 2, character H). The failure to add an exopodal seta at stage 10 (Appendix 2, character I) is shared by most cyclopids, and is also found in *Dioithona oculata, Coullana canadensis, Herrmannella saxidomi,* and *Pseudocalanus elongatus.* It is considered an independent, derived transformation of the ancestral state.

Table 2. Changes in numbers of setae on the distal segment of the exopod of leg 5 during copepodid stages 7–12. ml = male left side, mr = male right side. Remaining legend as for Table 1.

	Copepodid stages					
Taxon	7	8	9	10	11	12
0				a		
1f				a		
1m				a		a
2						
Notodelphys						
Doropygus					a	
Scolecodes					a	
Dioithona						
Limnoithona				a		
Cyclopina f				a		
Cyclopina m				a	a	
Procyclopina f				a		
Procyclopina m				a	a	a
Scottomyzon				a		
Longipedia				a	a	
Coullana						
Macrosetella f				a	a	
Macrosetella m				a		
Hemicyclops				a	a	
Leptinogaster				a		
Conchyliurus				a		
Midicola				a		
Herrmannella						
Ridgewayia f				a	a	l
Ridgewayia m				a		l
Pleuromamma f						
Pleuromamma m				a	a	l
Temora f						
Temora ml				a	a	
Temora mr				a	a	l
Acrocalanus f						
Acrocalanus ml					a	l
Acrocalanus mr						
Pseudocalanus f						
Pseudocalanus m						

P1–4

The complex development of the swimming legs is exemplified by P3 of the oithonid *Dioithona oculata* (Fig. 2A). P3 begins as a bilobed bud with 3 presumptive exopodal and two presumptive endopodal setae. During the following stage, it is transformed into a swimming leg, a biramal limb whose segments are flattened anterior-posteriorly, and which is united to its contralateral twin by an intercoxal sclerite. Segments are added proximally from the distal segment and, in general, setae are added proximally to the distal segment of the limb. In subsequent stages of development, these patterns of addition in different limbs depend upon the position of the limb along the anterior-posterior axis of the body (Ferrari, 1993).

Figure 3A shows information from the previous figure imposed upon the adult structure of the appendage, and new data from the development of leg 3 of *Thermocyclops decipiens* (Fig. 3B). With the exception of the medial seta on the proximal exopodal segment, setae of the proximal and middle segments of exopod and endopod are relatively younger than the segments upon which they are found, indicating that they initially are formed on the distal segment of their respective rami. These observations suggest that the complicated setal additions to these appendages can be reduced to a few simple patterns: (1) addition

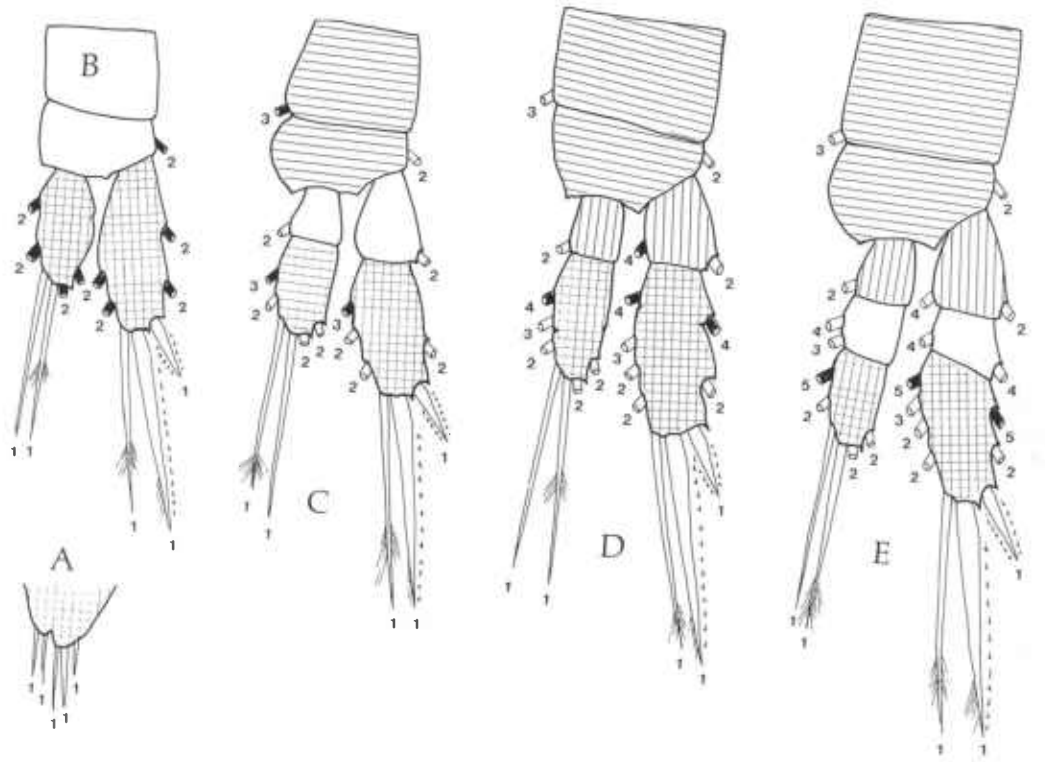

Fig. 2. Development of swimming leg 3 of *Dioithona oculata* (modified from Ferrari and Ambler, 1992). A, primary bud on copepodid I with 3 setae on the outer lobe (presumptive exopod) and 2 setae on the inner lobe (presumptive endopod); B–E, transformed legs of copepodids II–V, respectively. Oldest segment cross-hatched, youngest segment clear, oldest intermediate segment horizontally hatched, youngest intermediate segment vertically hatched. Oldest setae from copepodid I (numbered 1) are drawn completely; all others are cropped and new setae are black. New setae added to copepodids II–V are numbered 2–5, respectively.

or not of a medial seta to the basipod of P1 (Appendix 2, character J); (2) addition or not of a medial seta to the proximal exopodal segment (Appendix 2, characters K and L); (3) addition or not of the medial seta to the coxa, and the lateral seta to the basis (these do not vary among cyclopids); and (4) changes in numbers of setae on the distal segment of the exopod or endopod, which explain most of the variation in setal development of the appendages. Setal presence for characters J, K, and L is assumed to be ancestral, based on their presence in all other cyclopoid species studied.

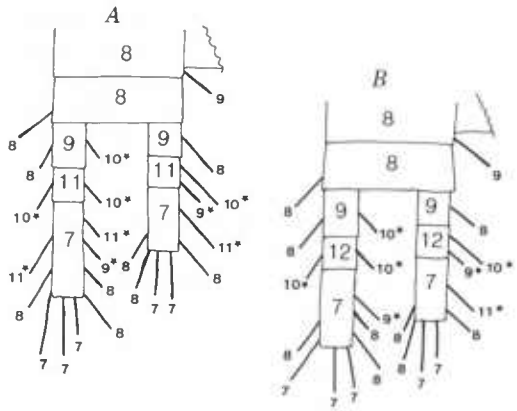

Fig. 3. Stylized representation of swimming leg 3. (A) *Dioithona oculata*; (B) *Thermocyclops decipiens*. Legend as for Fig. 1.

Changes in setal numbers on the distal exopodal or endopodal segments are compared to noncyclopids in Tables 3–10. For exopods of P1, P3, and P4, and the endopod of P2 (Tables 3, 7, 9, and 6), the ancestral cyclopid condition appears unambiguous, because only one state is shared with other noncyclopid cyclopoids, while the remaining states are unique to cyclopids. For endopods of P3 and P4 (Tables 8, 10), two patterns of setal changes during development are shared with

Table 3. Changes in numbers of setae on the distal segment of the exopod of swimming leg 1 during copepodid stages 7–12. p = polymorphic state; remaining legend as for Table 1.

	Copepodid stages					
Taxon	7	8	9	10	11	12
0	a					
1	a					1
2p	a					1
2p	a				1	
3	a				1	
4	a				a	a
Notodelphys	a					
Doropygus	a		1		1	
Scolecodes	a					
Dioithona	a					
Limnoithona	a					
Cyclopina	a					
Procyclopina	a					
Scottomyzon	a				1	
Longipedia	a				1	
Coullana f	a					1
Coullana m	a				1	
Macrosetella	a				1	
Hemicyclops	a					
Leptinogaster	a					
Conchyliurus	a					
Midicola	a					
Herrmannella	a					
Ridgewayia	a				1	
Pleuromamma	a				1	
Temora	a				1	
Acrocalanus	a	1				
Pseudocalanus	a				1	

Table 4. Changes in numbers of setae on the distal segment of the endopod of swimming leg 1 during copepodid stages 7–12. Legend as for Table 3.

	Copepodid stages					
Taxon	7	8	9	10	11	12
0	a		a		1	
1	a		a			1
2p	a		a			1
2p	a		a		1	
3	a	1	a		1	
4	a	1	a			1
5	a			a	1	
6	a	1				
Notodelphys	a	1		a	1	
Doropygus	a	1		a	1	
Scolecodes	a		1	a	1	
Dioithona	a	1	a		1	
Limnoithona	a	1	a		1	
Cyclopina	a	1	a		1	
Procyclopina	a	1	a		1	
Scottomyzon	a		a	1		
Longipedia	a	1	a			
Coullana	a					
Macrosetella	a	1	a			
Hemicyclops	a	1	a		1	
Leptinogaster	a	1	a		1	
Conchyliurus	a	1	a		1	
Midicola	a	1	a		1	
Herrmannella	a	1	a		1	
Ridgewayia	a		a		1	
Pleuromamma	a				1	
Temora	a		1			
Acrocalanus	a	1				
Pseudocalanus	a					

noncyclopids, but, in both of these cases, one of those patterns (number 4 of P3 endopod, number 6 of P4 endopod) results in a 2-segmented ramus in the cyclopids, while in the other copepods the pattern results in a 3-segmented ramus. These shared patterns are convergences and are considered unique to cyclopids. For the exopod of P2, comparisons are equivocal; both state 0 and state 1 (Table 5) are found among noncyclopids and both are associated with 3-segmented rami. However, state 0 is the only one shared with other cyclopoids and therefore is assumed to be ancestral to cyclopids.

Determination of the ancestral cyclopid state for the endopod of P1 is more problematical (Table 4). Pattern number 3 with a setal loss at stage 8 is the only pattern shared with other cyclopoids whose development has been studied here. This pattern results in an adult endopod with only one seta on the middle segment of the endopod. In most cyclopids, the second seta of that segment initially appears at stage 8 on the distal segment, and is later allocated to the middle segment when the arthrodial membrane separating the middle and distal segment forms during the molt to stage 11 (Ferrari and Benforado, in press). However, there are cyclopoids from the presumed oldest family, the Cyclopinidae, with two setae on the middle segment of the adult ramus (Huys and Boxshall, 1990). The hypothesis of Huys and Boxshall (1991) that the ancestral cyclopoid had two setae on that middle segment is accepted and here assumed for the ancestral cyclopid.

The interpretation of the complex changes from the ancestral states of both rami of P1–4 during development is best introduced by the examination of segmentation patterns of these appendages (Table 11). In *Macrocyclops albidus,* the segmentation patterns of P1 and P2 are identical; each begins as a bilobed bud at stage 6, the last naupliar stage. P1 and P2 are transformed appendages with 1-segmented rami at stage 7; these rami gain a second seg-

Table 5. Changes in numbers of setae on the distal segment of the exopod of swimming leg 2 during copepodid stages 7–12. Legend as for Table 3.

	Copepodid stages					
Taxon	7	8	9	10	11	12
0	a		a			
1	a		a		1	
2p	a		a		1	
2p	a		a			1
3	a		a		a	1
4	a					
Notodelphys	a		a			
Doropygus	a	a	a			
Scolecodes	a			a	1	
Dioithona	a		a			
Limnoithona	a		a			
Cyclopina	a		a			
Procyclopina	a		a			
Scottamyzon	a		a		1	
Longipedia	a	1	a		1	
Coullana f	a	1	a	a		1
Coullana m	a	1	a	a	1	
Macrosetella	a		a		1	
Hemicyclops	a		a			
Leptinogaster	a		a			
Conchyliurus	a		a			
Midicola	a		a			
Herrmannella	a		a			
Ridgewayia	a		a		1	
Pleuromamma	a		a			
Temora	a		a			
Acrocalanus	a		a		1	
Pseudocalanus	a		a		1	

Table 6. Changes in numbers of setae on the distal segment of the endopod of swimming leg 2 during copepodid stages 7–12. Legend as for Table 3.

	Copepodid stages					
Taxon	7	8	9	10	11	12
0	a		a	a	1	
1	a		a	a		1
2p	a		a	a		1
2p	a		a	a	1	
3	a		a			
4	a	1	a			
5	a	1				
6	a					
Notodelphys	a		a	a	1	
Doropygus	a		a	a	1	
Scolecodes	a	1	1	a		
Dioithona	a		a	a	1	
Limnoithona	a		a	a	1	
Cyclopina	a		a	a	1	
Procyclopina	a	1	a	a	1	
Scottomyzon	a		a	a	1	
Longipedia	a		a	a	1	
Coullana	a	1		a		
Macrosetella	a			a		1
Hemicyclops	a		a	a	1	
Leptinogaster	a		a	a	1	
Conchyliurus	a		a	a	1	
Midicola	a		a	a	1	
Herrmannella	a		a	a	1	
Ridgewayia	a	a	a			
Pleuromamma	a	a	a	a	1	
Temora	a	a	a	a	1	
Acrocalanus	a		a	a	1	
Pseudocalanus	a		1			

Table 7. Changes in numbers of setae on the distal segment of the exopod of swimming leg 3 during copepodid stages 7–12. Legend as for Table 3.

	Copepodid stages					
Taxon	7	8	9	10	11	12
0		a		a		
1		a		a		1
2p		a		a		1
2p		a		a	1	
3		a		a	a	1
4		a		a	1	
5		a				
Notodelphys		a		a		
Doropygus		a		a		
Scalecodes		a	1	a	1	
Dioithona		a		a		
Limnoithona		a		a		
Cyclapina		a		a		
Pracyclopina		a		a		
Scottomyzon		a		a	1	
Longipedia		a	1	a	1	
Coullana f		a	1	a		1
Coullana m		a	1	a	1	
Macrosetella		a	1	a	1	
Hemicyclops		a		a		
Leptinogaster		a		a		
Conchyliurus		a		a		
Midicola		a		a		
Herrmannella		a		a		
Ridgewayia		a		a		
Pleuromamma		a		a		
Temora		a	a	a	1	
Acrocalanus		a		a	1	
Pseudocalanus		a	1	a	1	

Table 8. Changes in numbers of setae on the distal segment of the endopod of swimming leg 3 during copepodid stages 7–12. Legend as for Table 3.

	Copepodid stages					
Taxon	7	8	9	10	11	12
0		a		a	1	
1		a		a	a	1
2p		a		a	a	1
2p		a		a	1	
3		a		a		
4		a	1	a		
5		a	1			
6f		a	1			
6m		a	1		1	
Notodelphys		a		a	1	
Dorapygus		a		a	1	
Scolecodes		a	1	a		
Dioithona		a		a	1	
Limnoithona		a		a	1	
Cyclopina		a		a	1	
Procyclopina		a	1	a	1	
Scottamyzon		a	1	a	1	
Longipedia		a	1	a		
Caullana		a	a	a		
Macrosetella		a		a	1	
Hemicyclops		a		a	1	
Leptinogaster		a		a	1	
Conchyliurus		a		a	1	
Midicola		a		a	1	
Herrmannella		a		a	1	
Ridgewayia		a	a	a		
Pleuromamma		a	a	a	1	
Temora		a	a	a	1	
Acrocalanus		a	a	a	1	
Pseudocalanus		a		a	1	

Table 9. Changes in numbers of setae on the distal segment of the exopod of swimming leg 4 during copepodid stages 7–12. Legend as for Table 3.

Taxon	Copepodid stages					
	7	8	9	10	11	12
0			a	a	l	
l			a	a		l
2p			a	a		l
2p			a	a	l	
3			a	a		
4f			a	a		
4m			a	a	l	
5			a			
6			a	l		
Notodelphys			a	a	l	
Doropygus			a	a	l	
Scolecodes				a	l	
Dioithona			a	a	l	
Limnoithona			a	a		
Cyclopina			a	a	l	
Procyclopina			a	a	l	
Scottomyzon			a	a	l	
Longipedia			a	a	l	
Coullana f			a			l
Coullana m			a		l	
Macrosetella			a	a	l	
Hemicyclops			a	a	l	
Leptinogaster			a	a		
Conchylirus			a	a		
Midicola			a	a		
Herrmannella			a	a	l	
Ridgewayia			a	a		
Pleuromamma			a	a		
Temora			a	a	l	
Acrocalanus			a	a	l	
Pseudocalanus			a	a	l	

Table 10. Changes in numbers of setae on the distal segment of the endopod of swimming leg 4 during copepodid stages 7–12. Legend as for Table 3.

Taxon	Copepodid stages					
	7	8	9	10	11	12
0			a		l	
l			a	a		l
2			a		a	l
3p			a		l	
3p			a		a	l
4			a			
5f			a			
5m			a		l	
6f			a			
6m			a	l		
7			a	l		
Notodelphys			a		l	a
Doropygus			a	a	l	a
Scolecodes				a	l	a
Dioithona			a		l	
Limnoithona			a		l	
Cyclopina			a		l	
Procyclopina			a		l	
Scottomyzon			a		l	
Longipedia			a	a	l	
Coullana			a			
Macrosetella			a	a	l	
Hemicyclops			a		l	
Leptinogaster			a		l	
Conchylirus			a		l	
Midicola			a		l	
Herrmannella			a		l	
Ridgewayia			a	l		
Pleuromamma			a	a	l	
Temora			a	a	a	l
Acrocalanus			a	l		
Pseudocalanus			a		l	

ment at stage 8, after which there is no change until stage 11. P3 develops similarly, but with one stage out of register with P1 and P2. It is a bilobed bud at stage 7, is transformed at stage 8, and adds its second segment at stage 9. P4 develops one stage out of register with P3; it is a bud at stage 8, is transformed at stage 9, and adds a second segment at stage 10. P1–4 add their third ramal segments simultaneously during the molt to stage 11. In general, both rami of each leg undergo two serial additions in stages immediately following the appearance of the bilobed leg bud; a simultaneous addition of the last segment of all rami occurs at stage 11. This pattern is the most widespread pattern found among copepods (represented in 50 genera and 22 families among six of 10 orders) including *Notodelphys affinis, Dioithona oculata, Limnoithona tetraspina, Procyclopina feiticeira, Cyclopina caroli, Scottomyzon gibberum, Longipedia americana, Hemicyclops ctenidis, Conchylirus quintus, Leptinogaster major, Midicola spinosus, Herrmannella saxidomi,* and *Ridgewayia klausmetzleri* among species studied here. For this reason, it is presumed to be the ancestral segmentation pattern for P1–4 in copepods (Ferrari, 1988).

Segmentation of the individual rami of P1–4 together for *Macrocyclops albidus* appears to be a coordinated process that results in an exopod and endopod of the same leg with equal numbers of segments throughout development and in 3-segmented rami for all adult legs. It is assumed here that this coordinated process is pleiotropically controlled by a single regulatory process, probably associated with serial somite formation during development. Segmentation of P1–4 of *Mesocyclops edax* (Table 11) is similar to that of *Macrocyclops albidus,* except that the simultaneous addition, during which the third segment is added to all rami, is delayed until the molt to stage 12. Segmentation pattern for P1–4 of *Apocyclops dimorphus* (Table 11) also begins like that of *Macrocyclops albidus,* but is truncated after the second serial addi-

Table 11. Addition of segments to swimming legs (P1–4) from last nauplius to adult showing the ancestral (*Macrocyclops albidus*), delayed (*Mesocyclops edax*), and truncated (*Apocyclops dimorphus*) pleiotropic patterns. b = leg bud; exopodal + endopodal segments.

Stage	P1–4, exopodal + endopodal segments			
	P1	P2	P3	P4
Macrocyclops albidus				
6	b	b		
7	1+1	1+1	b	
8	2+2	2+2	1+1	b
9	2+2	2+2	2+2	1+1
10	2+2	2+2	2+2	2+2
11	3+3	3+3	3+3	3+3
12	3+3	3+3	3+3	3+3
Mesocyclops edax				
6	b	b		
7	1+1	1+1	b	
8	2+2	2+2	1+1	b
9	2+2	2+2	2+2	1+1
10	2+2	2+2	2+2	2+2
11	2+2	2+2	2+2	2+2
12	3+3	3+3	3+3	3+3
Apocyclops dimorphus				
6	b	b		
7	1+1	1+1	b	
8	2+2	2+2	1+1	b
9	2+2	2+2	2+2	1+1
10	2+2	2+2	2+2	2+2
11	2+2	2+2	2+2	2+2
12	2+2	2+2	2+2	2+2

Table 12. Addition of segments to swimming legs (P1–4) from last nauplius to adult showing transformations of individual rami from the delayed (*Diacyclops dispinosus*) and truncated (*Graeteriella brehmi* male and *Bryocyclops caroli* female) pleiotropic patterns. Legend as for Table 11.

Stage	P1–4, exopodal + endopodal segments			
	P1	P2	P3	P4
Diacyclops dispinosus				
6	b	b		
7	1+1	1+1	b	
8	2+2	2+2	1+1	b
9	2+2	2+2	2+2	1+1
10	2+2	2+2	2+2	2+2
11	2+2	2+2	2+2	2+3
12	3+3	3+3	3+3	3+3
Graeteriella brehmi male				
6	b	b		
7	1+1	1+1	b	
8	2+2	2+2	1+1	b
9	2+2	2+2	2+2	1+1
10	2+2	2+2	2+2	2+2
11	2+2	2+2	2+2	3+3
12	2+2	2+2	2+2	3+3
Bryocyclops caroli female				
6	b	b		
7	1+1	1+1	b	
8	2+2	2+2	1+1	b
9	2+2	2+2	2+2	1+1
10	2+2	2+2	2+2	2+1
11	2+2	2+2	2+2	2+1
12	2+2	2+2	2+2	2+1

tion, i.e., after stage 8 for P1 and P2, after stage 9 for P3, and after stage 10 for P4. These latter two coordinated processes, delayed and truncated, also are assumed to be pleiotropically controlled. They also are assumed here to have evolved independently from the ancestral pleiotropic process, although an alternative would derive the truncated process from the delayed process.

Segmentation of P1–4 of *Diacyclops dispinosus* (Table 12) is similar to that of *Mesocyclops edax,* except that the endopod of P4 adds its third segment at stage 11, not at stage 12. It is assumed here that in addition to a delayed pleiotropic regulatory process, which affects the morphology of all rami together, there is a second regulatory process, acting after the pleiotropic one, which has affected only the morphology of the endopod of P4. The same set of processes may explain the segmentation pattern for P1–4 of both the male of *Graeteriella brehmi* and the female of *Bryocyclops caroli* (Table 12). The patterns are similar to that of *Apocyclops dimorphus,* except that the exopod and endopod of P4 each of *Graeteriella brehmi* add a third segment at stage 11, while the endopod of P4 of *Bryocyclops caroli* female fails to add a second segment at stage 10. In addition to the truncated pleiotropic process which affects the morphology of all rami together, a second regulatory process has affected the architecture of the exopod and, independently, the endopod of P4.

In general, developmental patterns of segmentation of P1–4 among copepods are assumed to result from two different regulatory processes which are expressed morphologically as two different characters. The early pleiotropic process determines the morphology of all eight rami together and is the first character. That character has three states in the Cyclopidae, ancestral and two derived, delayed and truncated, which have evolved independently from the ancestral state. In addition, there is a second set of eight regulatory processes which may act after the pleiotropic one; each of the eight processes determines

the morphology, and thus the eharaeter state, of only one ramus. The aneestral states of the eight eharacters are, by default, the morphology whieh results from the earlier pleiotropie regulatory proeess.

The aneestral pattern of swimming-leg segmentation is eorrelated with a pattern of setation for the distal segments of the rami, whieh ean be summarized as no ehange in setal numbers to the distal exopod of P1 after stage 8, of P2 after stage 9, of P3 after stage 10, and of P4 after stage 11, and setal loss to all distal endopodal segments at stage 11. The delayed pattern of swimming-leg segmentation results in a setation pattern whose apomorphy is setal losses to all distal exopodal and endopodal segments at stage 12 (Appendix 2, eharaeter M). The truneated pattern is assumed to have evolved independently of the delayed pattern and follows the aneestral pattern of setation early in development; its apomorphy is no ehange in setal numbers to the distal exopod or endopod of P1 after stage 8, of P2 after stage 9, of P3 after stage 10, and of P4 after stage 10 (Appendix 2, eharaeter N).

Individual morphologies whieh are derived from the aneestral pleiotropie pattern are found on the distal segment of the exopod and endopod of P1, the exopod of P3, and the endopod of P4 (Appendix 2, characters O–T). The distal segment of the exopod of P1–3 and of the endopod of P4 may express individual morphologies derived from the delayed pleiotropic pattern (Appendix 2, eharacters U–X). The distal segment of the exopod and of the endopod of P2–4 may express individual morphologies derived from the truncated pleiotropic pattern (Appendix 2, characters Hh–Nn). For the multistate characters (Appendix 2, Ii, Kk, Mm, and Nn), the pleiotropie state usually is transformed first into a pattern of no change in setal numbers, and later into a pattern of setal loss, rather than gain, during earlier eopepodid stages.

Sexual dimorphism in the setal developmental patterns of P1–4 is expressed in three speeies. For males of *Bryocyclops caroli,* the setation pattern of the endopod of P3 is unique among eyelopids, and the pattern for the endopod of P4 is shared with *Speocyclops racovitzai.* For males of *Graeteriella brehmi,* setation patterns of the distal exopodal and endopodal segments of P4 appear identical to the ancestral eyelopid eondition (Tables 9, 11), with which it also shares 3-segmented rami. However, the immediate aneestor of *Graeteriella brehmi* is hypothesized to have had a pleiotropieally truncated development. Therefore, the similarity of setal patterns results from convergenee. These two male morphologies are derived and are unique to cyclopids.

Polymorphisms are expressed in P1–4 of *Acanthocyclops robustus* and *A. carolinianus.* These polymorphisms are first apparent at stage 11, when individual rami may be either 2-segmented or 3-segmented. These two segmentation patterns result in three sets of setation patterns. One set, assoeiated with rami whieh are 2-segmented at stage 11, is present on exopods and endopods of P1–4, and is identieal to the delayed pleiotropic pattern. A seeond set, assoeiated with 3-segmented rami at stage 11, is present on the exopod of P4 and the endopod of P1–4; they appear to be identical to the aneestral pleiotropie pattern. A third set, also assoeiated with 3-segmented rami at stage 11, is present on the exopod of P1–3. These patterns are unique to eyclopids. The aneestor of *Acanthocyclops* is here assumed to have expressed the delayed pleiotropic pattern. The remaining eharaeter states eomprising the polymorphisms are derived from transformations of individual rami, some by apparent convergenee to aneestral patterns.

In addition, at stage 12 the distal exopodal segments of *Acanthocyclops* may exhibit one of two different setal numbers, depending on whether the proximal, lateral seta develops, and results in a well-known polymorphism (Ayeoek, 1942; H. C. Yeatman, personal eommunieation). However, beeause only the number of setae on the distal segment at stage 12 is affeeted and not the stage at which the change occurs, this polymorphism is not considered in the analysis.

Analysis

A matrix of the above eharaeter states is found in Table 13. There are five pairs of derived states of homologous struetures whieh are presumed to have been independently transformed (A and B, D and E, H and I, Hh and Ii, and Kk and Ll). Therefore, a state cannot be assigned to a group of speeies for one member of the pair. A similar outeome affeets the independently transformed pair of pleiotropie patterns, delayed and truneated (M and

Table 13. Matrix of character states. 2 beside genus name indicates that both species of the genus are identical; MEGA-complex is *Diacyclops navus, D. thomasi, Megacyclops latipes, Mesocyclops edax, M. longisetus,* and *Thermocyclops decipiens*; all other species names listed in Appendix 1; na = not applicable.

Name	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
Macrocyclops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Neocyclops	0	0	0	0	0	0	0	1	na	0	0	0	0	0	0	0	0	1	0	0
Eucyclops	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tropocyclops p	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Tropocyclops j	0	0	0	0	0	1	1	na	1	1	1	1	0	0	0	0	0	0	1	0
Paracyclops	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Halicyclops	0	0	0	0	0	0	0	1	na	0	0	0	0	0	1	1	1	0	1	1
MEGA complex	0	0	0	0	0	0	0	na	1	0	0	0	1	na	na	na	na	na	na	na
Mesocyclops r	0	0	0	0	0	0	0	na	1	1	0	0	1	na	na	na	na	na	na	na
Diacyclops d	0	0	0	0	0	0	0	0	1	0	0	0	1	na	na	na	na	na	na	na
Acanthocyclops 2	0	0	0	0	0	0	0	na	1	0	0	0	1	na	na	na	na	na	na	na
Microcyclops	0	0	0	0	0	1	0	na	1	0	0	0	na	1	na	na	na	na	na	na
Apocyclops 2	0	0	0	1	na	1	0	na	1	0	0	0	na	1	na	na	na	na	na	na
Allocyclops	1	na	0	1	na	1	0	na	1	0	0	0	na	1	na	na	na	na	na	na
Graeteriella	0	0	1	0	0	1	0	na	1	0	0	0	na	1	na	na	na	na	na	na
Bryocyclops	0	0	1	1	na	1	0	na	1	0	0	0	na	1	na	na	na	na	na	na
Speocyclops	0	0	1	1	na	1	0	na	1	0	0	0	na	1	na	na	na	na	na	na
Muscocyclops	na	1	1	na	1	1	0	na	1	1	1	1	na	1	na	na	na	na	na	na

	U	V	W	X	Y	Z	Aa	Bb	Cc	Dd	Ee	Ff	Gg	Hh	Ii	Jj	Kk	Ll	Mm	Nn
Macrocyclops	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Neocyclops	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Eucyclops	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Tropocyclops p	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Tropocyclops j	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Paracyclops	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
Halicyclops	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na	na
MEGA complex	0	0	0	0	0	0	0	0	0	0	0	0	na	na	na	na	na	na	na	na
Mesocyclops r	0	0	0	0	0	0	0	0	0	0	0	0	na	na	na	na	na	na	na	na
Diacyclops d	1	1	1	1	0	0	0	0	0	0	0	0	na	na	na	na	na	na	na	na
Acanthocyclops 2	0	0	0	0	1	1	1	1	1	1	1	1	na	na	na	na	na	na	na	na
Microcyclops	na	na	na	na	na	na	na	na	na	na	na	na	0	0	0	0	0	0	0	0
Apocyclops 2	na	na	na	na	na	na	na	na	na	na	na	na	0	0	0	0	0	0	0	0
Allocyclops	na	na	na	na	na	na	na	na	na	na	na	na	0	1	na	0	0	0	0	0
Graeteriella	na	na	na	na	na	na	na	na	na	na	na	na	0	na	1	0	0	0	1	1
Bryocyclops	na	na	na	na	na	na	na	na	na	na	na	na	0	na	2	0	na	1	2	2
Speocyclops	na	na	na	na	na	na	na	na	na	na	na	na	0	na	2	0	1	na	3	3
Muscocyclops	na	na	na	na	na	na	na	na	na	na	na	na	1	na	2	1	2	na	3	3

N), as well as the individual rami derived from them.

The following phylogenetic analysis (Fig. 4) assumes: (1) that the initial events which determined the phylogeny of the Cyclopidae were transformations of the distal exopodal and endopodal segments of P1–4 from the morphology of the ancestral pleiotropic process to the morphology of the delayed or, independently, to the truncated process; and (2) that subsequent transformations of the individual rami of P1–4 predict cyclopid evolution more accurately than transformations of other thoracic appendages. This results in a tree with 15 convergences (including a reversal) of which five (including the reversal) involve characters states associated with P5.

Macrocyclops albidus, Eucyclops agilis, and *Tropocyclops prasinus* retain the morphology for the distal exopodal and endopodal segments of P1–4 of the ancestral pleiotropic process. The latter two species cannot be separated with the characters used here, but share with *Tropocyclops jamaicensis* and *Paracyclops chiltoni* the absence of an articulation between the basipod and somite of P5 and the absence of the basipodal setae on P5. *Tropocyclops jamaicensis* and *P. chiltoni* have evolved independently, the former by transformations of P1, P4, and P5, and the latter by one transformation of P1, a character not homologous to the transformation of *T. jamaicensis. Neocyclops vicinus* and *Halicyclops aberrans* share a sexual di-

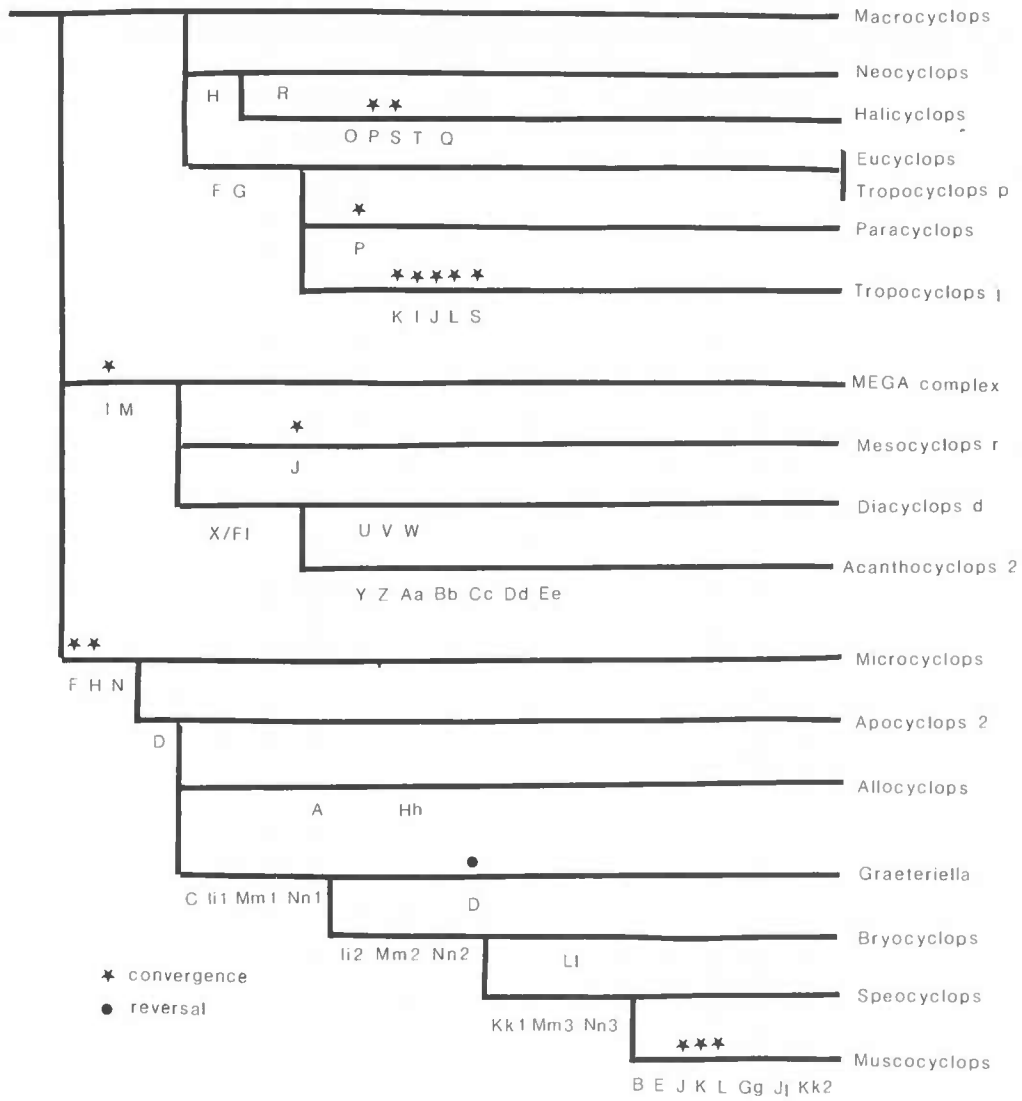

Fig. 4. Phylogenetic relationships for taxa and characters listed in Table 15.

morphism in a setal addition to the exopod of P5. A delayed setal addition to the distal endopodal segment of P1 is unique to *N. vicinus; H. aberrans* expresses derived character states for the distal endopodal segments of P1 and P4, and the distal exopodal segments of P3.

Among cyclopids in which the delayed pleiotropic process affects the morphology of the distal exopodal and endopodal segments of P1–4, there is an unresolved polychotomy of six species, *Diacyclops navus, D. thomasi, Megacyclops latipes, Mesocyclops edax, M. longisetus*, and *Thermocyclops decipiens* (the MEGA complex), from which *Mesocyclops ruttneri* is separated by a single transformation of P1. *Diacyclops dispinosus*, with the unresolved *Acanthocyclops carolinianus* and *A. robustus,* is also derived from the ancestor with the delayed pleiotropic process. One of the two derived polymorphic states of the endopod of P4 for *Acanthocyclops robustus* and *A. carolinianus* (setal loss at stage 11) is identical to the monomorphic derived state of the endopod of P4 for *Diacyclops dispinosus.* The characters have been listed separately in Appendix 2 and Table 14, because one is polymorphic and the other monomorphic. However, the identical morphology is assumed to indicate a common ancestor for the

three species. *Diacyclops dispiuosus* exhibits transformations of the distal exopodal segments of P1–3 and P5, and the distal endopodal segment of P4. *Acanthocyclops caroliniauus* and *A. robustus* exhibit polymorphisms in the distal exopodal and endopodal segments of P1–4 which resulted from eight independent transformations.

The remaining cyclopids share an ancestor in which the truncated pleiotropic process affected the morphology of the distal exopodal and endopodal segments of P1–4. The unresolved *Apocyclops dimorphus* and *A. panamensis* are separated from *Microcyclops rubellus* by a single change of P5. *Allocyclops silvaticus* is derived independently from *Graeteriella brehmi, Muscocyclops operculatus, Bryocyclops caroli,* and *Speocyclops racovitzai.* The latter four species can be separated by transformations of the maxilliped, of the distal endopodal segments of P2–4, of the distal exopodal segments of P4 and of P5.

Discussion

The phylogenetic hypothesis derived from the analysis of 40 characters with 46 derived states of setal developmental patterns results in 12 character-state convergences, of which one is a reversal. Twenty-seven states result in 33 autapomorphies which may prove to be synapomorphies when more information about development of cyclopids becomes known. For example, a recent study of development of *Paracyclops fimbriatus* by Karaytug and Boxshall (1996) indicates that this species shares with *P. chiltoni* the setal developmental pattern for the distal endopodal segment of P1 resulting in a single seta on the middle segment of that ramus.

Developmental patterns, however, fail to provide a separate identity for two congeneric pairs, *Acanthocyclops caroliniauus* and *A. robustus,* and *Apocyclops dimorphus* and *A. panamensis,* or for the species groups *Eucyclops agilis* and *Tropocyclops prasinus,* and the MEGA complex (*Diacyclops navus, D. thomasi, Megacyclops latipes, Mesocyclops edax, M. longisetus,* and *Thermocyclops decipiens*). Developmental patterns also fail to resolve several relationships (Fig. 4). Some of these problems subsequently may be solved by adding developmental patterns of the cephalic appendages, or by adding the initial morphology of transformed appendages and differentiating setae by morphology and position on an appendage segment.

In the case of assumed pleiotropic effects to P1–4, the choice here has been to weight regulatory processes and not morphology. In the obverse case, where morphology presumably is affected by more than one regulatory process, the choice here has been to allow the early pleiotropic process to determine the ancestral character state of any later individual process. In cases such as these, establishing an ancestral condition involves surveying on the same animal the serially homologous appendages presumably affected by the early pleiotropic process rather than surveying the same appendage among related copepods.

Two kinds of reversals in ramal segmentation are masked by the treatment of dimorphisms. The 3-segmented exopod and endopod of P4 of *Graeteriella brehmi* males (2-segmented in females) appear to be reversals to the ancestral segment number for cyclopids. However, the setation pattern does not match the one resulting from the ancestral pleiotropic process. There is one seta fewer on all exopodal segments and on the middle endopodal segment. The immediate ancestor of *G. brehmi* is presumed to have had 2-segmented rami, whose setal morphology resulted from the truncated pleiotropic process, and the 3-segmented rami of P4 of the males is unique to the lineage.

The endopod of P4 of *Diacyclops dispiuosus* is 3-segmented at stage 11 and its setation pattern is identical to the homologous ramus of the ancestral pleiotropic pattern. This is the case in the endopods of P1–4 and the exopod of P4 of one morph of *Acanthocyclops robustus* and *A. caroliniauus,* which are also 3-segmented at stage 11. However, the remaining seven rami of *D. dispiuosus* and all rami of one morph of *A. robustus* and *A. caroliniauus* express setal morphology resulting from the delayed pleiotropic process, suggesting that the ancestor of this group had 2-segmented rami at stage 11. These examples of 3-segmented rami at stage 11 are true character state reversals; they do not simply represent the retention of the ancestral condition.

Setation patterns of P1–4 for all cyclopids examined here with 2-segmented rami appear to be derived from the ancestral pleiotropic process, which was truncated after the second

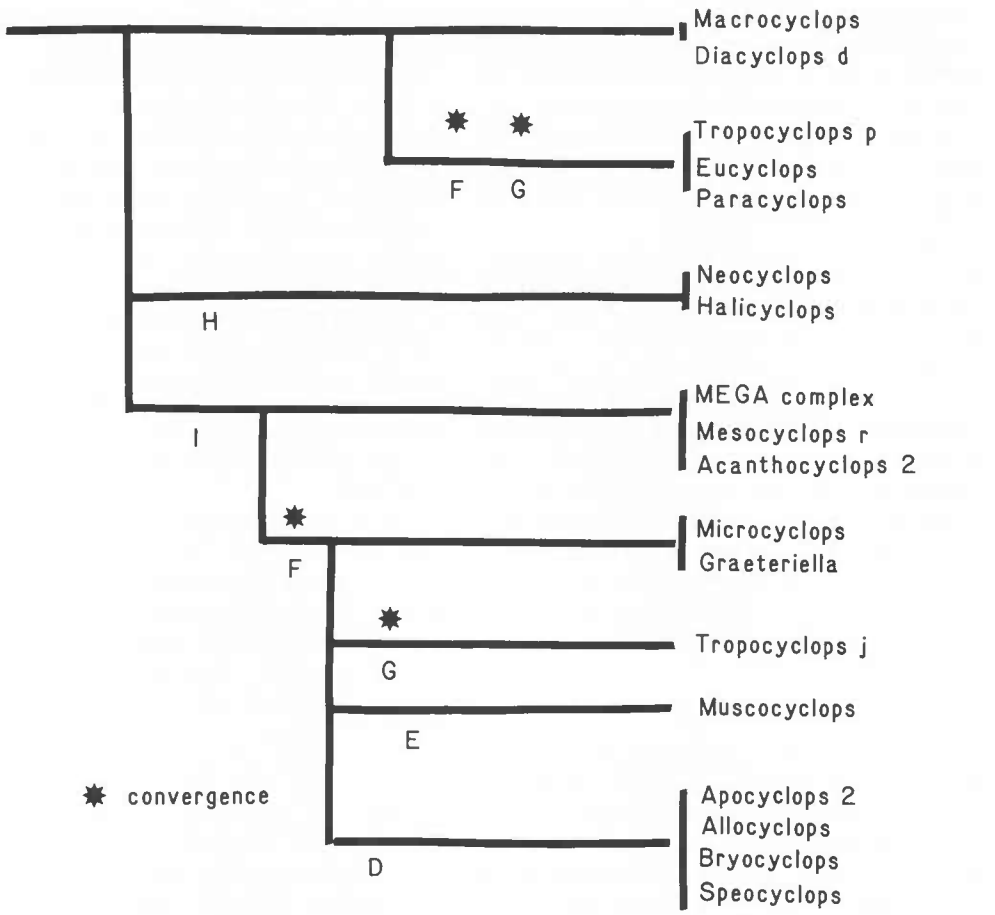

Fig. 5. Phylogenetic relationships for taxa listed in Table 15; characters are those of P5 only; initial divergence determined by number of setae on the exopodal segment.

serial addition. It is possible to consider a second kind of setation pattern for 2-segmented rami in which the rami continue their ancestral pleiotropic pattern of setal development but delay the addition of the third segment through the terminal adult molt, a true neoteny. This developmental pattern will result in 2-segmented rami with seven or eight setae on the distal segment of both rami of swimming leg 1, and eight or nine setae on the distal segment of the exopod and seven or eight setae on the distal segment of the endopod of swimming legs 2–4. Discovery of this developmental pattern would suggest another lineage within the MEGA complex.

The phylogenetic hypothesis proposed here differs from the cyclopid groups proposed by Ferrari (1991), which were based on segmental developmental patterns derived from literature reports. The differences are due to patterns used for *Acanthocyclops viridis* and *Thermocyclops minutus,* whose literature accounts do not agree with the species of those genera reported here, and to the pattern used for *Diacyclops thomasi,* whose literature account does not agree with the results here.

The above hypothesis also differs from the system of the subfamilies *Halicyclopinae, Eucyclopinae,* and *Cyclopinae* proposed by Kiefer (1927, 1928), which is based on the number of setae on the distal segment of P5. Gurney (1933) reviewed the literature prior to the work of Kiefer. Subsequently, Monchenko (1975) established the Euryteinae; there are currently four subfamilies into which the cyclopid genera are placed. Figure 5 is an abbreviated hypothesis based only on the five characters associated with P5. The carliest transformations are: (1) addition of a seta at stage 12 to the distal segment of the

exopod (H) of males, in effect separating the two species of Halicyclopinae; (2) failure to add a seta to the distal exopodal segment (I), which results in two groups of species with either three setae, the Eucyclopinae, or with two setae on that segment, the Cyclopinae. P5 of *Diacyclops dispinosus* is identical to that of *Macrocyclops albidus,* but these two species share no setal developmental patterns of the rami of P1–4. The distal segment of five of eight rami of *D. dispinosus* is identical in morphology to that resulting from the delayed pleiotropic process of the MEGA complex, while the distal exopodal segments of P1–3 are unique to cyclopids. *Macrocyclops albidus* retains the ancestral pleiotropic process in determining the morphology of the rami of P1–4.

Tropocyclops jamaicensis, with two setae on the distal exopodal segment of P5, differs from the remaining species of the proposed lineage whose morphology of P1–4 is derived from the truncated pleiotropic process. The rami of P1–4 of *T. jamaicensis* are derived from the ancestral pleiotropic pattern. The conclusion of Gurney (1933:17) to reject Kiefer's cyclopid subfamilies is accepted here. The hypothesis favored here is that transformations of P1–4 more clearly reflect evolution of the Cyclopidae, and that convergences, including reversals, are more likely to have occurred to P5.

An incomplete series of copepodid stages were obtained for two interesting cyclopids. No data are available for stage 10 of *Cyclops scutifer* Sars, 1863, a species of the type genus of the family. Analysis of the remaining stages suggests that it retains the ancestral pattern of development of mxp and P6. The ancestral pleiotropic process determines the morphology of the endopods of P1–4 and exopods of P1, P2, and P4. The distal segment of the exopod of P3 has eight setae rather than the ancestral nine setae at stage 11, suggesting a failure to add a seta at stage 10, which would be unique to the lineage. Failure to add a third seta to the exopod of P5 at stage 10 is the only other derived state for the species; *C. scutifer* appears to share a common ancestor with *Macrocyclops albidus.*

No data are available for stage 11 of *Troglocyclops janstocki* Rocha and Iliffe, 1994. It apparently has retained the ancestral state of development for P6 and the ancestral pleiotropic process for the morphology of P1–4, but exhibits the derived sexual dimorphism of the exopod of P5. *Troglocyclops janstocki* is similar to *Neocyclops vicinus* in these character states. However, its maxilliped expresses a setal developmental pattern similar to a copepod with a 5-segmented endopod (Ferrari and Dahms, 1998); in effect, its middle endopodal segment is a complex of three segments. This pattern may be considered ancestral to the remaining cyclopids, all of which have a derived 2-segmented endopod. This interpretation would place *T. janstocki* at the base of Fig. 4. Alternately, the endopod of the maxilliped may represent a character-state reversal. This would suggest that *T. janstocki* shares a common ancestor with *N. vicinus* and *Halicyclops aberrans.*

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Appendix 1. Species studies and sources of specimens.

Cyclopidae
Halicyclopinae
Halicyclops aberrans Rocha, 1983; preserved specimens from Rocha.
Neocyclops vicinus (Herbst, 1955); preserved specimens from Rocha.

Eucyclopinae
Eucyclops agilis (Koch, 1838); from Reid, cultured.
Macrocyclops albidus (Jurine, 1820); from Reid, cultured by Wyngaard.
Paracyclops chiltoni (Thompson, 1883); from Reid, cultured.
Tropocyclops jamaicensis Reid and Janetzky, 1996; preserved specimens from Janetzky.
Tropocyclops prasinus (Fischer, 1860); from Reid, cultured by Wyngaard.

Cyclopinae
Acanthocyclops carolinianus (Yeatman, 1944); from Reid, cultured.
Acanthocyclops robustus (Sars, 1863); from Marten, cultured by Wyngaard.
Allocyclops silvaticus Rocha and Bjornberg, 1988; from Rocha, cultured: and Rocha and Bjornberg, unpublished observations.
Apocyclops dimorphus (Johnson, 1953); preserved specimens from Buskey.
Apocyclops panamensis (Marsh, 1913); preserved specimens.
Bryocyclops caroli Bjornberg, 1985; from Rocha, cultured; and Bjornberg, unpublished observations.
Diacyclops dispinosus Ishida, 1994; preserved specimens from Ishida.
Diacyclops navus (Herrick, 1882); from White, cultured.
Diacyclops thomasi (Forbes, 1882); from Reid, cultured.
Graeteriella brehmi (Lescher-Moutoué, 1968); preserved specimens from Lescher-Moutoué.
Megacyclops latipes (Lowndes, 1927); from Marten, cultured by Wyngaard.
Mesocyclops edax (Forbes, 1891); cultured by Wyngaard.
Mesocyclops longisetus (Thiébaud, 1914); from Marten, cultured by Wyngaard.
Mesocyclops ruttneri Kiefer, 1981; from Marten, cultured by Wyngaard.
Microcyclops rubellus (Lilljeborg, 1901); from Reid, cultured.
Muscocyclops operculatus (Chappuis, 1917); preserved specimens from Rocha.
Speocyclops racovitzai (Chappuis, 1923); preserved specimens from Lescher-Moutoué.
Thermocyclops decipiens (Kiefer, 1929); preserved specimens from Reid.

Other Cyclopoida
Notodelphyidae
Doropygus seclusus Illg, 1958; from Dudley (1966).
Notodelphys affinis Illg, 1958; from Dudley (1966).
Scolecodes huntsmani (Henderson, 1931); from Dudley (1966).

Oithonidae
Dioithona oculata (Farran, 1913); from Ferrari and Ambler (1992).
Limnoithona tetraspina Zhang and Li, 1976; preserved specimens from Orsi.

Cyclopinidae
Cyclopina caroli Lotufo, 1994; preserved specimens from Lotufo.
Procyclopina feiticeira Lotufo, 1995; preserved specimens from Lotufo.

Harpacticoida
Canuellidae
Coullana canadensis (Willey, 1923); cultured by Lonsdale.
Longipediidae
Longipedia americana Wells, 1980; cultured by Fofonoff.
Miraciidae
Macrosetella gracilis (Dana, 1847); preserved specimens from Böttger-Schnack.

Poecilostomatoida
Clausidiidae
Conchyliurus quintus Tanaka, 1961; preserved specimens from Kim.
Hemicyclops adhaerens (Williams, 1907); cultured by Fofonoff.
Leptinogaster major (Williams, 1907); preserved specimens from Humes.

Myicolidae
Midicola spinosus (Raffaele and Monticelli, 1885); from Do, Kajihara, and Ho (1984).

Sabelliphilidae
Herrmannella saxidomi Illg, 1949; preserved specimens from Humes.

Siphonostomatoida
Asterocheridae
Scottomyzon gibberum (T. Scott and A. Scott, 1894); preserved specimens from Ivanenko.

Calanoida
Ridgewayiidae (Pseudocyclopoidea)
Ridgewayia klausruetzleri Ferrari, 1995; from Ferrari (1995).
Metridinidae (Augaptiloidea)
Pleuromamma xiphias (Giesbrecht, 1889); from Ferrari (1985) and preserved specimens.
Temoridae (Centropagoidea)
Temora longicornis (Muller, 1792); cultured by Klein Breteler.
Paracalanidae (Megacalanoidea)
Acrocalanus gibber Giesbrecht, 1888; cultured by McKinnon.
Clausocalanidae (Clausocalanoidea)
Pseudocalanus elongatus (Boeck, 1865); cultured by Klein Breteler.

Appendix 2. States for 40 characters (A–Nn) of thoracopod developmental patterns. mxp = maxilliped; P1–4 = swimming legs 1–4; P5 and 6 = legs 5 and 6; f = female, m = male.

A: P6
- 0 – setal addition at stage 11.
- 1 – sexual dimorphism: setal addition at stage 11 [f] and no setal addition at stage 11 [m].

B: P6
- 0 – setal addition at stage 11.
- 1 – no setal addition at stage 11.

C: Mxp
- 0 – setal addition to syncoxa at stage 9.
- 1 – no setal addition to syncoxa at stage 9.

D: P5
- 0 – formation of an articulation between basipod and exopod at stage 10.
- 1 – no articulation between basipod and exopod.

E: P5
- 0 – formation of an articulation between basipod and exopod at stage 10.
- 1 – formation of an articulation between basipod and exopod at stage 12.

F: P5
- 0 – formation of an articulation between basipod and somite at stage 10.
- 1 – no articulation between basipod and somite.

G: basipod of P5
- 0 – setal addition at stage 10.
- 1 – no setal addition at stage 10.

H: distal segment of exopod of P5
- 0 – setal addition at stage 10, no addition at stage 12.
- 1 – sexual dimorphism: setal addition at stage 10 [f] and setal addition at stage 12 [m].

I: distal segment of exopod of P5
- 0 – setal addition at stage 10, no addition at stage 12.
- 1 – no setal addition at stages 10 and 12.

J: basipod of P1
- 0 – setal addition at stage 8.
- 1 – no setal addition at stage 8.

K: proximal segment of exopod of P1
- 0 – setal addition at stage 9.
- 1 – no setal addition at stage 9.

L: proximal segment of exopod of P4
- 0 – setal addition at stage 11.
- 1 – no setal addition at stage 11.

M: P1–4 after transformation
- 0 – distal segment of exopods: no change to P1; addition at stage 9 to P2; addition at stage 10 to P3; addition at stage 10, loss at stage 11 to P4; distal segment of endopods: addition at stage 9, loss at stage 9 to P1; addition at stages 9 and 10, loss at stage 11 to P2; addition at stage 10, loss at stage 11 to P3; loss at stage 11 to P4.
- 1 – distal segment of exopods: loss at stage 12 to P1; addition at stage 9, loss at stage 12 to P2; addition at stage 10, loss at stage 12 to P3; addition at stage 10, loss at stage 12 to P4; distal segment of endopods: addition at stage 9, loss at stage 12 to P1; addition at stages 9 and 10, loss at stage 12 to P2; addition at stages 10 and 11, loss at stage 12 to P3; addition at stage 11, loss at stage 12 to P4.

N: P1–4 after transformation
- 0 – distal segment of exopods: no change to P1; addition at stage 9 to P2; addition at stage 10 to P3; addition at stage 10, loss at stage 11 to P4; distal segment of endopods: addition at stage 9, loss at stage 9 to P1; addition at stages 9 and 10, loss at stage 11 to P2; addition at stage 10, loss at stage 11 to P3; loss at stage 11 to P4.
- 1 – distal segment of exopods: no change after stage 8 to P1; no change after stage 9 to P2; no change after stage 10 to P3; no change after stage 10 to P4; distal segment of endopods: no change after stage 8 to P1; no change after stage 9 to P2; no change after stage 10 to P3; no change after stage 10 to P4.

O: distal segment of exopod of P1 after transformation
- 0 – no change.
- 1 – setal loss at stage 11.

P: distal segment of endopod of P1 after transformation
- 0 – no change at stage 8.
- 1 – setal loss at stage 8.

Q: distal segment of endopod of P1 after transformation
- 0 – setal loss at stage 11.
- 1 – setal loss at stage 12.

R: distal segment of endopod of P1 after transformation
- 0 – setal addition at stage 9, and no change at stage 10.
- 1 – no change at stage 9, and setal addition at stage 10.

S: distal segment of exopod of P3 after transformation
- 0 – no change at stage 11.
- 1 – loss at stage 11.

T: distal segment of endopod of P4 after transformation
- 0 – no change at stage 10, setal loss at stage 11, and no change at stage 12.
- 1 – setal addition at stage 10, no change at stage 11, and setal loss at stage 12.

U: distal segment of exopod of P1 after transformation
- 0 – setal loss at stage 12.
- 1 – setal addition at stage 11 and loss at stage 12.

V: distal segment of exopod of P2 after transformation
- 0 – setal addition at stage 9, loss at stage 12.
- 1 – setal additions at stages 9 and 11, loss at stage 12.

W: distal segment of exopod of P3 after transformation
- 0 – setal addition at stage 10, loss at stage 12.
- 1 – setal additions at stages 10 and 11, loss at stage 12.

X: distal segment of endopod of P4 after transformation
- 0 – setal addition at stage 11, loss at stage 12.
- 1 – setal loss at stage 11.

Y: distal segment of exopod of P1 after transformation
- 0 – loss at stage 12.
- 1 – loss at stage 11 or loss at stage 12.

Z: distal segment of endopod of P1 after transformation
- 0 – addition at stage 9, loss at stage 12.
- 1 – addition at stage 9, loss at stage 11 or addition at stage 9, loss at stage 12.

Aa: distal segment of exopod of P2 after transformation
- 0 – addition at stage 9, loss at stage 12.
- 1 – addition at stage 9, loss at stage 11 or addition at stage 9, loss at stage 12.

Appendix 2. Continued.

Bh: distal segment of endopod of P2 after transformation
- 0 – addition at stages 9 and 10, loss at 12.
- 1 – addition at stage 9, loss at stage 11 or addition at stages 9 and 10, loss at stage 12.

Cc: distal segment of exopod of P3 after transformation
- 0 – addition at stage 10, loss at stage 12.
- 1 – addition at stage 10, loss at stage 11 or addition at stage 10, loss at stage 12.

Dd: distal segment of endopod of P3 after transformation
- 0 – addition at stages 10 and 11, loss at stage 12.
- 1 – addition at stage 10, loss at stage 11 or addition at stages 10 and 11, loss at stage 12.

Ec: distal segment of exopod of P4 after transformation
- 0 – addition at stage 10, loss at stage 12.
- 1 – addition at stage 10, loss at stage 11 or addition at stage 10, loss at stage 12.

Ff: distal segment of endopod of P4 after transformation
- 0 – addition at stage 11, loss at stage 12.
- 1 – loss at stage 11 or addition at stage 11, loss at stage 12.

Gg: distal segment of exopod of P2 after transformation
- 0 – addition at stage 9.
- 1 – no change at stage 9.

Hh: distal segment of endopod of P2 after transformation
- 0 – setal addition at stage 9.
- 1 – no change at stage 9.

Ii: distal segment of endopod of P2 after transformation
- 0 – no change at stage 8, setal addition at stage 9.
- 1 – setal loss at stage 8, setal addition at stage 9.
- 2 – setal loss at stage 8, no change at stage 9.

Jj: distal segment of exopod of P3 after transformation
- 0 – setal addition at stage 10.
- 1 – no change at stage 10.

Kk: distal segment of endopod of P3 after transformation
- 0 – no change at stage 9, setal addition at stage 10.
- 1 – setal loss at stage 9, addition at stage 10.
- 2 – setal loss at stage 9, no change at stage 10.

Ll: distal segment of endopod of P3 after transformation
- 0 – no change at stage 9, setal addition at stage 10.
- 1 – sexual dimorphism: no change at stages 9 and 10 [f] and setal loss at stage 9, no change at stage 10 [m].

Mm: distal segment of exopod of P4 after transformation
- 0 – setal addition at stage 10, no change at stage 11.
- 1 – sexual dimorphism: setal addition at stage 10, no change at stage 11 [f] and setal addition at stage 10, loss at stage 11 [m].
- 2 – no change at stages 10 and 11.
- 3 – setal loss at stage 10, no change at stage 11.

Nn: distal segment of endopod of P4 after transformation
- 0 – no change at stages 10 and 11.
- 1 – sexual dimorphism: no change at stages 10 and 11 [f] and no change at stage 10, setal loss at stage 11 [m].
- 2 – sexual dimorphism: no change at stages 10 and 11 [f] and setal loss at stage 10, no change at stage 11 [m].
- 3 – setal loss at stage 10, no change at stage 11.