

EXCEPTIONS TO THE RULE OF DEVELOPMENT THAT ANTERIOR IS OLDER AMONG SERIALY HOMOLOGOUS SEGMENTS OF POSTMAXILLIPEDAL LEGS IN COPEPODS

Frank D. Ferrari

ABSTRACT

A survey of more than 250 species of copepods shows about 4% of the rami on postmaxillipedal legs have a segment that is formed later in development, and therefore is younger, than homologous segments on legs located on more posterior body somites. These younger segments are exceptions to the general rule of development that, among serially homologous segments, those found on anterior legs are older than their homologues on more posterior legs. Exceptions to this rule occur more frequently on leg 1 than expected, and appear to have originated more than once during copepod evolution. These younger segments more often are added during the terminal adult molt, which is an unusual developmental pattern for copepods.

During copepodid development of copepods, new somites are added anteriorly from the posteriormost somite (Hulsemann, 1991; Huys and Boxshall, 1991; Izawa, 1991). As a result of this process, successively older somites are located more anteriorly along the body. Izawa (1991) documented exceptions to this rule for somites in some members of the order Poecilostomatoida. New segments of each postmaxillipedal leg (hereafter "leg") on a thoracic somite are added proximally from the distalmost segment (Hulsemann, 1991; Ferrari and Ambler, 1992) (Fig. 1). All of the legs on the body of a copepod often exhibit a coordinated pattern of development; the addition of a segment on any leg usually is one stage of development out of register with the addition of its serial homologues on legs immediately anterior and posterior (Ferrari, 1988). Thus, for segments on serially homologous legs, an "anterior-is-older" rule applies, because successively older segments are encountered more anteriorly along the anterior-posterior axis of the body (Fig. 2). A corollary to this rule follows: changes in leg morphology one copepodid stage forward in time can be predicted from the morphology of the leg found one somite anteriorly in space.

While developmental patterns of legs 1-4 are similar among species of the same copepod genus (Ferrari, 1991, for information about 10 species of *Labidocera*), many differences among genera have been documented (Ferrari, 1988). These differ-

ences are responsible for exceptions to the coordinated pattern of development (Ferrari, 1988), and some of these expectations vitiate the strict anterior-is-older polarity. For example, in *Tropodiptomus informis* the endopod of leg 1 is 1-segmented on copepodid II (CII) and the endopod of leg 2 is 2-segmented (Fig. 3). During the molt to CIII a second, proximal, segment is added to the endopod of leg 1 (Rama Devi and Ranga Reddy, 1990). This second segment is homologous to the proximal endopodal segment of leg 2, and is younger than its posterior homologue on leg 2, because it is added later in development.

This paper documents this and similar kinds of exceptions to an anterior-is-older rule of development which result in leg segments that are younger than a posterior homologue (hereinafter "younger-anterior" segments). The frequency of these younger-anterior segments is described, and their occurrence among copepod taxa is discussed.

MATERIALS AND METHODS

In this paper legs 1-6 are identified as the appendages of thoracic somites 2-7; they include the swimming legs on thoracic somites 2-5. These legs develop during the last nauplius and copepodid stages. Information presented here was retrieved from a database of developmental patterns of these legs for copepod genera. Data about a genus have been entered into the database if 3 or more stages of development are known for 1 or more species in that genus. Each developmental stage is a record in the database; more than 1 record per stage is entered if bilateral asymmetry or sexual dimorphism are expressed in that stage. If 2 or more different patterns of leg development have been de-

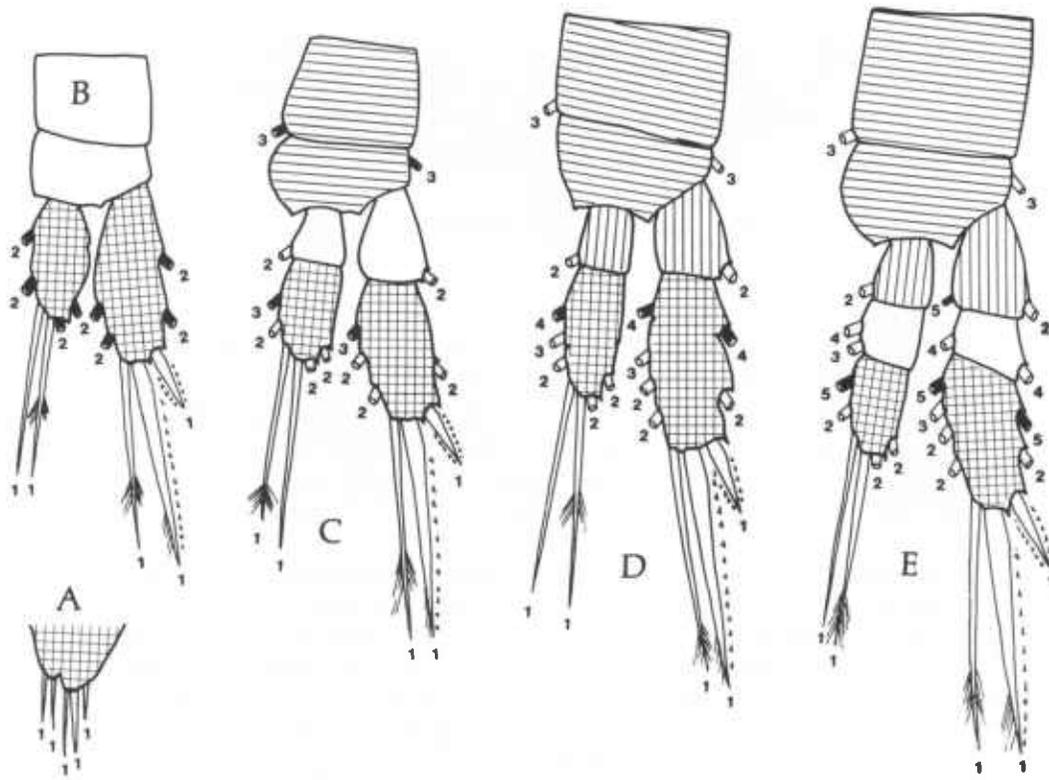


Fig. 1. Development of leg 3 of *Dioithona oculata* (from Ferrari and Ambler, 1992): A, primary bud of copepodid I with 3 setae on outer lobe and 2 setae on inner lobe; B-E, reorganized legs of copepodids II-V, respectively. Oldest segment cross-hatched, youngest segment clear, oldest intermediate segment 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.

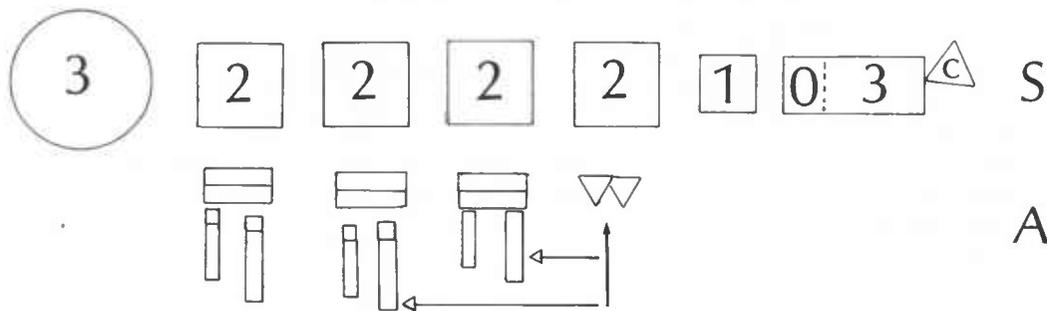


Fig. 2. Schematic illustration of somites, somite complexes (S line), and postmaxillipedal legs (A line) for CII of *Dioithona oculata*. Circle is a complex of 5 cephalic plus first thoracic somites, and bears premaxillipedal legs and maxilliped; somites are square; terminal somite is rectangular (c is caudal ramus). Numbers in somites indicate presumed relative ages (after Ferrari and Ambler, 1992); 1 is youngest somite, 0 indicates proximal part of distalmost somite which will form the new somite of CIII. The relative age of a somite is assigned when that somite appears during development, not when the appendages of the somite appear. A leg bud is represented by interlocking triangles; basipodal segments are horizontal bars; rami are vertical bars; exopod is right branch and endopod is left branch. Vertical arrow is on bud of leg 4; short horizontal arrow indicates the morphology of that leg one stage forward in time (=one somite anteriorly in space); long horizontal arrow indicates the morphology of that leg two stages forward in time (=two somites anteriorly in space).

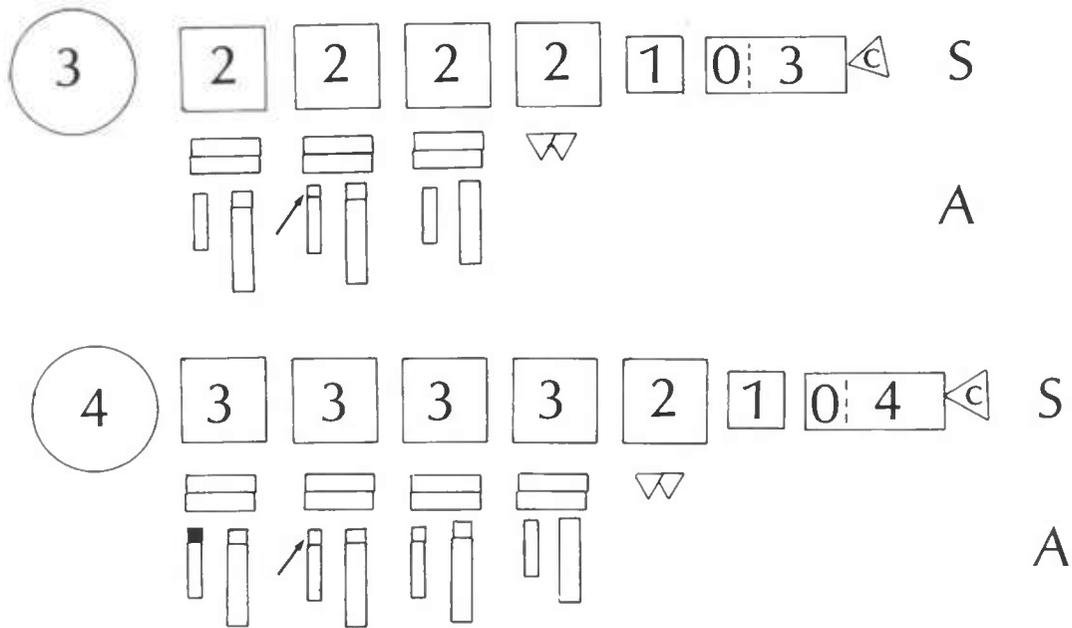


Fig. 3. Schematic illustration of changes in somites, somite complexes (S line), and postmaxillipedal legs (A line) of *Tropodiaptomus informis* from CII (top) to CIII (bottom). The second endopodal segment on leg 1 of CIII (dark) is younger than its homologue on leg 2 (arrow), because the latter already is present on CII (arrow). Numbers and other symbols as in Fig. 2.

scribed among species within a genus, each unique pattern has been entered. The database at present comprises segment numbers for legs in 273 species of 236 genera belonging to 87 families in 7 of the 10 known orders of copepods. Further information about the database, including a list of taxa and sources for descriptions of legs, is available from the author.

Because not all stages of development have been described for all of the copepods represented in the database, these numbers of developmental patterns for the following legs are available for analysis: leg 1 = 177, leg 2 = 177, leg 3 = 175, leg 4 = 179, leg 5 = 178. The present survey involves 708 cases known for any of legs 1-4. Leg 5 is not included in the analysis of younger-anterior segments; segments on leg 5 are never younger than homologues on leg 6 because leg 6 does not develop beyond the earliest leg bud condition.

In this paper, numerical designations of homologous segments on the rami of legs are not proximal-to-distal as is the usual case for copepod descriptions. Instead, numerical designations follow the developmental age of ramal segments, and are defined as follows (see Fig. 1). The homologue of the single segment of a 1-segmented ramus is the distal-most segment of a 2- or 3-segmented ramus; it is accordingly called the *first* segment. The *second* segment of a 2-segmented leg is proximal to the distal segment and immediately distal to the basipod. This *second* segment has no homologue in a 1-segmented ramus; in a 3-segmented ramus its homologue also is immediately distal to the basipod. The *third* segment of a 3-segmented ramus is immediately proximal to the distal-most segment and has no homologue in a 2-segmented or 1-segmented ramus.

Thus, in a 3-segmented ramus, the proximal segment is the *second* segment, the middle segment is the *third* segment, and the distal segment is the *first* segment.

RESULTS

Among 708 legs, 25 (4%) have an endopodal segment that is younger than at least one of its posterior homologues (Table 1). These 25 endopods are found on 24 copepod species, and a majority, 19, of these younger-anterior endopodal segments occur on leg 1. On 22 of these 25 endopods, the younger-anterior segment is the last one formed during development, and in 11 of these 22 cases that segment is the third (middle) endopodal segment. In 9 of 25 endopods, a younger-anterior segment appears during the molt to CVI. Among the 19 cases for which a younger-anterior segment is found on the endopod of leg 1, in 6 of those cases, that younger-anterior segment is younger than its homologues on all posterior legs (legs 2-5); 3 of 3 cases are known in which a segment on leg 2 is younger than all posterior homologues.

There are 22 of 708 legs (3%) with an exopodal segment younger than at least one of its posterior homologues (Table 2). These

Table 1. Copepods with an endopodal segment that is younger than at least one of its posterior homologues. Sg is the younger-anterior segment; Lg is the postmaxillipedal leg on which that segment occurs; St is the copepodid stage (I–VI) during which the younger-anterior segment initially appears. Ls indicates whether the younger-anterior segment is the last one formed on that ramus; 2, 3, 4 indicate the posterior legs which possess older segments. y = yes, n = no, u = not applicable for that leg, m = male only.

Genus	Species	Lg	Sg	St	Ls	2	3	4
<i>Aglaodiaptomus</i>	<i>clavipes</i>	1	2	4	y	y	y	n
<i>Allodiaptomus</i>	<i>raoi</i>	1	2	3	y	y	n	n
<i>Megadiaptomus</i>	<i>pseudohebes</i>	1	2	3	y	y	n	n
<i>Notodiaptomus</i>	<i>conifera</i>	1	2	3	y	y	n	n
<i>Paradiaptomus</i>	<i>greeni</i>	1	2	2	y	y	n	n
<i>Tropodiaptomus</i>	<i>informis</i>	1	2	3	y	y	n	n
<i>Chiridius</i>	<i>armatus</i>	2	2	6	y	u	y	y
<i>Gaetanus</i>	<i>kruppi</i>	2	2	5	y	u	y	y
<i>Parvocalanus</i>	<i>crassirostris</i>	1	2	5	y	y	y	y
<i>Neocalanus</i>	<i>tonsus</i>	3	3	6	y	u	u	y
<i>Undinula</i>	<i>vulgaris</i>	1	2	3	n	y	n	n
<i>Parastenocaris</i>	<i>phyllura</i>	3	1	6	y	u	u	y
<i>Paramphiascella</i>	<i>fulvofasciata</i>	1	3	6	y	y	y	y
<i>Schizopera</i>	<i>knabeni</i>	1	3	6	y	y	y	y
<i>Diarthrodes</i>	<i>cystoecus</i>	1	3	5	y	n	y	y
<i>Diarthrodes</i>	<i>cystoecus</i>	2	3	5	y	u	y	y
<i>Thalestris</i>	<i>longimana</i>	1	3	6	y	y	y	y
<i>Platychelipus</i>	<i>littoralis</i> m	3	1	5	n	u	u	y
<i>Alteutha</i>	<i>interrupta</i>	1	2	3	n	y	n	n
<i>Tisbe</i>	<i>longisetosa</i>	1	3	6	y	y	y	y
<i>Diacyclops</i>	<i>bicuspidatus</i>	1	3	6	y	y	y	y
<i>Macrocyclops</i>	<i>albidus</i> m	1	3	5	y	n	y	n
<i>Thermocyclops</i>	<i>minutus</i>	1	3	5	y	y	y	n
<i>Taeniacanthus</i>	<i>legocephali</i>	1	2	3	y	y	n	n
<i>Caligus</i>	<i>spinosus</i>	1	1	6	y	y	y	n

exopods are found on 19 species, 9 of which also have a younger-anterior endopod. Eighteen of the younger-anterior exopodal segments are found on leg 1. Among these 18 cases, in 11 the younger-anterior segment is younger than its homologues on all posterior legs (legs 2–5). There are no known cases in which a segment on leg 2 is younger than its homologues on all posterior legs. On 18 of 22 exopods the younger-anterior segment is the last one formed during development and in 15 of these cases that segment is the third (middle) exopodal segment. On 8 of 22 exopods, the younger-anterior segment appears during the molt to CVI.

DISCUSSION

Incidences of younger-anterior ramal segments are significant for three reasons: (1) there is a greater number of incidences for leg 1 than leg 2; (2) younger-anterior segments occur frequently during the molt to CVI; and (3) incidences are not confined to particular orders, suborders, or superfamilies.

Segment additions to rami of legs 1 and 2 are identical during the development of many copepods (Ferrari, 1988). Buds of these two legs usually appear at the last naupliar stage and segment additions are synchronous. If the occurrence of a younger-anterior segment is equally probable for these two synchronously developing legs, then leg 1 should exhibit about one-third (1.33 times) more cases because there are four posterior legs which may have older, serial homologues, as opposed to only three posterior legs for leg 2. However, the appearance of a younger-anterior segment is 6.2 times more likely to occur on leg 1 than on leg 2; among 47 cases, 37 are reported for leg 1 and only 8 for leg 2.

The addition of a younger-anterior segment occurs during the molt to CVI in 17 of 47 rami (36%). Changes in segment numbers during this molt usually are rare among copepods (Ferrari, 1988). There are 287 species whose leg-segment number is known for both CV and CVI; 12 species also exhibit sexual dimorphism in segment number. Among these 299 cases, each with four legs

Table 2. Copepods with an exopodal segment that is younger than at least one of its posterior homologues. Abbreviations as in Table 1.

Genus	Species	Lg	Sg	St	Ls	2	3	4
<i>Acartia</i>	<i>californiensis</i>	1	3	6	y	y	y	y
<i>Acartia</i>	<i>clausi</i>	1	3	6	y	y	y	y
<i>Aglaodiaptomus</i>	<i>clavipes</i>	1	3	5	y	n	y	n
<i>Aglaodiaptomus</i>	<i>clavipes</i>	2	3	5	y	u	y	n
<i>Eudiaptomus</i>	<i>vulgaris</i>	2	2	4	n	u	y	n
<i>Paradiaptomus</i>	<i>greeni</i>	1	2	2	n	y	n	n
<i>Tumediaptomus</i>	<i>diabolicus</i>	1	3	5	y	y	y	y
<i>Euchirella</i>	<i>maxima</i>	1	2	5	y	y	y	y
<i>Euchirella</i>	<i>messinensis</i>	1	2	5	y	y	y	y
<i>Gaetanus</i>	<i>kruppi</i>	1	2	5	n	y	y	y
<i>Euchaeta</i>	<i>japonica</i>	1	2	5	y	y	y	y
<i>Euchaeta</i>	<i>japonica</i> m	1	3	6	y	y	y	y
<i>Neocalanus</i>	<i>tonsus</i>	3	3	6	y	u	u	y
<i>Parastenocaris</i>	<i>phyllura</i>	1	3	5	y	y	n	y
<i>Diarthrodes</i>	<i>cystoecus</i>	1	2	5	y	y	n	n
<i>Noodorthopsyllus</i>	<i>stocki</i> m	1	3	6	y	y	y	y
<i>Saccodiscus</i>	<i>ovalis</i>	1	2	2	n	y	n	n
<i>Diacyclops</i>	<i>bicuspidatus</i>	1	3	6	y	y	y	y
<i>Macrocyclus</i>	<i>albidus</i> m	1	3	5	y	n	y	n
<i>Macrocyclus</i>	<i>albidus</i> m	2	3	5	y	u	y	n
<i>Thermocyclops</i>	<i>minutus</i>	1	3	6	y	y	y	n
<i>Lamproglena</i>	<i>chinensis</i> m	1	3	6	y	y	y	y

of two rami each, only 173 of the resulting 2,392 rami (7%) change segment numbers during the molt to CVI. A change of segment numbers during the molt to CVI will involve the addition of a younger-anterior segment about 5 times more frequently.

Most examples of younger-anterior segments reported to date are found in the copepod orders Calanoida and Harpacticoida. The evolution of younger-anterior segments has originated independently more than once within copepod orders, because their developmental patterns are not restricted to specific orders in the way that legs with unequal numbers of ramal segments are (Ferrari, 1992a). Among calanoid superfamilies, younger-anterior exopods and endopods are found in the Diaptomidae and the Acartiidae of the Centropagoidea, the Euchaetidae and the Aetideidae of the Clausocalanoidea, and the Calanidae of the Megacalanoidea. These occurrences are not restricted to closely related families, because derived families of the Clausocalanoidea are not close relatives of the Centropagoidea or the Megacalanoidea (Park, 1986; Mauchline, 1988). Among harpacticoid superfamilies, younger-anterior exopods are found in the Parastenocaridae of the Ameiroidea, the Cristacoxidae of the Laophonoidca, the Thalestridae and the Diosacci-

dae of the Thalestroidea, and the Tisbidae of the Tisboidea. Younger-anterior endopods occur in the first three superfamilies. These superfamilies are distributed among all infraorders (Bowman and Abele, 1982) of Lang's (1948) oligarthra harpacticoids. A determination of whether younger-anterior segments are restricted to related genera within the above-mentioned families must await descriptions of the development of more calanoid and harpacticoid genera.

The occurrence and frequency of patterns of leg development which result in younger-anterior segments or legs with unequal numbers of ramal segments (Ferrari, 1992a) provide information about the diversity and unique features of copepod development. Knowledge about these developmental patterns also contributes to a framework for future studies of the developmental genetics of body somites and appendage segments in these and other arthropods. This framework in turn will provide a better understanding of character transformations and convergences, which will contribute to correct phylogenetic inferences (Ferrari, 1992b).

ACKNOWLEDGEMENTS

This paper is dedicated to Kuni Hulsemann, Biologische Anstalt Helgoland, whose research has emphasized the relationship between a linear arrangement of

copepod somites and segments and their developmental age, and to Edward Lewis, California Institute of Technology, whose model of insect development suggests a relationship between a linear arrangement of insect somites and the regulation of their development. I thank Dr. Thomas E. Bowman and Dr. Janet Reid of the Smithsonian Institution, Dr. Hans-Uwe Dahms of the University of Waterloo, and Dr. Mark Grygier of the University of The Ryukyus for their valuable comments and suggestions.

LITERATURE CITED

- Bowman, T., and L. Abele. 1982. Classification of the Recent Crustacea.—In: D. E. Bliss, editor-in-chief, The biology of Crustacea. Vol. 1, L. G. Abele, ed., Systematics, the fossil record, and biogeography. Pp. 1–27. Academic Press, New York, New York.
- Ferrari, F. 1988. Developmental patterns in numbers of ramal segments of copepod post-maxillipedal legs.—*Crustaceana* 54: 256–293.
- . 1991. Using patterns of appendage development to group taxa of *Labidocera*, Diaptomidae and Cyclopidae (Copepoda).—*Bulletin of the Plankton Society of Japan, Special Volume*, pp. 115–127.
- . 1992a. Development of copepod swimming legs with unequal numbers of ramal segments.—*Journal of Crustacean Biology* 12: 392–396.
- . 1992b. The antennal exopod of *Noodtorhopsyllus* and the next evolutionary synthesis (Copepoda).—*Crustaceana* 61: 128–132.
- , and J. Ambler. 1992. Nauplii and copepodids of the cyclopoid copepod *Dioithona oculata* (Oithonidae) from a mangrove cay in Belize.—*Proceedings of the Biological Society of Washington* 105: 275–298.
- Hulsemann, K. 1991. The copepodid stages of *Drepanopus forcipatus* Giesbrecht, with notes on the genus and a comparison to other members of the family Clausocalanidae (Copepoda Calanoida).—*Helgoländer Meeresuntersuchungen* 45: 199–224.
- Huys, R., and G. Boxshall. 1991. Copepod evolution.—The Ray Society, London, England. Pp. 1–648.
- Izawa, K. 1991. Evolutionary reduction of body segments in the poecilostome Cyclopoida (Crustacea: Copepoda).—*Plankton Society of Japan, Special Volume*, pp. 71–88.
- Lang, K. 1948. *Monographie der Harpacticiden*.—Two volumes, pp. 1–1682. Håkan Ohlsson, Lund, Sweden.
- Mauchline, J. 1988. Taxonomic value of pore pattern in the integument of calanoid copepods (Crustacea).—*Journal of Zoology* 214: 697–749.
- Park, T. 1986. Phylogeny of calanoid copepods.—*Syllogeus* 58: 191–196.
- Rama Devi, C., and Y. Ranga Reddy. 1990. The complete postembryonic development of *Tropodiptomus informis* Kiefer, 1936 (Copepoda: Calanoida) reared in the laboratory.—*Journal of Plankton Research* 12: 55–75.

RECEIVED: 8 September 1992.

ACCEPTED: 4 January 1993.

Address: Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.