RELATIONSHIPS BETWEEN ARTHRODIAL MEMBRANE FORMATION AND ADDITION OF SETAE TO SWIMMING LEGS 1-4 DURING DEVELOPMENT OF *DIOITHONA OCULATA*, *RIDGEWAYIA KLAUSRUETZLERI*, *PLEUROMAMMA XIPHIAS*, AND *TEMORA LONGICORNIS* (COPEPODA)

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ABSTRACT

Relationships between arthrodial membrane formation and the addition of setae to the exopod and endopod of swimming leg 3 of the cyclopoid copepod *Dioithona oculata* are derived from formation homologies during development. Based on this information, these relationships are inferred for the remaining swimming legs of the cyclopoid and the swimming legs of three calanoids, *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Temora longicornis*. Most of the variation in setal numbers for a leg among the four copepods is expressed in the distal segment of each ramus. The most striking differences in architecture result from a delay or failure in expression of the arthrodial membranes which separate the proximal segment or the middle segment of the ramus from the distal segment. Inferring a composite model for relationships between arthrodial membrane formation and addition of setae to the exopod and endopod of a swimming leg is complicated by differences in swimming leg 1 and the remaining swimming legs which includes an earlier allocation of the proximal seta of the middle (third) segment to both rami of swimming leg 1. These developmental patterns are presumed to be derived, and the endopod of all thoracopods of the ancestral copepod immediately after the transformation of the leg bud is presumed to have been 2-segmented with one medial seta on the proximal segment.

RÉSUMÉ

Les relations entre la formation de la membrane arthrodiale et l'addition de soies sur l'exopodite et l'endopodite de la patte natatoire 3 du copépode cyclopoïde *Dioithona oculata* sont dérivées d'homologies de formation au cours du développement. D'après cette information, ces relations sont déduites pour les autres pattes natatoires du cyclopoïde et de trois calanoïdes, *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, et *Temora longicornis*. La variation la plus grande dans le nombre de soies pour une patte parmi les quatre copépodes est exprimée dans l'article distal de chaque rame. Les différences les plus frappantes dans l'architecture résultent d'un délai ou d'un manque dans l'expression des membranes arthrodiales qui séparent l'article proximal ou l'article médian de la rame de l'article distal. La déduction d'un modèle composite pour les relations entre

membranes arthrodiales et addition de soies à l'exopodite et à l'endopodite d'une patte natatoire est compliquée par les différences entre la patte natatoire 1 et les autres pattes natatoires, ce qui inclut une affectation précoce de la soie proximale de l'article médian (le troisième) aux deux rames de la patte natatoire 1. Ces modèles de développement sont présumés dérivés, et l'endopodite de tous les thoracopodes du copépode ancestral, immédiatement après la transformation du bourgeon de patte, est présumé avoir été 2-segmenté, avec une soie médiane sur l'article proximal.

INTRODUCTION

The exoskeleton of the ramus of a copepod swimming leg, in a simple way, can be thought of as one or more setae placed between a proximal and a distal arthrodial membrane. While variation in segmentation of swimming legs 1-4 (thoracopods 2-5) during copepodid development has been documented among different kinds of copepods (Ferrari, 1988), relationships between arthrodial membrane formation and setal additions during development have not been explored. Here we describe arthrodial membrane formation and setation during development of swimming legs 1-4 of the cyclopoid *Dioithona oculata* (Farran, 1913) and three calanoids, *Ridgewayia klausruetzleri* Ferrari, 1995, *Pleuromamma xiphias* (Giesbrecht, 1889) and *Temora longicornis* (Müller, 1792), and discuss the relationship between arthrodial membrane formation and setal addition. We also derive composite models which generalize arthrodial membrane formation and setal addition during development of the exopod and endopod. Variability of the models is discussed.

METHODS

Complete development of swimming legs 1-4 of *D. oculata* during the naupliar and copepodid phases was described by Ferrari & Ambler (1992). Development of swimming legs 1-4 of *R. klausruetzleri* during its copepodid phase and of *P. xiphias* for copepodids II-VI was described by Ferrari (1985, 1995). Here we include unpublished observations of swimming legs 1-3 of CI of *P. xiphias* and illustrate segmentation and setation of swimming legs 1-4 of CI-VI of *T. longicornis*. Specimens of *P. xiphias* and *T. longicornis* which were fixed and preserved with 4% formaldehyde/96% seawater, cleared in steps through 50.0% lactic acid/50.0% freshwater to 100% lactic acid and examined with differential interference optics, or stained by adding a solution of chlorazol black E dissolved in 70.0% ethanol/30.0% freshwater and examined with bright-field optics.

An hypothesis about the phylogenetic relationship among the 270 calanoid genera has yet to be proposed. The 43 calanoid families have been grouped into 11 superfamilies, and phylogenetic relationships among 8 or 10 of those

superfamilies has been hypothesized by Andronov (1980) and Park (1986), respectively. *Ridgewayia klausruetzleri* [Ridgewayiidae, 3 genera] belongs to the Pseudoeyclopoidea [3 families], one of the presumed oldest calanoid superfamilies, along with Epacteriscioidea. *Pleuromamma xiphias* [Metridinidae, 3 genera] belongs to the Arietelloidea [8 families], the next derived superfamily and the oldest superfamily of planktonie ealanoids. *Temora longicornis* [Temoridae, 7 nominal genera] belongs to the Diaptomoidea [10 families], the next derived superfamily. *Dioithona oculata* belongs to the Oithonidae, a relatively older cyelopoid family (Ho, 1994). The Cyelopoida is one of the youngest eopepod orders; the Calanoida is one of the oldest (Ho, 1990).

Analysis of the segmentation and setation of swimming leg 3 of *D. oculata* based on formation homology (Ferrari & Ambler, 1992) permits a derivation of the relationship between arthrodial membrane formation and setal addition of both exopod and endopod of this biramal appendage. Analyses of formation homology for segmentation and setation of the other swimming legs of *D. oculata* and the swimming legs of the three ealanoids discussed here is not available. Relationships between arthrodial membrane formation and setal addition during different steps of development are inferred here by assuming the following generalizations: (1) events of the developmental pattern of swimming leg 3 of *D. oculata* are eonserved whenever possible; and (2) losses of setae during development are minimized.

RESULTS

Development of swimming leg 3 (fig. 1) takes plaee in four steps, A-D, for the exopod and four steps, W-Z, for the endopod. These steps (tables I-II) eorrespond to the molts to CII, CIII, CIV and CV respeetively. During the molt to CII (step A, table I), the leg bud of CI with three exopodal setae, which will be alloeated to the presumptive distal segment as a lateral, a terminal and a medial seta, is transformed into an appendage with a 1-segmented exopod armed with seven setae, four of which are new setae. Three of the new setae (one lateral and two medial) will remain on the distal segment, and the proximal, lateral seta on the distal segment will be alloeated to the presumptive proximal (second) segment. During the molt to CIII (step B), an arthrodial membrane develops which separates the proximal segment (with its lateral seta) and the distal segment, and a medial seta is added to the distal segment. During the molt to CIV (step C), a medial seta is added to the proximal segment and two new setae, one lateral and one medial, are added to the distal segment. These two, new setae will be allocated to the presumptive middle (third) segment. During

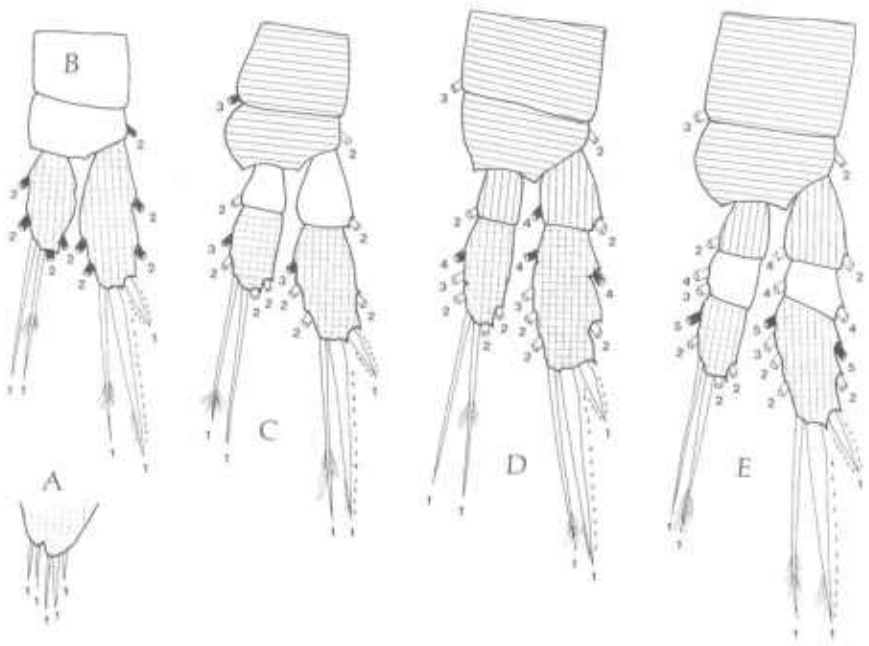

Fig. 1. Development of swimming leg 3 of *Dioithona oculata* (Farran, 1913) (modified from Ferrari & Ambler, 1992). A, primary bud on copepodid 1 with 3 setae on the outer lobe (presumptive exopod) and 2 setae on the inner lobe (presumptive endopod); B-E, transformed legs of copepodids II-V, respectively. Oldest segment cross-hatched, youngest segment clear, oldest intermediate segment horizontally hatched, youngest intermediate segment vertically hatched. Oldest setae from copepodid 1 (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.

the molt to CV (step D), an arthrodial membrane forms which separates the middle segment (with its lateral and medial seta) and the distal segment, and two new setae (lateral and medial) are added to the distal segment. It is unclear whether these two setae are being allocated to a presumptive, but unformed, fourth segment.

Development of the endopod (table II) is similar but not identical to that of the exopod. Step W corresponds to step A. The three new setae on the distal segment are lateral, terminal and medial; the proximal medial seta will be allocated to the presumptive proximal (second) segment. During the molt to CIII (step X) an arthrodial membrane develops which separates the proximal and distal segments, and a medial seta is added to the distal segment which will be allocated to the presumptive, middle segment. During the molt to CIV (step Y) another medial setae is added to the distal segment which will be allocated to the middle segment; its position is proximal to the seta allocated in step X. During the molt to CV (step Z) an arthrodial membrane develops which separates the

TABLE I

Arthrodial membrane formation (+) and number of setae added (arabic numerals) to the exopod of swimming leg 3 of *Dioithona oculata* (Farran, 1913). Column 1 = number of setae added to distal segment; 2 = setae allocated to proximal segment; 3 = arthrodial membrane forms between distal and proximal segments; 4 = setae allocated to middle segment; 5 = arthrodial membrane forms between distal and middle segments; parentheses indicate setae may be allocated to a presumptive, but unformed, fourth segment

Step	1	2	3	4	5
A	3	1			
B	1		+		
C		1		2	
D	(2)				+

TABLE II

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 3 of *Dioithona oculata* (Farran, 1913). Legend as for table I

Step	1	2	3	4	5
W	3	1			
X			+	1	
Y				1	
Z	(1)				+

TABLE III

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 2 of *Dioithona oculata* (Farran, 1913). Legend as for table I

Step	1	2	3	4	5
W	3	1			
X			+	1	
Y				1	
Z1	(1)				
Z2					+

middle segment (with its two medial setae) and the distal segment, and a new medial seta is added to the distal segment. It is not clear whether this medial seta is being allocated to a presumptive, but unformed, fourth segment.

Development of the exopod of swimming leg 2 of *D. oculata* takes place during the molts to CI, CII, CIII and CV. Based on the three assumptions mentioned above, development is identical to swimming leg 3. Development of the endopod takes place during the molts to CI, CII, CIII, CIV and CV (table III); step Z has been subdivided so that the formation of the arthrodial membrane between the

TABLE IV

Arthrodial membrane formation and number of setae added to the exopod of swimming leg 4 of *Dioithona oculata* (Farran, 1913). Legend as for table I

Step	1	2	3	4	5
A	3	1			
B/C	1		+	2	
C/D	(1)	1			+

TABLE V

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 4 of *Dioithona oculata* (Farran, 1913). Legend as for table I

Step	1	2	3	4	5
W	3	1			
X			+	1	
Y/Z				1	+

middle and distal segment takes place during the molt to CV (step Z2), one molt after the medial seta is added to the distal segment (table III, step Z1).

Swimming leg 4 develops during molts to CIII, CIV and CV. For the exopod, the events of step C are combined with step B or step D (table IV); one seta fewer is added to the distal segment at step D. Steps Y and Z are combined in the endopod and no medial seta is added to the distal segment at step Y/Z (table V).

The rami of swimming leg 1 develop during molts to CI, CII, CIII, and CV. During the molt to CI (table VI, step A), the leg bud with four presumptive exopodal setae (two lateral, one terminal and one medial) is transformed into an appendage with a 1-segmented exopod armed with eight setae. Of the four new setae, one lateral seta each is allocated to the proximal and middle segments; a lateral and a medial seta will remain on the distal segment. No seta is added to the distal segment at step B, the molt to CII, but a second medial seta is allocated to the presumptive, middle segment, and the arthrodial membrane forms which separates the proximal (second) and distal segment. During the molt to CIII (step C) a medial seta is added to the proximal segment; step D is identical to the exopod of leg 3. There are other hypotheses which can explain the distribution of exopodal setae; our interpretation is constrained by exopod development of *P. xiphias* and *T. longicornis*.

During endopodal development of swimming leg 1, at the molt to CI (step W, table VII), five new setae are added with three remaining on the distal segment and one each allocated to the presumptive proximal and middle segments. During

TABLE VI

Arthrodial membrane formation and number of setae added to the exopod of swimming leg 1 of *Dioithona oculata* (Farran, 1913). Legend as for table I

Step	1	2	3	4	5
A	2	1		1	
B			+	1	
C		1			
D	(2)				+

TABLE VII

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 1 of *Dioithona oculata* (Farran, 1913). Legend as for table I

Step	1	2	3	4	5
W	3	1		1	
X			+		
Y	1				
Z					+

the molt to CII (step X), an arthrodial membrane develops which separates the proximal and distal segments. During the molt to CIII (step Y) a medial seta is added to the distal segment and during the molt to CV an arthrodial membrane develops which separates the middle (with its medial seta) and distal segments.

Copepodid development of the exopods of swimming legs 2 and 3 of *R. klausruetzleri* is identical to those of *D. oculata* (table I); the last naupliar stage of this calanoid is unknown, but like swimming leg 3, the bud of swimming leg 2 is assumed to bear three setae which will be allocated to the presumptive distal segment of the exopod and two setae which will be allocated to the presumptive distal segment of the endopod. Development of the endopod of swimming leg 2 (table VIII) and swimming leg 3 is identical to one another, and similar to those of *D. oculata* with the following exceptions. At step X, a seta is added to the distal segment and at step Z1/Z2 two setae are added to the distal segment. Development of the exopod of swimming leg 4 of *R. klausruetzleri* is similar to *D. oculata* (table IV) with the following exception; at step D two setae, not one, are added to the distal segment. Development of the endopod of swimming leg 4 of *R. klausruetzleri* differs from *D. oculata* (table II). At step X a seta is added to the distal segment and at step Y/Z another seta is added to the distal segment.

The last naupliar stage of *R. klausruetzleri* is unknown; however, the bud of swimming leg 1, like that of *T. longicornis* or *Acrocalanus gibber* Giesbrecht, 1888 (unpublished observations), is assumed to bear four setae on a lateral lobe which will be allocated to the presumptive distal segment of the exopod, and

TABLE VIII

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 2 of *Ridgewayia klausruetzleri* Ferrari, 1995. Legend as for table I

Step	1	2	3	4	5
W	3	1			
X	1		+	1	
Y				1	
Z1/Z2	(2)				+

TABLE IX

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 1 of *Ridgewayia klausruetzleri* Ferrari, 1995. Legend as for table I

Step	1	2	3	4	5
W	2	1		1	
X			+	1	
Y	1				
Z					+

three setae on a medial lobe which will be allocated to the presumptive distal segment of the endopod. Copepodid development of the exopod of swimming leg 1 is similar to that of *D. oculata* (table VI) with the following exception; at step D one seta, not two, is added to the distal segment. Development of the endopod of *R. klausruetzleri* (table IX) is similar to that of *D. oculata*. At step W (molt to CI), only four new setae are added; the lateral and terminal setae remain on the distal segment, and the two medial setae are allocated to the presumptive proximal and middle segments respectively. During the molt to CII (step X) an arthrodial membrane develops which separates the proximal and distal segments, and a second medial seta, proximal to the one added at step W, is allocated to the presumptive middle segment. During the molt to CIII (step Y) a medial seta is added to the distal segment. During the molt to CV (step Z) an arthrodial membrane develops which separates the middle (with its medial seta) and distal segments.

Swimming legs 1-3 of CI of *P. xiphias* are illustrated in fig. 2. Development of the exopods of swimming legs 2 and 3 of *P. xiphias* is identical to that of *D. oculata* (table I). However, development of the endopod of swimming legs 2 and 3 differs from that of *D. oculata* (tables II, III); at step X the arthrodial membrane which would separate the proximal (second) and distal segments fails to form and at step Y the proximal seta of leg 2 is lost. At step Z two setae are added to the distal segment, and both of the arthrodial membranes form; they separate the proximal and distal segments, and the middle and distal segments.

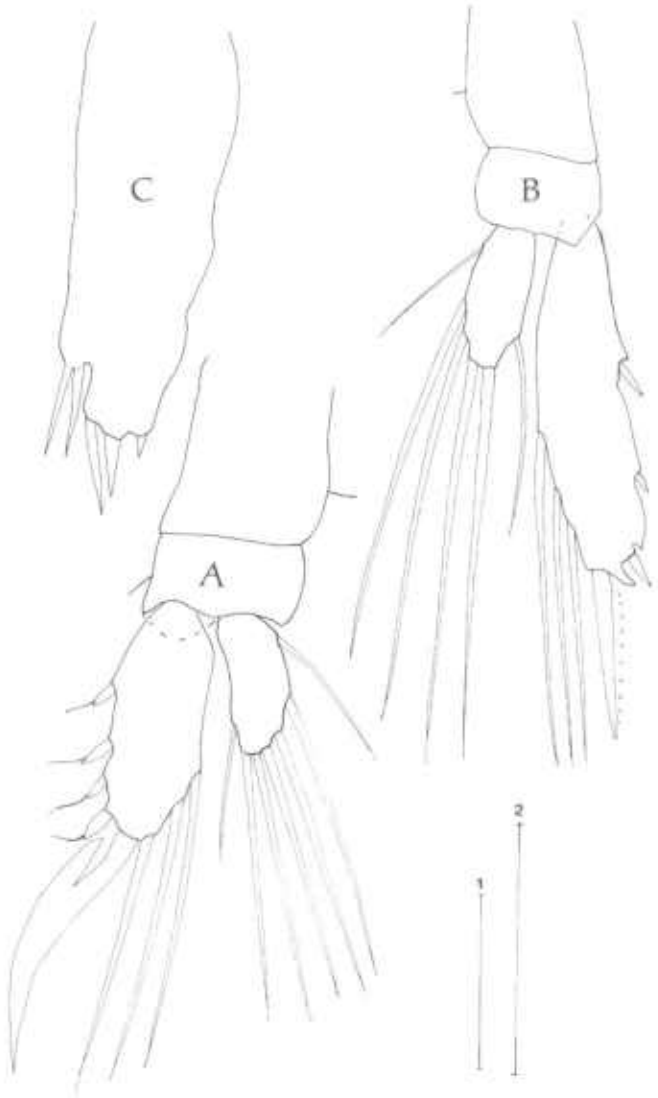

Fig. 2. *Pleuromamma xiphias* (Giesbrecht, 1889), copepodid I. A, swimming leg 1, anterior; B, swimming leg 2, posterior; C, swimming leg 3, posterior. Line 1 is 0.05 mm for A; line 2 is 0.10 mm for B, C.

Development of the exopod of swimming leg 4 of *P. xiphias* is similar to that of *D. oculata* (table IV) and identical to that of *R. klausruetzleri*. At step D two setae, not one, are added to the distal segment. Development of the endopod of *P. xiphias* differs from that of *D. oculata* (table V). At step X, both setae of the presumptive middle segment are added, a seta is added to the distal segment, but the arthrodial membrane between the proximal and distal segment fails to form.

TABLE X

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 1 of *Pleuromamma xiphias* (Giesbrecht, 1889). Legend as for table I

Step	1	2	3	4	5
W	2	1		1	
X/Y			+	1	
Z					+

TABLE XI

Arthrodial membrane formation and number of setae added to the exopod of swimming leg 3 of *Temora longicornis* (Müller, 1792). – = loss of arthrodial membrane; remaining legend as for table I

Step	1	2	3	4	5
A	3	1			
B	1				
C		1		2	
D	(2)		+		+
E			–		

TABLE XII

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 3 of *Temora longicornis* (Müller, 1792). Legend as for table I

Step	1	2	3	4	5
W	3	1			
X				1	
Y				1	
Z	(1)				+

At step Y/Z both of the arthrodial membranes form; they separate the proximal and distal segments, and the middle and distal segments.

The last naupliar stage of *P. xiphias* is unknown but the bud of swimming leg 1 also is assumed to bear four setae on a lateral lobe which will be allocated to the presumptive distal segment of the exopod, and three setae on a medial lobe which will be allocated to the presumptive distal segment of the endopod. Development of the exopod of swimming leg 1 of *P. xiphias* is identical to that in *R. klausruetzleri* and is similar to that of *D. oculata* (table VI). Development of the endopod of swimming leg 1 of *P. xiphias* (table X) differs from that of *D. oculata*. During the molt to CII (step X) a second medial seta is added to the presumptive middle segment, and an arthrodial membrane forms between the proximal and distal segments. During the molt to CIII (step Y), no new medial

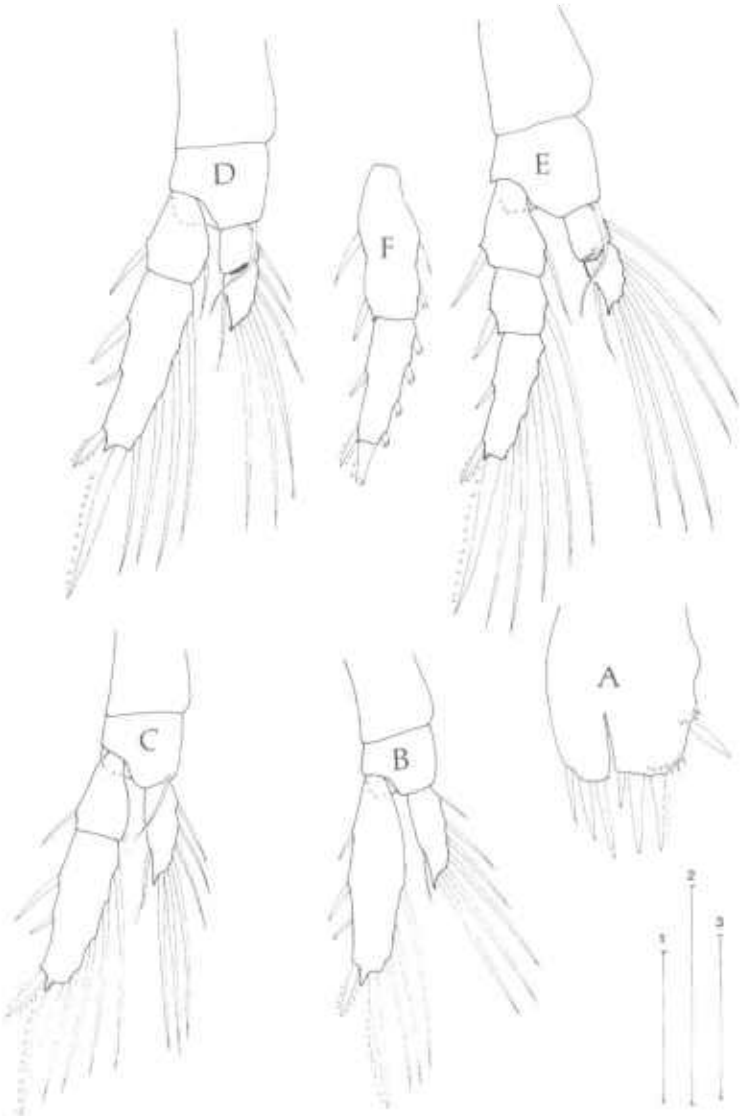

Fig. 3. *Temora longicornis* (Müller, 1792), swimming leg 1, anterior. A, N6; B, CI; C, CII; D, CIII; E, CV; F, CVI, exopod. Line 1 is 0.05 mm for A; line 2 is 0.10 mm for B, C, D; line 3 is 0.10 mm for E, F.

seta is added to the distal segment; because no event occurs in this step we have arbitrarily combined this step and step X. During the molt to CV (step Z), the arthrodial membrane separating the middle and distal segments forms.

Swimming legs 1-4 of *T. longicornis* are illustrated in figs. 3-6 and their development is summarized in tables XI-XVI. Development of the exopods of

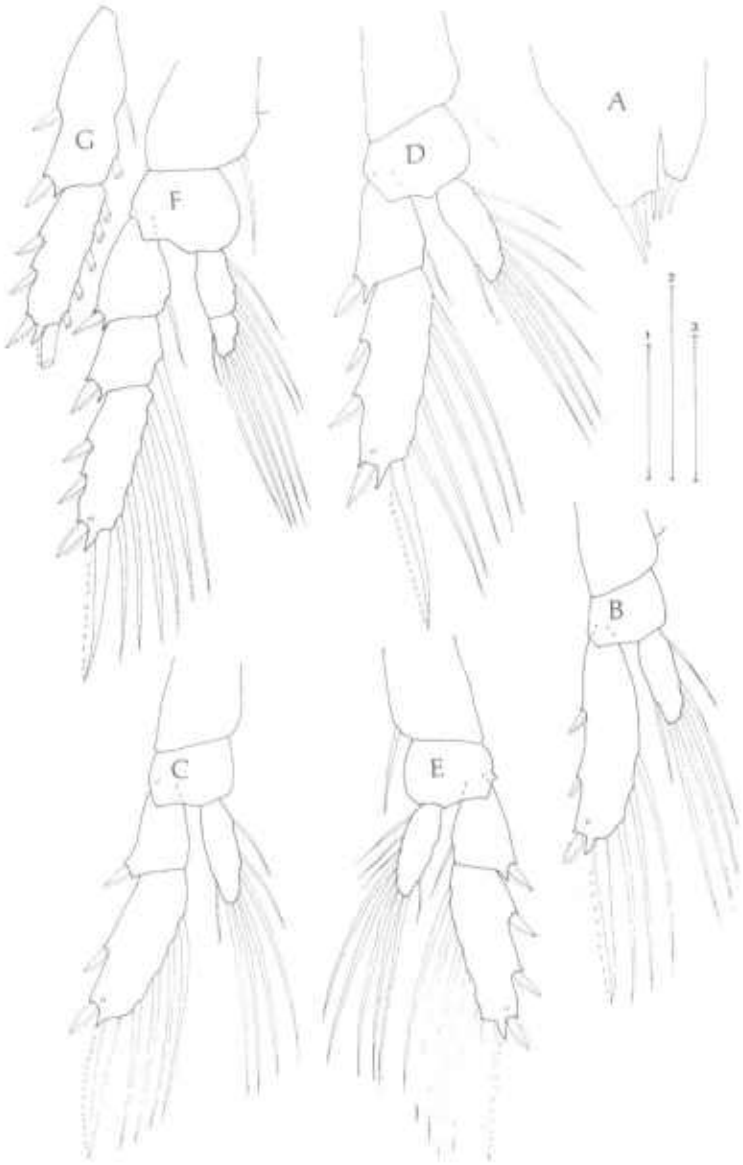

Fig. 4. *Temora longicornis* (Müller, 1792), swimming leg 2, posterior. A, N6; B, CI; C, CII; D, CIII; E, CIV; F, CV; G, CVI, exopod. Line 1 is 0.05 mm for A; line 2 is 0.10 mm for B, C, D; line 3 is 0.10 mm for E, F, G.

swimming legs 2 and 3 of *T. longicornis* (table XI) is similar to those of *D. oculata* except that formation of the arthrodial membrane between the proximal and distal segments is delayed until step D. Step E has been added to accommodate the subsequent loss of that membrane in the adult. Development of the endopod

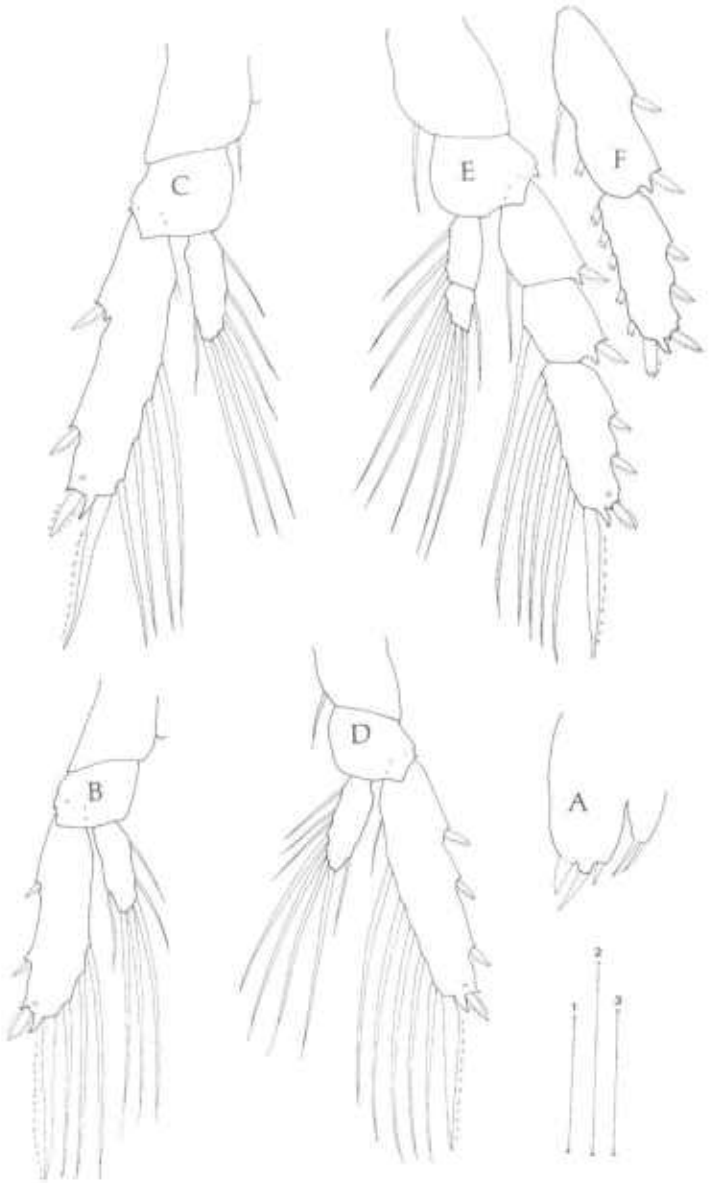

Fig. 5. *Temora longicornis* (Müller, 1792), swimming leg 3, posterior. A, CI; B, CII; C, CIII; D, CIV; E, CV; F, CVI, exopod. Line 1 is 0.05 mm for A; line 2 is 0.10 mm for B, C; line 3 is 0.10 mm for D, E, F.

of swimming legs 2 and 3 (tables XII and XIII) is similar to that of *D. oculata* (including a subdivision of step Z for swimming leg 2) with the exception that for both rami the arthrodial membrane between the proximal (second) and distal segments fails to form.

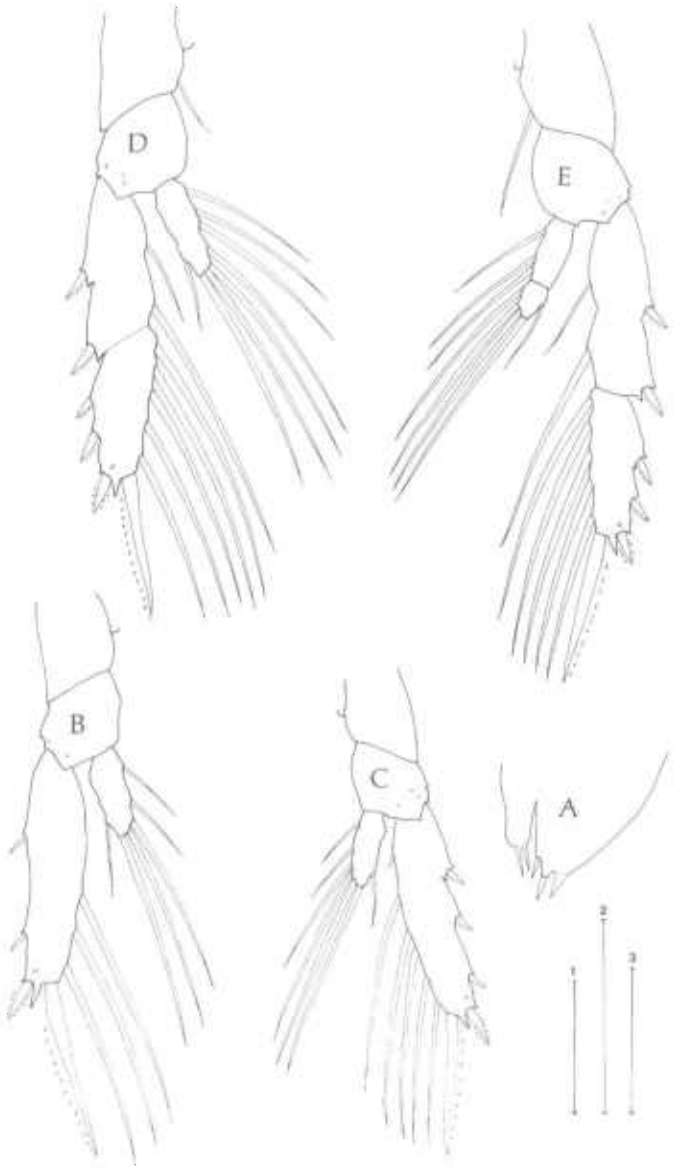

Fig. 6. *Temora longicornis* (Müller, 1792), swimming leg 4, posterior. A, CII; B, CIII; C, CIV; D, CV; E, CVI. Line 1 is 0.05 mm for A; line 2 is 0.10 mm for B; line 3 is 0.10 mm for C, D, E.

Development of the exopod of swimming leg 4 (table XIV) of *T. longicornis* is similar to that of *D. oculata* with the following exceptions: one more seta is added to the distal segment at step D; and an arthrodial membrane which would have separated the proximal and distal segments fails to form. Development of the endopod of swimming leg 4 (table XV) occurs during molts to CIII, CIV,

TABLE XIII

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 2 of *Temora longicornis* (Müller, 1792). Legend as for table I

Step	1	2	3	4	5
W	3	1			
X				1	
Y				1	
Z1	(1)				
Z2					+

TABLE XIV

Arthrodial membrane formation and number of setae added to the exopod of swimming leg 4 of *Temora longicornis* (Müller, 1792). Legend as for table I

Step	1	2	3	4	5
A	3	1			
B/C	1			2	
D	(2)	1			+

TABLE XV

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 4 of *Temora longicornis* (Müller, 1792). Legend as for table I

Step	1	2	3	4	5
W	3	1			
X				1	
Y				1	
Z					+

CV and CVI; steps Y and Z are not combined as they are in *D. oculata*, and the arthrodial membrane which would have separated the proximal and distal segments fails to form. Development of the exopod of swimming leg 1 (table XVI) of *T. longicornis* is similar to that of *D. oculata* but one more seta is added to the distal segment at step C/D, and the formation of the arthrodial membrane between the proximal and distal segments is delayed until step D. Step E has been added to accommodate the subsequent loss of that membrane. Development of the endopod of swimming leg 1 (table XVII) differs from that of *D. oculata*; it appears to have been truncated after step X.

TABLE XVI

Arthrodial membrane formation and number of setae added to the exopod of swimming leg 1 of *Temora longicornis* (Müller, 1792). Legend as for table XI

Step	1	2	3	4	5
A	2	1		1	
B			+	1	
C/D	(1)				+
E			–		

TABLE XVII

Arthrodial membrane formation and number of setae added to the endopod of swimming leg 1 of *Temora longicornis* (Müller, 1792). Legend as for table I

Step	1	2	3	4	5
W	2	1		1	
X			+		

DISCUSSION

Based on our hypothesized generalizations and the above analyses, variation in setal addition and allocation to the same serial appendage among the four species consists for swimming leg 1 of:

(1) one (for calanoids) or two (for the cyclopoid) setae added to the distal segment of the exopod at step C or C/D;
(2) no (*D. oculata* and *T. longicornis*) or one (*R. klausruetzleri* and *P. xiphias*) seta allocated to the middle segment of the endopod at step X;
(3) no (*P. xiphias* and *T. longicornis*) or one (*D. oculata* and *R. klausruetzleri*) seta added to the distal segment of the endopod at step Y;

for swimming leg 2 of:

(4) one (*R. klausruetzleri*) or two (*D. oculata*, *P. xiphias* and *T. longicornis*) setae added to the distal segment of the exopod at step D;
(5) no (*D. oculata* and *T. longicornis*) or one (*R. klausruetzleri* and *P. xiphias*) seta added to the distal segment of the endopod at step X;
(6) no (*R. klausruetzleri* and *P. xiphias*) or one (*D. oculata* and *T. longicornis*) seta added to the distal segment of the endopod at step Y;
(7) no (*D. oculata*), one (*T. longicornis*) or two (*R. klausruetzleri* and *P. xiphias*) setae added to the distal segment of the endopod at step Z;

for swimming leg 3 of:

(8) no (*D. oculata* and *T. longicornis*) or one (*R. klausruetzleri* and *P. xiphias*) seta added to the distal segment of the endopod at step X;

(9) no (*R. klausruetzleri* and *P. xiphias*) or one (*D. oculata* and *T. longicornis*) seta added to the distal segment of the endopod at step Y;

(10) no (*D. oculata*), one (*T. longicornis*) or two (*R. klausruetzleri* and *P. xiphias*) setae added to the distal segment of the endopod at step Z;

for swimming leg 4 of:

(11) one (for calanoids) or two (for the cyclopoid) setae added to the distal segment of the endopod at step D;

(12) no (*D. oculata* and *T. longicornis*) or one (*R. klausruetzleri* and *P. xiphias*) seta added to the distal segment of the endopod at step X;

(13) no (*D. oculata* and *T. longicornis*) or one (*R. klausruetzleri* and *P. xiphias*) seta added to the distal segment of the endopod at step Y/Z.

Variation in arthrodial membrane formation is distinctive for the calanoids *P. xiphias* and *T. longicornis*. For endopods of swimming legs 2-4 of *P. xiphias*, the arthrodial membrane separating the proximal segment is delayed until the molt to CV and synchronized with formation of the arthrodial membrane separating the middle and distal segments; the latter arthrodial membrane shows no variation from rami of other copepods. For *T. longicornis*, formation of the arthrodial membrane separating the middle and distal segments of the endopods of swimming legs 1-4 also exhibits no variation from rami of other copepods. However, the arthrodial membrane between the proximal and distal segment of the endopods of swimming legs 1-4 fails to form, resulting in a 2-segmented ramus peculiar to species of the centropagoidean families Acartiidae, Candaciidae, Parapontellidae, Pontellidae, Temoridae and Tortanidae whose proximal segment bears the setae of both the proximal and middle segments of a 3-segmented ramus (Giesbrecht, 1892: 334, pl. 17 fig. 13). Variation in formation of the arthrodial membrane between the proximal and distal segment of the exopods is more complex: for swimming leg 1 it forms at CII as is usual for the other copepods but then fails to form during the molt to CVI; for swimming legs 2-3 its formation is delayed until the molt to CV and synchronized with formation of the arthrodial membrane separating the middle and distal segments and fails to form during the molt to CVI (step E). It fails to form on swimming leg 4.

In attempting to derive composite models for the exopod and for the endopod (tables XVIII, XIX), we have allotted four steps for development of each ramus: A-D for the exopod and W-Z for the endopod. Formation of arthrodial membranes occurs at the second and fourth steps, i.e., steps B and D for the exopod

TABLE XVIII

Composite model of arthrodial membrane formation and number of setae added to the exopod of a copepod swimming leg. Legend as for table I

Step	1	2	3	4	5
A	3	1			
B	1		+		
C		1		2	
D	(1-2)				+

TABLE XIX

Composite model of arthrodial membrane formation and number of setae added to the endopod of a copepod swimming leg. Legend as for table I

Step	1	2	3	4	5
W	3	1			
X			+	1	
Y				1	
Z	(0-1)				+

and steps X and Z for the endopod. Additions of setae to the distal segment of the exopod occur during the first, second, and fourth steps, and during the first and fourth steps to the distal segment of the endopod. Those setae added in the fourth step may be allocated to a presumptive, but unarticulated, fourth segment (see Von Vaupel Klein, 1984) whose arthrodial membrane does not normally form in copepods.

The most significant problem for the composite models is a difference in setal allocation to the middle ramal segments between swimming leg 1 and swimming legs 2-4. The lateral seta of the presumptive middle segment of the exopod of swimming leg 1 is allocated at step A and its medial seta is allocated at step B. For the exopod of swimming legs 2-4 both setae are allocated at step C. For the composite exopod, we have adopted the latter set of events simply because it has more explanatory power. Allocation of the proximal and the distal (if present) medial setae on the middle segment of the endopod of swimming leg 1 occurs during step W and step X respectively. For swimming legs 2-4, these setae are allocated during step X and step Y, respectively. For the composite endopod, we again have adopted the latter set of events because it has greater explanatory power.

The developmental patterns for the exopod and endopod of swimming leg 1, and particularly the allocation of a seta to the middle (third) segment immediately after transformation of the leg bud, do not result from a simple change to the developmental patterns of swimming legs 2-4. In the case of the endopod of swimming leg 1, setae of the middle segment appear one step earlier than for

swimming legs 2-4. However, in the case of the exopod, the inner seta of the middle segment appears one step earlier than for swimming legs 2-4 but the outer seta appears two steps earlier. We also note that the bud of swimming leg 1 of calanoids and cyclopoids first appears at naupliar stage 6, the same stage as the first appearence of the bud of swimming leg 2, and one stage later than would be expected if the addition of each leg bud occurred in register and one stage later than the serial addition of its somite (Ferrari, unpubl. obs.). Subsequent additions of segments to swimming legs 1 and 2 also are synchronous (Ferrari, 1988). The developmental patterns of the rami of swimming leg 1 may be a derived condition linked to the synchronous development of swimming legs 1-2, or they may represent a state retained by copepods from an ancestor to the copepods.

The endopod of the maxilliped of many copepods, like the endopod of swimming legs 2-4, is 2-segmented or presumptively 2-segmented immediately after the transformation of its bud, and the proximal segment bears one inner seta (Ferrari & Dahms, 1998). Endopod development of leg 5 is suppressed for most podopleans like *D. oculata* and for many gymnoplean calanoids like *P. xiphias*, or if the endopod is present in calanoids the proximal segment is naked, e.g., in *R. klausruetzleri*. These presumably are derived states. The adult females of the arietelloidean *Lucicutia grandis* (Giesbrecht, 1895) has a 3-segmented endopod with a medial seta on the proximal segment. Immediately after transformation of its bud at CIV, the endopod of leg 5 is presumptively 2-segmented with one medial seta on the proximal segment (Ferrari, unpubl. obs.). These data suggest that the endopod of all thoracopods of the ancestral copepod immediately after the transformation of the leg bud was 2-segmented with one medial seta on the proximal segment. The developmental pattern for swimming leg 1 with its earlier allocation of a seta to the middle segment of both rami and its segmentation synchronous with swimming leg 2, is presumed to be derived.

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