

# Antennular development during the copepodid phase in the family Cyclopidae (Copepoda, Cyclopoida)

**Maria Luisa Motta SCHUTZE**

Instituto de Ciências Biológicas e Ambientais,  
Universidade Santa Úrsula, Rua Fernando Ferrari, 75,  
22231-040 Rio de Janeiro (Brazil)  
mlmschutze@ax.apc.org.br

**Carlos Eduardo Falavigna da ROCHA**

Departamento de Zoologia, Instituto de Biociências,  
Universidade de São Paulo, Caixa Postal 11461,  
05422-970 São Paulo (Brazil)  
cefrocha@usp.br

**Geoffrey A. BOXSHALL**

Department of Zoology, The Natural History Museum,  
Cromwell Road, London SW7 5BD (United Kingdom)  
g.boxshall@nhm.ac.uk

Schutze M. L. M., Rocha C. E. F. da & Boxshall G. A. 2000. — Antennular development during the copepodid phase in the family Cyclopidae (Copepoda, Cyclopoida). *Zoosystema* 22 (4) : 749-806.

## ABSTRACT

The development of the antennules through the copepodid phase to adult female was studied in 35 species representing to 29 genera of the subfamilies Euryteinae, Halicyclopiniae, Eucyclopiniae and Cyclopiniae of the family Cyclopidae. The homology of the antennular segments was established by comparing the distribution of the setae on each expressed segment with reference to the position of particular elements recognized here as markers. Ten developmental patterns were recognized. The most common pattern generates adult female antennules with 11 to 17 expressed segments, and is found in *Cyclops* sp., *Megacyclops viridis* s.l., *Acanthocyclops* sp., *Mesocyclops meridianus*, *Thermocyclops decipiens*, *Kieferiella delamarei*, *Macrocyclus albidus albidus*, *Troglocyclops janstocki*, *Diacyclops bicuspidatus odessanus*, *D. uruguayensis*, *Metacyclops laticornis*, *M. hirsutus*, *Microcyclus anceps anceps*, *M. ceibaensis*, *M. alius*, *Apocyclops dengizicus*, *Hesperocyclops stocki*, *Speocyclops racovitzaei*, *Graeteriella (Graeteriella) brehmi*, *Bryocyclops caroli*, *Muscocyclops operculatus* and *Fimbricyclops jimhensoni*. A second pattern was shared by *Tropocyclops schubarti schubarti*, *Cryptocyclops linjanticus* and *Apocyclops procerus*. The third pattern links together *Neutrocyclops* sp. and *Alloccyclops*

**KEY WORDS**Cyclopidae,  
copepodid,  
antennule,  
development.

*silvaticus*, *Afrocylops gibsoni*, *Ancheuryte notabilis*, *Eucyclops (Eucyclops) ensifer*, *Neocylops (Neocylops) vicinus*, *Paracyclops chiltoni*, *Halicyclops aberrans* and two species of *Ectocylops* (*E. strenzkei* and *E. rubescens*), each having unique development patterns. After the moult to copepodid I, new segments are formed only in the median and proximal regions of the antennule. An increase in the number of segments due to the expression of new intersegmental articulations was commonly observed during the ontogeny of the antennules. Reduction in expressed segment numbers occurred within phylogenetic lineages due to failure of expression of intersegmental articulations, but fusion of previously separate segments was never observed in females. Eight species of Cyclopinae and one of Halicyclopinae have neotenic antennules in which segmentation patterns typical of earlier copepodid stages are retained in adults. The significance of antennular developmental data in establishing a robust scheme of phylogenetic relationships between the taxa within the Cyclopidae is emphasized.

**RÉSUMÉ**

*Développement des antennules des copépodites dans la famille Cyclopidae (Copepoda, Cyclopoidea).*

Le développement des antennules des copépodites femelles dans la famille des Cyclopidae a été étudié chez 35 espèces appartenant à 29 genres des sous-familles Euryteinae, Halicyclopinae, Eucyclopinae et Cyclopinae. L'homologie des articles antennulaires a été établie en comparant l'arrangement des soies de chaque article avec la présence d'éléments d'ornementation reconnus ici comme marqueurs. Dix modèles de développement ont été dénombrés. Le modèle le plus fréquent concerne les antennules avec 11 à 17 articles chez les femelles adultes. Ce modèle a été trouvé chez *Cyclops* sp., *Megacyclops viridis* s.l., *Acanthocylops* sp., *Mesocylops meridianus*, *Thermocylops decipiens*, *Kieferiella delamarei*, *Macrocylops albidus albidus*, *Troglocylops janstocki*, *Diacylops biscupidatus odessanus*, *D. uruguayensis*, *Metacylops laticornis*, *M. hirsutus*, *Microcylops anceps anceps*, *M. ceibaensis*, *M. alius*, *Apocylops dengizicus*, *Hesperocylops stocki*, *Speocylops racovitzai*, *Graeteriella (Graeteriella) brehmi*, *Bryocylops caroli*, *Muscocylops operculatus* et *Fimbricylops jimbenoni*. Le deuxième modèle est trouvé chez *Tropocylops schubarti schubarti*, *Cryptocylops linjanticus* et *Apocylops procerus*. Le troisième modèle réunit *Allocylops silvaticus* et *Neutrocylops* sp. Des modèles uniques de développement ont été respectivement trouvés chez *Afrocylops gibsoni*, *Ancheuryte notabilis*, *Eucyclops (Eucyclops) ensifer*, *Neocylops (Neocylops) vicinus*, *Paracyclops chiltoni*, *Halicyclops aberrans* et en deux espèces de *Ectocylops* (*E. strenzkei* et *E. rubescens*). Après la mue en copépodite I, de nouveaux articles se forment seulement dans les régions médiane et proximale de l'antennule. Une augmentation du nombre d'articles due à l'expression des nouvelles articulations entre les articles a souvent été observée pendant l'ontogénie des antennules. Une réduction du nombre d'articles se produit dans certaines lignées phylogénétiques du fait de l'échec de l'expression d'articulations entre les articles, mais la fusion de segments précédemment séparés n'a jamais été observée chez les femelles. Huit espèces de Cyclopinae et une d'Halicyclopinae présentent des antennules néoténiques. Les informations sur le développement des antennules sont très importantes comme source de nouveaux caractères pour la reconstruction phylogénétique chez les Cyclopidae.

**MOTS CLÉS**Cyclopidae,  
copépodite,  
antennule,  
développement.

## INTRODUCTION

The first attempts to trace the homologies of the antennular segments of copepods were based exclusively on the comparative morphology of these appendages in adults (Giesbrecht 1892, 1899; Claus 1893; Mrázek 1893; Burckhardt 1913; Sewell 1949).

The highest number of antennular segments in an adult female copepod described to date (27) is found in the Calanoida and Misophrioida (Huys & Boxshall 1991). Based on the structure of the antennules of calanoid copepods, Gurney (1931) concluded that the antennule of the ancestral copepod consisted of 27 or 28 segments. Comparing calanoid and misophrioid antennules, Boxshall (1983) proposed that the antennule of the ancestral copepod consisted of 28 segments. This number has since been used in different studies concerning the homology of antennular segments in copepods (Huys & Boxshall 1991).

The assumption that the evolution of copepods has proceeded predominantly by oligomerisation has always been present in studies on the phylogeny of the group. In the Cyclopidae, antennules with 21 segments, the largest number yet recorded in the family, are found in species of *Euryte* Philippi, 1843. Ho (1986) considered the antennule of *Euryte* to be the most plesiomorphic in the family. Similarly, the 26-segmented antennule of the adult female of the cyclopinid *Cyclopicina longifurcata* (Scott, 1901) was referred to as the most plesiomorphic state for the order Cyclopoidea by Huys & Boxshall (1991). Similarly, Reid (1993) defined as plesiomorphic the antennules of 16 or 17 segments within the Cyclopininae, a subfamily of Cyclopidae. Such treatments indicate that, in the evolution of copepods, the most widely accepted process has been the trend towards the fusion and reduction in number of segments; the multi-segmented antennule being inferred to be more primitive than the antennule with few expressed segments (Boxshall *et al.* 1984).

The derivation of the antennular segments through development in cyclopid copepodids was first followed by Gurney (1933), using stages

of *Cyclops* Muller, 1776, *Halicyclops* Norman, 1903 and *Euryte*. Karaytug & Boxshall (1996) vertically traced the homologies of the antennular segments through from copepodid I to adult in both sexes of *Paracyclops chiltoni* as *P. fimbriatus*. For other groups of copepods, developmental studies have been provided by Haq (1965), Dahms (1989) and Huys & Böttger-Schnack (1994) in harpacticoids, Ferrari & Benforado (1998) in three species of calanoids, and Boxshall & Huys (1998) who established a model of antennular development in copepods after comparative study of representatives of six orders, Calanoida, Platycopioidea, Misophrioida, Siphonostomatoida, Poecilostomatoida and Harpacticoida.

The pioneering developmental study of the swimming legs through the copepodid phase, by Ferrari (1988), was the first to demonstrate conclusions concerning phylogenetic relationships, based on development rather than simply relying on adult morphology. Ho (1990) also emphasized the potential of developmental patterns as characters in his cladistic analysis of the relationships between the copepod orders.

The number of antennular segments in adult female cyclopids has long been considered to be a taxonomically important character. For each taxon described, the number of antennular segments is usually mentioned, but no reference is made to the development or to the homology of those segments. Such a procedure renders impossible the adequate use of segmental data in evaluating the systematics of the group.

The aims of this paper are to describe the development of the antennule through the copepodid phase of several genera of cyclopids, to establish the homologies of the segments, and to identify patterns of antennular development within the family.

## MATERIAL AND METHODS

Copepodids and adult females were selected from existing preserved samples in the collections of the Department of Zoology of the University of

São Paulo, or were obtained from foreign institutions by donation or loan.

Material of one or more species of as many genera as possible from each of the four subfamilies of Cyclopidae was selected. Specimens of 35 species representing 29 genera were studied, and these are distributed across the subfamilies as follows: one species of Euryteinae, three of Halicyclopininae, seven of Eucyclopinae and 24 of Cyclopinae.

SPECIES STUDIED AND COLLECTION DATA

*Ancheuryte notabilis* Herbst, 1989.

Brazil. Vitória Island, State of São Paulo, 1.1993, coll. J. M. M. Nogueira.

*Halicyclops aberrans* Rocha, 1983.

Brazil. Guamá River, Bujarú, State of Pará, 17.XII.1983, coll. M. L. Carvalho.

*Neocyclops (Neocyclops) vicinus* (Herbst, 1955).

Brazil. Segredo Beach, São Sebastião, State of São Paulo, 12.II.1985, coll. C. E. F. da Rocha.

*Troglocyclops janstocki* Rocha & Iliffe, 1994.

Bahamas. Hatcher Bay Cave, Eleuthera Island, 15.VI.1986, coll. T. M. Iliffe.

*Macrocyclus albidus albidus* (Jurine, 1820).

Brazil. Itingussu River, Iguape, State of São Paulo, 12.II.1985, coll. C. E. F. da Rocha.

*Eucyclops (Eucyclops) ensifer* Kiefer, 1936.

Brazil. Jaraguá State Park, São Paulo, 6.VII.1994, coll. C. E. F. da Rocha.

*Afrocyclus gibsoni* s.l. (Brady, 1904).

Israel. 'En Tamar, 24.II.1967, coll. Y. Cohen, copepods I to IV and adult female. — Lago Hula, 15.II.1995, coll. F. D. Por, copepodid V.

*Tropocyclops schubarti schubarti* (Kiefer, 1935).

Brazil. Itabaiana Massif (in bromeliad pools), State of Sergipe, 6.XI.1993, coll. C. E. F. da Rocha.

*Paracyclops chiltoni* (Thomson, 1882).

Brazil. Itabaiana Massif (in moss), State of Sergipe, 6.XI.1993, coll. C. E. F. da Rocha.

*Ectocyclops strenzkei* Herbst, 1959.

Brazil. Piçarra, State of Santa Catarina (in bromeliad pools), 23.I.1990, coll. C. E. F. da Rocha.

*Ectocyclops rubescens* Brady, 1904.

Brazil. Boracéia Biological Station, Salesópolis, State of São Paulo, 7.VIII.1986, coll. C. E. F. da Rocha.

*Cyclops* sp.

Hungary. Szarvas, 46°50'N, 20°30'E, 29.V.1992, coll. M. Holyńska, adults; 6.I.1994, copepodids.

*Megacyclops viridis* s.l. (Jurine, 1820).

Israel. 'Ein Duyuk, near Dead Sea, 2.III.1984, coll. Y. Spira.

*Acanthocyclops* sp.

Hungary. Szarvas, 46°50'N, 20°30'E, 29.VIII.1989, coll. M. Holyńska.

*Diacyclops bicuspidatus odessanus* (Schmankevitch, 1875).

Israel. Ma'agar Zin, near Dead Sea, 12.IV.1994, coll. Ch. Dimentmann.

*Diacyclops uruguayensis* Kiefer, 1935.

Brazil. Piçarras (among decaying leaves on moist soil), State of Santa Catarina, 23.I.1990, coll. C. E. F. da Rocha.

*Metacyclops laticornis* (Lowndes, 1934).

Brazil. Miranda River, Bodejão Bay, Corumbá State of Mato Grosso do Sul, 20.VII.1994, coll. C. E. F. da Rocha.

*Metacyclops hirsutus* Rocha, 1994.

Brazil. Comprida Island, State of São Paulo, 24°37'S, 47°30'W, 9.VI.1991, coll. C. E. F. da Rocha.

*Microcyclops anceps anceps* (Richard, 1897).

Brazil. Quirino Lake, Paraíba do Sul River, Jacareí, State of São Paulo, 27.I.1993, coll. CETESB staff.

*Microcyclops alius* Kiefer, 1935.

Brazil. Quirino Lake, Paraíba do Sul River, Jacareí, State of São Paulo, 27.I.1993, coll. CETESB staff.

*Microcyclops ceibaensis* (Marsh, 1920).

Brazil. Miranda River, Bodejão Bay, Corumbá, State of Mato Grosso do Sul, 2.III.1993, coll. C. E. F. da Rocha.

*Cryptocyclops linjanticus* (Kiefer, 1928).

Israel. 'En Tamar, 2.II.1967, coll. Y. Cohen.

*Apocyclops procerus* (Herbst, 1955).

Brazil. Rodrigo de Freitas Lagoon, State of Rio de Janeiro, without date or collector.

*Apocyclops dengizicus* (Lepeschkin, 1900).

Mexico. Laguna Salgada, Vale de Cuatro Ciénegas, Coahuyla State, without date, coll. A. Z. Valdez.

*Hesperocyclops stocki* (Pesce, 1985).

Anguilla. Island Harbour, 3.III.1989, coll. Natan, J. W. Reid det. (USNM-250584).

*Mesocyclops meridianus* (Kiefer, 1926).

Brazil. Balbina Power Station, State of Amazonas, 21.X.1987, coll. M. Vassiliou.

*Thermocyclops decipiens* Kiefer, 1929.

Brazil. Balbina Power Station, State of Amazonas, 21.X.1987, coll. M. Vassiliou.

*Kieferiella delamarei* (Lescher-Moutoué, 1971).

France. Terrieu, Hérault, without date, coll. F. Lescher-Moutoué and det. (USNM-264075).

*Neutrocyclops* sp.

Brazil. Comprida Island (wet organic soil), State of São Paulo, 24°37'S, 47°30'W, 10.VIII.1993, coll. C. E. F. da Rocha.

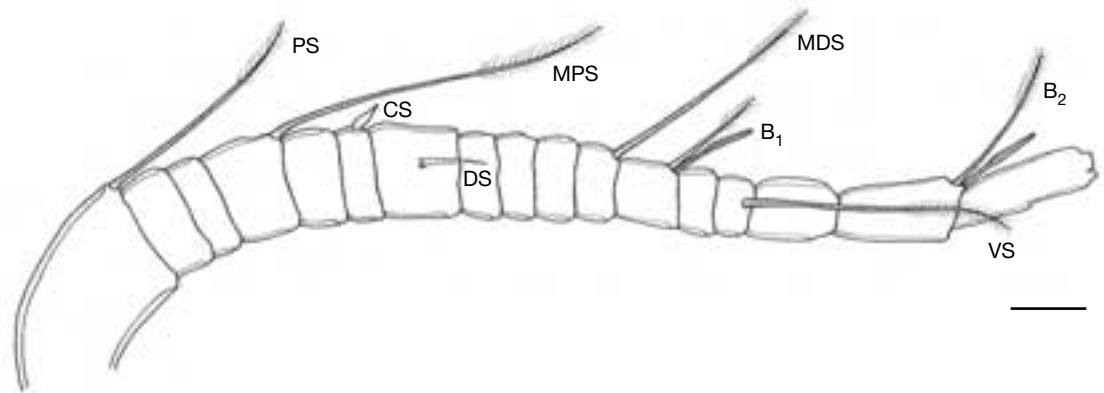


FIG. 1. — *Cyclops* sp., composite figure showing marker setae. Abbreviations: **PS**, proximal seta; **MPS**, median proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, median distal seta; **VS**, ventral seta; **B1**, **B2**, bithek (aesthetasc/seta complex). Scale bar: 50  $\mu$ m.

*Speocyclops racovitzai* (Chappuis, 1923).

France. Fontaine de la Biele, Ariège, 30.I.1970, without collector (USNM-417617).

*Graeteriella (Graeteriella) brehmi* Lescher-Moutoué, 1968.

France. Fontaine de la Biele, Ariège, 30.I.1970, without collector (USNM-417617).

*Bryocyclops caroli* Bjornberg, 1985.

Brazil. State of São Paulo, São Paulo, Cidade Universitária, without date, coll. M. H. G. de C. Bjornberg.

*Fimbricyclops jimbensoi* Reid, 1993.

Puerto Rico. Luquillo, El Yunque, 26.III.1992, coll. Suarez & Amador, J. W. Reid det. (USNM 251906) and (USNM 151905).

*Muscocyclops operculatus* (Chappuis, 1917).

Brazil. Itereí Farm (in moss near streamlet), km 350 Regis Bittencourt Highway, Miracatú, State of São Paulo, 8.IV.1994, coll. C. E. F. da Rocha.

*Allocyclops silvaticus* Rocha & Bjornberg, 1988.

Brazil. Comprida Island (wet organic soil), State of São Paulo, 24°37'S, 47°30'W, II.1994, coll. C. E. F. da Rocha.

*Cyclopicina longifurcata* (Scott, 1901).

Açores south-west, *Discovery*, stn 10379, 35°N, 33°W, 2980 m depth, R. Huys det. (The Natural History Museum, London. Reg. No. 1989.473, 6 slides).

#### REMARKS

Copepodids and whole adult females were observed in temporary preparations in 80% lactic acid. Fragments of coverslip were placed between the slide and the coverslip to avoid crushing and to permit changes in the position of the specimen by moving the coverslip. Such a procedure al-

lowed the examination of the antennules from various angles. Antennules were also dissected under a stereomicroscope and mounted as semi-permanent preparations in glycerine.

Observations were made using an optical microscope equipped with phase contrast and 100 $\times$  objective. Drawings were made with the aid of a camera lucida.

In Figures 2 to 23 the derivation of the segments during development is indicated by dotted lines linking an original segment to its derivatives, from the copepodid I stage to the adult (copepodid VI). Segment derivation was established by back tracking from the antennule of the adult female, with reference to the number and position of the setae on each segment and, principally, to the position of marker setae. Figure 1 illustrates the antennule of adult female *Cyclops* sp., showing the marker setae: PS, proximal seta; MPS, mid proximal seta; CS, conical seta; DS, dorsal seta; MDS, mid distal seta; VS, ventral seta; B1, proximal bithek; B2, distal bithek. Additional evidence used for the determination of the origin of new segments included the presence of transverse lines in the tissues in some specimens, interpreted as incipient articulations.

The description of the antennular segments of each species starts with the proximal most segment (1) of the antennule of copepodid I and continues describing the segments that originate from it during the subsequent copepodid stages

(until the adult). Then, the second segment of copepodid I is described, followed by descriptions of its derivatives until the adult, and so on until the most distal antennular segment of copepodid I and its derivatives are considered.

The antennule of *Cyclops* sp. was taken as a reference for the comparative descriptions of the other species investigated.

Diagrams showing the patterns of antennular development (Figs 24–40) were constructed based on antennule segmentation of copepodids I to VI, taking as baseline reference the segmentation of the antennule of adult female *Cyclopicina longifurcata* (Scott, 1901). This species was selected as it has the antennule with the largest number of expressed segments among the Cyclopoida. Numbers and roman numerals at the top of each diagram indicate the segments of *C. longifurcata*. Colours were used in the diagrams, to show segmental derivation. However, in Figure 24, segment 1 of copepodid I, which is formed by homologues of segments I–XI of *C. longifurcata*, is represented by the colour burgundy, thus allowing us to follow its derivatives through to the adult stage. For segment 2, a lighter shade of burgundy was used because in some species, as seen in Figure 38, segment 1 is formed by homologues of segments I–XX of *C. longifurcata*. The same procedure was adopted for the blue and green sequence and their lighter shades, used to highlight the derivation of the following segments. In order to analyze the appearance of intersegmental articulations and of setation elements we have used the hypothetical ancestral developmental sequence of copepod antennules (Boxshall & Huys 1998) as an out-sequence.

The abbreviations used in the text and figures are: CI–CV, first to fifth stage copepodid; A ♀, adult female.

## RESULTS

### ANTENNULARY DEVELOPMENT PATTERNS

Fifteen different sequences of development of antennular segmentation from copepodid I to adult female were observed in the 35 species of

cyclopids studied. These sequences are identified by different colours in Table 1.

The Cyclopinae was the most homogeneous of the cyclopid subfamilies. Although the antennular development of some genera in the subfamily remains either unknown (for example, the rare genera *Goniocyclops* Kiefer, 1955 *Cochlacocyclops* Kiefer, 1955 *Idiocyclops* Herbst, 1987 etc.), or only partly described, members of the Cyclopinae typically start the copepodid phase with six segments, this number increasing to seven in copepodid II and to nine in copepodid III. Thereafter, the antennule either retains the same nine segments in copepodid IV or becomes 10-segmented. Antennules of nine segments in copepodid IV change to 10 in copepodid V whereas antennules of 10 segments in copepodid IV increase to 11 in copepodid V. Antennules of 10 segments in copepodid V always give rise to 11-segmented antennules in the adult female. Antennules of 11 segments in copepodid V either maintain the same number in the adult (and thus can be considered as neotenic), or divide to produce 12, 14, or 17 segments in the adult.

Species of different genera can share common antennular development patterns, as in *Microcyclops alius* Kiefer, 1935, *Speocyclops* Kiefer, 1937, *Graeteriella* Brehm, 1926, *Bryocyclops* Kiefer, 1927, *Muscocyclops* Kiefer, 1937 and *Fimbricyclops* Reid, 1993 or in *Cryptocyclops* G. O. Sars, 1927, *Apocyclops procerus* (Herbst, 1955) and *Allocyclops* Kiefer, 1932 or in *Metacyclops* Kiefer, 1927 and *Microcyclops* Claus, 1893. Alternatively, congeneric species such as *Apocyclops procerus* (Herbst, 1955) and *A. dengizicus* (Lepeschkin, 1900) can have adult females with the same number of expressed segments, but which are generated via developmental and, thus, could be considered as not completely homologous.

The most common developmental sequence from copepodid I to V among the cyclopines was also found in *Macrocyclops albidus albidus*, a member of the Eucyclopinae, and in *Troglocyclops janstocki*, a member of the Halicyclopinae. The other genera investigated showed peculiar sequences, indicating a high level of heterogeneity within the Halicyclopinae and Eucyclopinae.

TABLE I. — Number of antennular segments of copepodids I to V and adult female (A ♀) of 35 cyclopoid species. Numbers in parentheses are presumed segment numbers of stages unavailable for study. The colours indicate the different segmentation sequences in the family.

SPECIES / STAGES	I	II	III	IV	V	A ♀
EURYTEINAE						
<i>Ancheuryte notabilis</i>	6	6	7	10	11	19
HALICYCLOPINAE						
<i>Halicyclops aberrans</i>	3	3	4	5	6	6
<i>Neocyclops (Neocyclops) vicinus</i>	5	5	7	7	8	12
<i>Troglocyclops janstocki</i>	6	7	9	10	11	15
EUCYCLOPINAE						
<i>Macrocyclops albidus albidus</i>	6	7	9	10	11	17
<i>Eucyclops (Eucyclops) ensifer</i>	6	6	7	8	9	12
<i>Afrocyclus gibsoni</i> s.l.	6	7	9	10	10	12
<i>Tropocyclops schubarti schubarti</i>	6	7	9	9	10	12
<i>Paracyclops chiltoni</i>	5	5	6	6	7	8
<i>Ectocyclops strenzkei</i>	4	4	5	5	5	8
<i>Ectocyclops rubescens</i>	4	4	5	5	5	11
CYCLOPINAE						
<i>Cyclops</i> sp.	6	7	9	10	11	17
<i>Megacyclops viridis</i> s.l.	6	7	9	10	11	17
<i>Acanthocyclops</i> sp.	6	7	9	10	11	17
<i>Diacyclops biscupidatus odessanus</i>	(6)	(7)	9	10	11	14
<i>Diacyclops uruguayensis</i>	6	(7)	9	10	11	17
<i>Metacyclops laticornis</i>	6	7	9	10	11	12
<i>Metacyclops hirsutus</i>	6	7	9	10	11	12
<i>Microcyclops alius</i>	6	7	9	10	11	11
<i>Microcyclops anceps anceps</i>	6	7	9	10	11	12
<i>Microcyclops ceibaensis</i>	6	7	9	10	11	12
<i>Cryptocyclops linjanticus</i>	(6)	(7)	9	9	10	11
<i>Apocyclops procerus</i>	6	7	9	9	10	11
<i>Apocyclops dengizicus</i>	6	7	9	10	11	11
<i>Hesperocyclops stocki</i>	(6)	7	9	(10)	11	11
<i>Mesocyclops meridianus</i>	6	7	9	10	11	17
<i>Thermocyclops decipiens</i>	6	7	9	10	11	17
<i>Kieferiella delamarei</i>	6	7	9	10	11	17
<i>Neutrocyclops</i> sp.	6	7	9	9	10	11
<i>Speocyclops racovitzae</i>	(6)	7	9	10	11	11
<i>Graeteriella (Graeteriella) brehmi</i>	6	7	9	10	(11)	11
<i>Bryocyclops caroli</i>	6	7	9	10	11	11
<i>Muscocyclops operculatus</i>	6	7	9	10	11	11
<i>Fimbricyclops jimhensoni</i>	6	7	9	10	(11)	11
<i>Allocyclops silvaticus</i>	6	7	9	9	10	11

Little can be deduced for the Euryteinae since antennular development in the copepodid phase is known only for one of the two included genera. However, *Ancheuryte notabilis* shares with *Eucyclops (E.) ensifer* the same number of segments in antennules of copepodids I to III.

#### DESCRIPTION OF THE ANTENNULES

*Cyclops* sp. (Fig. 2)

The copepodid I antennule consists of six segments and already possesses the marker setae:

MPS on segment 1, MDS on segment 2, bithek B1 and VS on segment 3, and bithek B2 on segment 5. Segment 1 carries MPS plus two smooth setae. This segment is unchanged at the moult to copepodid II, except for the addition of one seta. In copepodid III, segment 1 divides into two segments, each with three setae; MPS is located at the distal corner of segment 2. In copepodid III another marker seta appears, the PS, at the distal angle of segment 1. From copepodid III, segment 1 does not divide, only adding new setae to give

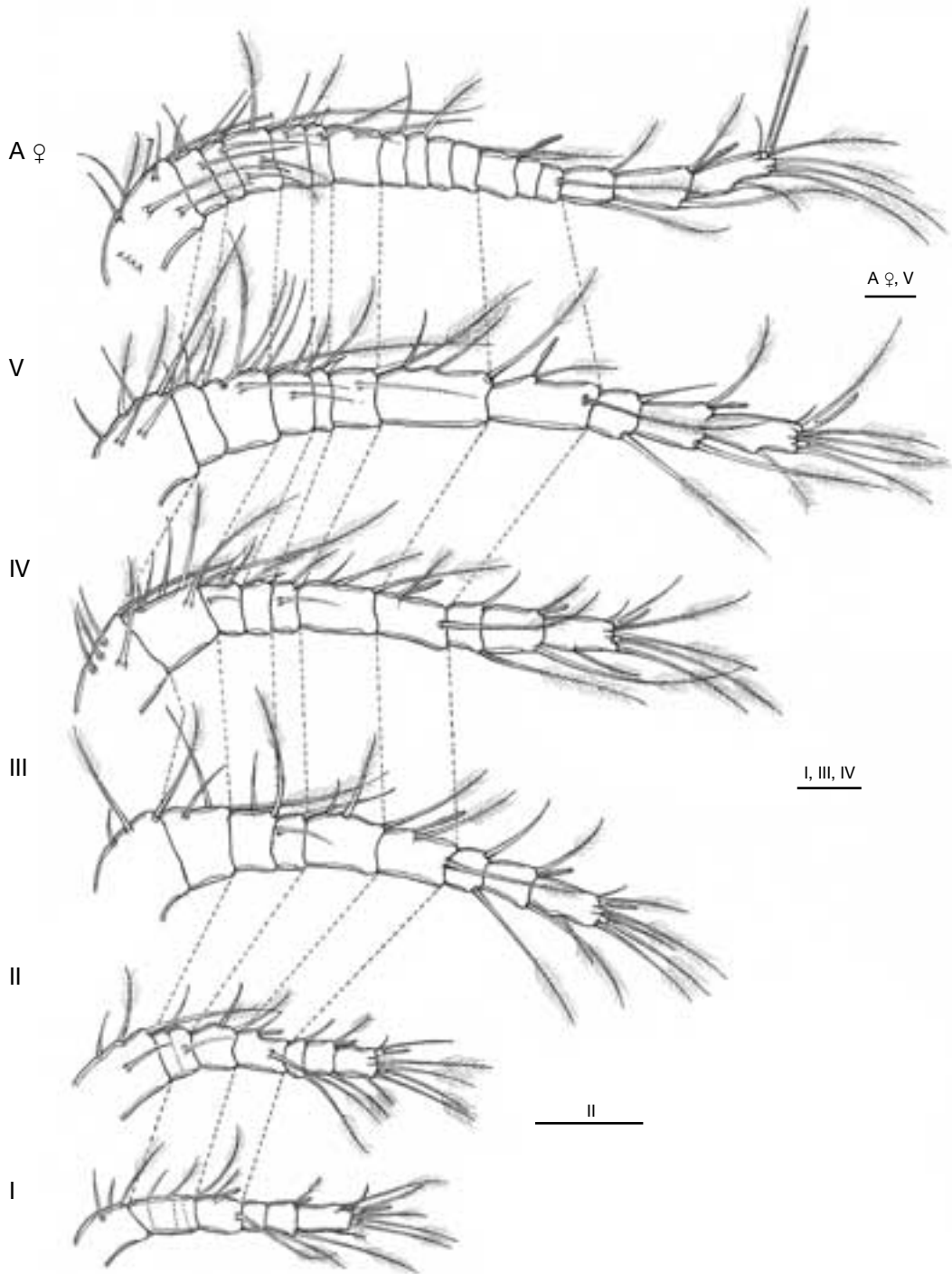


FIG. 2. — Development of antennule of female *Cyclops* sp.; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50 µm.



totals of five in copepodid IV, six in copepodid V and eight in the adult. Segment 2 of copepodid III shows an increase to six in copepodid IV. It then divides into two segments, by the separation of the proximal third at the moult to copepodid V; three setae are added to the four existing setae in the distal part and a further smooth seta is added to the three setae on the newly separated second segment. Segment 2 of the copepodid V antennule corresponds to segment 2 of the adult. Segment 3 gives rise to segments 3 and 4 in the adult without change in setal numbers. MPS is implanted at the distal angle of segment 4.

Segment 2 of the copepodid I antennule possesses three setae and three transverse furrows. This segment typically gives rise to segments 5 to 11 of the adult female. In the moult to copepodid II, it divides into a proximal segment with one furrow and two setae (one marginal and the dorsal, marker seta, DS) and a distal segment with two setae. The latter bears three setae in copepodid III, and remains undivided with the same number of setae until copepodid V; it then divides to form segments 8 to 11 in the adult female; with the MDS seta inserted at the distal angle of segment 11. The second segment of copepodid II, forms segments 3 and 4 of copepodid III, each with two setae. Segment 4 simply increases in length in the subsequent stages and corresponds to segment 7 of the adult. Segment 3 divides to form segments 3 (with three setae) and 4 of the copepodid IV. This moult marks the first appearance of another marker element: the conical seta (CS) at the distal corner of segment 4. The latter two segments do not change during subsequent moults, and are homologous with segments 5 and 6 of the adult.

Segment 3 of copepodid I bears two marker elements, the VS and bithek B1. This segment does not divide until copepodid V, but gives rise to segments 12, 13 and 14 of the adult. Bithek B1 is located at the distal corner of segment 12, and VS is implanted on segment 14 in the adult, segment 13 remains unarmed.

Segment 4 of copepodid I is armed with a long posterior seta. In copepodid II a new seta appears at the anterior distal corner. This segment

remains undivided and carries the same setae from copepodid II until the adult.

Segment 5 of copepodid I carries bithek B2 at the distal corner and a long seta posteriorly. This segment does not change in its setation from copepodid I to adult.

Apical segment 6 of copepodid I has the same setation as the adult: a short smooth seta, an aesthetasc fused at its base to the adjacent seta, four long, plumose setae around the apex, and a short plumose seta on the posterior margin.

The three distal antennulary segments of the adult female are ornamented with a strip of hyaline membrane along the posterior margin.

*Megacyclops viridis s.l.*; *Acanthocyclops sp.*; *Diacyclops uruguayensis*; *Mesocyclops meridianus*; *Thermocyclops decipiens*; *Kieferiella delamarei*; *Macrocyclus albidus albidus*

The development pattern of these species follows that observed in *Cyclops sp.* as regards the number and sequence of appearance of segments. However there are some differences in setation. In *Acanthocyclops sp.* (Fig. 3), *Mesocyclops meridianus*, *Thermocyclops decipiens* and *Kieferiella delamarei* (Fig. 4), segment 1 of copepodid III has five setae and segments 1, 2 and 3 of copepodid V carry seven, four and eight setae, respectively. In *K. delamarei* there are six setae on segment 1. In *Macrocyclus albidus albidus* (Fig. 5), marker seta DS first appears on segment 4 at copepodid III. Segment 2 of copepodid V has setae, as does the adult. Segment 5 has one additional marginal setae. The antennule of copepodid II of *Diacyclops uruguayensis* was not observed.

*Troglocyclops janstocki* (Fig. 6)

The copepodid I antennule is 6-segmented and carries the marker setae MPS on segment 1, MDS on segment 2, VS and bithek B1 on segment 3, and bithek B2 on segment 5.

The segmental subdivisions from copepodid I to V follow the same sequence as in *Cyclops sp.* The position of the marker setae also follows the *Cyclops* pattern. There are, however, some differences in the numbers of setae: segment 1 of

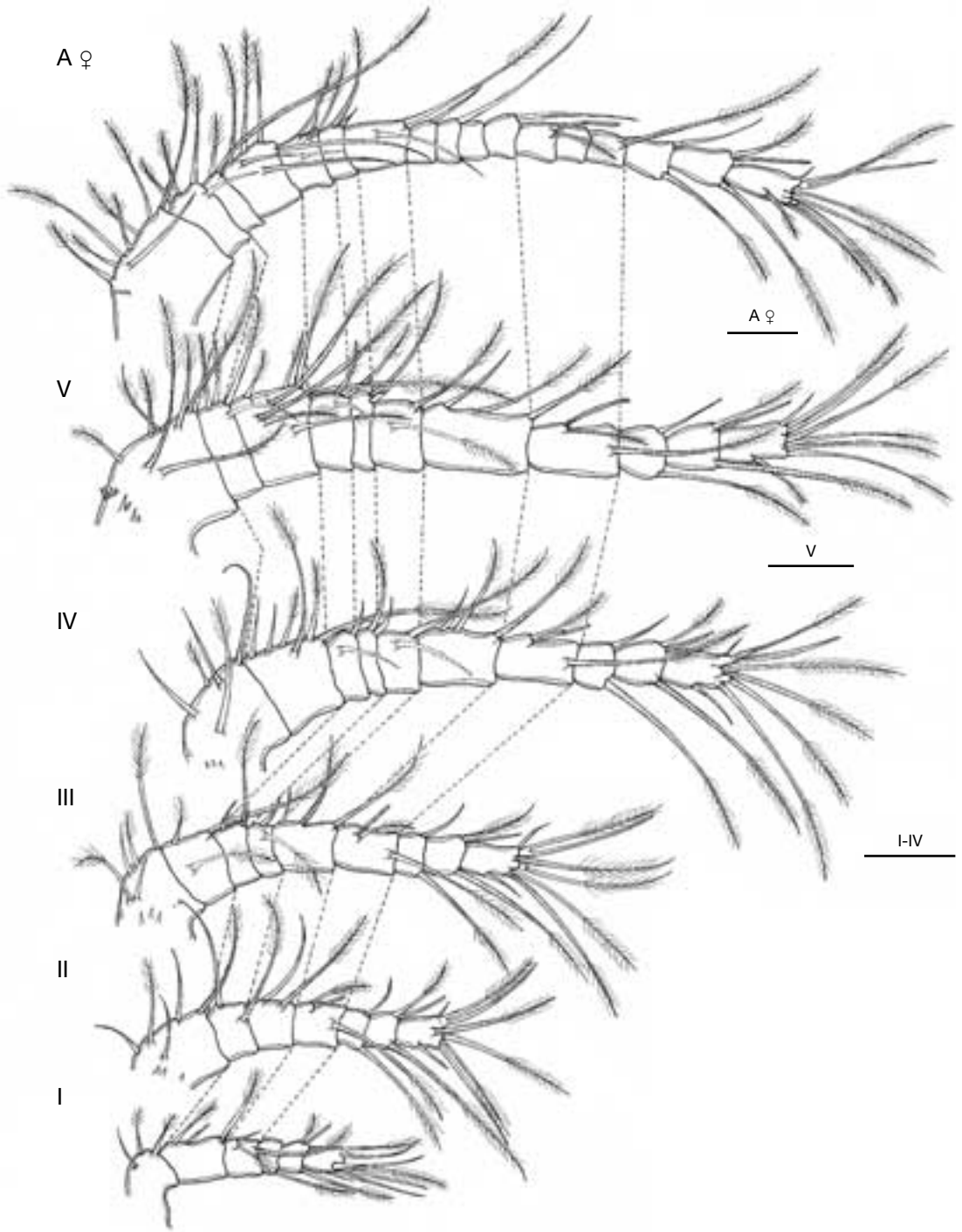


FIG. 3. — Development of antennule of female *Acanthocyclops* sp.; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

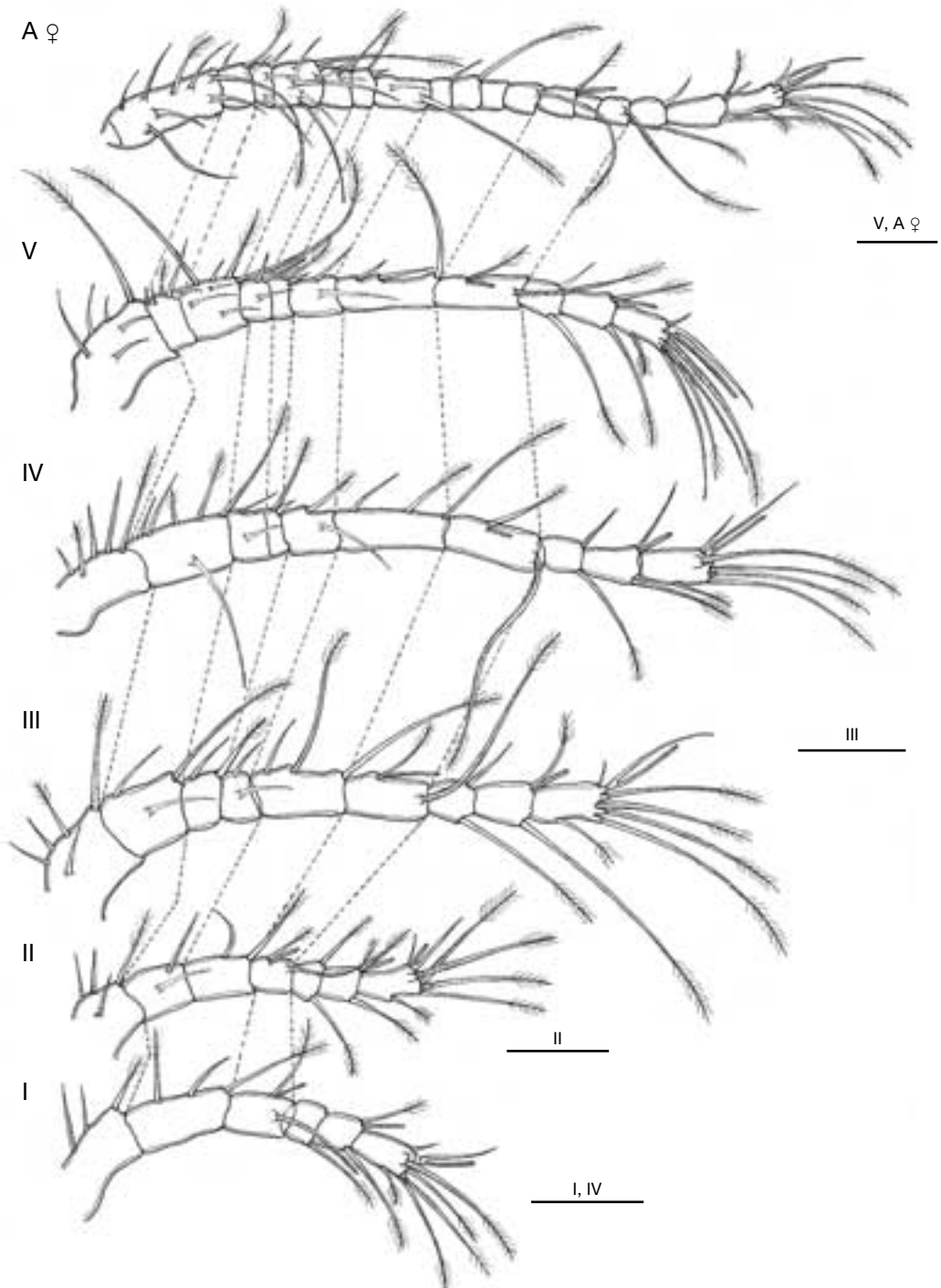


FIG. 4. — Development of antennule of female *Kieferiella delamarei* (Lescher-Moutoué, 1971); dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50 µm.

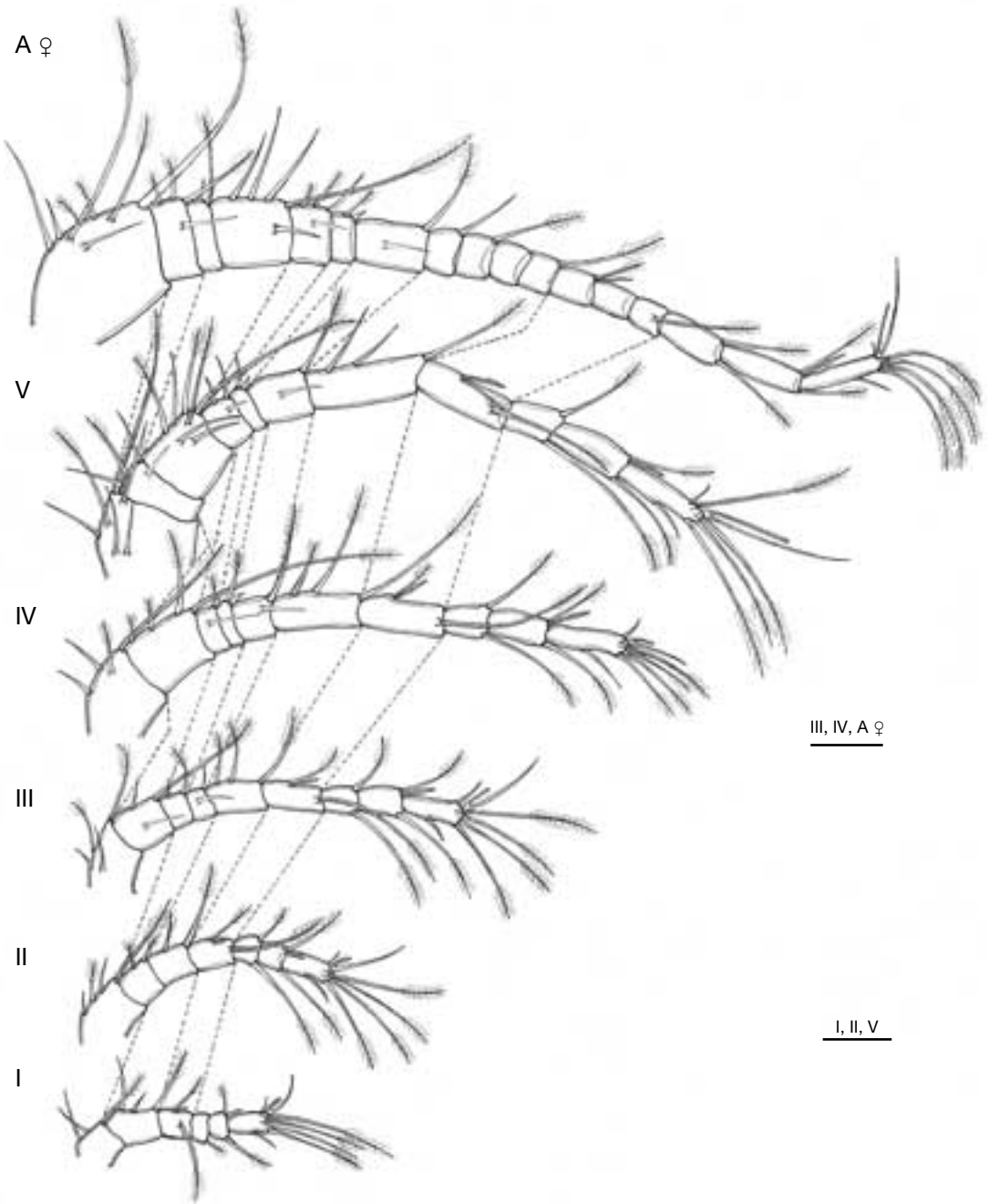


FIG. 5. — Development of antennule of female *Macrocyclus albidus albidus* (Jurine, 1820); dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50 µm.

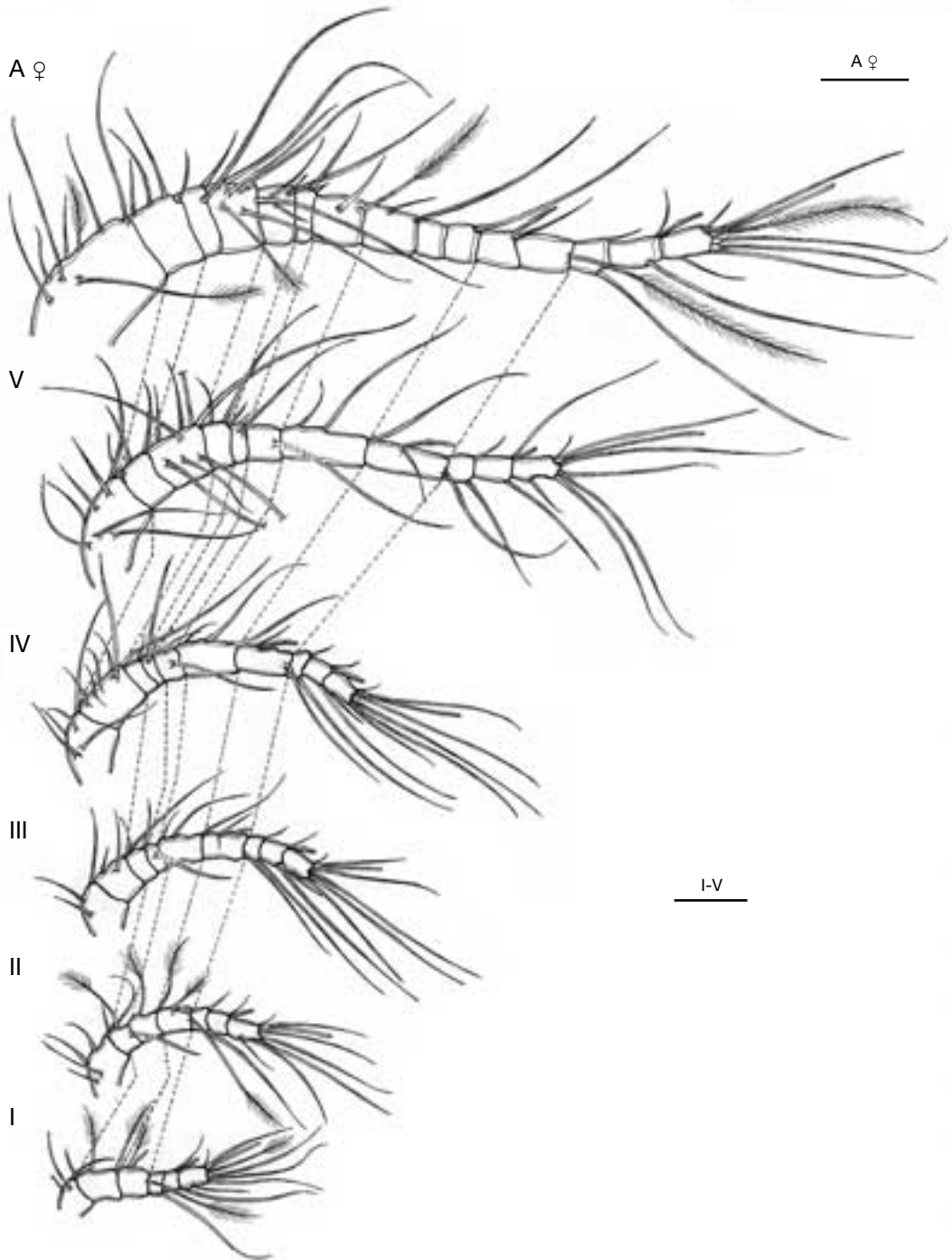


FIG. 6. — Development of antennule of female *Troglocyclops janstocki* Rocha & Iliffe, 1994; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50 µm.

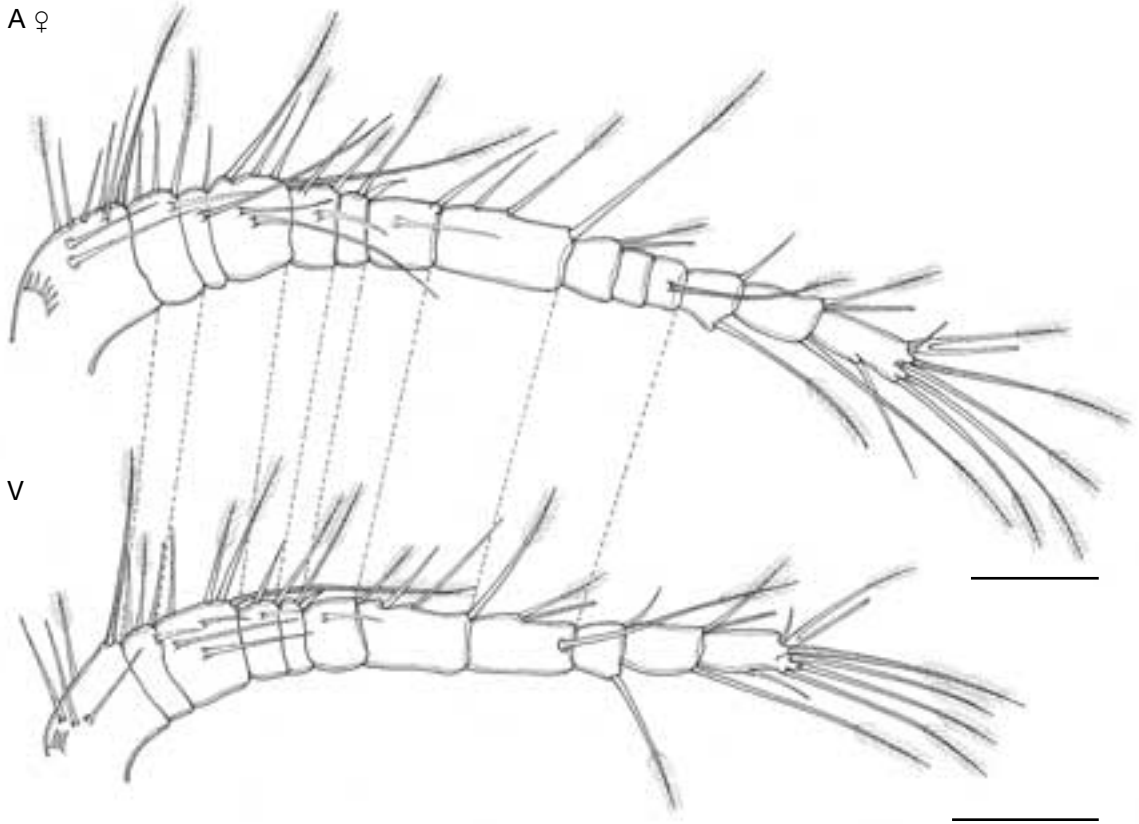


FIG. 7. — Development of antennule of female *Diacyclops bicuspidatus odessanus* (Schmankevitch, 1875); dotted lines indicate derivation of segments. Abbreviations: V, copepodid V; A ♀, adult female. Scale bars: 50 µm.

copepodid II has one extra seta; segment 4 of copepodid III has one less; segments 1 and 3 of copepodid V each possess one extra seta; segments 4 and 5 of the adult female each have one more seta.

Segment 7 of the copepodid V antennule, with three setae, divides to form segments 8, 9 and 10 of the adult. The MDS is ultimately located at the distal angle of segment 10, segment 9 is unarmed and segment 8 has two marginal setae, already present on the precursor segment (7) of copepodid V.

Segment 8 of the copepodid V antennule possesses the markers VS and bithek B1. This segment gives rise to segments 11 and 12 of the adult, in which the bithek is positioned at

the distal corner of segment 11 and the VS on segment 12.

In *Cyclops* sp., segments 7 and 8 of copepodid V divide into four and three segments in the adult, respectively, thereby generating the 17-segmented antennule of adult *Cyclops* sp., compared to the 15-segmented adult limb of *Troglocyclops janstocki*.

*Diacyclops bicuspidatus odessanus* (Fig. 7)

Copepodids I and II were not observed. The development from copepodid III to V is similar to that of *Cyclops* sp. Segment 1 of copepodid V has one seta less than in *Cyclops* sp. while segment 2 has one more; segment 4 of the adult female also has one more seta. Segment 7 of copepodid

V fails to divide at the moult to the next stage, so the adult female retains 14 segments.

*Metacyclops hirsutus* (Fig. 8); *Metacyclops laticornis*

The segmental developmental pattern in copepodids I to V follows that of *Cyclops* sp. However, setal development on the segments originating from segment 1 of copepodid II is different from that of *Cyclops* sp. It is noteworthy that the marker MDS appears at copepodid II whereas in all previously mentioned species it is already present on distal corner of segment 2 at copepodid I. Segment 8 of copepodid V divides to form segments 8 and 9 of the adult. Segments 3 and 7 of copepodid V remain undivided in the adult female and can, therefore, be interpreted as neotenic.

*Microcyclops anceps anceps* (Fig. 9); *Microcyclops ceibaensis*

The pattern of segmental derivation is similar to that found in *Metacyclops hirsutus*, except that segment 3 of copepodid V gives rise to segments 3 and 4 of the adult. In the two *Metacyclops* studied antennular segment 8 of copepodid V divides into two segments as described above. In both cases, the final segment number in the adult female is 12. In these *Microcyclops* species, MDS appears on segment 2 at copepodid I, as in *Cyclops* and allied species. However, copepodid I bears 1 seta at the corner of segment 4; this seta only appears at the copepodid II stage in all previously described species. Figures 8 and 9 show other differences in setation.

*Microcyclops alius* (Fig. 10); *Apocyclops dengizicus* (Fig. 11); *Hesperocyclops stocki*; *Speocyclops racovitzai*, *Graeteriella* (G.) *brehmi*, *Bryocyclops caroli* (Fig. 12); *Muscocyclops operculatus*; *Fimbricyclops jimhensoni*

The developmental pattern of the listed species follows that of *Cyclops* sp. until copepodid V. The antennule of the adult is 11-segmented, as in copepodid V.

In *Hesperocyclops stocki*, *Speocyclops racovitzai*, *Graeteriella* (G.) *brehmi* and *Bryocyclops caroli*,

segment 2 of copepodid II does not carry marker DS; this first appears later, on segment 4 of copepodid III.

The setation of the copepodids of *B. caroli* and *M. operculatus* is almost the same as in *Cyclops* sp. They differ only by the presence of one more seta on segment 3 of copepodids IV and V than in *Cyclops* sp. In *M. alius*, there are setation differences on segment 3 of copepodid IV as well as segments 1 and 3 of copepodid V.

The antennules of copepodid V of *Fimbricyclops jimhensoni* and *Graeteriella* (G.) *brehmi*, copepodids I and IV of *Hesperocyclops stocki*, and copepodid I of *Speocyclops racovitzai* were not studied.

*Afrocyclops gibsoni* s.l. (Fig. 13)

Copepodids I to III show the same developmental pattern as *Cyclops* sp. Nevertheless, differences can be detected in setation. Segment 1 of copepodids I and II have two and three marginal setae, respectively. Segment 2 of copepodid I exhibits two setae and two incomplete frontal furrows; this segment gives rise to segments 2 and 3 of copepodid II and segments 3, 4 and 5 of copepodid III. Marker DS appears on segment 4 in copepodid III.

Segment 2 of copepodid III, with a marginal seta and MPS, divides to form segments 2 and 3 of copepodid IV. In *Cyclops* sp., this division only occurs at copepodid V. Segment 2 of copepodid IV remains undivided and with the same setation until the adult. Segment 3 of copepodid IV has one seta added at copepodid V. In the moult to adult, this segment divides to form adult segments 3, with two setae, and 4 with four setae, one of which is the MPS inserted distally. Segment 4 of copepodid V divides to form adult segments 5 and 6.

Segment 3 of copepodid III carries two setae; its homologues in copepodids IV and V carry four setae, including the CS. In the adult female, the two segments originating from it each bear two setae.

Copepodids IV and V possess antennules of 10 segments, with a similar arrangement of setae, except for segment 1, which has five setae in copepodid IV and seven in copepodid V.

Segment 4 of copepodid III remains undivided and retains the same number of setae through to the adult.

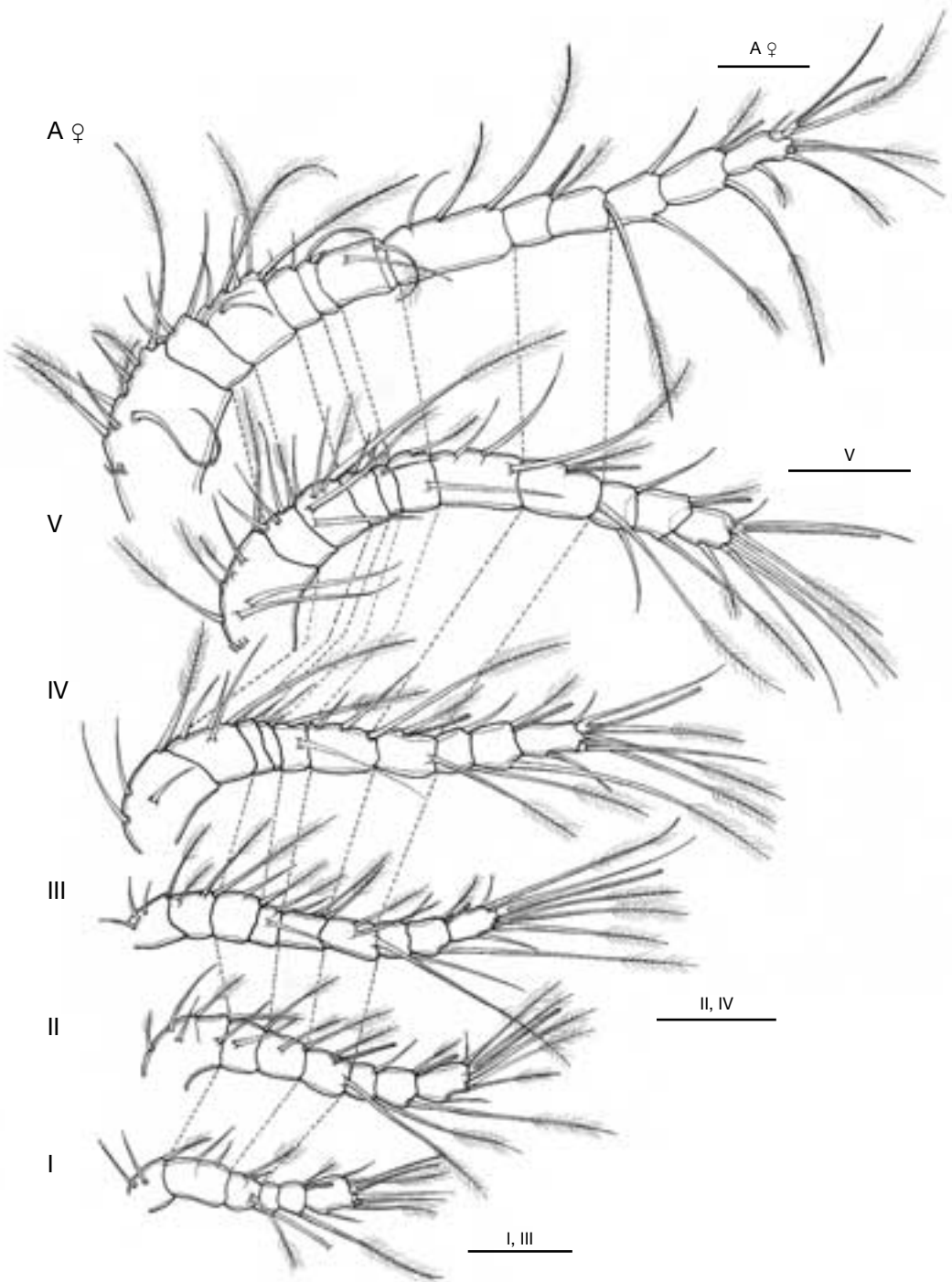


FIG. 8. — Development of antennule of female *Metacyclops hirsutus* Rocha, 1994; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.



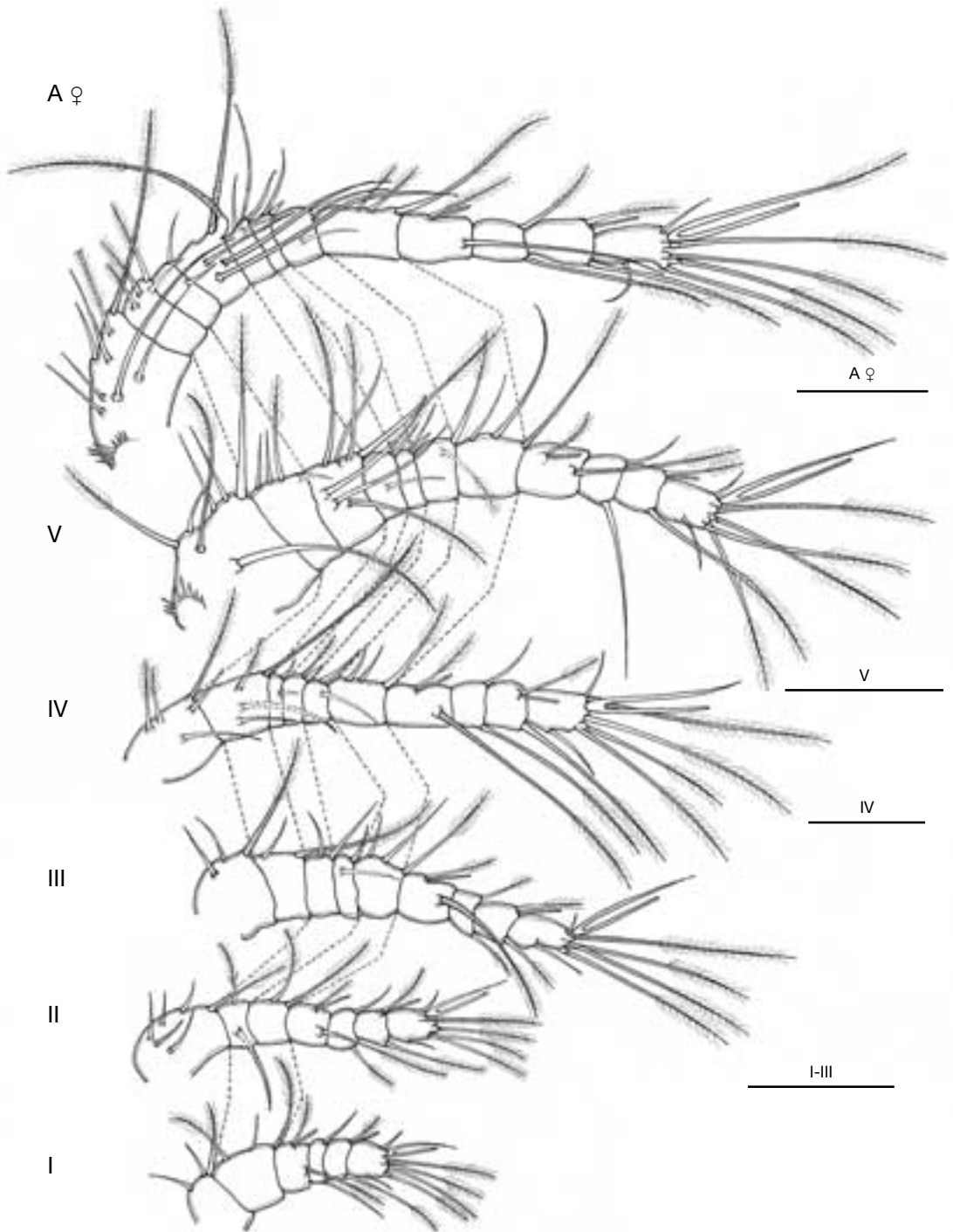


FIG. 9. — Development of antennule of female *Microcyclops anceps anceps* (Richard, 1987); dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

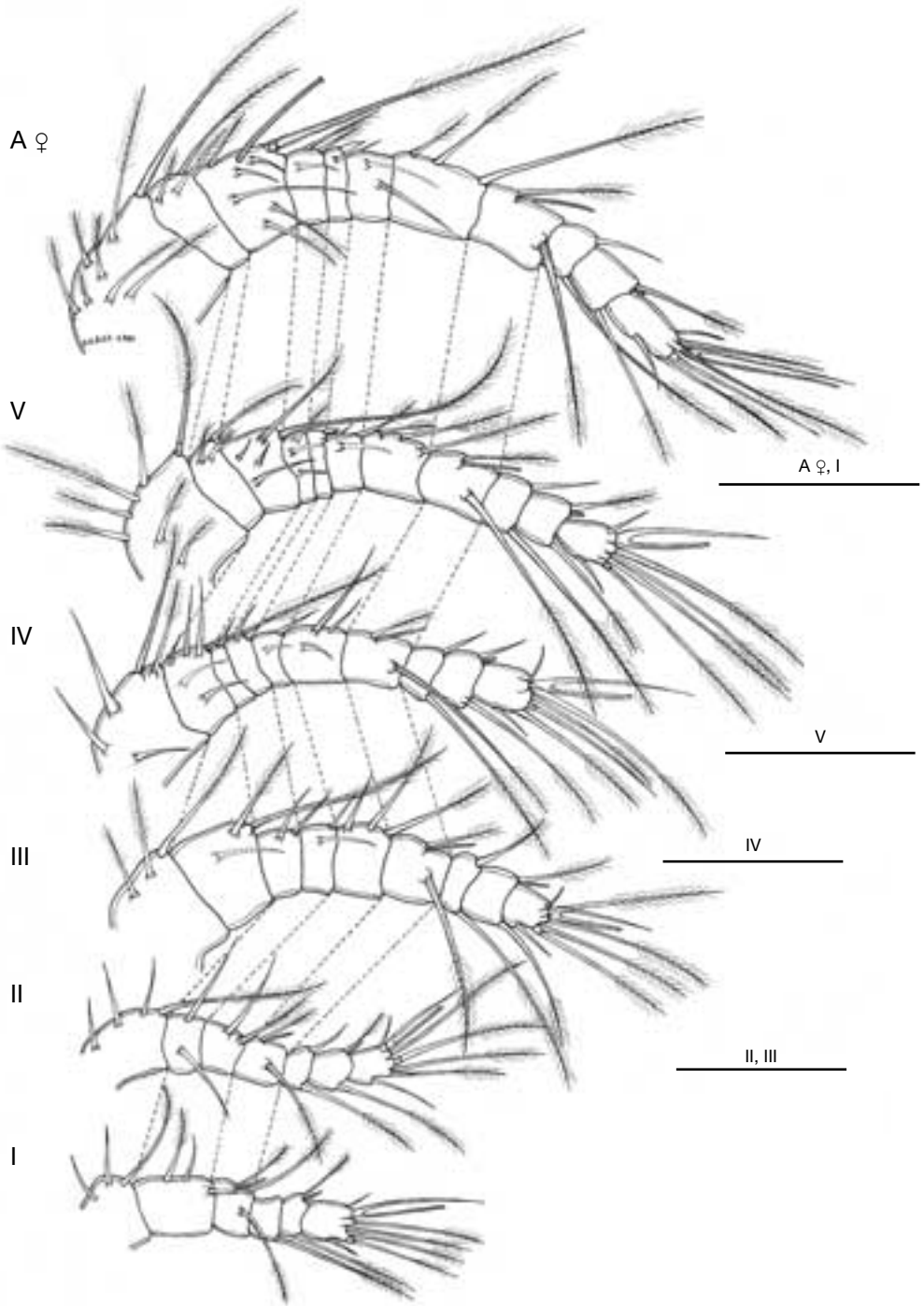


FIG. 10. — Development of antennule of female *Microcyclops alius* Kiefer, 1935; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

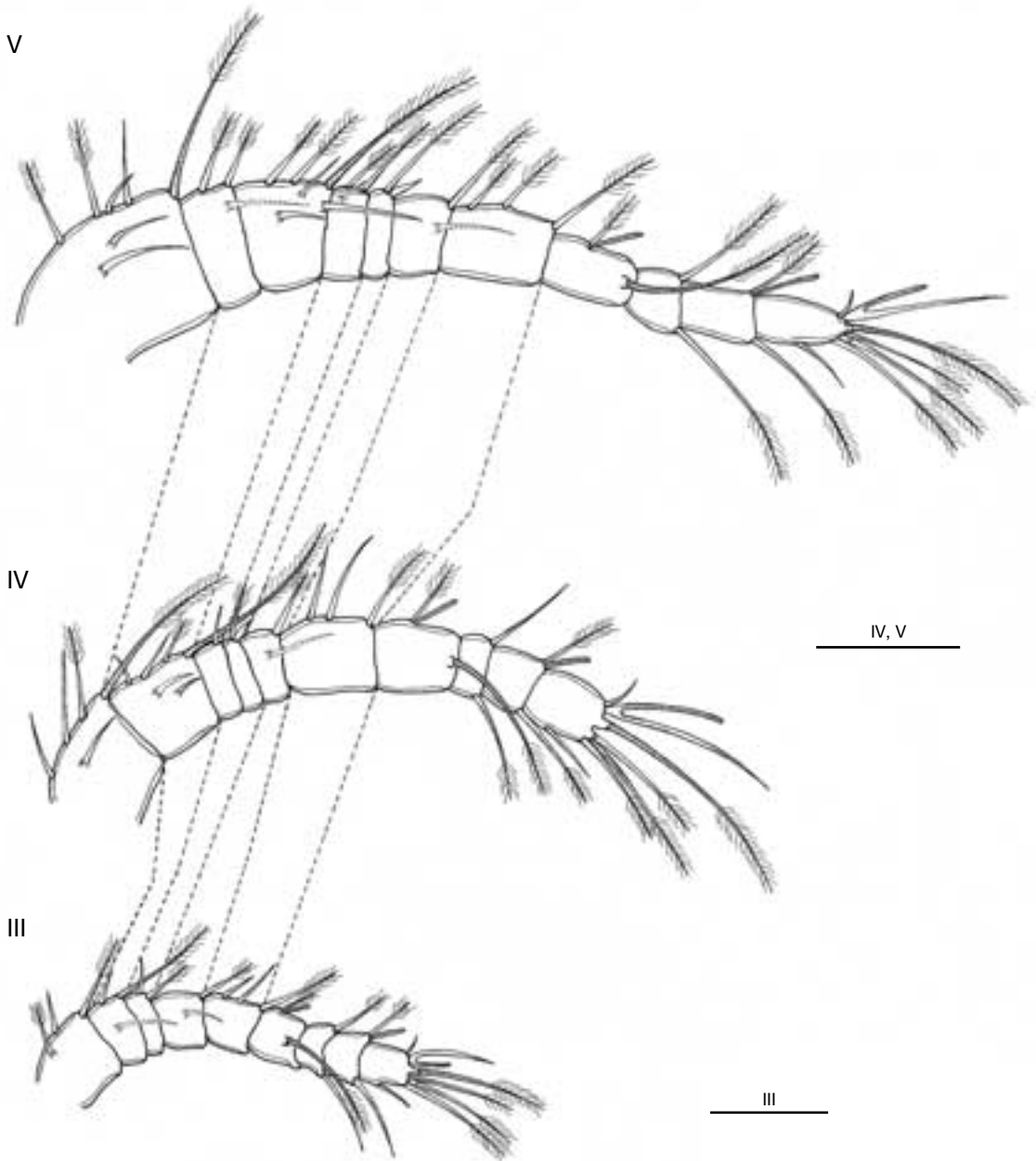


FIG. 11. — Development of antennule of female *Apocyclops dengizicus* (Lepeschkin, 1900); dotted lines indicate derivation of segments. Abbreviations: III-V, copepodid III-V; A ♀, adult female. Scale bars: 50 μm.

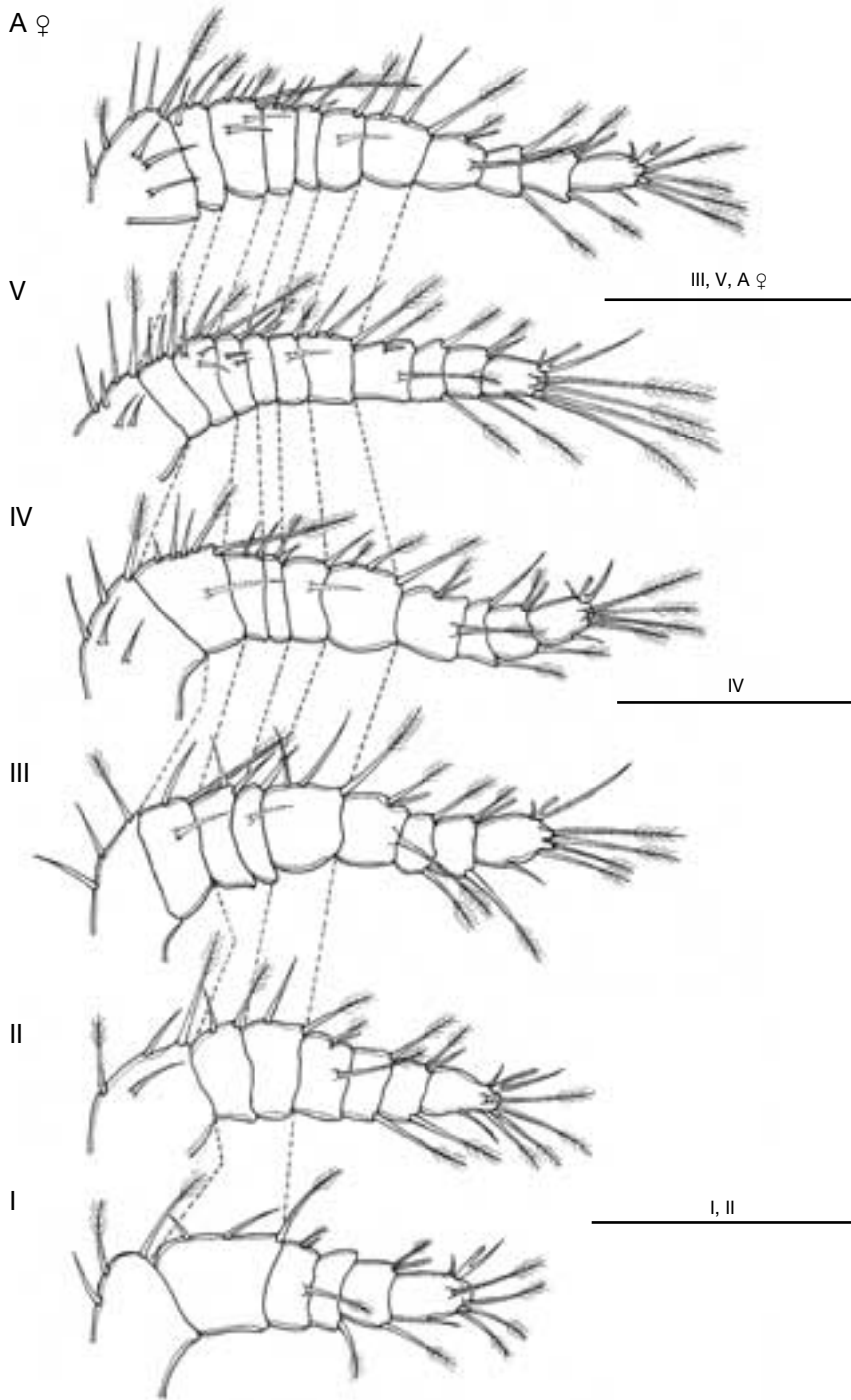


FIG. 12. — Development of antennule of female *Bryocyclops caroli* Bjornberg, 1985; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50 µm.

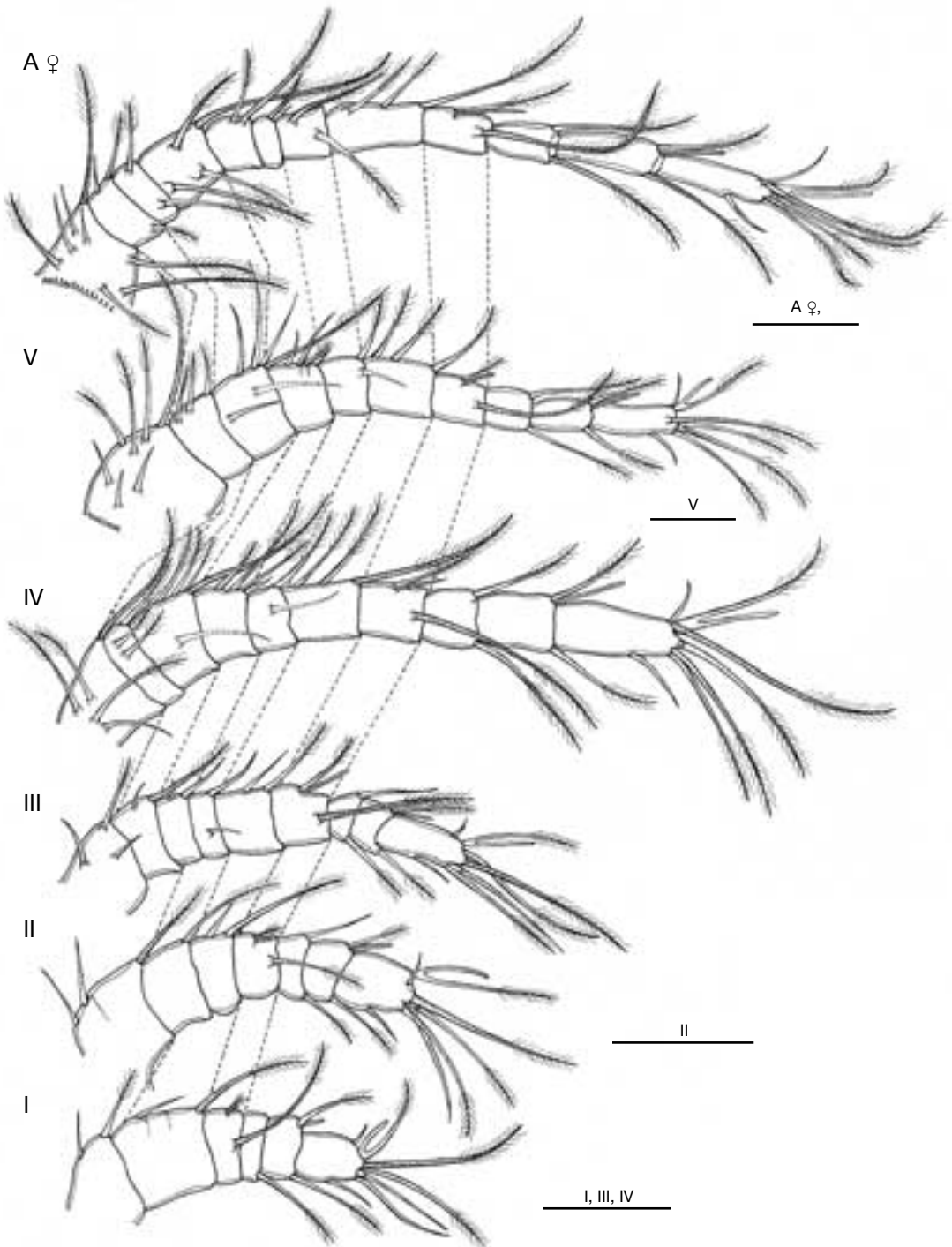


FIG. 13. — Development of antennule of female *Afrocylops gibsoni* s.l. (Brady, 1904); dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

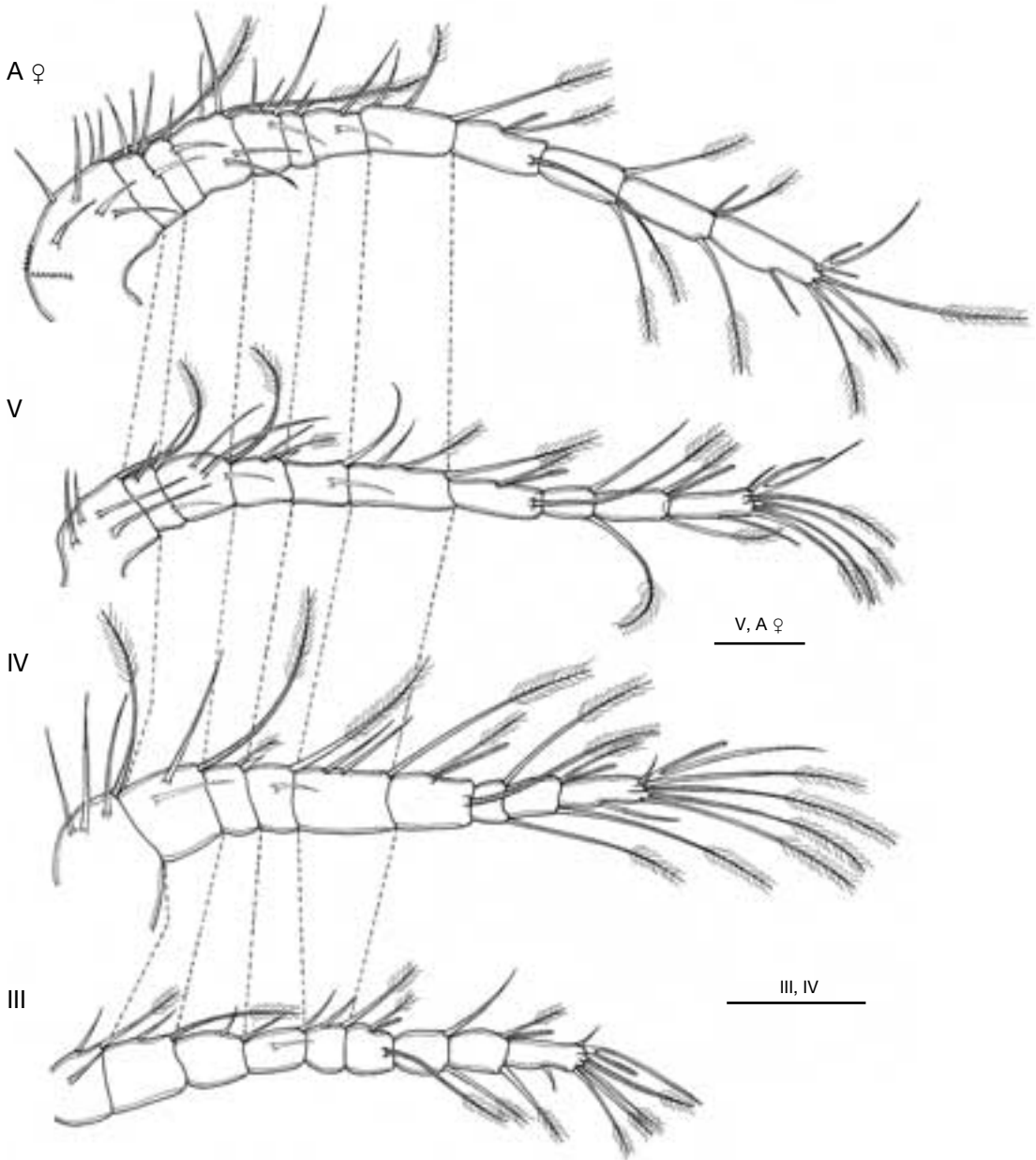


FIG. 14. — Development of antennule of female *Tropocyclops schubarti schubarti* (Kiefer, 1935); dotted lines indicate derivation of segments. Abbreviations: III-V, copepod III-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

Segment 5 of copepodid III appears with a middle seta and marker MDS at the distal angle. A proximal seta appears on this segment at copepodid IV. This segment remains undivided and retains the same number of setae through to the adult. The four terminal antennular segments of copepodid I follow the same development pattern as in *Cyclops* sp. until copepodid V. Segment 7 of copepodid V does not split into three segments as its homologue in *Cyclops* sp. does.

#### *Tropocyclops schubarti schubarti* (Fig. 14)

The antennular development of this species is very similar to that of *Afrocyclus gibsoni*. The only difference is in copepodid IV, which possesses nine segments due to a failure in the division of antennular segment 2 at the copepodid III stage.

#### *Apocyclops procerus* (Fig. 15); *Cryptocyclops linjanticus*

The antennules of copepodids I, II and III differ from those of *Cyclops* only in having one seta less on segment 1 in copepodid II. In copepodid IV the same number of segments is retained as in the previous stage, however the three proximal segments all show an increase in number of setae; marker CS appears on segment 3.

Segment 2 of copepodid IV gives rise to segments 2 and 3 of copepodid V.

Segment 4 of copepodid V divides to form segments 4 and 5 of the 11-segmented antennule of the adult female.

The antennule of adult *A. procerus* is identical in segmentation to that of copepodid V of *Cyclops* sp. but there are two setae more on segment 1, and 2 setae less on segment 3 in *A. procerus*.

Copepodid stages I and II of *Cryptocyclops linjanticus* were not observed.

#### *Alloicyclus silvaticus* (Fig. 16); *Neutrocyclops* sp.

The number of antennular segments from copepodid I to adult female of *A. silvaticus* and *Neutrocyclops* sp. is the same as in *A. procerus* and *C. linjanticus*, that is: 6-7-9-9-10-11. However, the segments expressed at copepodid V are not homologous. Segment 3 of copepodid IV divides

into two at copepodid V of *A. silvaticus* and *Neutrocyclops* sp.; in *A. procerus* and *C. linjanticus*, however, it is segment 2 of copepodid IV which splits during the moult to copepodid V.

The antennular segments of copepodid V and adult female of *A. silvaticus* and *Neutrocyclops* sp. are homologous to those of copepodids IV and V of *Cyclops* sp.

#### *Ancheuryte notabilis* (Fig. 17)

The antennule of copepodid I possesses six segments, and these remain undivided in copepodid II. In both stages, marker MPS is on segment 1, MDS on segment-2, bithek B1 and VS on segment 3, and bithek B2 on segment 5.

Antennular segment 1 remains undivided until copepodid III, exhibiting only an increase in number of setae. At copepodid IV, it splits into two segments, the first with four setae and the second with five. Marker seta MPS inserts distally on the second segment, while PS is placed at the antero-distal angle of the first segment. This segment does not divide further, changing only by the addition of new setae: four in copepodid IV, six in copepodid V and eight in the adult. Segment 2 of copepodid IV splits into two in copepodid V; the proximal segment, with three setae, remains undivided until the adult and adds only one more seta; the distal segment, with eight setae, has MPS inserted at the distal angle. This segment divides into four in the adult, giving rise to segments 3 to 6, with marker MPS originating on segment 6.

Segment 2 of copepodid I, with a proximal seta and the MDS distally, remains undivided and retains the same number of setae in copepodid II. This segment splits into two segments in copepodid III. In copepodid IV, segment 2 of copepodid III, already bearing the DS, divides into three, giving rise to segments 3, 4 and 5. Segment 3, with one seta, does not change until the adult except for the addition of two setae in copepodid V. This segment corresponds to antennular segment 7 of the adult, which shows a transverse furrow ventrally, at the level of the DS implantation; this furrow can be confused with a subdivision of the segment. Segment 4 of copepodid IV

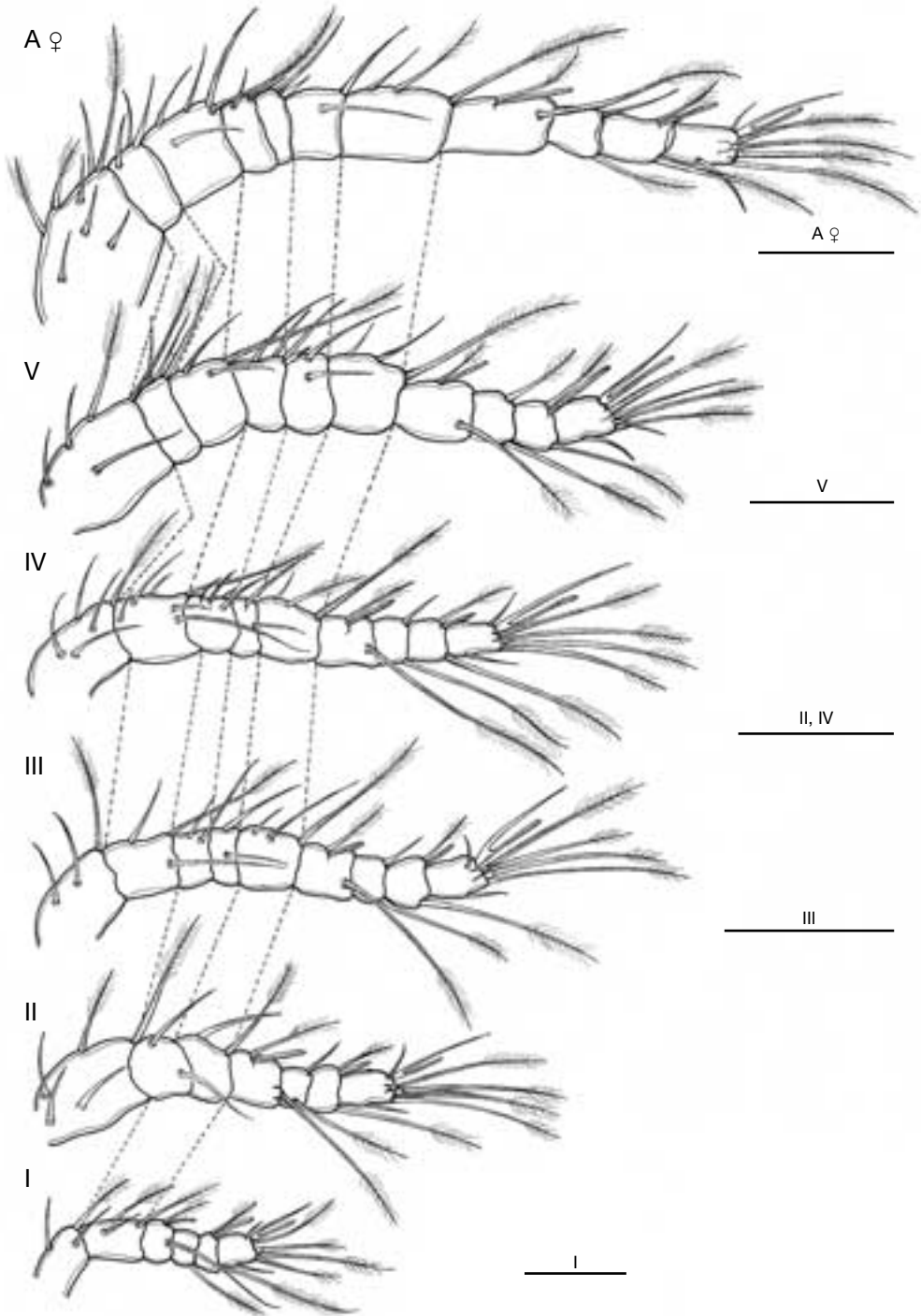


FIG. 15. — Development of antennule of female *Apocyclops procerus* (Herbst, 1955); dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.



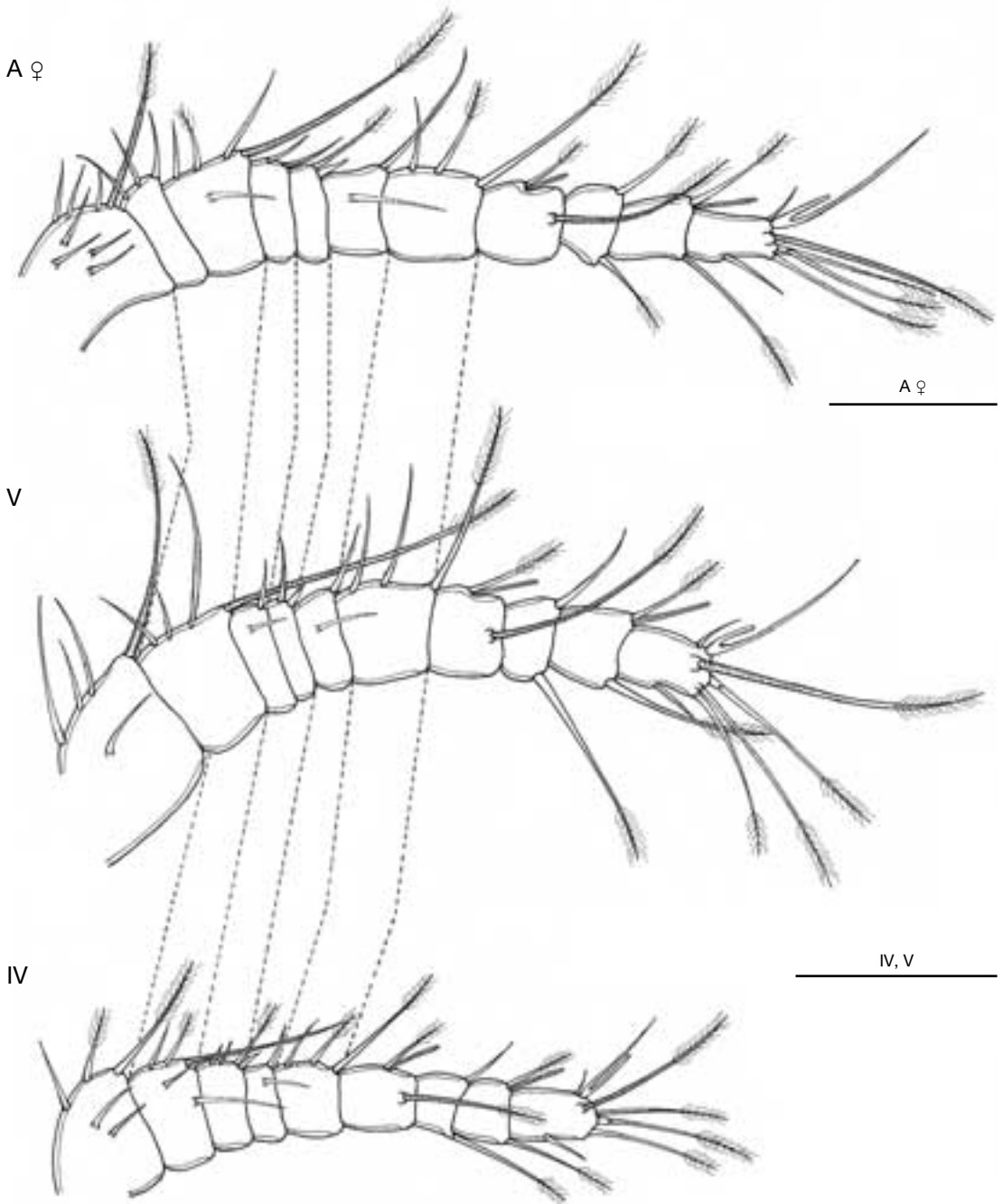


FIG. 16. — Development of antennule of female *Allocyclops silvaticus* Rocha & Bjornberg, 1988; dotted lines indicate derivation of segments. Abbreviations: **IV-V**, copepodid IV-V; **A ♀**, adult female. Scale bars: 50  $\mu$ m.

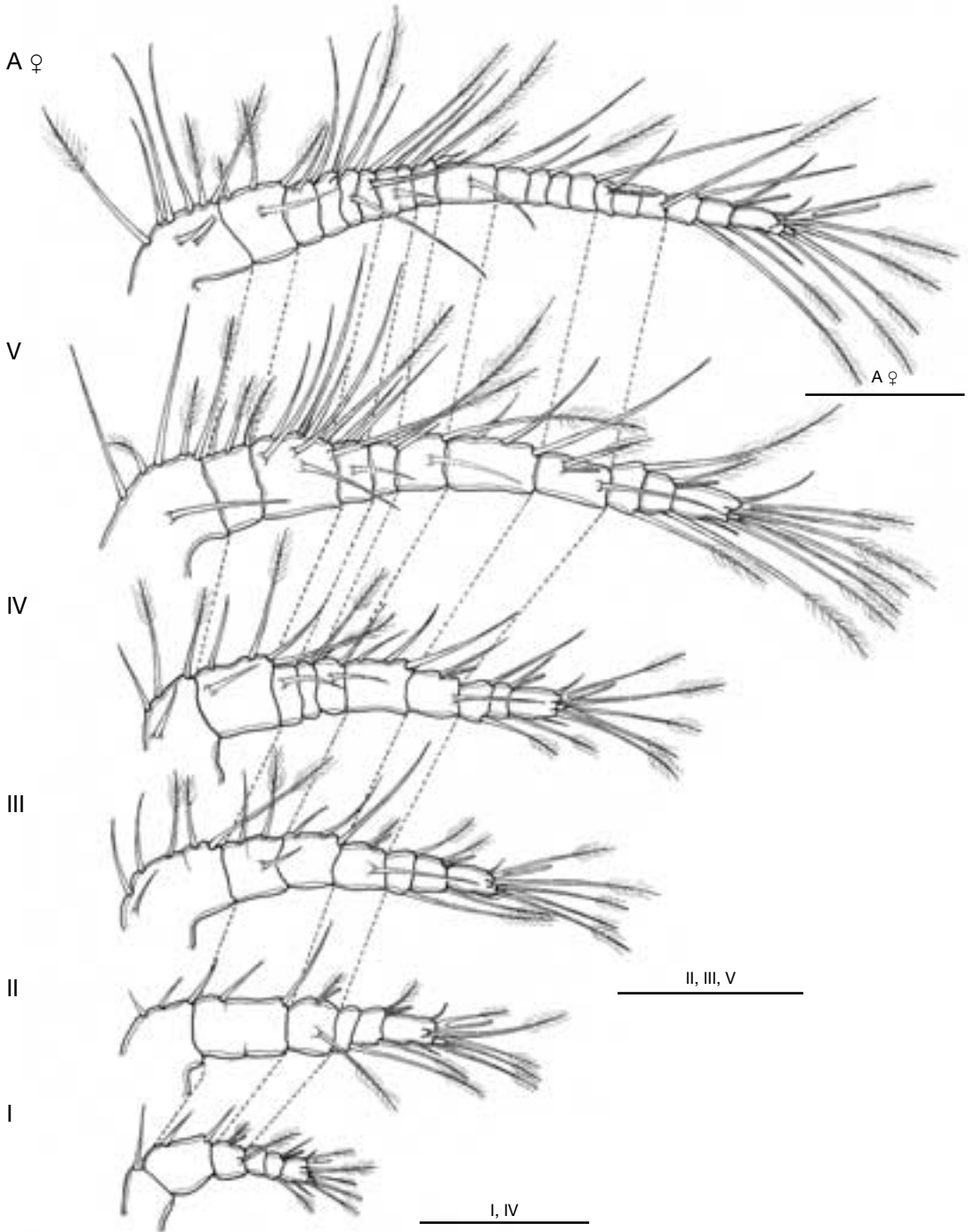


FIG. 17. — Development of antennule of female *Ancheuryte notabilis* Herbst, 1989; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

possesses a plumose seta and the CS. This segment remains undivided and with the same arrangement of setae through to the adult, as does segment 5.

Segment 3 of copepodid III has three setae, including the MDS at the distal angle. This segment gives rise to segments 10 to 13 in the adult; segments 10 and 11 each bear a distal seta, segment 12 is unarmed and segment 13 has the MDS.

Segment 3 of copepodid I possesses the VS and B1. This segment remains undivided until the moult to adult, when segments 14 to 16 are formed. Segment 14 carries bithek B1, segment 15 is unarmed, and segment 16 carries VS.

Segment 4 of copepodid I lacks setae. In copepodid II, a long inner distal seta appears. In copepodid III, a further seta is added at the distal corner. Segment 5, with bithek B2, and segment 6 of copepodid I are unchanged through to adult.

#### *Eucyclops* (*Eucyclops*) *ensifer* (Fig. 18)

The antennule of copepodid I possesses six segments and has the same setation as in *Cyclops* sp. In copepodid II, the number of segments is maintained, but the number of setae increases to five on segment 1; DS appears on segment 2, raising to four the number of setae; and segment 4 has one seta at the distal corner.

Segment 1 of copepodid II remains undivided in copepodid III and retains the same armature. This segment divides in copepodid IV, giving rise to the most proximal antennular segment, with five setae, including the PS at the distal corner. From copepodid IV the number of setae increases to seven in copepodid V and eight in the adult. Segment 2 of copepodid IV possesses six setae, including the MPS. This segment splits into two in copepodid V, giving rise to segment 2 bearing two marginal setae (the number of setae of this segment increases to four in the adult) and segment 3, with seven setae. The latter segment divides into two in the adult: segment 3, with two setae, and segment 4, with five setae including the MPS at the distal angle.

Segment 2 of copepodid II divides into two in copepodid III. Segment 2 of copepodid III, with two setae, remains undivided in copepodid IV; in

this stage the CS appears at the distal corner. In copepodid V, a further seta is added. In the adult, this segment gives rise to segments 5 and 6, each bearing two setae one of which is the CS on segment 6. Segment 3 of copepodid III carries the MDS at the distal corner, the DS, and two marginal setae. This segment remains undivided until copepodid V, where a further seta appears. At the moult to adult, it divides into segment 7, with a marginal seta and the DS, and segment 8, with two marginal setae and the MDS at the distal angle.

The final four segments of copepodid III carry the same setation as in *Cyclops* sp. These segments maintain the same setation through to the adult. The three distal segments have a hyaline membrane on posterior margin from copepodid IV to adult.

#### *Neocyclops* (*Neocyclops*) *vicinus* (Fig. 19)

The antennule of copepodid I of *Neocyclops* (*N.*) *vicinus* has five segments: segment 1 carries three setae including the MPS at the distal angle; segment 2 is armed with two setae, one being the MDS; segment 3 carries bithek B1, the VS and an inner distal seta; segment four with bithek B2 inserted at the outer distal corner and a long inner seta at the posterior distal angle; and segment 5 has a bithek and six setae. From copepodid I to adult, the latter two segments change only in their proportions and in the lengths of their setae.

Copepodid II retains the same number of segments, but there are increases in the number of setae. Segment 1 has four setae and divides into two at the moult to copepodid III: segment 1 having five setae, including the PS, and segment 2 three setae, including the MPS inserted at the distal angle. Segment 1 of copepodid III does not divide again, increasing only in size and in number of setae. Segment 2 of copepodid III remains undivided in copepodid IV, with only the addition of two setae. At the moult to copepodid V, this segment gives rise to segment 2, bearing three setae, which remains undivided and with the same number of setae through to the adult, and segment 3, with seven setae, including the

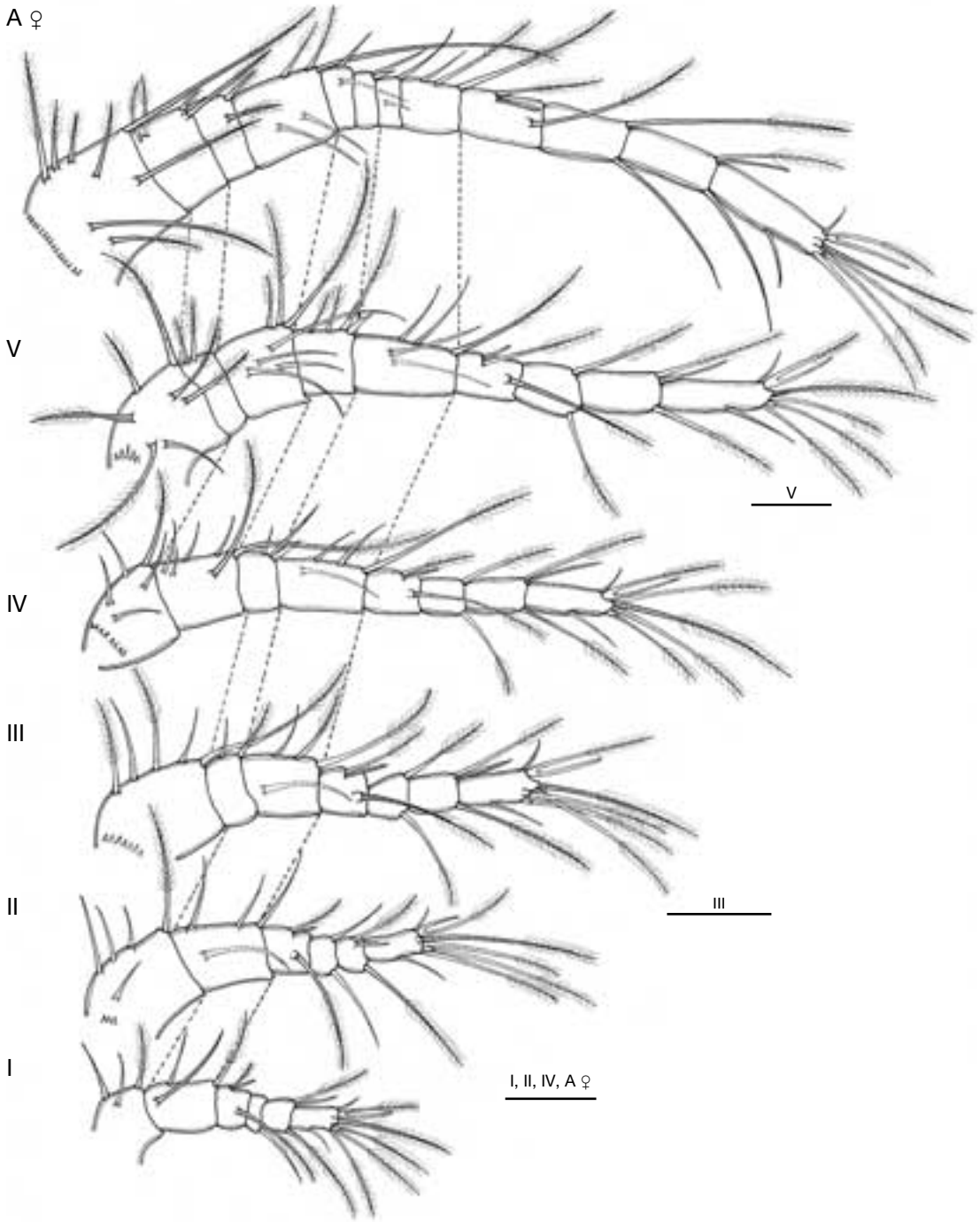


FIG. 18. — Development of antennule of female *Eucyclops* (*Eucyclops*) *ensifer* Kiefer, 1936; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

MPS implanted distally. This segment divides into two in the adult, giving rise to segment 3, bearing two setae, and segment 4, with five setae, plus the MPS.

Segment 2 of copepodid II, with two setae, becomes segments 3 and 4 of copepodid III. Segment 2 of copepodid III has two setae. This segment gains seta CS at copepodid IV remains undivided in copepodid V, then gives rise to segments 5, with three setae, and 6, with a long seta plus the CS in the adult. Segment 4 of copepodid III, carries three setae, adding two more (one being the DS) in the following stage. This segment gives rise to segment 7, with one seta plus the DS, and segment 8, with two setae plus the MDS inserted at the distal angle in the adult.

Segment 3 of copepodid II remains undivided and retains the same armature until copepodid V, when it divides to form segment 9, with B1 and VS, and segment 10, with two setae, in the adult. The distal two antennulary segments of copepodid I remain unchanged and show the same setation through to the adult.

#### *Paracyclops chiltoni* (Fig. 20)

The antennule of copepodid I differs from that of *N. (N.) vicinus* only in the presence of one extra seta on segment 2. The last two segments have the same setation through to the adult.

The antennule of copepodid II has the same number of segments as the previous stage. Segment 1 has two additional setae and a row of seven spinules. From copepodid II to V, this segment only increases in size and in the number of setae, which reaches a total of 19. In the adult, it divides to form segment 1 with eight setae including the PS inserted distally, and segment 2, with 12 setae.

Segment 2 of copepodid II bears 5 setae, including the DS. In copepodid III, this segment gives rise to segments 2 with two setae, and 3 with five setae. These latter two segments remain undivided through to the adult. The number of setae on segment 2 increases progressively at each moult and CS appears at copepodid IV. The number of setae of segment 3 remains constant through to the adult.

Segment 3 of copepodid II differs from that of copepodid I only in having one seta at the antero-distal corner. This segment divides to form segments 4 and 5 of copepodid V.

The aesthetasc of bithek B2 resembles a seta, differing from the aesthetascs found in the other species examined.

#### *Ectocyclops rubescens* (Fig. 21)

The antennule of copepodid II differs from that of copepodid I only in having one extra seta on segments 1 and 2. At the moult to copepodid III, segment 1 divides to form segments 1 and 2, with five and four setae respectively. The number of antennulary segments remains unchanged until copepodid V. Then, segment 1 divides into the five first segments, segment 2 gives rise to segments 6 and 7, and segment 3 divides into segments 8 and 9 of the adult.

#### *Ectocyclops strenzkei* (Fig. 22)

The antennules of copepodids I to V of *E. strenzkei* are similar to those of *E. rubescens* in segmentation. Antennules of both species also share the same setation in copepodids I and II. However, segment 1 of copepodids III, IV and V bears more setae (8, 12 and 21) in *E. strenzkei* than in *E. rubescens* (5, 10 and 13).

In copepodid V segment 1 is partially subdivided by four furrows. It gives rise in the adult, to segment 1 with eight setae, including the PS at the distal angle; segment 2, with 10 setae, including the MPS inserted at the distal corner; segment 3 with two setae; and segment 4 with a long marginal seta and the CS.

Segment 2 of copepodid V corresponds to segment 5 of the adult and has the following setation: two marginal setae, the MDS inserted at the distal angle, and the DS.

#### *Halicyclops aberrans* (Fig. 23)

The antennule of copepodid I consists of three segments. In copepodid II it is still 3-segmented, but carries one additional seta on segment 1. Segment 1 divides to form segments 1 and 2 of the copepodid III stage. The first antennulary segment of copepodid III has five setae plus the

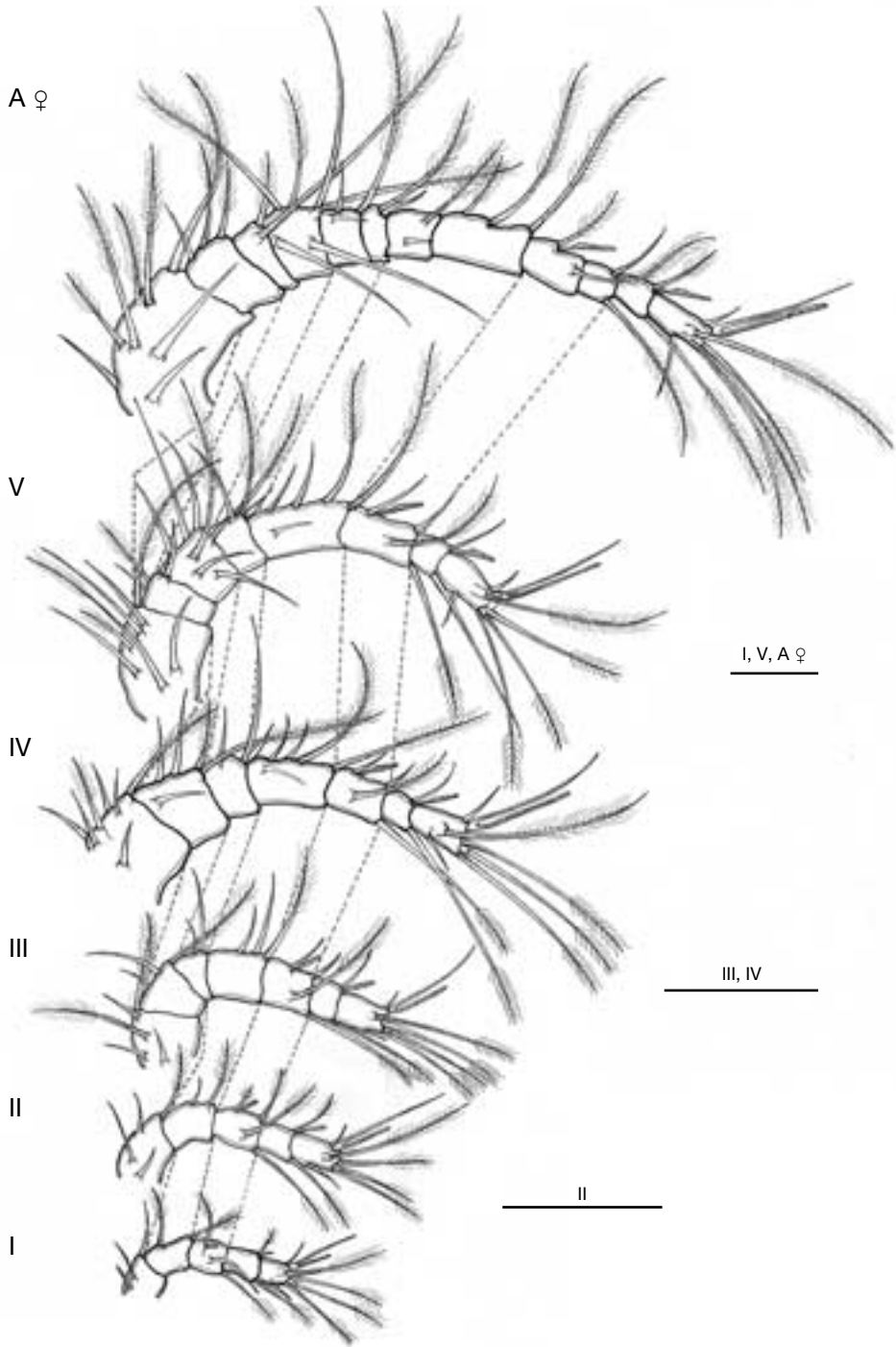


FIG. 19. — Development of antennule of female *Neocyclops* (*Neocyclops*) *vicinus* (Herbst, 1955); dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

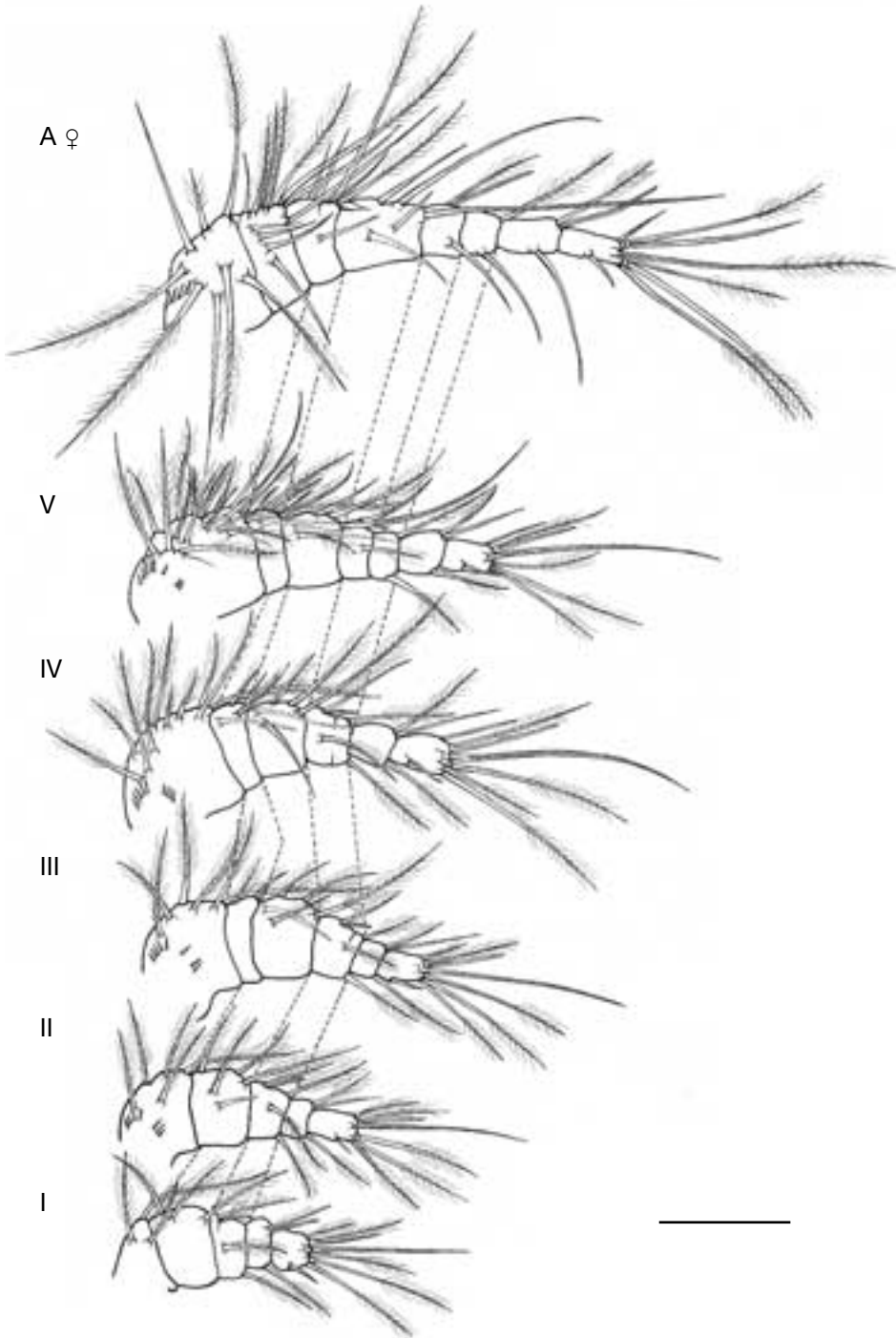


FIG. 20. — Development of antennule of female *Paracyclops chiltoni* (Thomson, 1882); dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bar: 50  $\mu$ m.

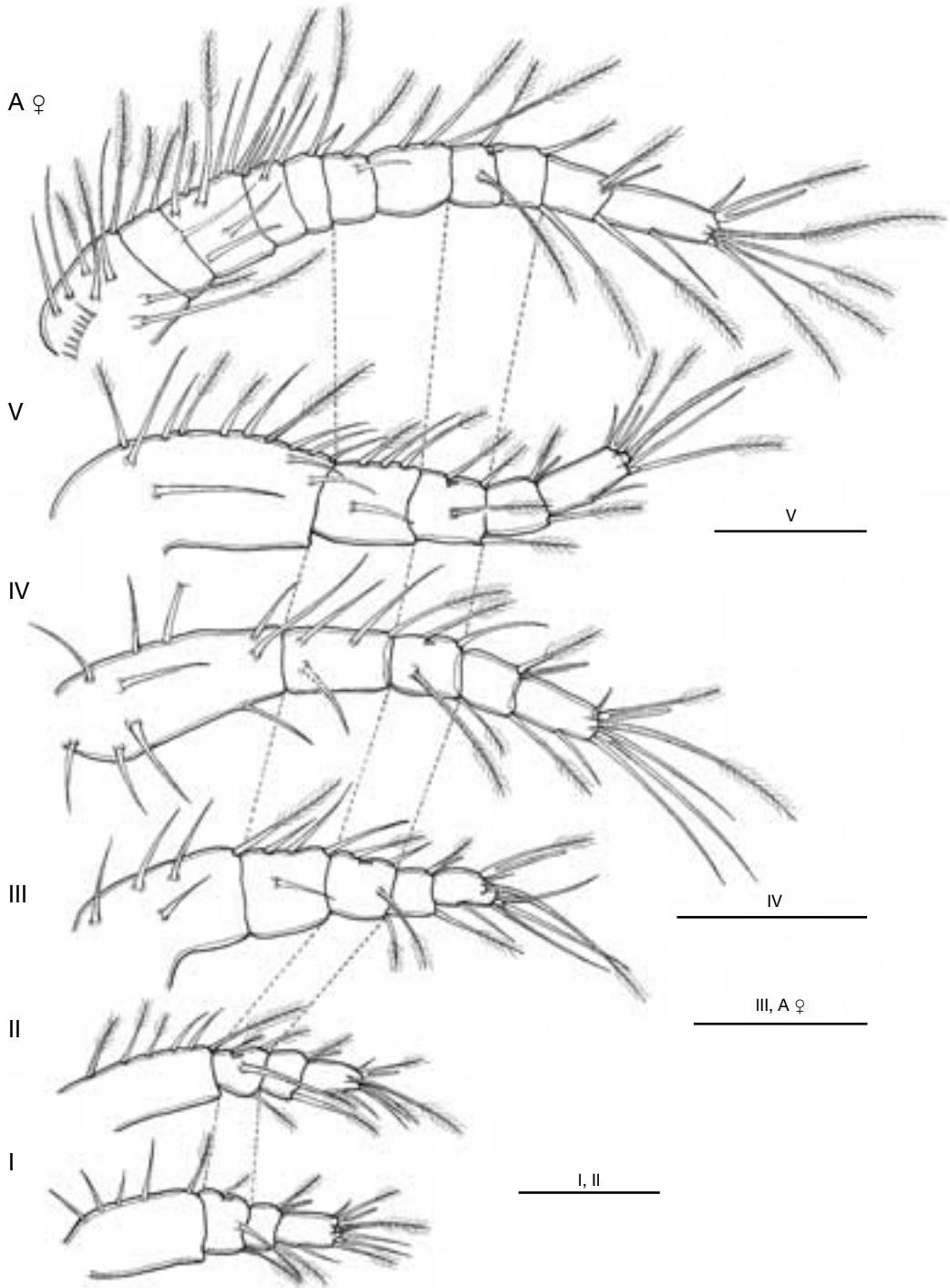


FIG. 21. — Development of antennule of female *Ectocyclops rubescens* Brady, 1904; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.



MPS; in copepodid IV, the number of setae increases to 11 and a furrow appears proximally. At the moult to copepodid V, this segment divides along the furrow giving rise to two segments, with eight and 12 setae respectively; the PS is inserted at the distal corner of segment 1 of copepodid V. Segment 2 of copepodid III carries seven setae, including the MDS positioned distally and the DS in the mid-section. This segment divides to form antennular segment 2 of copepodid IV, with four setae, including the CS, and segment 3, bearing five setae. Segments 2 and 3 of copepodid IV remain undivided until the adult, only adding two setae on the third segment in the copepodid V stage.

Segment 2 of copepodid I possesses a seta at the posterior distal corner, the VS and bithek B1. This bithek is inserted very close to the proximal edge of segment. The segment maintains the same arrangement of setae through to the adult. Segment 3 of copepodid I bears an anterior marginal seta, five setae and a terminal bithek around the apex, and two posterior marginal setae. One anterior marginal seta is added to the proximal half of this segment at the moult to copepodid III. The arrangement of setae then remains unchanged to the adult stage.

#### ANALYSIS OF PATTERNS

Analysis of patterns of antennular development within the Cyclopidae is facilitated by the construction of schematics which emphasizes the derivation of the segments and the sequence of appearance of the setal elements used as markers in this study.

Considering only the development of the antennules from copepodid I to V, 10 patterns were recognised as follows.

##### *Pattern I (Figs 24-29)*

This pattern is shared by *Cyclops* sp., *Megacyclops viridis*, *Acanthocyclops* sp., *Diacyclops uruguayensis*, *Mesocyclops meridianus*, *Thermocyclops decipiens*, *Kieferiella delamarei*, *Diacyclops bicuspidatus odessanus*, *Metacyclops laticornis*, *M. hirsutus*, *Microcyclops anceps anceps*, *M. ceibaensis*, *M. alius*, *Apocyclops dengizicus*, *Hespero-*

*cyclops stocki*, *Speocyclops racovitzai*, *Graeteriella (G.) brehmi*, *Bryocyclops caroli*, *Muscocyclops operculatus*, *Fimbricyclops jimbensoi*, all belonging to Cyclopinae; *Troglocyclops janstocki*, a member of the Halicyclopinae, and *Macrocyclus albidus albidus*, a member of the Eucyclopinae. This group of species represents about 63% of the taxa studied. It is characterised by the expression, from copepodid I, of ancestral articulations XI-XII, XX-XXI, XXIII-XXIV, XXIV-XXV and XXV-XXVI. In copepodid II, articulation XVI-XVII is first expressed, in copepodid III, articulations V-VI and XIV-XV; in copepodid IV, articulation XIII-XIV; and, finally, in copepodid V, articulation VII-VIII. In the moult to adult, various arrangements can occur. The number of segments can remain unaltered at 11 or be increased by the expression of articulation VIII-IX, or one or more articulations in the antennular portion corresponding to segments XXI-XXIII, or of two or three articulations in the region XVII-XX.

##### *Pattern II (Figs 31; 32)*

This was found in *Tropocyclops s. schubarti*, *Cryptocyclops linjanticus* and *Apocyclops procerus*. It differs from the previous pattern only in failure of expression of articulation XIII-XIV from copepodid IV. This articulation appears later, in the antennule of the adult female. Articulation VIII-IX may or may not be expressed.

##### *Pattern III (Fig. 33)*

This occurs in *Allocyclops silvaticus* and *Neutrocyclops* sp. It is distinguished from pattern I by the delay in expression of articulation XIII-XIV, which only appears in copepodid V, and by the differentiation of the articulation VII-VIII only in the adult antennule.

##### *Pattern IV (Fig. 30)*

This presents two differences from Pattern I: articulation XIII-XIV appears only in the adult and articulation VII-VIII differentiates earlier, in copepodid IV. This pattern was found in *Afrocyclops gibsoni*.

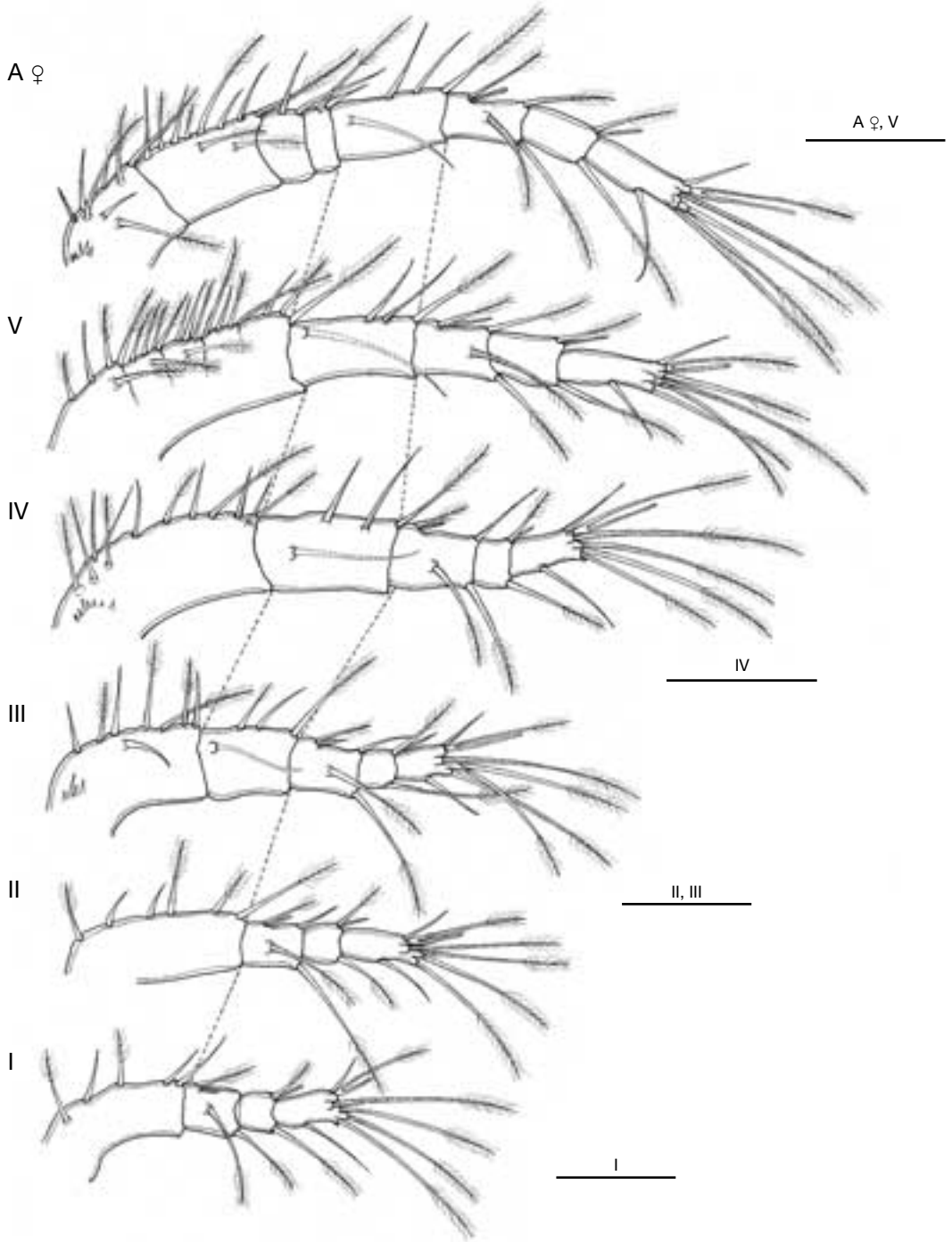


FIG. 22. — Development of antennule of female *Ectocyclops strenzkei* Herbst, 1959; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

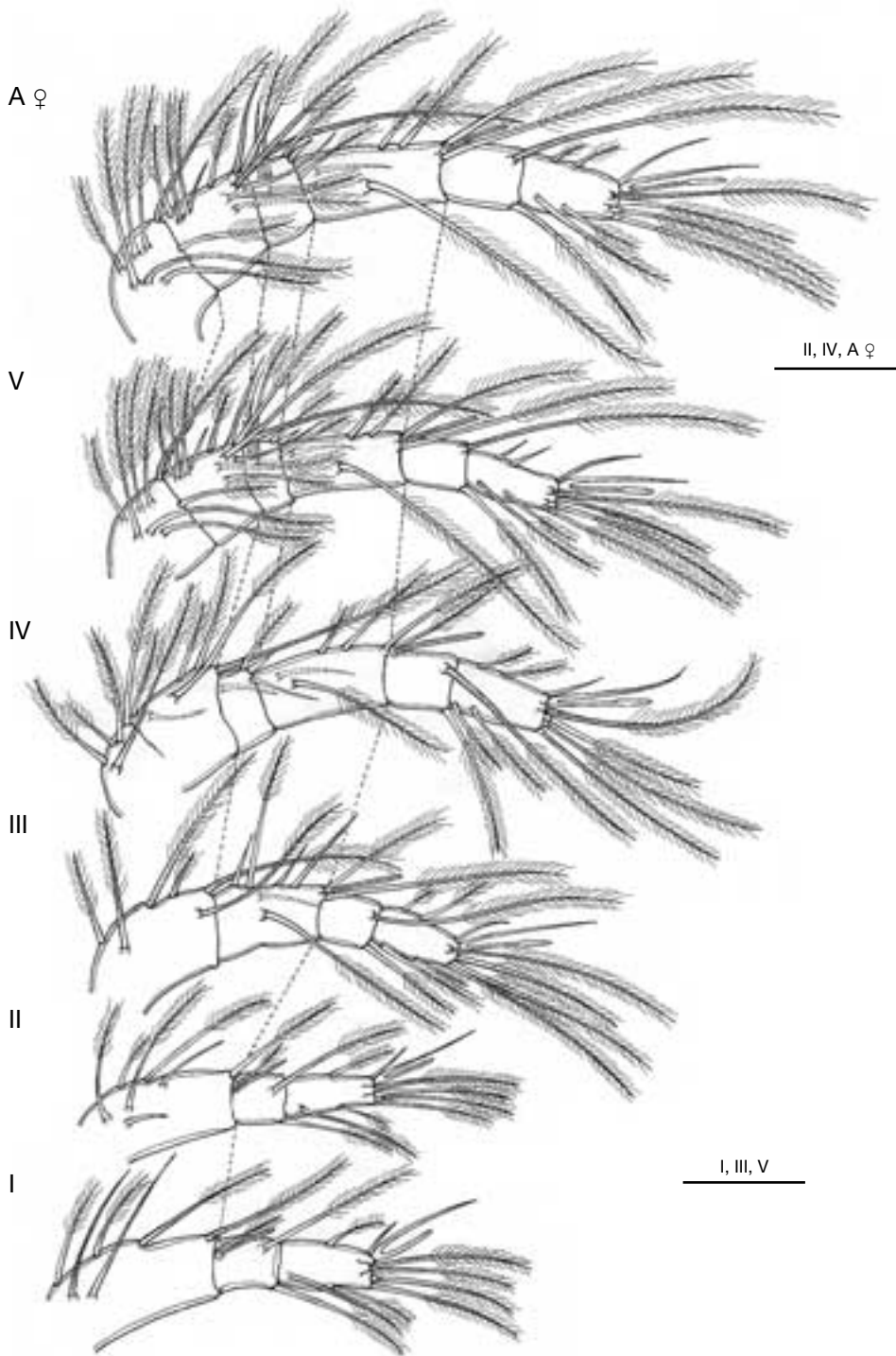


FIG. 23. — Development of antennule of female *Halicyclops aberrans* Rocha, 1983; dotted lines indicate derivation of segments. Abbreviations: I-V, copepodid I-V; A ♀, adult female. Scale bars: 50  $\mu$ m.

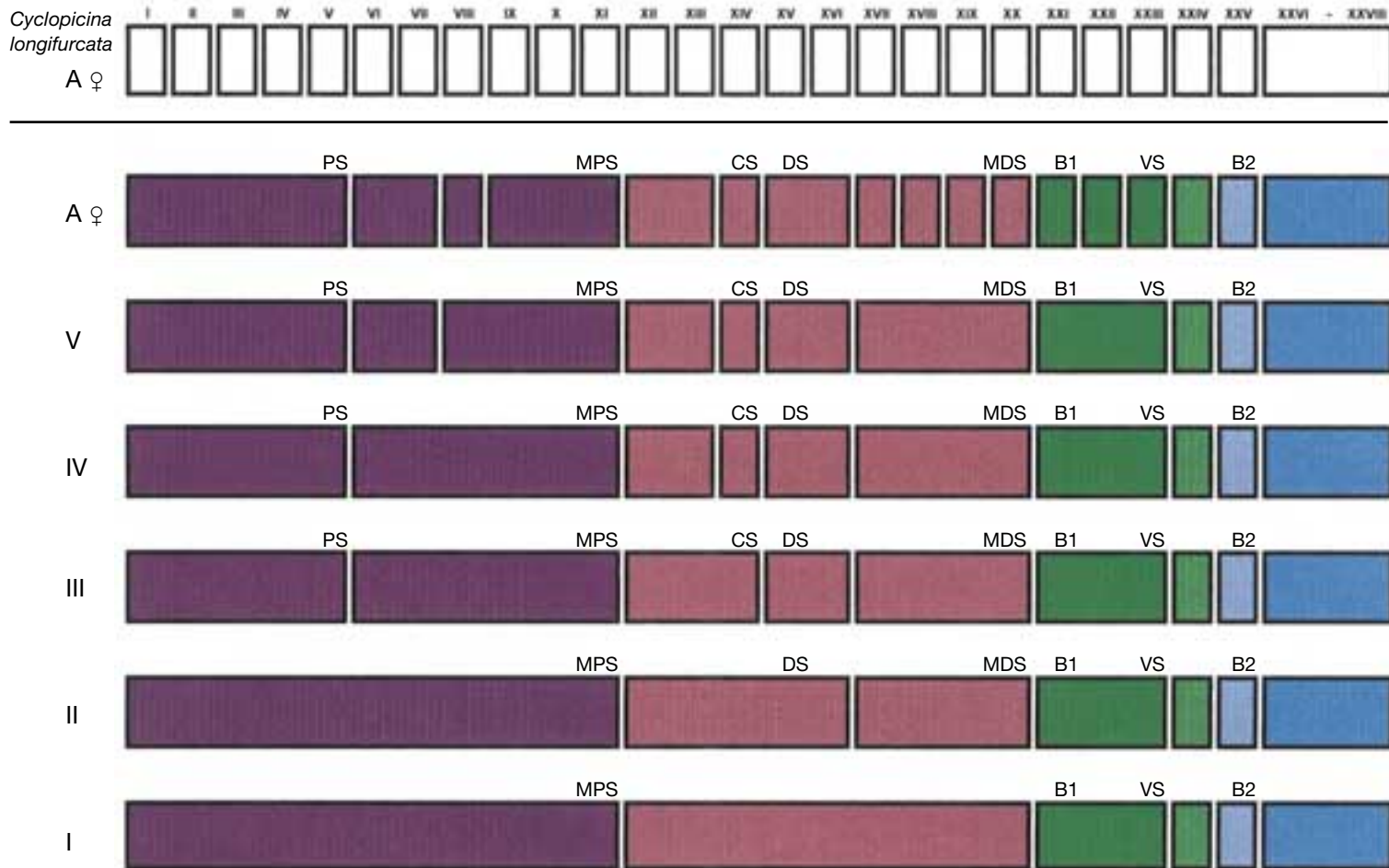


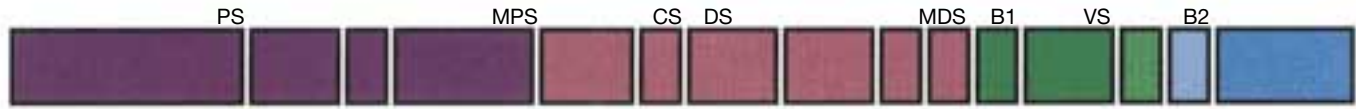
FIG. 24. — Schematic representation of antennular segmentation development from copepodid I to V and adult female (A ♀). *Cyclops* sp., *Megacyclops viridis* s.l., *Acanthocyclops* sp., *Diacyclops uruguayensis*, *Mesocyclops meridianus*, *Thermocyclops decipiens*, *Kieferiella delamarei* are Cyclopinae; *Macrocyclus albidus albidus* belongs to Eucyclopinae. Antennule of adult female (A ♀) *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

*Cyclopicina longifurcata*

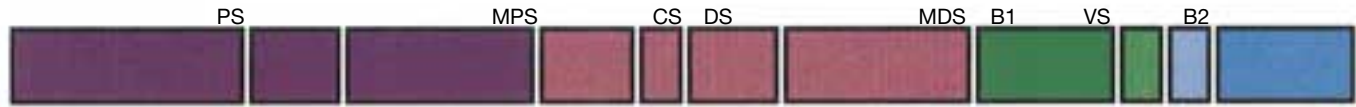
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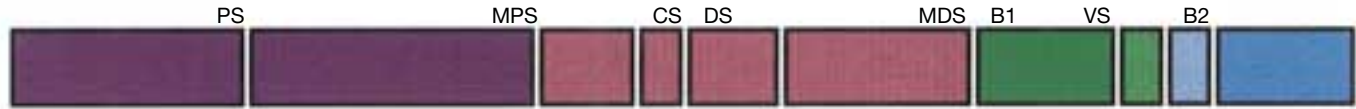
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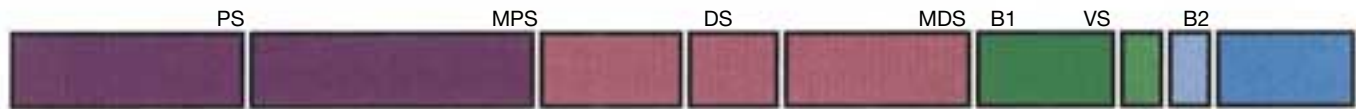
V



IV



III



II



I



FIG. 25. — Schematic representation of antennular segmentation development from copepodid I to V and the adult female (A ♀) of *Troglocyclops janstocki*. Antennule of adult female (A ♀) *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

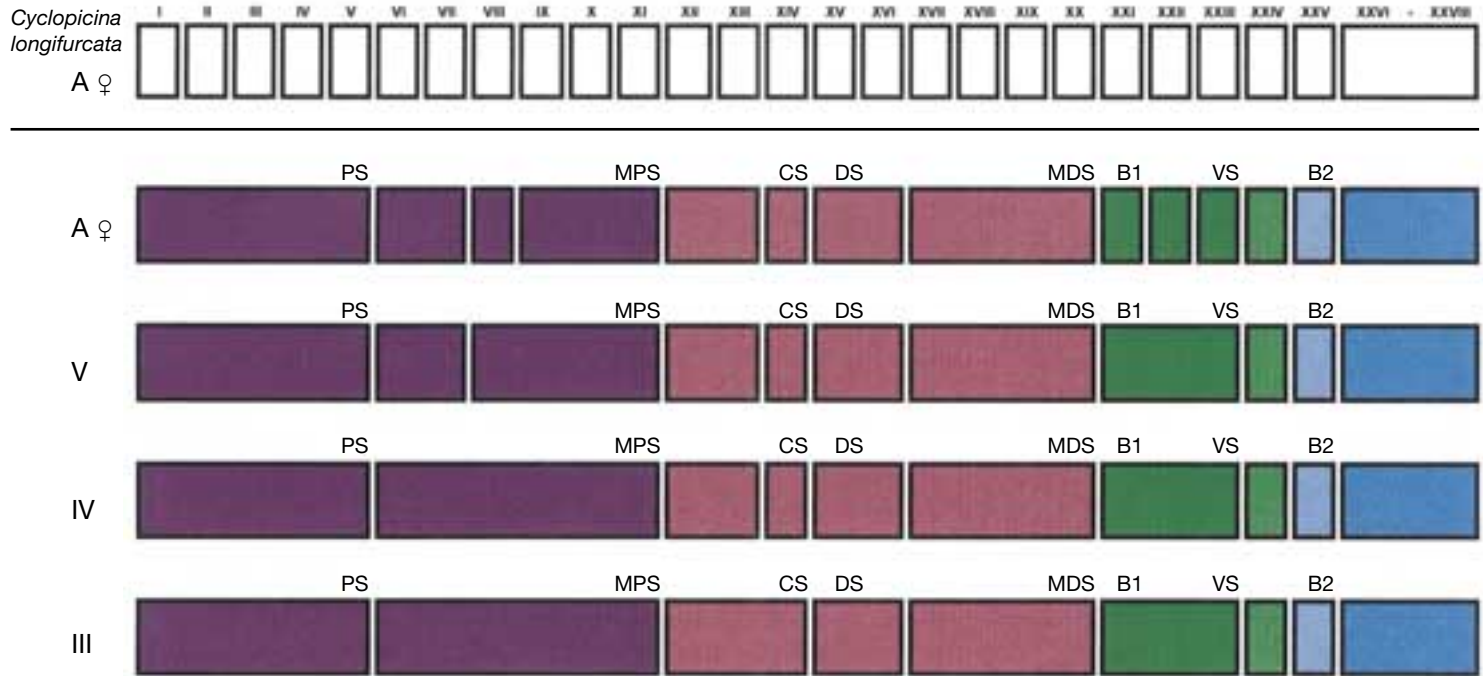


FIG. 26. — Schematic representation of antennular segmentation development of copepodid III to V and the adult female (A ♀) of *Diacyclops bicuspidatus odessanus*. Antennule of adult female (A ♀) *Cyclopocina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

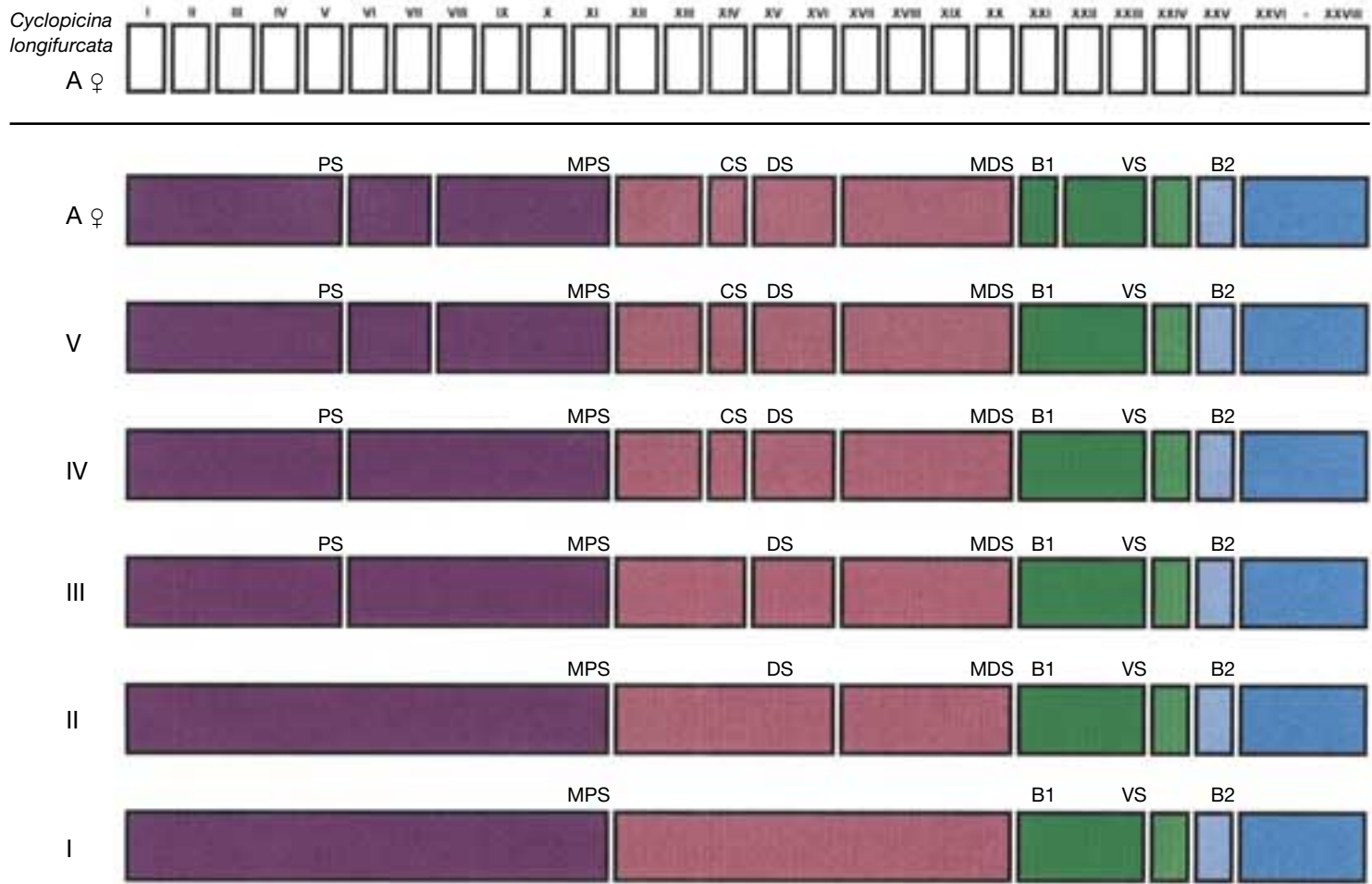


Fig. 27. — Schematic representation of antennary segmentation development of copepodid I to V and adult female (A ♀) of *Metacyclops hirsutus* and *Metacyclops laticornis*. Antennule of adult female (A ♀) *Cyclopocina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.



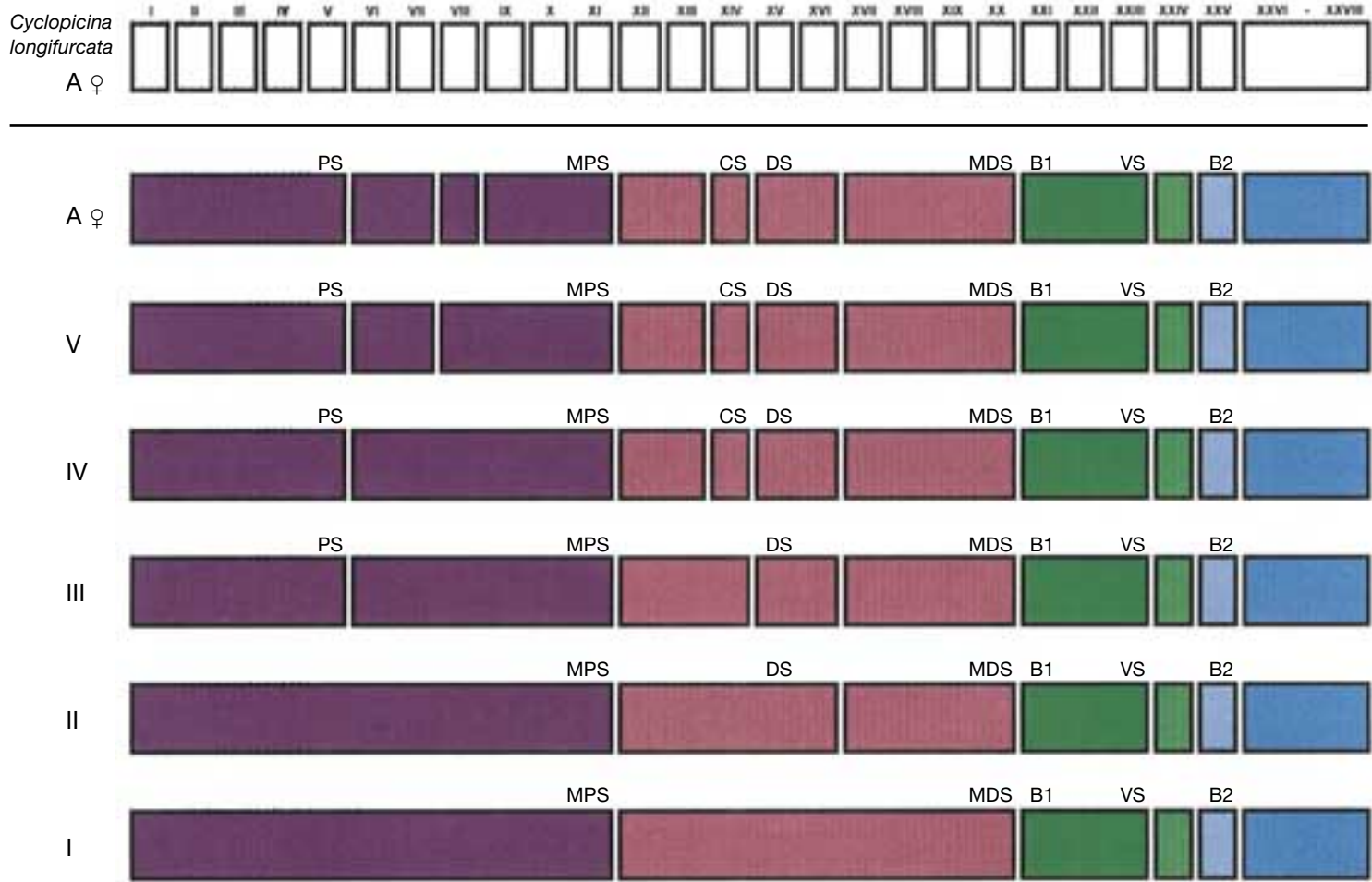


Fig. 28. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Microcyclops anceps anceps* and *Microcyclops ceibaensis*. Antennule of adult female (A ♀) *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.



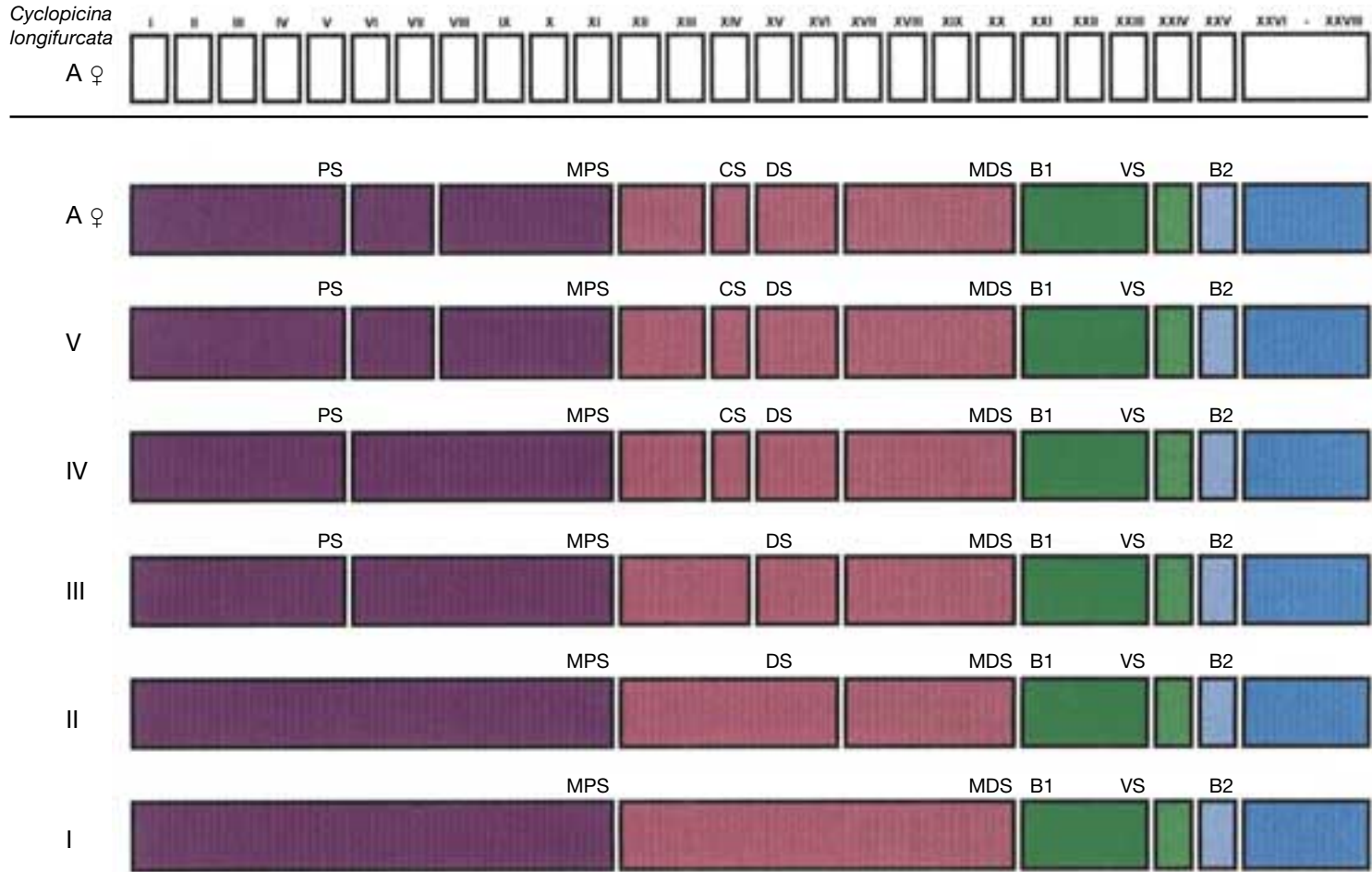
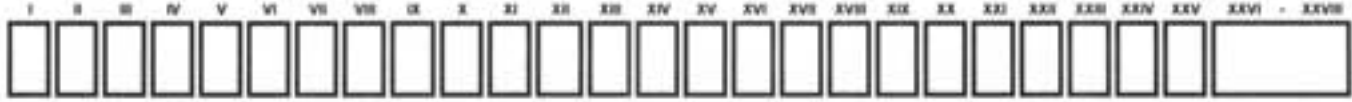


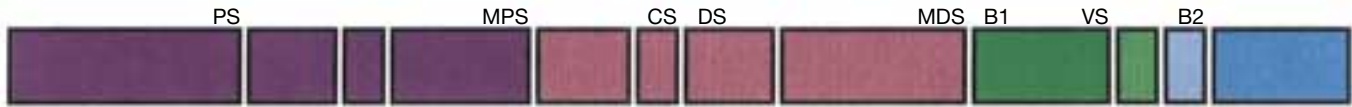
FIG. 29. — Schematic representation of antennular segmentation development from copepodid I to V and adult female (A ♀) of *Microcyclops alius*, *Apocyclops dengizicus*, *Hesperocyclops stocki*, *Graeteriella* (*Graeteriella*) *brehmi*, *Speocyclops racovitzai*, *Bryocyclops caroli*, *Muscocyclops operculatus* and *Fimbricyclops jimhensoni*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

*Cyclopicina longifurcata*

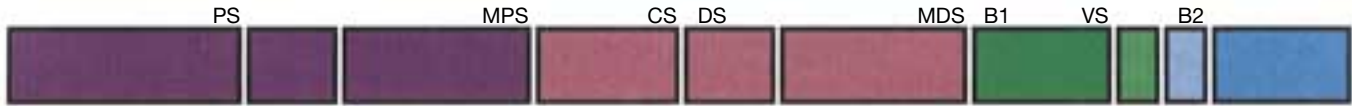
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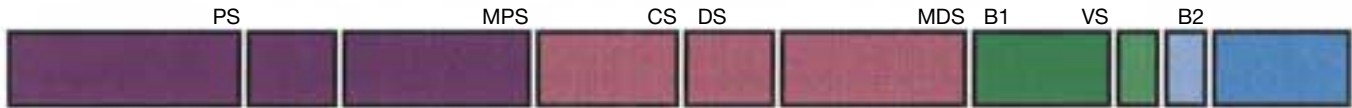
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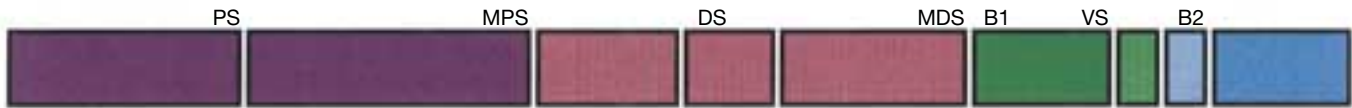
V



IV



III



II



I



FIG. 30. — Schematic representation of antennular segmentation development from copepodid I to V and adult female (A ♀) of *Afrocylops gibsoni* s.l. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

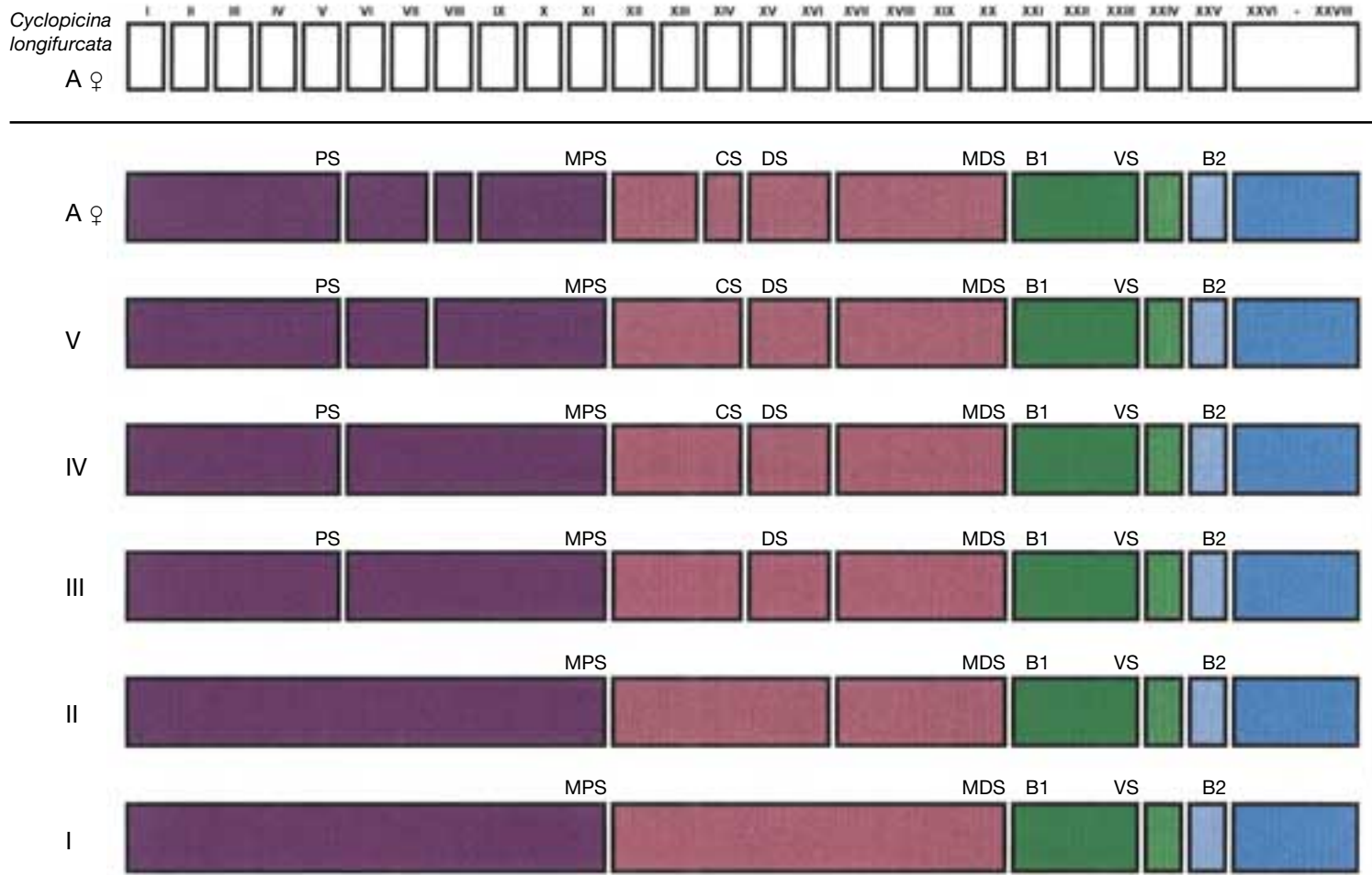


Fig. 31. — Schematic representation of antennular segmentation development from copepodid I to V and adult female (A ♀) of *Tropocyclops schubarti schubarti*. Antennule of adult female (A ♀) of *Cyclopocina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

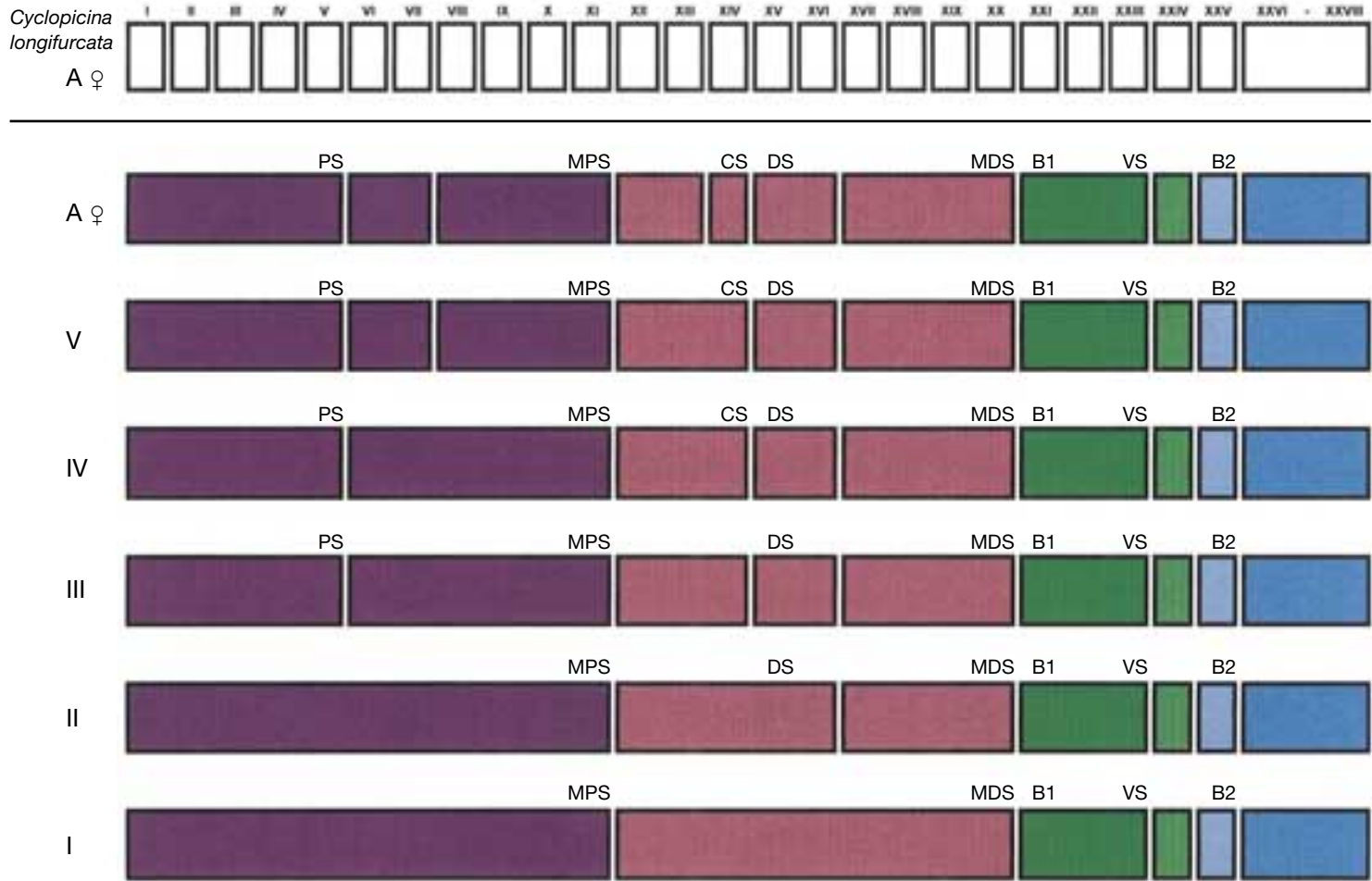


FIG. 32. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Apocyclops procerus* and *Cryptocyclops linjanticus*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

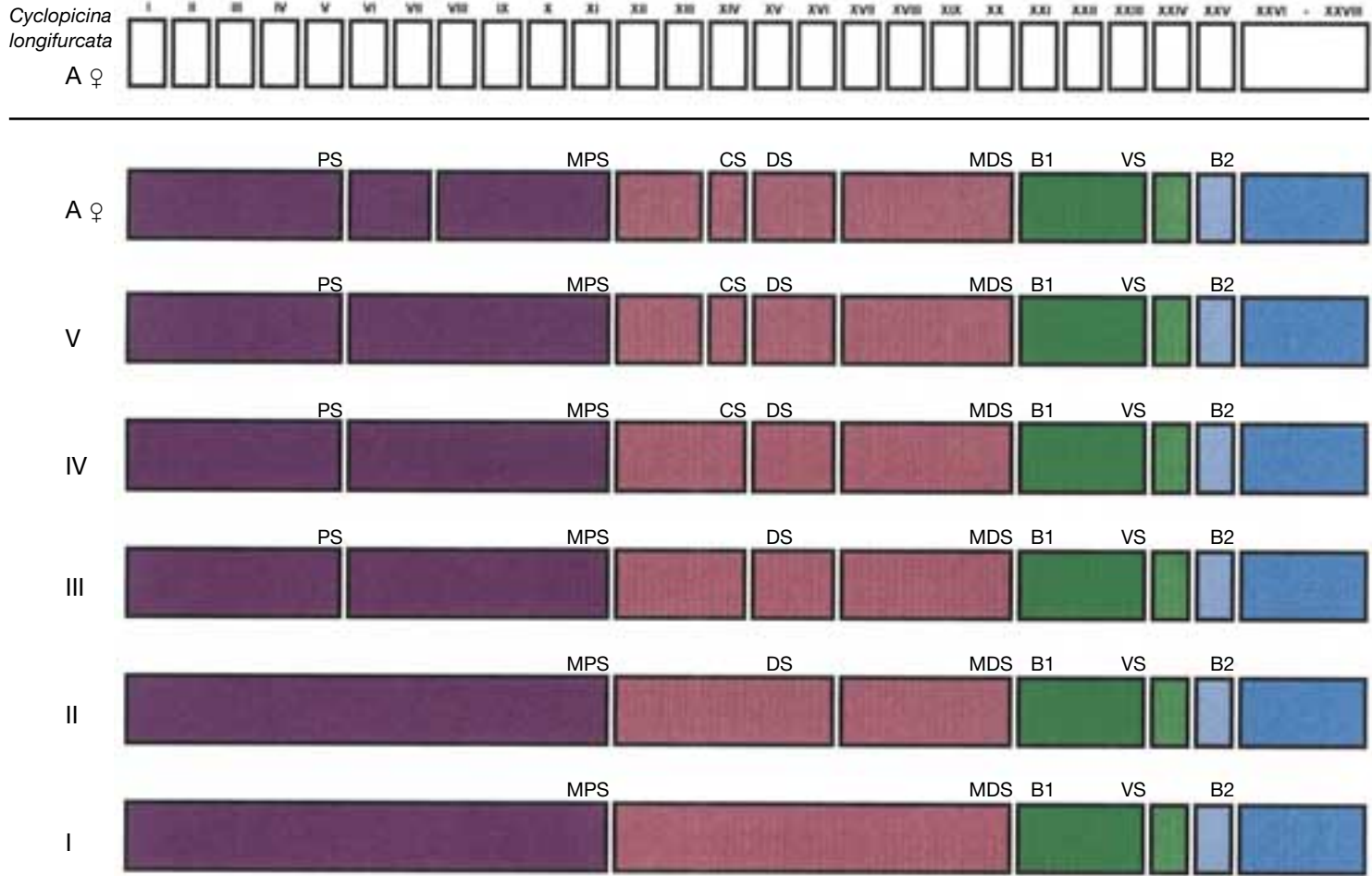


FIG. 33. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Alloctyclops silvaticus* and *Neotroctyclops* sp. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

*Pattern V (Fig. 34)*

This is exclusive to *Ancheuryte notabilis*. Copepodids I and II possess antennules with the same number of segments. So, articulation XVI-XVII, which appears at copepodid II in Pattern I, appears here only in copepodid III. The same segmentation is shared by copepodids IV and V in both patterns. The delay in expression of articulation XVI-XVII observed in *A. notabilis* might be correlated with the suppression of the antennular development step represented by copepodid III of Pattern I.

As in *A. notabilis*, the patterns which follow share an unaltered number of segments in the antennules of both copepodids I and II.

*Pattern VI (Fig. 35)*

This was observed in *Eucyclops (E.) ensifer*. Copepodid I has the same initial segmentation as Pattern I, which it maintains unaltered in copepodid II. In copepodid III, articulation XIV-XV appears; in copepodid IV, articulation V-VI; and, in copepodid V, articulation VII-VIII. In the adult the articulations between segments VIII-IX and XIII-XIV are expressed; the articulation between segments XVI-XVII also appears first in the adult. In addition to retaining the antennular segmentation of copepodid I in copepodid II, the following four patterns are characterised by having the antennular part comprising segments XXI to XXIV undivided through most of development or even until the adult phase.

*Pattern VII (Fig. 36)*

Shares with Pattern VI the same development of antennular portions XII-XX and XXV-XXVIII. But articulation XXIII-XXIV is expressed only at the moult to adult; while articulation V-VI differentiates at the moult to copepodid III. It occurs in *Neocyclops (N.) vicinus*.

*Pattern VIII (Fig. 37)*

The characteristic of this pattern, exclusive to *Paracyclops chiltoni*, is the retention of antennular sector I-XI undivided until the adult, when articulation V-VI appears. The articulation XIV-XV is expressed in copepodid III, while articulation XXIII-XXIV is formed at the moult to copepodid V.

*Pattern IX (Figs 38; 39)*

This is displayed in *Ectocyclops*. The antennules of copepodid I express articulations XX-XXI, XXIV-XXV and XXV-XXVI. In copepodid III, there is an additional articulation, XIV-XV. Articulation XI-XII appears only in the moult to adult; the delayed appearance of this articulation (XI-XII) has been verified only in this genus. Articulations VII-VIII and XVI-XVII are expressed or not, depending on species.

*Pattern X (Fig. 40)*

This is exclusive to *Halicyclops aberrans*. The first two copepodid stages show only articulations XX-XXI and XXIV-XXV. The appearance of articulation XI-XII, present in copepodid I in all other patterns (except pattern IX), is delayed until copepodid III. Articulation XIV-XV differentiates in copepodid IV, and V-VI, in copepodid V. The antennule does not show any changes in number of segments in the moult to adult.

## DISCUSSION

The study of the development of antennules within the family Cyclopidae has demonstrated that a number of different sequences exists (Table 1). Of the 17 different sequences identified, six of them generated an adult antennule of 12 segments (Figs 27; 28), and four resulted in an adult antennule of 11 segments (Figs 32; 33). This occurred in species of both the Eucyclopinæ and Cyclopinæ. Seven species of Cyclopinæ and one of Eucyclopinæ show a common pattern resulting in an adult female with 17 expressed segments (Schutze 1997). Antennules with the same number of segments in the copepodid V and in the adult female were found within the Cyclopinæ and in *Halicyclops aberrans*, suggesting that neotenic processes may be involved in these taxa. In cases where the antennule of copepodid V and the adult female had 11 segments, Gurney (1933) interpreted them as being due to the persistence of a larval character in the adult phase.

The origin of the newly differentiated segments was clearly evidenced by the presence of trans-



*Cyclopicina longifurcata*

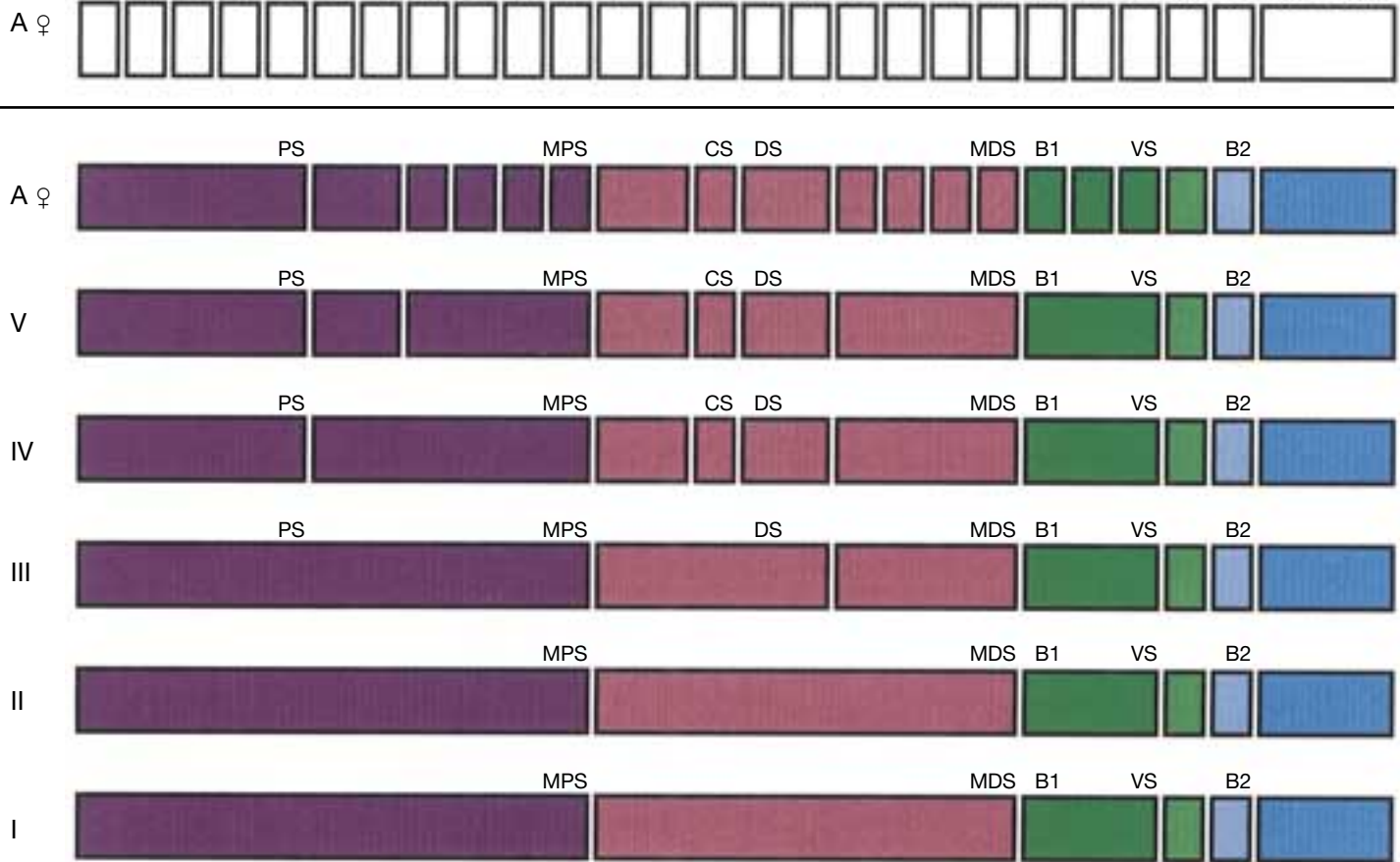


FIG. 34. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Ancheuryte notabilis*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

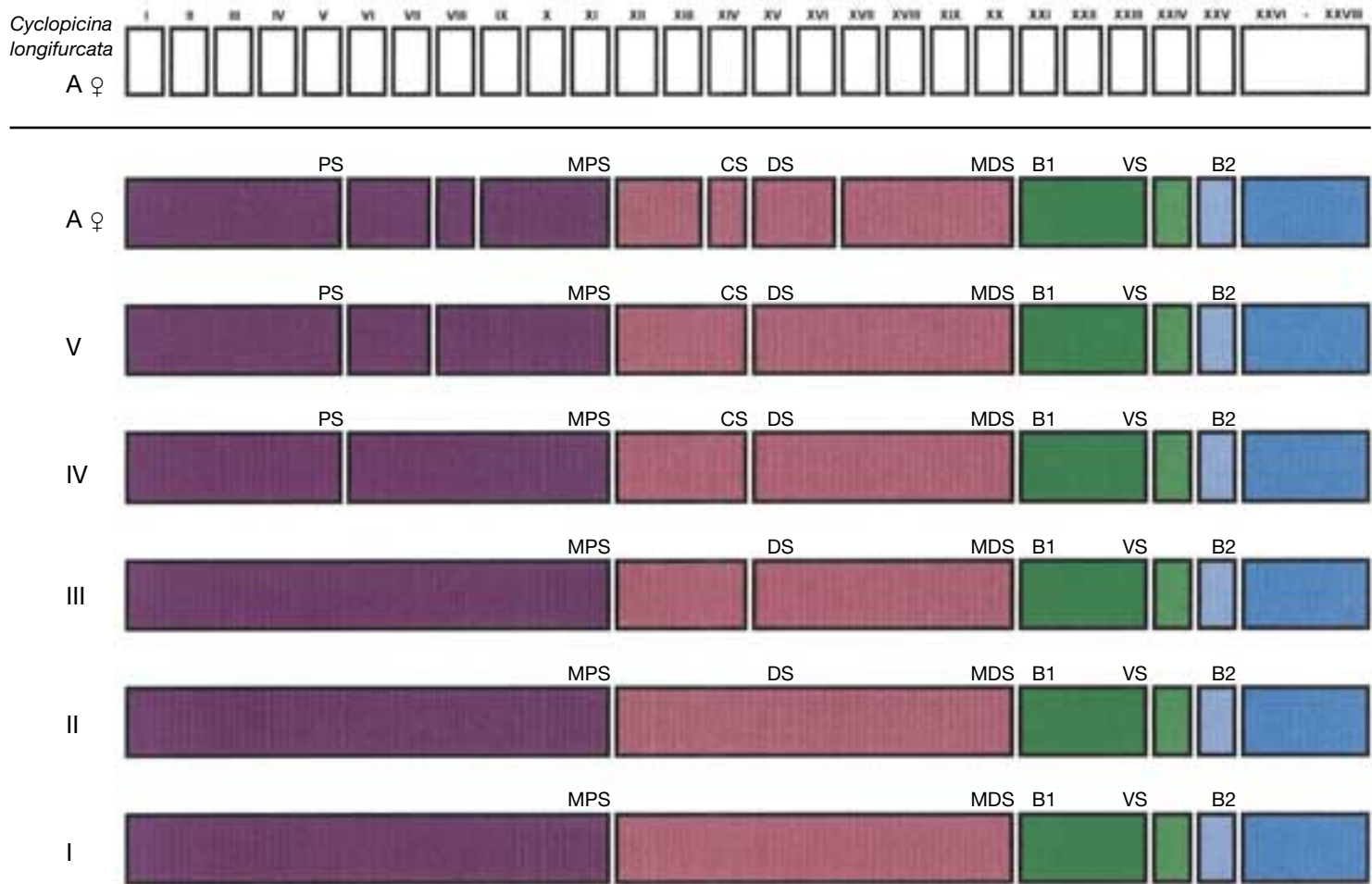


FIG. 35. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Eucyclops (Eucyclops) ensifer*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.



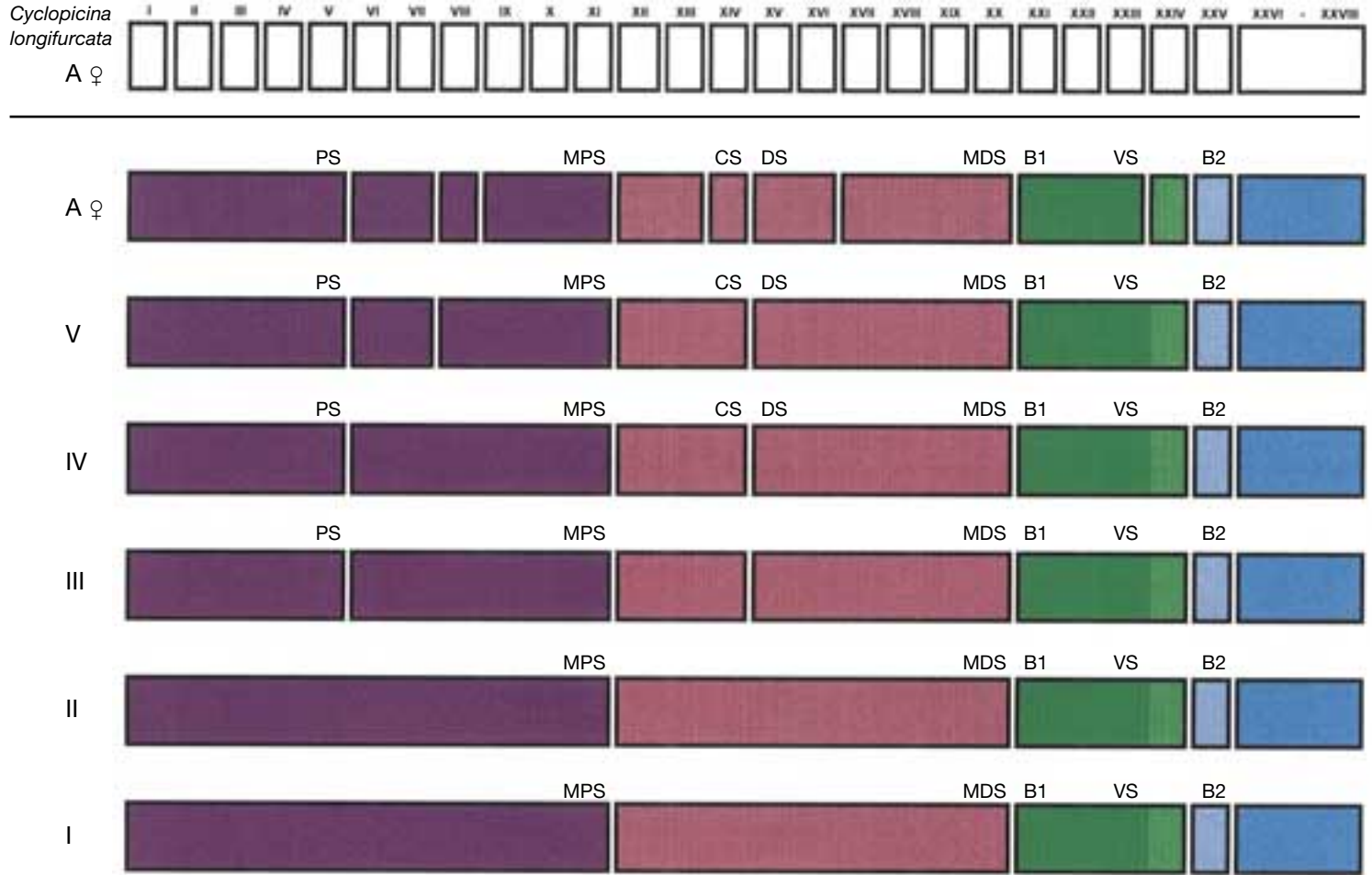


Fig. 36. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Neocyclops (Neocyclops) vicinus*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal biramous; **B2**, distal biramous.

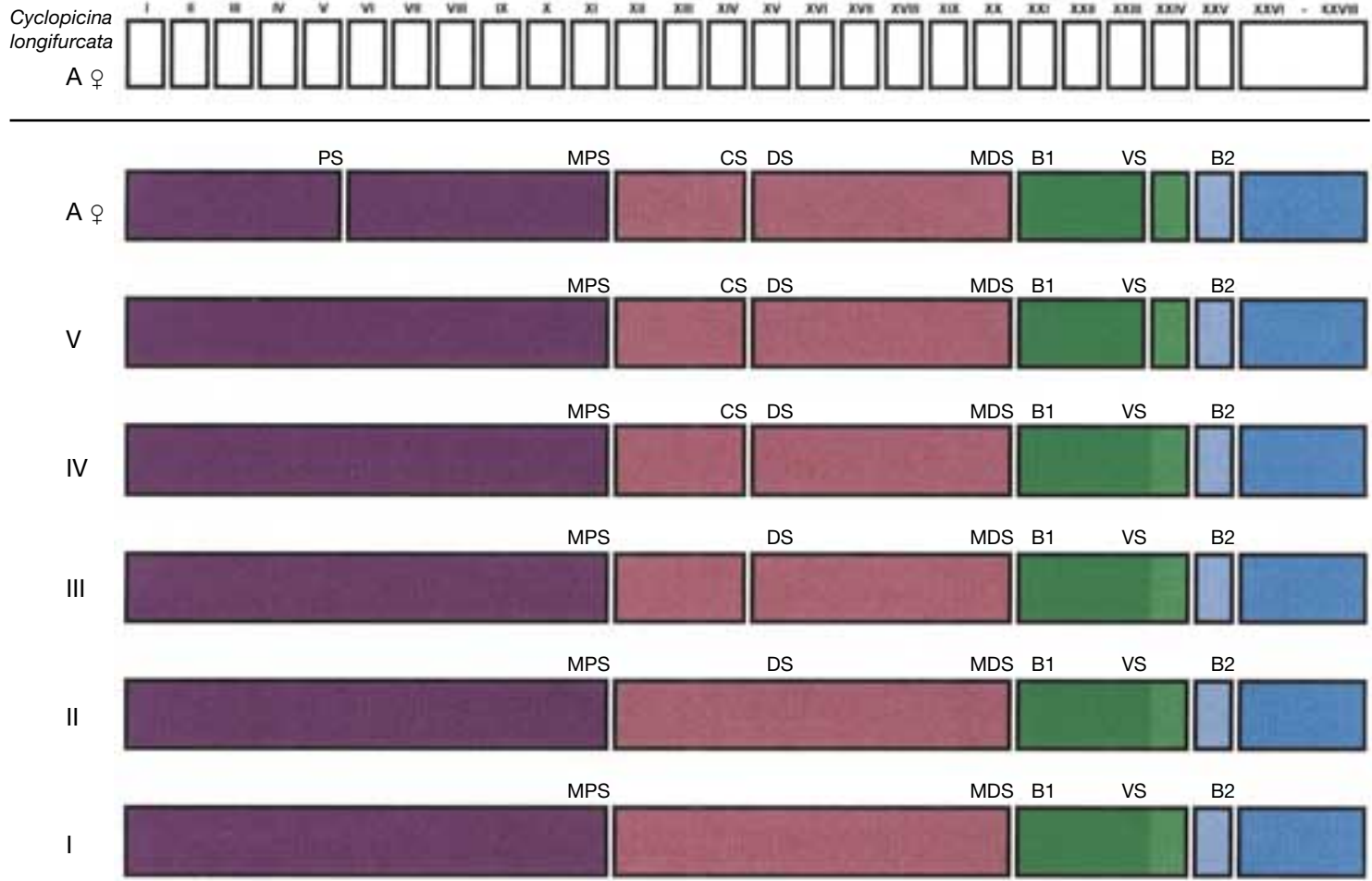


FIG. 37. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Paracyclops chiltoni*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

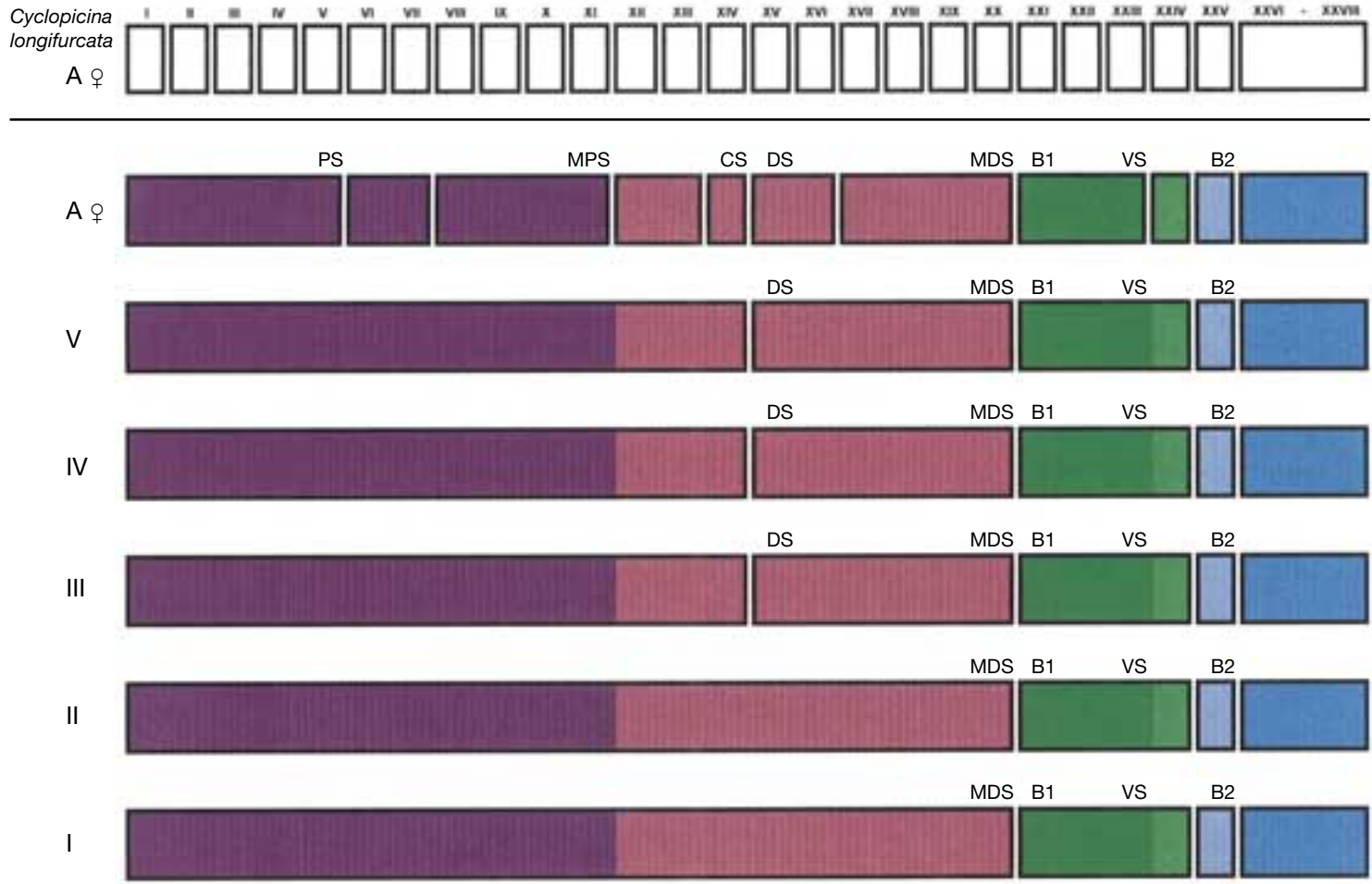


FIG. 38. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Ectocyclops rubescens*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

*Cyclopicina longifurcata*

A ♀

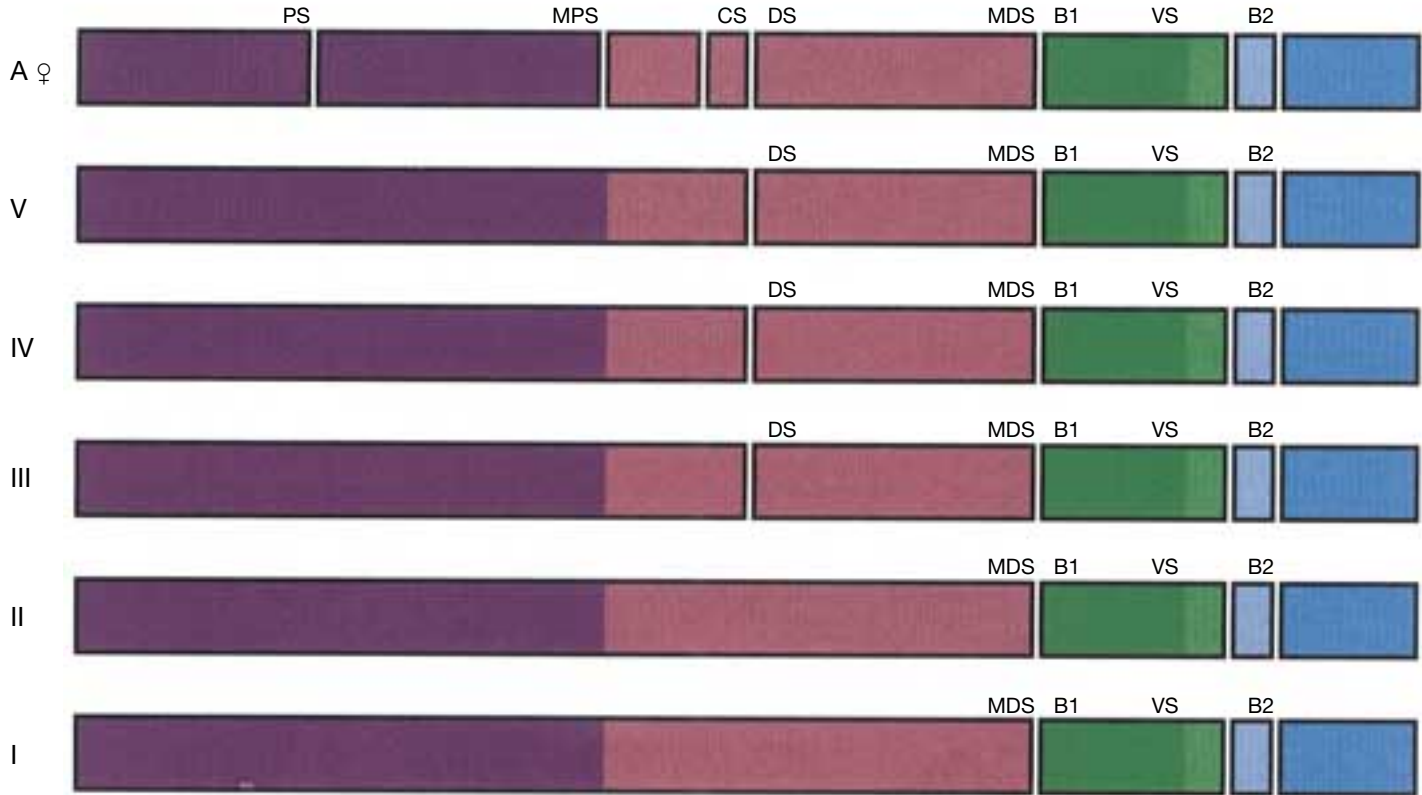
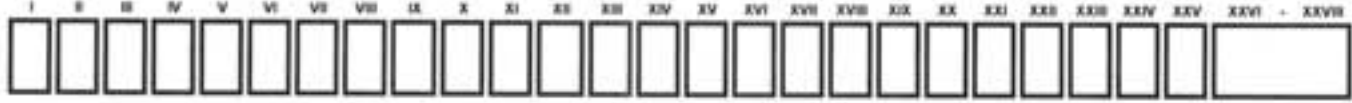


FIG. 39. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Ectocyclops strenzkei*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

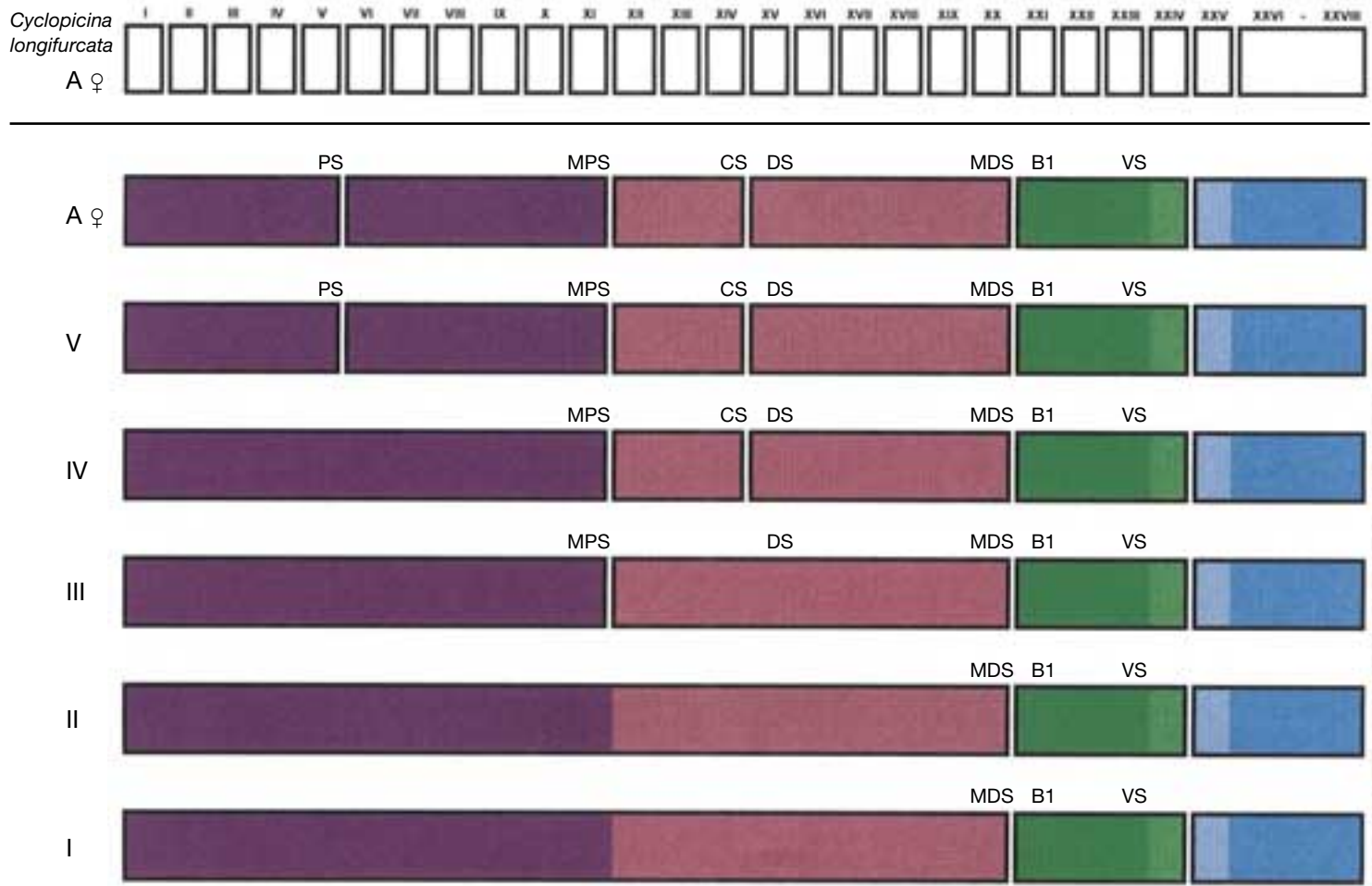


FIG. 40. — Schematic representation of antennular segmentation development of copepodid I to V and adult female (A ♀) of *Halicyclops aberrans*. Antennule of adult female (A ♀) of *Cyclopicina longifurcata* shown as reference. Abbreviations: **PS**, proximal seta; **MPS**, mid proximal seta; **CS**, conical seta; **DS**, dorsal seta; **MDS**, mid distal seta; **VS**, ventral seta; **B1**, proximal bithek; **B2**, distal bithek.

verse furrows and marker setae, by the number of setae, and by the relative lengths of the segments. Division on only one side of a segment was observed only in *Ancheuryte notabilis* however, it is quite a common occurrence, as reported, for example, by Dahms (1989), in *Tisbe gracilis* (T. Scott, 1985) and *Drescheriella glacialis* Dahms & Dieckman, 1987 (Harpacticoida), and by Reid (1992) in *Acanthocyclops pennaki* Reid, 1992.

In general, copepodid descriptions in the literature do not detail either the setation or the antennular segmentation. These descriptions, moreover, do not aid in the identification of the homologies of the segments. Tracing the homologies of the segments here has demonstrated that the development of the antennules of all female cyclopids examined involves an increase in the number of segments through the expression of one more additional articulations during the copepodid phase. There are many examples of failure of expression of particular articulations but none of reducing segment numbers by secondary fusion of segments, although this occurs in males.

The increase in number of segments occurred in the proximal and median regions of the antennule. Only in *Neocyclops* (*N.*) *vicinus*, *Paracyclops chiltoni* and *Ectocyclops rubescens* did any changes occur in the three terminal segments. Increasing numbers of segments, during development, only in the median part of the appendage was observed in Harpacticoida by Itô (1970) and Dahms (1989). As a general rule, during the development of copepods, the anteriorly located somites and appendages are formed earlier than the most posterior ones (Hulsemann 1991; Huys & Boxshall 1991; Ferrari 1993). Nevertheless, a few examples of retrograde morphogenesis were recognized by Izawa (1991). In the antennules of Cyclopidae, however, the first segments to be differentiated are located in the distal region, as in other copepods (Boxshall & Huys 1998). The apical segment of the antennules in the Cyclopidae appears already formed as a compound segment XXVI-XXVIII at the copepodid I. No increase in the number of setae and no subdivisions are found, with the exception of *Halicyclops*

*aberrans*, which showed a unique compound apical segment derived from segments XXV-XXVIII. This was also the only species lacking bithek B2 on segment XXV. In *Halicyclops aberrans* a proximal anterior seta appears at copepodid III on the compound apical segment 4 (Fig. 23). There are two possible interpretations of this: 1) the distal antennular segment of *H. aberrans* is in part derived from segment XXIV and the new seta represents the anterior seta from ancestral segment XXIV (since this seta usually appears at the moult to copepod II in copepods); 2) the seta is the anterior seta of segment XXV which is, uniquely, delayed in appearance in *Halicyclops aberrans*. We favour the latter interpretation.

Segment 1 at the adult female cyclopids represents ancestral segments I-V that never differentiate during development. An apical segment, corresponding to segments XXVI-XXVIII, is found in the antennules of Cyclopoida, Harpacticoida, Siphonostomatoida and Poecilostomatoida (Huys & Boxshall 1991).

Some pairs of species from the genera *Metacyclops* and *Microcyclops* display identical segment-numbers at all stages and this might lead to the erroneous inference that the developmental pattern is the same in each member of the pair. For example, the pairs species *Metacyclops hirsutus*/*Metacyclops laticornis* (Fig. 8) and *Microcyclops a. anceps*/*Microcyclops ceibaensis* (Fig. 9) each possess the same number of antennular segments in all stages of development (Table 1). In the adult, however, the derivations of the segments from copepodid V are not the same. In the former pair of species, it is segment 8 of copepodid V that splits into two; segment 3 does not split. In the latter pair of species, the subdivision occurs in segment 3 of copepodid V, segment 8 remaining undivided. In the eight species with antennules of 12 segments in the adult, the last five segments (XVII-XX; XXI-XXIII; XXIV; XXV; XXVI-XXVIII) are homologous in all, with the exception of *Metacyclops laticornis* and *M. hirsutus*.

The same occurs in the pairs of species *Apocyclops procerus*/*Cryptocyclops linjanticus* and *Alloicyclops silvaticus*/*Neutrocyclops* sp. (Table 1).

The number of segments is similar in all stages of development. The difference occurs in segment 2 of copepodid IV, which splits into two at the moult to copepodid V in *A. procerus* and *C. linjanticus* (Fig. 32), whereas in *A. silvaticus* and *Neutrocyclops* sp. (Fig. 33), it is segment 3 of copepodid IV which splits into two in copepodid V. The antennules of the adult females show the same segmentation in both pairs of species, but it is derived through the subdivision of segment 4 of copepodid V in the former pair of species, and of segment 2 of copepodid V in the latter pair.

Failures of segmental expression were observed in all four subfamilies of Cyclopidae and in all copepodid stages. Identical segmentation and setal counts in successive stages could indicate that there has been a failure in the ancestral sequence of development. The compound antennular segments of *Paracyclops chiltoni* were considered by Karaytug & Boxshall (1996) to be derived either as a result of secondary fusion of segments that had been separate at an earlier developmental stage, or as a result of failure in separation (i.e. by the failure of expressive of an articulation). Secondary fusions were observed only in males, the majority of compound segments in both sexes arising as a result of failures of expression of ancestral articulations.

In all the species of Cyclopinae observed, the development of the antennules was identical from copepodid I to copepodid III. In copepodids IV and V, few variations were observed, always relating to a developmental failure during ontogeny. Ferrari (1988) observed failures in development of the swimming legs of Cyclopidae.

The present study generates new evidence relevant to the current debate on systematics at the subfamily level in the Cyclopidae.

As we observed, *Macrocyclus a. albidus*, which belongs to the Eucyclopinae, possesses the same number of segments and the same pattern of antennular development as a large group of species of Cyclopinae. Fiers & Van de Velde (1984) considered *Macrocyclus* as a primitive genus and positioned it close to the separation of the

Eucyclopinae and Cyclopinae lineages. The plesiomorphic status of *Macrocyclus* was also pointed out by Fryer (1957). The sharing of developmental sequences between *Macrocyclus* and the group of cyclopine species may, however represent a symplesiomorphy and not be indicative of a close phylogenetic relationship.

Rocha & Iliffe (1994) included *Troglocyclops janstocki* in the Halicyclopinae because of the plesiomorphic structure of its fifth leg. This study reveals a close similarity in antennular development between *T. janstocki* and many cyclopine species, the only difference being the presence in the adult of 15 antennular segments, in the former. However, this too may be a symplesiomorphy.

*Eucyclops* and *Afrocyclus* have been considered to be closely related genera, but on the basis of the species studied here they differ considerably in antennular segmentation from the copepodid II onwards, despite both having 12 segmented antennules in the adult female. *Afrocyclus gibsoni* exhibits a closer resemblance to *T. s. schubarti*. *Ancheuryte notabilis* and *Eucyclops (E.) ensifer* are included in different subfamilies but share a similar development from copepodid I to copepodid III. *Halicyclops aberrans*, *Neocyclus (N.) vicinus* and *Paracyclops chiltoni* all show patterns of development that are very distinct from the rest of the Cyclopidae, and the pattern in *Ectocyclops* is unique in the family.

*Apocyclops procerus* and *A. dengizicus* bear antennules with the same number of segments in most stages, except copepodids IV and V. In *A. procerus* a development failure occurs in copepodid IV, which maintains the same number of segments (nine) as in copepodid III. In *A. dengizicus*, the failure in development occurs in the adult female which retains eleven segments, in the two last stages of development. Both species have the same adult number of antennular segments. This difference in the development pattern corroborates the recognition of the different species groups "panamensis", including *A. procerus*, and "dengizicus", represented only by *A. dengizicus*.

The articulations between segments XX and XXI and segments XXIV and XXV are always ex-



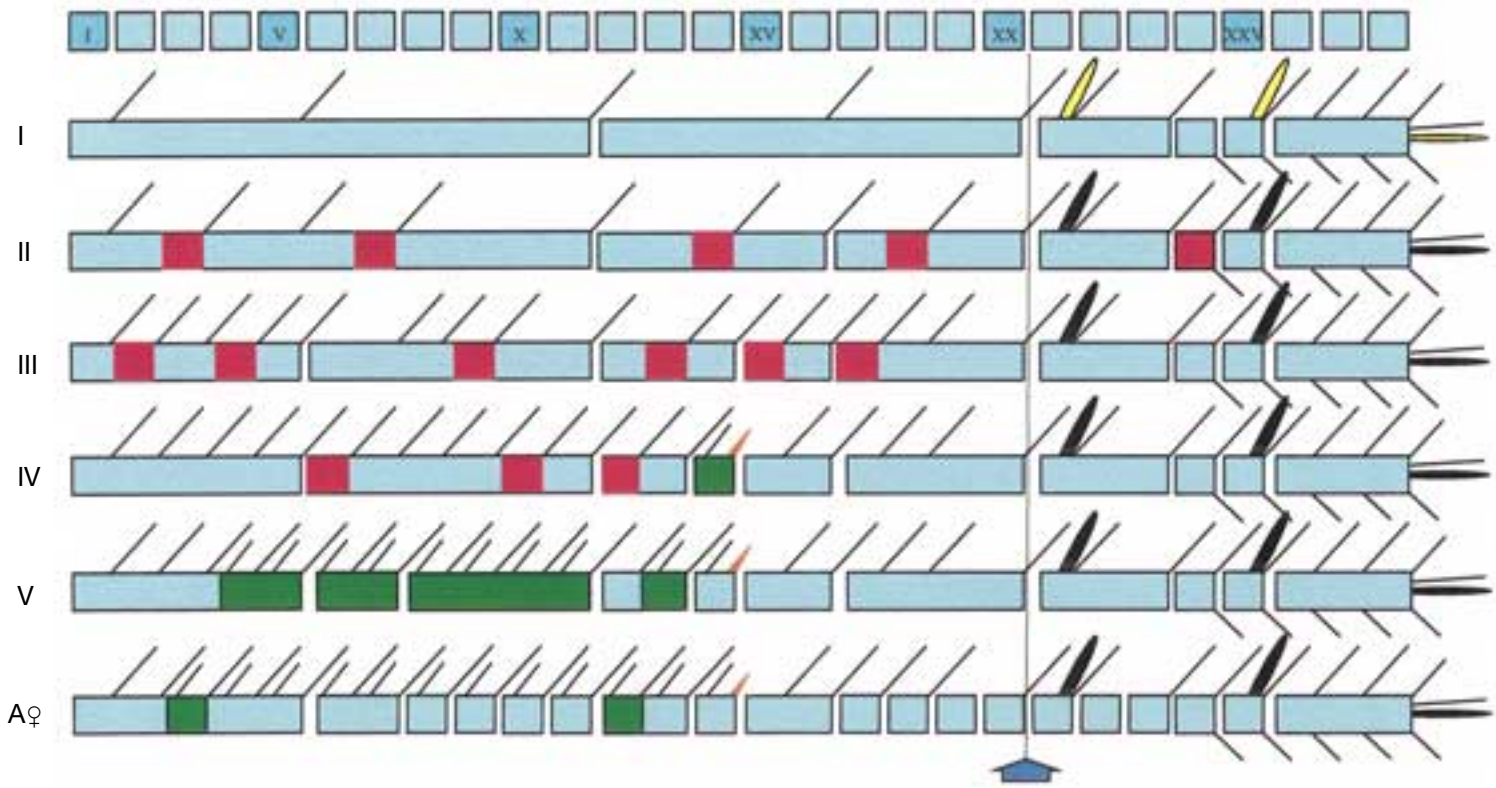


FIG. 41. — Schematic representation of the development of segmentation and setation through the copepodid stages of hypothetical ancestral antennules of Cyclopidae. Armature elements are shown as setae, spines or aesthetascs. Segments carrying a seta not present at the preceding copepodid stage are shown in red if the newly added seta is the anterodistal member of a trithek, in green if it is the anteroproximal member. The plane of the XX to XXI articulation is indicated by a vertical dotted line. Aesthetasc are shown in yellow when they first appear, then in black. I-V, copepodid stages I to V; ♀, female. The scale at the top indicates the presumed 28 segments of the ancestral copepod (see Huys & Boxshall 1991).



pressed in all copepodid stages of all Cyclopidae examined and are regarded here as symplesiomorphic.

Articulations V-VI, XI-XII and XIV-XV are expressed in all adult Cyclopidae but appear at different copepodid stages in different taxa. According to Boxshall & Huys (1998), the articulation between segments V and VI is already expressed in copepodid I in the hypothetical ancestral developmental pattern of copepod antennules. A delay of at least two moults was observed in the appearance of this articulation in all cyclopids studied.

The articulation between segments XI and XII appears in copepodid II in the hypothetical ancestral copepod antennules (Boxshall & Huys 1998). In cyclopids its appearance is delayed in *Ectocyclops strenzkei*, *Ectocyclops rubescens* (Eucyclopinae) and *Halicyclops aberrans* (Halicyclopinae) but in all other species the appearance of articulation is accelerated.

The articulation between segments XIV and XV appears in copepodid II in the hypothetical ancestral sequence (Boxshall & Huys 1998), but was delayed in all cyclopids studied.

A schematic showing the development of antennular segmentation and setation through the copepodid stages of the female hypothetical ancestor of the Cyclopidae is presented (Fig. 41). Only one seta is added distal to the XX-XXI articulation in the copepodid phase, the anterior seta on segment XXIV at the moult to copepodid IV, exactly as typical for other copepods. Unique features are the lack of any setal elements on segments XIX and XXII at any stage, plus the failure to develop of the proximal setae on segments XV to XX, which would typically appear at moult to copepodid IV. Segment XXI also lacks the proximal seta, which usually appears at the moult to copepodid III.

The distal seta on segment XIV appears at copepodid II, but transforms to a spine (often referred to as the conical seta) at the moult to copepodid IV. This setal transformation occurs at exactly the same moult as in the Siphonostomatoida and the Misophrioida (Boxshall & Huys 1998), suggesting that this is probably a highly conserved, plesiomorphic feature of development.

## Acknowledgements

We would like to thank Dr Jeanete Maron Ramos Chancellor of Santa Ursula University for her encouragement and support and Dr Damia Jaume of IMEDEA (CSIC, UIB), Spain, for commenting on the manuscript.

## REFERENCES

- Boxshall G. A. 1983. — Three new genera of misophrioid copepods from the near bottom plankton community in the North Atlantic Ocean. *Bulletin of the British Museum Natural History, zoology* 44 (2): 103-124.
- Boxshall G. A., Ferrari F. & Tiemann H. 1984. — The ancestral copepod: towards a consensus of opinion at the First International Conference on Copepoda 1981. *Crustaceana*, supplement 7: 68-84.
- Boxshall G. A. & Huys R. 1998. — The ontogeny and phylogeny of copepod antennules. *Philosophical Transactions of the Royal Society of London* 353 (B): 765-786.
- Burckhardt G. 1913. — Wissenschaftliche Ergebnisse einer Reise um die Erde von M. Pernod und C. Schröter. III: Zooplankton aus ost und süd-asiatischen Binnengewässern. *Zoologische Jahrbücher, Abteilung für Systematik* 34: 341-372.
- Claus C. 1893. — Neue Beobachtungen über die Organisation und Entwicklung von *Cyclops*. Ein Beitrag zur Systematik der Cyclopiden. *Arbeiten aus den Zoologischen Instituten der Universität Wien* 10: 283-356.
- Dahms H. U. 1989. — Antennule development during copepodite phase of some representatives of Harpacticoida (Copepoda, Crustacea). *Bijdragen tot de Dierkunde* 59 (3): 159-189.
- Ferrari F. D. 1988. — Developmental patterns in numbers of ramal segments of copepod post-maxillipedal legs. *Crustaceana* 54 (3): 256-293.
- Ferrari F. D. 1993. — Exceptions to the rule of the development that anterior is older among serially homologous segments of postmaxillipedal legs in Copepods. *Journal of Crustacean Biology* 13 (4): 763-768.
- Ferrari F. D. & Benforado A. 1998. — Setation and setal groups on antenna 1 of *Ridgewayia klausruetzleri*, *Pleuromamma xiphias*, and *Pseudocalanus elongatus* (Crustacea: Copepoda: Calanoida) during the copepodid phase of their development. *Proceedings of the Biological Society of Washington* 111 (1): 209-221.
- Fiers F. & Van de Velde I. 1984. — Morphology of the antenna and its importance in the systematics of the Cyclopidae. *Crustaceana* supplement 7: 182-199.
- Fryer G. 1957. — The feeding mechanism of some freshwater cyclopoid copepods. *Proceedings of the Zoological Society of London* 129: 1-25.
- Giesbrecht W. 1892. — Systematik und Faunistik der Pelagischen Copepoden des Golfes von Neapel.

- Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte* 19: 1-831.
- Giesbrecht W. 1899. — Die Asterocheriden des Golfes von Neapel und der angrenzenden Meeresabschnitte. *Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte* 25: 1-217.
- Grygier M. J. 1987. — Nauplii, antennular ontogeny and the position of the Ascothoracida within the Maxillopoda. *Journal of Crustacean Biology* 7 (1): 87-104.
- Gurney R. 1931. — *British Fresh-Water Copepoda*. Vol. 1. The Ray Society, London, 236 p.
- Gurney R. 1933. — *British Fresh-Water Copepoda*. Vol. 3. The Ray Society, London, 384 p.
- Haq S. M. 1965. — Development of the copepod *Euterpina acutifrons* with reference to dimorphism in the male. *Proceedings of the Zoological Society of London* 144: 175-201.
- Ho J. S. 1986. — Phylogeny of Cyclopoida. *Syllogeus* 58: 117-183.
- Ho J. S. 1990. — Phylogenetic analysis of copepod orders. *Journal of Crustacean Biology* 10 (3): 528-536.
- Hulsemann K. 1991. — Tracing homologies in appendages during ontogenetic development of Calanoid Copepods. *Bulletin of Plankton Society of Japan*, special volume: 105-114.
- Huys R. & Boxshall G. A. 1991. — *Copepod Evolution*. The Ray Society, London, 468 p.
- Huys R. & Böttger-Schnack R. 1994. — Taxonomy, biology and philogeny of Miracidae (Copepoda: Harpacticoida). *Sarsia* 10 (3): 207-283.
- Itô T. 1970. — The biology of a Harpacticoid Copepod, *Tigriopus japonicus* Mori. *Journal of the Faculty of Science Hokkaido University*, series 6, zoology 17 (3): 474-502.
- Izawa K. 1991. — Evolutionary reduction of body segments in the Poecilostome Cyclopoida (Crustacea: Copepoda). *Bulletin of Plankton Society of Japan*, special volume: 71-86.
- Karaytug S. & Boxshall G. A. 1996. — The life cycle of *Paracyclops fimbriatus* (Fischer, 1853) (Copepoda, Cyclopoida). *Bulletin of The Natural History Museum*, zoology 62 (1): 41-70.
- Mrázek A. 1893. — Über die Systematik der Cyclopiden und die Segmentation der Antennen. *Zoologischen Anzeiger* 16 (425): 285-289.
- Reid J. W. 1992. — *Acanthocyclops pennaki* n. sp. (Copepoda: Cyclopoida) from the Hyporheic Zone of the South Platte River, Colorado, U.S.A. *Transactions of the American Microscopical Society* 111 (4): 269-277.
- Reid J. W. 1993. — *Fimbricyclops jimhensoni*, new genus, new species (Copepoda: Cyclopoida: Cyclopidae), from bromeliads in Puerto Rico. *Journal of Crustacean Biology* 13 (2): 383-392.
- Rocha C. E. F. da & Iliffe T. M. 1994. — *Troglocyclops janstocki*, new genus, new species, a very primitive cyclopoid (Copepoda: Cyclopoida) from an anchialine cave in the Bahamas. *Hydrobiologia* 292/293: 105-111.
- Schutze M. L. M. 1997. — *Desenvolvimento das antênulas de copepóditos na família Cyclopidae (Copepoda, Cyclopoida)*. [=Antennular development during the copepodid phase in the family Cyclopidae (Copepoda, Cyclopoida)]. Ph.D. thesis, São Paulo University, São Paulo, Brazil, 105 p.
- Sewell R. B. S. 1949. — The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida. *Scientific Report John Murray Expedition* 9 (2): 17-199.

Submitted on 21 October 1999;  
accepted on 17 July 2000.