

## Postmarsupial development of *Sinelobus stanfordi* (Richardson, 1901) (Tanaidacea: Tanaidae)

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### Abstract

A description of the postmarsupial development stages of the tanaid *Sinelobus stanfordi* was carried out from specimens collected from brackish waters of Paranaguá Bay, and reared in the laboratory. Culture water temperature oscillated from 21 to 25°C; a mush of cnidarian colonies was provided for food. The following stages were obtained: Mancas II and III, Juveniles I and II, Copulatory Males I, II, III and IV, Preparatory Females I and II, and Copulatory Females I and II. Juvenile II stage in the development of *S. stanfordi* females is unique among tanaid species. The habitus and the appendages of these stages were drawn. The number of stages was different according to the sex. *S. stanfordi* is a gonochoristic species and, as males do not suffer from degeneration of mouth appendages, they are not rare as other tanaid species. A life history sequence for the species is proposed which seems to be species-specific. Notes on behavioral aspects and the duration of developmental stages are included.

Key words: Life history, gonochoristic, Paranaguá Bay, Brazil.

### Introduction

Tanaids constitute an important component of coastal communities, as they are found in a variety of marine and brackish habitats such as hardy, sandy and muddy bottom, associated or not with algae, hydroids, empty seashells, polychaete tubes and sponges (Lang 1956, Gardiner 1975a, Masunari 1982, 1983a, Johnson and Attramadal 1982a). High densities of *Zeuxo coralensis* Sieg 1980 and *Leptochelia savignyi* (Kröyer, 1842) were reported by Masunari and Sieg (1980), Masunari (1983b) and Fonseca and D'Incao (2003, 2006) from Brazilian shallow waters, and of *Tanais cavolinii* Milne-Edwards, 1829 by Johnson and Attramadal (1982a) from Bergen area, Norway. Due to the abundance and smallness of these animals, surely, they are an excellent food resource for higher trophic level

consumers including commercially important fishes and crabs (Dauvin and Gentil, 1990).

Although the study of the postmarsupial development in Tanaidacea has been started more than 50 years ago (Lang 1953), investigations on tanaids reared in laboratories were carried out only by few authors: Lang (1958) with *Sinelobus stanfordi* f. *sylviae* (Richardson, 1901), Bückle-Ramirez (1965) with *Heterotanais oerstedii* Kröyer, Johnson and Attramadal (1982b) with *Tanais cavolinii*, Hammers and Franke (2000) with *T. dulongii* (Audouin, 1826), and Messing (1983) with *Pagurapseudes largoensis* McSweeney, 1982. These authors found a varied number of stages as these species belong to different families. On the other hand, Gardiner (1975b), Masunari and Sieg (1980) and Masunari (1983b) reconstructed life histories of members of the deep sea family Neotanaidae, *Z. coralensis*

and *L. savignyi*, respectively, based on preserved material. More recently, Schmidt *et al.* (2002) described the postembryonic development of two species occurring in cold waters of Magellanic and sub-Antarctic regions—*Apsudes heroae* Sieg 1986 and *Allotanais hirsutus* (Beddard, 1886). This study was based on preserved specimens.

*Sinelobus stanfordi* (Richardson, 1901) is a tropical world wide distributed species, occurring in the Atlantic coast from Florida (U.S.A.) to South America, in the Pacific coast of Central America, Peru and Galapagos, Kurile Islands, Polinesia, Australia, New Zealand and Indian Ocean (Sieg, 1983a, 1980; Suárez-Morales, 2004). The biology of this species is poorly known and the literature about it is restricted to systematic and occurrence. The present work aims to describe the life history of this tanaid based on material reared in laboratory.

## Material and Methods

Alive samples of *S. stanfordi* were collected from brackish waters of Paranaguá Bay Complex, Parana State (25°31'–25°32'S and 48°30'–48°31'W), southern Brazil. Their tubes were attached to branches of cnidarian colonies of *Eudendrium* sp., that were carefully scraped from an immersed solid surface of floating anchorages in the riverside of Itibere River. As these anchorages were continuously floating, *Eudendrium* colonies were always submerged without any dryness condition, even during low tides.

The collection site has a strong influence from mangrove ecosystem of Parana Bay Complex and from anthropogenic activities, as those anchorages support a harbor for ferry boats that cross the canal between Parana city and Valadares Island.

Detached *Eudendrium* colonies were brought to the laboratory in plastic galloon containing local seawater; the transportation lasted about an hour, from collection site to Curitiba city, where the laboratory is located. The collection was carried out from June 1983 to June 1985, during which period the local air temperature oscillated from 20.0 to 33.0°C, the surface water temperature from 22.0 to 29.5°C, and the surface water salinity from 16.3‰ to 24.5‰.

In the laboratory, cnidarian colonies were transferred to two-liters glass containers filled with collection site seawater that was aerated with an aquarium pump. The culture water temperature varied from 20°C to 25°C and its abrupt oscillation was avoided by keeping these glass containers partially submerged into 50 liters freshwater aquarium: the surface level of the freshwater in the aquarium was always a little lower than the upper border of glass containers. As in Curitiba city the air temperature can drop to -2°C during the winter period, the aquarium was warmed with a heater in order to minimize the oscillation of water temperature.

Tanaids for the development observation were sorted from *Eudendrium* branches by tearing their delicate tubes with thin forceps under stereoscopic microscope, and they were moved to Petri dishes (8.0 cm diameter and 1.8 cm high) containing seawater. Following Johnson and Attramadal (1982a), pieces of glass capillarity were offered for these tanaids in order to be colonized. As natural tubes were made of fine sediment glued with organic matter and totally opaque, this procedure improved a better visualization.

Couples ready for copulation and fertilized females were maintained in Petri dishes, while juveniles and manca stages were kept individually in ice tray compartments (4.5 cm long, 3.0 cm wide and 2.5 cm high). All culture Petri dishes and ice trays were filled with seawater from collection site and partially immersed in the freshwater aquarium at temperature from 20°C to 25°C. The culture experiments were carried out in summer, autumn and winter of 1984 and 1985.

After several unsuccessful attempts for feeding tanaids, a mush of *Eudendrium* colonies was obtained by “smashing” living colonies in a grail; this constituted the best food for all tanaid developmental stages. Culture containers were inspected for exuvies everyday, and in the case of occurrence, they were preserved in alcohol 70%. In alternate days, the culture compartments were cleaned by swabbing their internal walls with the aid of a fine brush, the seawater renewed for a half with a pipette and the animals fed with above mentioned cnidarian mush. All procedures were made under stereoscopic microscope.

Special attention was given to juvenile stages when they became able to traverse from a com-

partment to another in the ice tray: the culture water level was lowered to the least possible in order to avoid this transposition and eventual misinterpretation about the life history.

All body measurements were made in preserved specimens, under binocular microscope provided with *camera lucida* for stages MII, MIII, JUVI and ♀JUVII, and under stereomicroscope provided with ocular scale for remaining ones. The morphological terminology and the developmental stages nomenclature followed Messing (1980, 1983) and Larsen (2003).

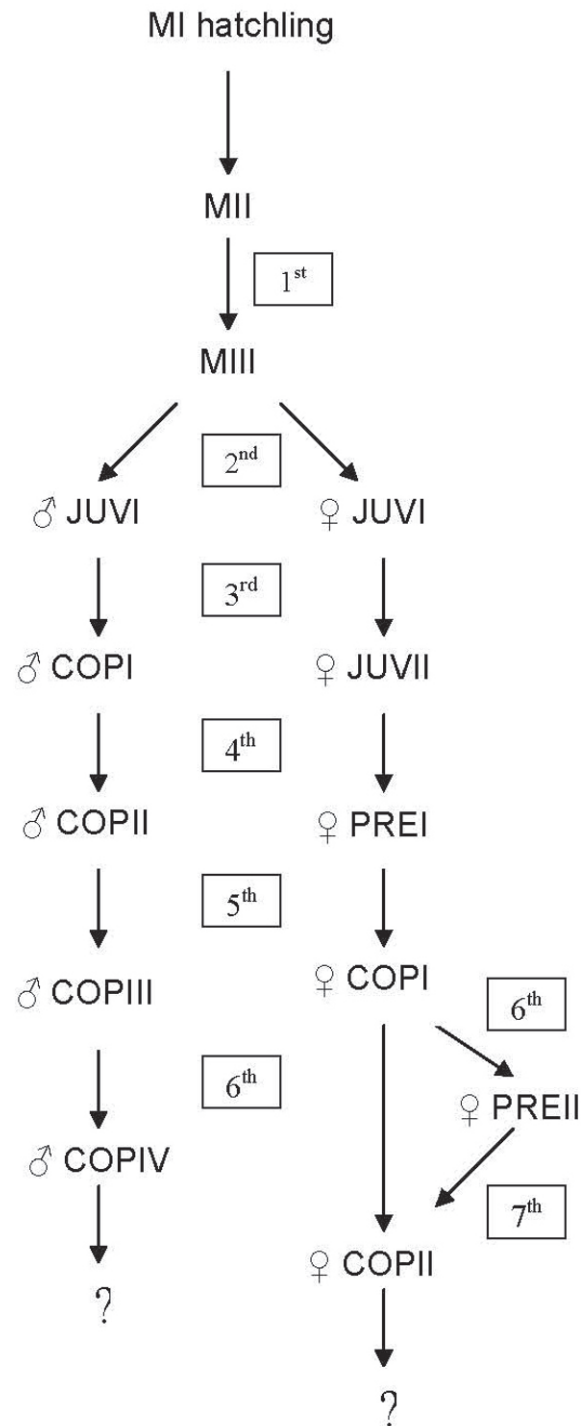
## Results

### Life history

A total of 544 tanaids were analyzed including those obtained in the collection site and those were born in the laboratory. The following postmarsupial developmental stages were recognized and described in *S. stanfordi*: Manca II and III (MII, MIII), Juvenile I and II (♀JUVI, ♂JUVI, ♀JUVII), Copulatory Male I, II, III and IV (♂COPI, ♂COPII, ♂COPIII, ♂COPIV), Preparatory Female I and II (♀PREI, ♀PREII), and Copulatory Female I and II (♀COPI, ♀COPII). The stage of Manca I hatchling, in the sense of Larsen (2003), was observed but its morphology was not described. No external evidence of protandry, protogyny or hermaphroditism was observed in *S. stanfordi*.

The first stage released from the female marsupium was Manca II, that did not have any sexual dimorphism. This stage gave origin to Manca III and after, to Juvenile I; in this stage, it was possible to discriminate males by the observation of copulatory cones in exuvies, that were hardly seen in alive or preserved animals. Males were able to copulate from the next stage (♂COPI), and they passed through successive stages of Copulatory Male II, III and IV. On the other hand, females had two additional immature stages after Juvenile I: Juvenile II and Preparatory Female I. Only after the fifth ecdysis females became able to copulate (♀COPI). Once the first spawning had occurred, females had two ways to perform a second spawning: by molting directly to copulatory stage (♀CO-

PII) or indirectly, by passing once again through a preparatory stage (♀PREII). Figure 1 summarizes the life history of this species. As females bred at least two times during their life span, that lasted about 35 days in summer cohort (Fig. 17), it is clear that *S. stanfordi* is a multiparous species.



**Figure 1.** *Sinelobus stanfordi*. Proposed life history. M = manca, JUV = juvenile, PREP = preparatory, COP = copulatory. The ordinal sequence of ecdysis is also presented.

### Description of developmental stages

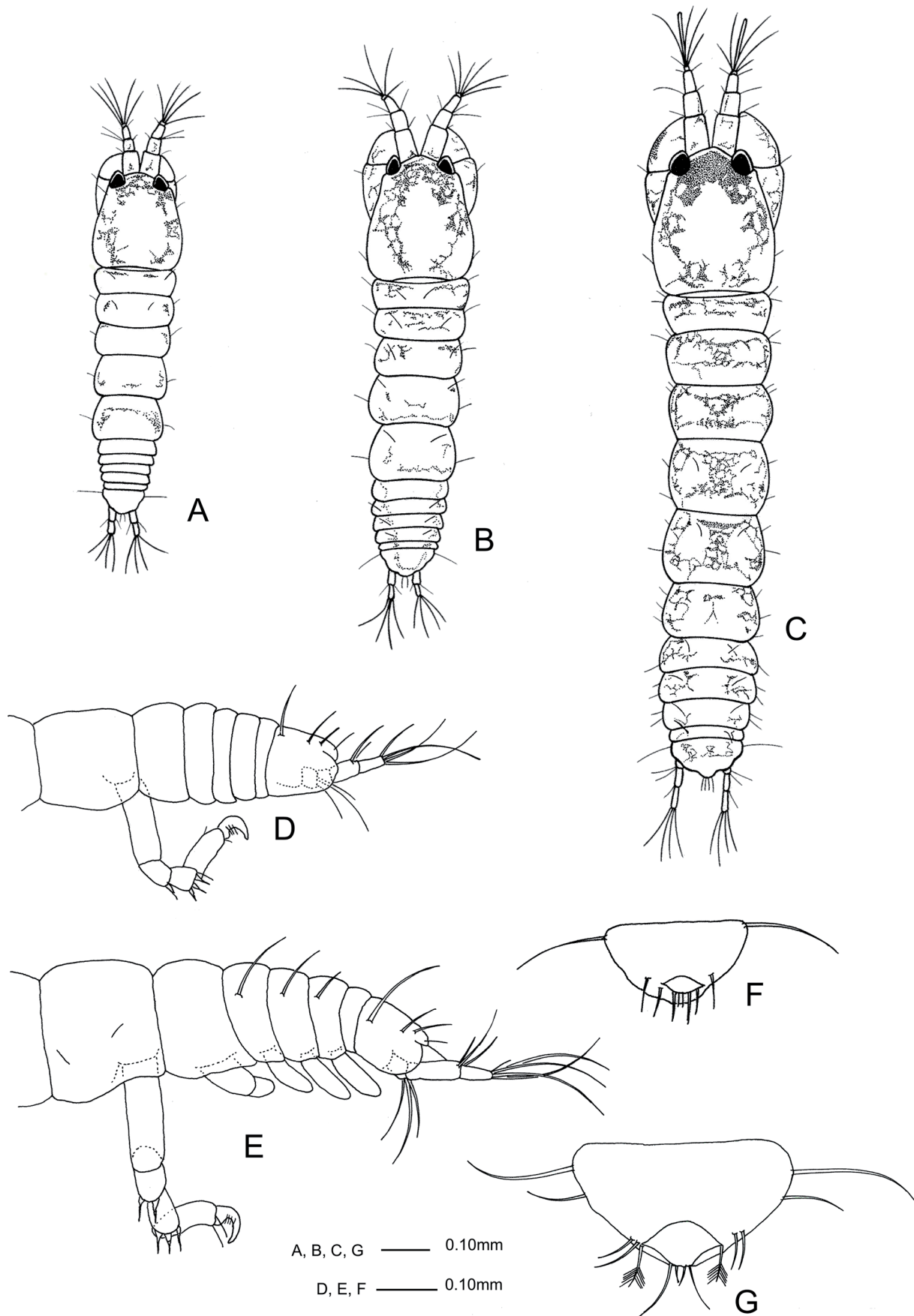
MANCA I HATCHLING: young mancas still staying inside the mother marsupium. After the first meal (yellowish food produced in the marsupium), this stage gave origin to Manca II without any moulting. Only Manca I hatchling that fed this “yolk” could survive and molt to next stages. MANCA II (Fig. 2A): the 1<sup>st</sup> postmarsupial developmental stage, none ecdysis occurred. The mean body length was 0.61 mm (range: 0.53-0.69 mm); pleonite 6 short, pereopods 6 and all pleopods absent (Fig. 2D), pleotelson triangular with one pair of setae as long as pleotelson width at the anterior corners, and three pairs of setae in the posterior marginal area, the innermost about half in length (Fig. 2F). MANCA III (Fig. 2B): reared from the 1<sup>st</sup> ecdysis. The mean body length was 0.78 mm (range: 0.62-0.94 mm); pleonite 6 a little longer than MII one, appearance of pereopods 6 and three pairs of rudimentary pleopods (Fig. 2E). JUVENILE I (Fig. 2C): reared from the 2<sup>nd</sup> ecdysis. The mean body length was 1.04 mm (range: 0.80-1.28 mm); pleonite 6 about three times longer than MII one, pereopods 6 with total number of articles and pleopods fully developed. It was possible to recognize the sex, although any copulation was observed in this stage. Male Juvenile I with a pair of small genital cones in the sternite 6 (Fig. 4A); it grew directly to sexually mature Copulatory Male I. Female Juvenile I without any genital cones; it grew to Juvenile II. FEMALE JUVENILE II (Fig. 3E): female reared from the 3<sup>rd</sup> molting. Except for the lacking of genital cones, there was not any sexual dimorphism. Oostegites were also lacking. Mean body length 1.54 mm (range = 1.16-1.92 mm). It grew to Preparatory female I. COPULATORY MALE I, II, III AND IV (Fig. 3A, B, C, D): reared from 3<sup>rd</sup>, 4<sup>th</sup>, 5<sup>th</sup> and 6<sup>th</sup> molting, respectively. They were provided with a pair of well developed genital cones and able to copulate (Fig. 4B, C, D, E). The mean body lengths of respective stages were: 1.54 mm (range = 1.16-1.92 mm), 1.90 mm (1.70-2.10 mm), 2.21 mm (1.86-2.57 mm) and 2.48 mm (1.96-3.00 mm). No sexual dimorphism was observed in ♂COPI, except for the presence of the genital cones. However, from ♂COPII, antennules, antennas and chelipeds became gra-

dually stronger and longer in relation to the body dimensions. In ♂COPIV, males acquired the most characteristic morphology of the species: strong sexual dimorphism performed by extremely developed isochelous chelipeds and a long carapace tapering anteriorly. No further ecdysis was obtained in laboratory, but, as males much bigger than this stage were collected in nature, it is probable that successive molts occur in *S. stanfordi* after attaining maturity. ♂COPI had lower copulation frequency than other stages, but two males in this stage as long as 1.60 mm and 1.70 mm copulated with females 2.60 mm and 3.16 mm long, respectively. PREPARATORY FEMALE I AND II (Fig. 3F, H): reared from the fourth and sixth ecdysis, with mean body lengths of 2.08 mm (range: 1.72-2.44 mm) and 2.86 mm (2.64-3.08 mm), respectively. They were provided with a pair of oostegites in the base of pereopods 4. These oostegites were small and translucent soon after the ecdysis, but gradually grew and became opaque in the end of the stage, by membrane thickening. They molted to the Copulatory Female I and II, respectively. COPULATORY FEMALE I (Fig. 3-G) and II: reared from the 5<sup>th</sup> and 6<sup>th</sup> or 7<sup>th</sup> ecdysis (Fig. 1) and provided with a fully developed marsupium; ♀COPI was preceded by ♀PREI, but ♀COPII came both directly from ♀COPI or indirectly from ♀PREII. Mean body length was 2.26 mm (range: 1.76-2.76 mm) for ♀COPI and 2.96 mm (2.68-3.24 mm) for ♀COPII.

### Morphology of postmarsupial developmental stages

#### Body somites

CARAPACE (Fig. 2, 3): trapezoid, proportion between length and largest width subequal in MII, MIII and JUVI. From JUVII and ♂COPI, the sexual dimorphism became apparent. Male carapace grew longer than wide and narrowed anteriorly, while the female's maintained the general shape of juvenile stages. In MII, the carapace pigmentation was weak and restricted to marginal area. In the sequence of development, it became gradually stronger in tone and relatively larger in area, leaving blank only small central



**Figure 2.** *Sinelobus stanfordi*. A-C, habitus, dorsal view; D-E, peronites 5-6 and pleon, lateral view; F-G, pleotelson, dorsal view. A, D, F, MII; B, E, MIII; C, ♂JUVI; G, ♂COPIII.

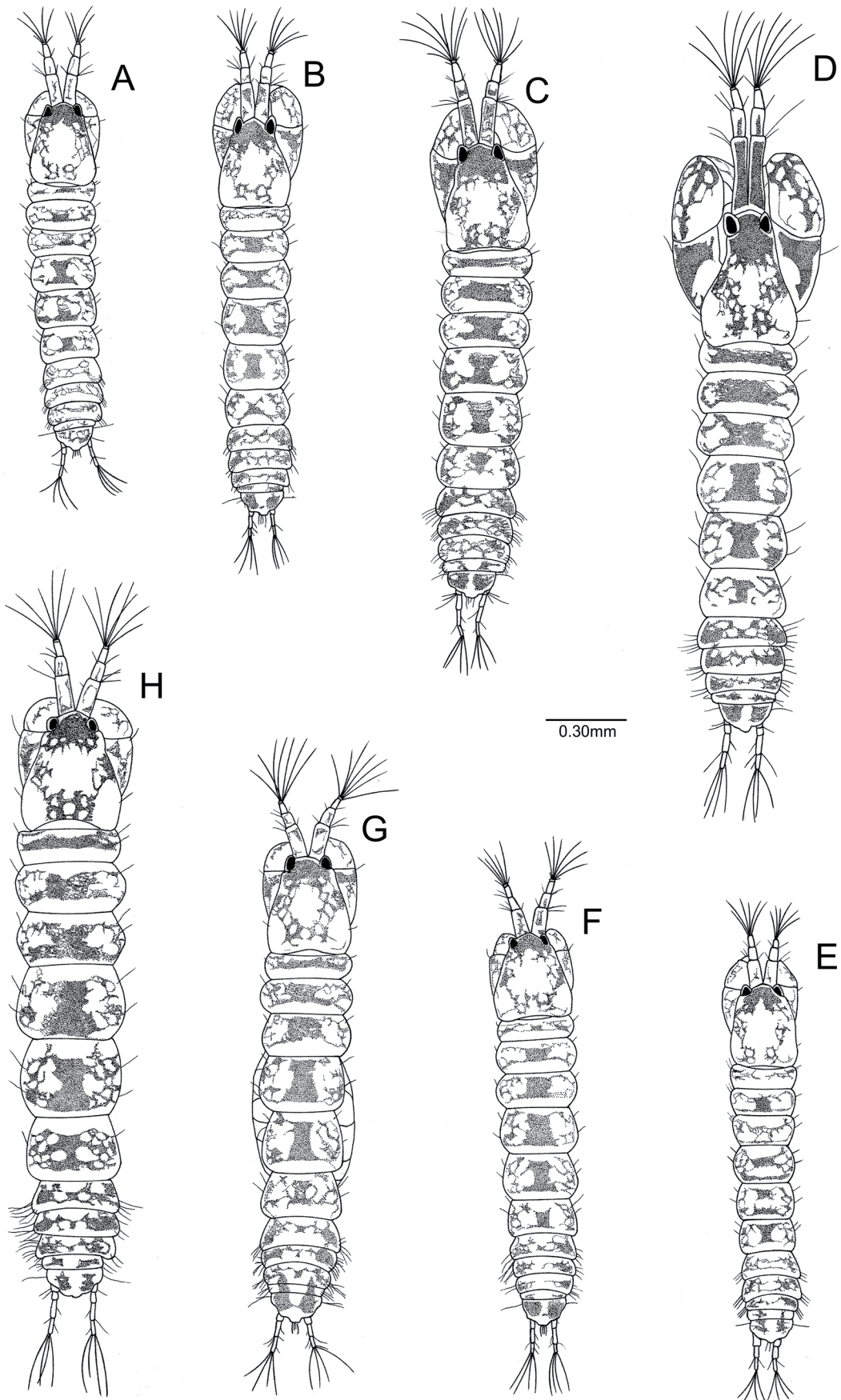
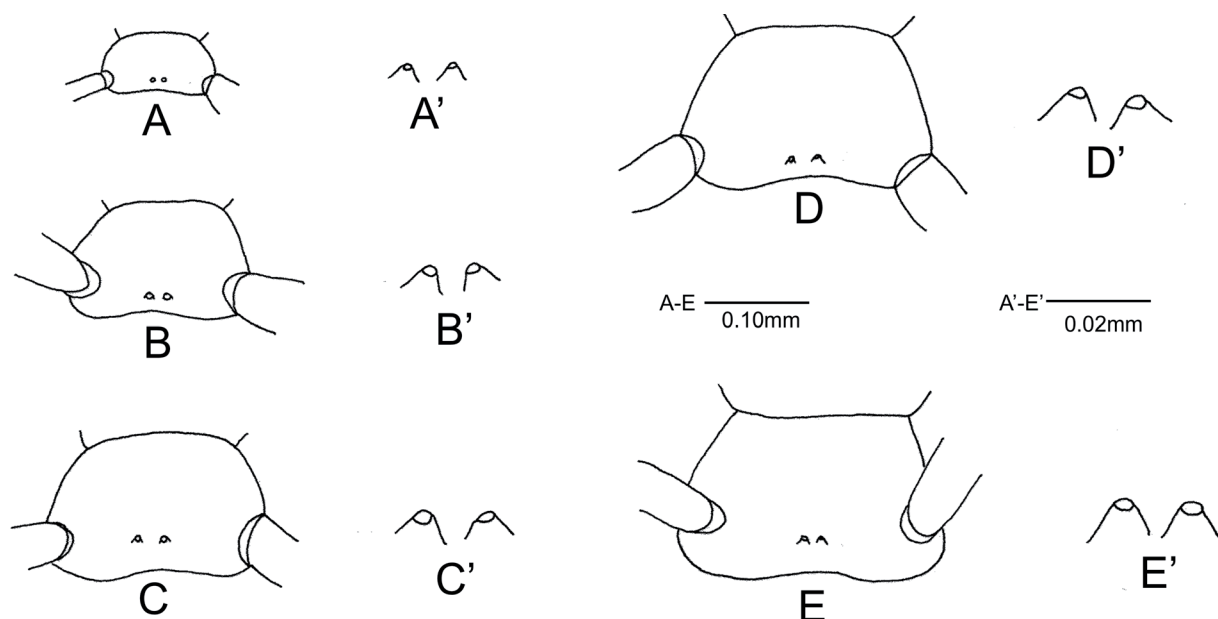


Figure 3. *Sinelobus stanfordi*. A-H, habitus, dorsal view. A, ♂COPI; B, ♂COPII; C, ♂COPIII; D, ♂COPIV; E, ♀JUVII; F, ♀PREI; G, ♀COPI; H, ♀PREII.

and posterior lateral areas; the male's pigmentation always stronger than the female's. A pair of setae in the outer margin of all stages, except in MII. PEREONITES (Fig. 2, 3): all pereonites rectangular and, in a general way, the proportion length/width increased with the advance of the development. The pigmentation area also increased gradually in a defined pattern. All stages with pereonites 1-6 bearing sparse setae on dorsal surface and lateral margins. PLEONITES (Fig. 2, 3): the proportion of length/width increased through the developmental progress. The pigmentation became gradually stronger as in pereonites. Pleonites 1-4 naked in MII (Fig. 2D), but with a pair of dorsal simple setae on each pleonites 1-3 in MIII (Fig. 2E); these simple seta were replaced by plumose ones in JUVI that increased in number during the development and became distributed mainly in lateral side of all pleonites. PLEOTELSON (Fig. 2F, G): triangular, with proportion length/width near 0.6; pigmentation sequence as in pleonites. One long simple seta in each anterior proximal corner and 1 short simple seta in each upside of the uropod insertion in all stages; from JUVI the posterior central marginal lobe provided with increasing number of simple and plumose setae as the postmarsupial development advanced.

## Appendages

ANTENNULE (Fig. 5). Four-articulated in all developmental stages. The length/width ratio of the articles changed throughout the development, among which the 1<sup>st</sup> one showed the most striking sexual dimorphism, reaching 5.4 among males, ♂COPIV (Fig. 5G) and 3.1 among females, ♀PREII (Fig. 5K); this article is also provided with denticules combs in the proximal area of the dorsal surface, that increased progressively in number from MII to adult stages. First three stages had identical setation in both sexes, but males had 3 aesthetes from ♂COPI and females only 2 from JUVI. First article with 3 short simple setae in the middle of the outer margin in manca and juvenile stages, but they change to proximal margin in adult stages, with 4-5 simple setae in the anterior margin from MII, additional 1 simple seta from JUVI, 1 simple and 1 plumose setae from 4<sup>th</sup> molt and 1 simple seta from 5<sup>th</sup> molt; 2<sup>nd</sup> article with 4-6 simple setae along the anterior margin in MII, additional 2 simple setae from MIII, 1 simple seta from 3<sup>rd</sup> molt and 1 plumose setae from 4<sup>th</sup> molt; 3<sup>rd</sup> article with 2-4 simple setae along the anterior margin in MII, 1 additional simple seta from 5<sup>th</sup> molt; 4<sup>th</sup> article with 1 aesthete plus 4 long setae and 1-2 short setae in the distal end in MII, 1 additional



**Figure 4.** *Sinelobus stanfordi*. A-E, 6<sup>th</sup> thoracic sternite of males with genital cones, ventral view; A'-E', detailed genital cones. A, A', JUVI; B, B', ♂COPI; C, C', ♂COPII; D, D', ♂COPIII; E, E', ♂COPIV.

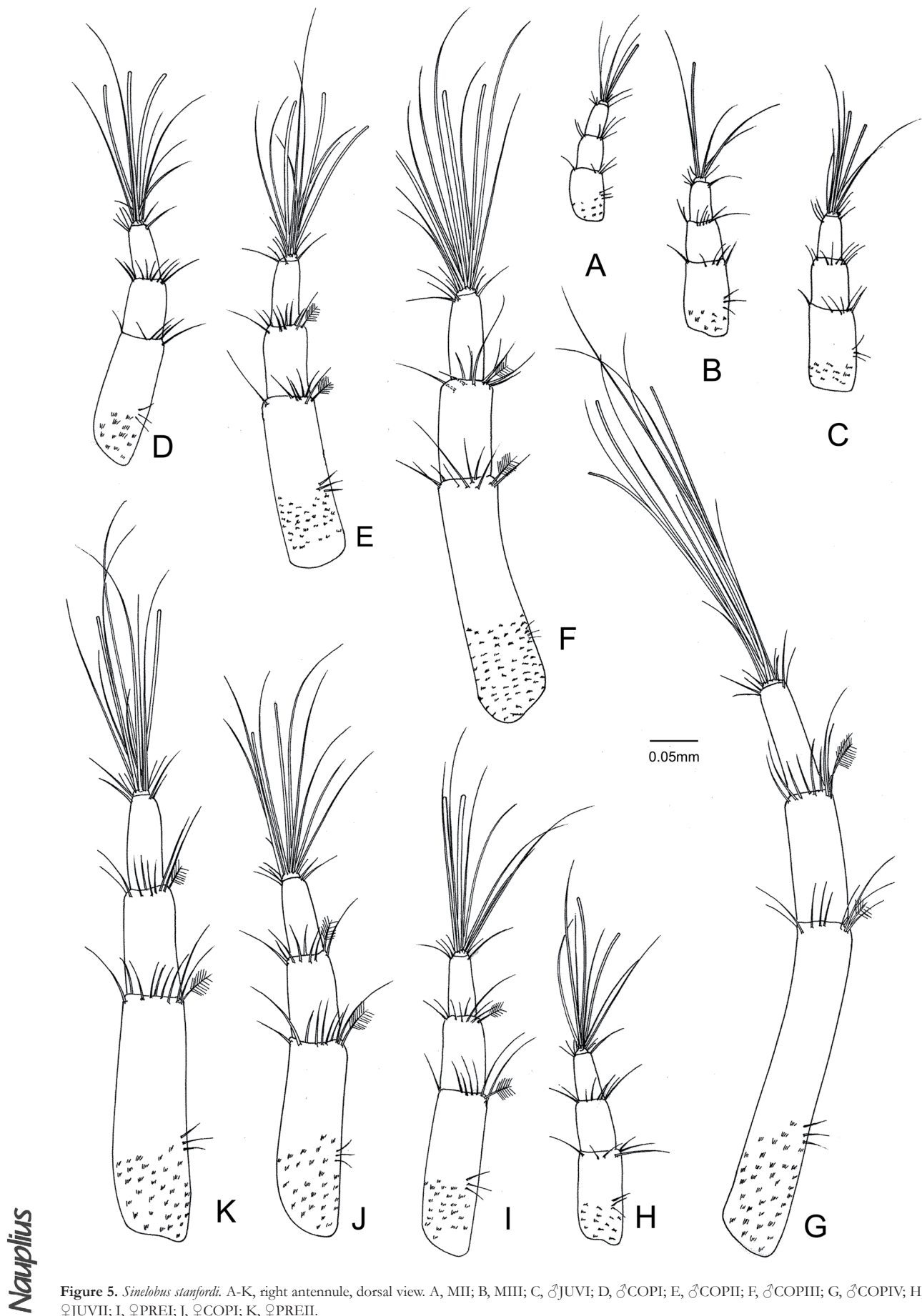


Figure 5. *Sinelobus stanfordi*. A-K, right antennule, dorsal view. A, MII; B, MIII; C, ♂JUVI; D, ♂COPI; E, ♂COPII; F, ♂COPIII; G, ♂COPIV; H, ♀JUVII; I, ♀PREI; J, ♀COPI; K, ♀PREII.



aesthete after 2<sup>nd</sup> molt, 1 additional simple seta after 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> molts, adult males with 3 aesthetes while females had only 2. ANTENNA (Fig. 6). Same length as antennule, 6-articulated in all developmental stages; 2<sup>nd</sup> article with a dorsal concavity over which the 1<sup>st</sup> article of antennule rests; 2<sup>nd</sup> and 3<sup>rd</sup> bearing denticule combs in the dorsal outer surface that rose in number with development. Striking sexual dimorphism in the 4<sup>th</sup> article that take a length/width proportion of 5.4 in males (♂COPIV, Fig. 6G) and 3.0 in females (♀PREII, Fig. 6K). First and third articles naked, remainder ones provided with simple setae; 2<sup>nd</sup> article bearing 1 anterior inner seta in MII, but with 3 from JUVI and 4 from 6<sup>th</sup> molt (♂COPIV, Fig. 6G and ♀PREII, Fig. 6K); 4<sup>th</sup> article with 1 anterior outer seta in former stages, but with 2 from 5<sup>th</sup> molt (♂COPIII, Fig. 6F and ♀COPII) and 3 from 6<sup>th</sup> molt; 5<sup>th</sup> article with 5-6 setae of varied length along the dorsal anterior margin that maintained in number till 6<sup>th</sup> molt; 6<sup>th</sup> article with 5 long setae and 3 short setae distally and from 5<sup>th</sup> molt, with 2 additional long setae. MOUTH-PARTS: morphologically similar from manca to adult stages: only the size and the number of denticles, setae, denticles combs and spines grew with the development. No sexual dimorphism was observed in these appendages. LABRUM (Fig. 7A). Tubular in lateral view, with prominent posterior side and ventral surface provided with hairy setae that grew in number, length and diameter with the development. MANDIBLES (Fig. 8). Incisors chitinized, faced innerly, inner margin provided with irregular relief that is unequal in each mandible; *lacinia mobilis* with irregular anterior margin in both mandibles, but the right one is triangular and transparent while the left one, almost square and chitinized; 2 plumose setae at the base of both *lacinia mobilis*; molar strong and almost perpendicular to incisor, with a chewing surface provided with denticles that grew in number with the development. MAXILLULE (Fig. 9). Endite sigmoid with 8 spines in the anterior end, among which 6 serrated from 5<sup>th</sup> molt (♂COPIII, Fig. 9F), and 2 oblique rows of simple setae anteriorly, ventral surface covered medially with denticule combs; palp tapering posteriorly and provided with 2 long simple setae almost two times the palp length at the posterior end. MAXILLA (Fig. 9). Oval, located at posterior

third of the maxillule endite and with setulose anterior margin from ♀JUVII. LABIUM (Fig. 7 B). Composed of 2 bilobed and overlapped structures, without palps or processes; all developmental stages with denticles combs on ventral surface and with several simple setae on anterior area from MIII. MAXILLIPED (Fig. 10). Composed of coxa, basis, palp and endite that grew about 3.5 times from MII to ♂COPIV, but without any change in the article shape. Coxa naked in MII and MIII, but with a long simple seta in anterior inner corner from JUVI; basis with denticles combs on ventral surface in all developmental stages and an additional simple seta in inner margin from JUVI; palp 4-articulated, the 1<sup>st</sup> and last articles provided with denticles combs in all developmental stages and the 3<sup>rd</sup> one only from JUVI, number of simple setae grew with development and, among them, about 1/3 substituted gradually by plumose ones, with the following seta formula: MII and MIII = (0, 5+1, 5, 6), JUVI = (0, 5+1, 6, 7), ♂COPI, ♀JUVII = (0, 5+1, 8, 9), ♂COPII, ♀PREI, ♂COPIII, ♀COPI and ♂COPIV, ♀PREII = (0, 5+1, 9, 10); endite with terminal surface provided with 2 plumose setae, 3 simple short and basally large setae. EPIGNATH. This appendage was not described. CHELIPED (Fig. 11). sexual dimorphism apparent from ♂COPI, ♀JUVII when all articles grew faster in males than in females; in ♂COPIV, merus and carpus provided with projection issuing from ventral margin, dactylus with strong curvature, distal margin of fixed finger with a rectangular shape and propodus 2 times the female's (Fig. 11-G and 11-K). Proximal inner surface of dactylus and ventral inner surface of basis, merus and carpus covered with denticule combs that rose in number through the development, in both sexes. Few simple setae in the 1<sup>st</sup> four articles of all stages: coxa with 1 outer middorsal seta, basis with 1 outer and 1 inner setae, merus with 1 ventral seta (MII to JUVI) or plus 1 outer (from 3<sup>rd</sup> molt, in both sexes), and carpus with 3 dorsal and 2 ventral setae. Propodus with 2 simple setae near the dactylus insertion and 4 simple setae near unguis of fixed finger in MII: 2 additional simple setae in MIII; 2 additional simple setae after 3<sup>rd</sup> molt in both sexes; dactylus with 1 simple midinner seta and 4 simple setae in the ventral margin and 1 plumose near unguis in MII, 2 additional simple setae and unguis

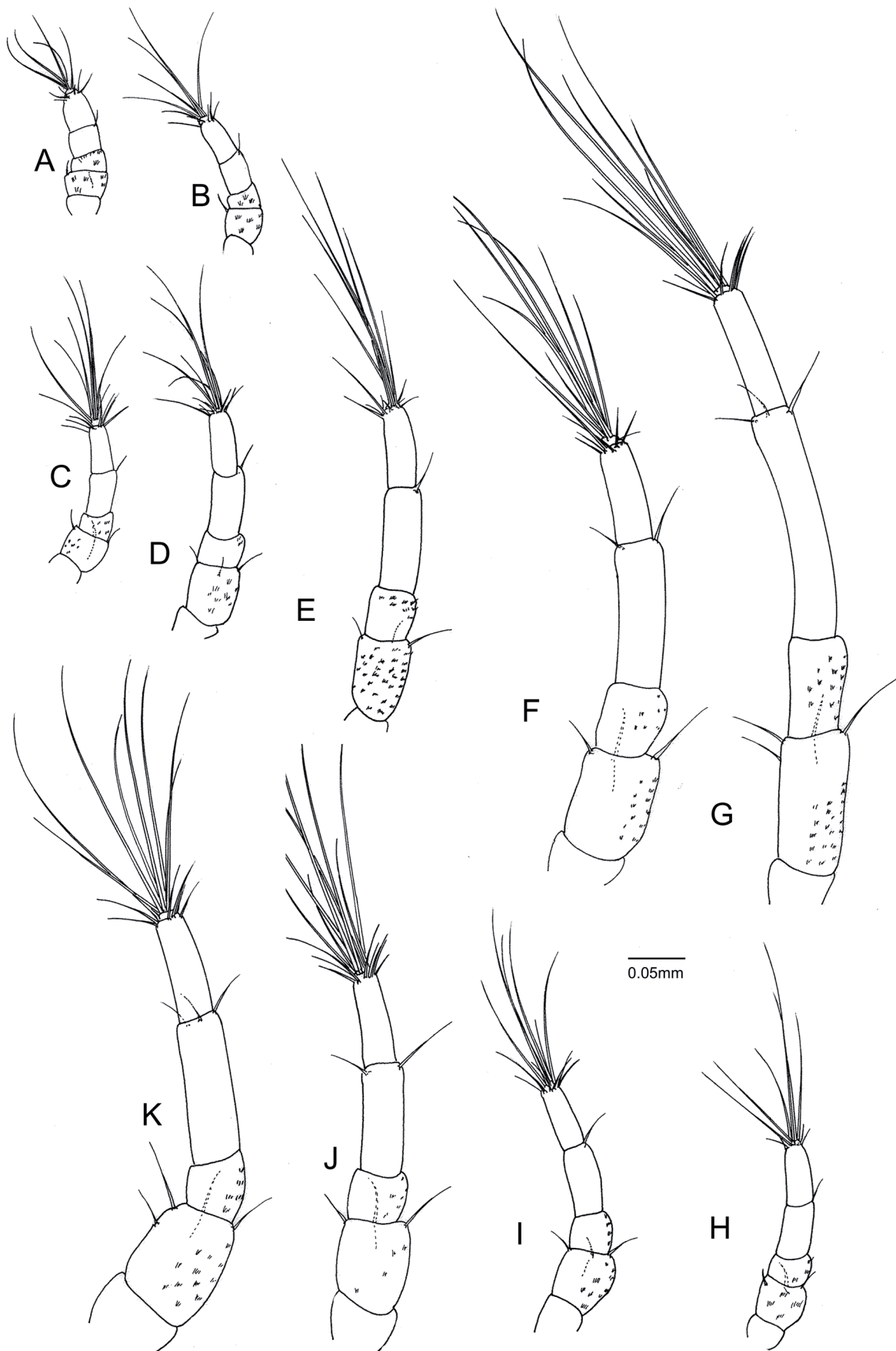
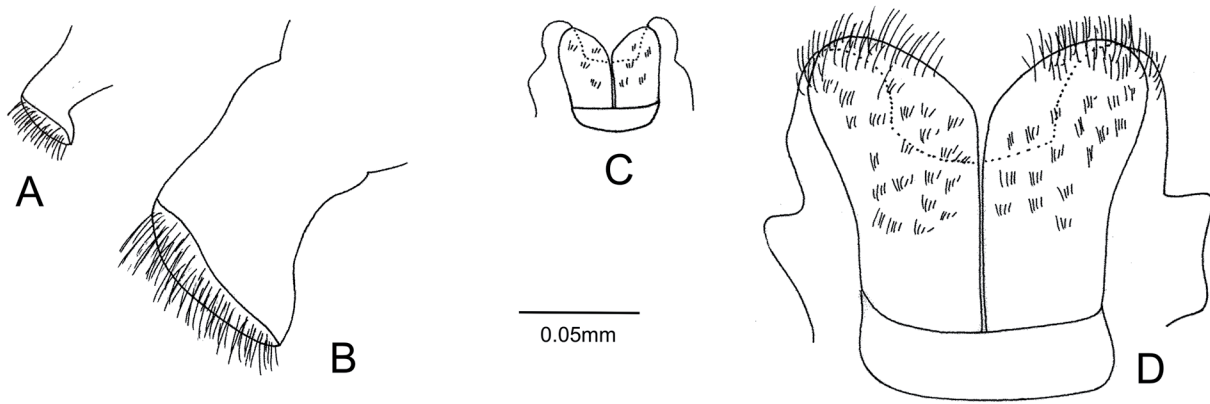


Figure 6. *Sinelobus stanfordi*. A-K, right antenna, dorsal view. A, MII; B, MIII; C, ♂JUVI; D, ♂COPI; E, ♂COPII; F, ♂COPIII; G, ♂COPIV; H, ♀JUVII; I, ♀PREI; J, ♀COPI; K, ♀PREII.



**Figure 7.** *Sinelobus stanfordi*. A-B, labrum, lateral view; C-D, labium, ventral view. A, C, MII; B, D, ♂COPIV.

tip split into 2 branches in MIII, 1-2 additional simple seta after 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> molts in both sexes. PEREPODS 1-6 (Fig. 12, 13, Tab. I). Six-articulated in all developmental stages, with the exception of MII and MIII, when Pr-6 was still lacking or unarticulated, respectively (Fig. 12); without any sexual dimorphism. Pereopods 1-3 facing anteriorly, provided with free dactylus and unguis; the first pair is the thinnest and called spinning legs, but no thread secretion pore was observed in the magnification of optical equipments. Pereopods 4-6 facing posteriorly, provided with dactylus and unguis fused in a claw. In a general way, the more advanced the developmental stage, the more numerous are simple setae, spines and denticle combs over the surface; plumose setae appear only from JUVI (Tab. I): simple setae present on all articles, mainly on propodus of all developmental stages. Pr-1 provided only with simple setae. Spines occurring only on merus and carpus, plumose setae only on basis and propodus and denticle combs on the inner surface of the ventral distal area of merus, carpus and propodus of all developmental stages. The number of setae and spines was not constant for all individuals of the same stage, mainly those occurring on merus and carpus; unequal number was observed even between appendages of the same pair. Pr4-6 with claws ornamented with a row of fine spines on both sides. PLEOPODS 1-3 (Fig. 14, Tab. II). Absent in MII, 3 pairs of rudimentary appendages without setae and composed of short basal article and fused endopod and exopod in MIII. From JUVI, 3 pairs with well defined articles, among which the 2<sup>nd</sup> is the biggest and 3<sup>rd</sup>, the smallest; no sexual dimorphism. Basal article square with plumose setae in

the outer margin and, from ♂COPII, ♀PREI, with 1 plumose seta in the inner margin; endopod ellipsoid, unarticulated, with 1 long plumose seta in the upper inner margin followed by a row of short setae that varies from 5 to 14 according to stage, proximal end with 1 short plumose seta, outer margin with a row of plumose setae that shorten in length towards dorsal distal corner and the number varies from 5 to 12; exopod ellipsoid, unarticulated, inner margin naked, outer margin more convex and provided with 14-23 long plumose setae that shorten in length towards dorsal distal corner (Tab. II). The number of plumose setae was highly variable among individuals of the same stage, mainly advanced ones, and between appendages of the same pair. UROPOD (Fig. 15). Composed of a basal article and a 3-articulated endopod in all developmental stages, but unclear delimitation between 1<sup>st</sup> and 2<sup>nd</sup> articles in MII and MIII; no sexual dimorphism. Basal article with 3 long simple setae in distal outer corner, and endopod 1<sup>st</sup> article naked in all developmental stages; endopod 2<sup>nd</sup> article with 3 simple setae in MII, among which 1 was replaced by a plumose in JUVI and 2 additional simple setae appeared from ♀JU-VII (Fig. 15D); endopod 3<sup>rd</sup> article with 4 long and 2 short simple setae distally in MII, among which 1 was replaced by a short plumose in JUVI.

### Behavioral notes

CONSTRUCTION OF TUBES. Tanaids easily accepted to inhabit glass tubes, if they were also provided with hydroid colony mush, as this constituted both food and the raw material for

the elaboration of the natural tube with pereopods 1-3. Soon after these animals have entered into glass tubes, they began fast and rhythmic move-

ments of spinning legs. Firstly, tanaids wove a fine mesh lining the glass tube with mucus secretion and cnidarian mush (Fig. 16); soon after, they be-

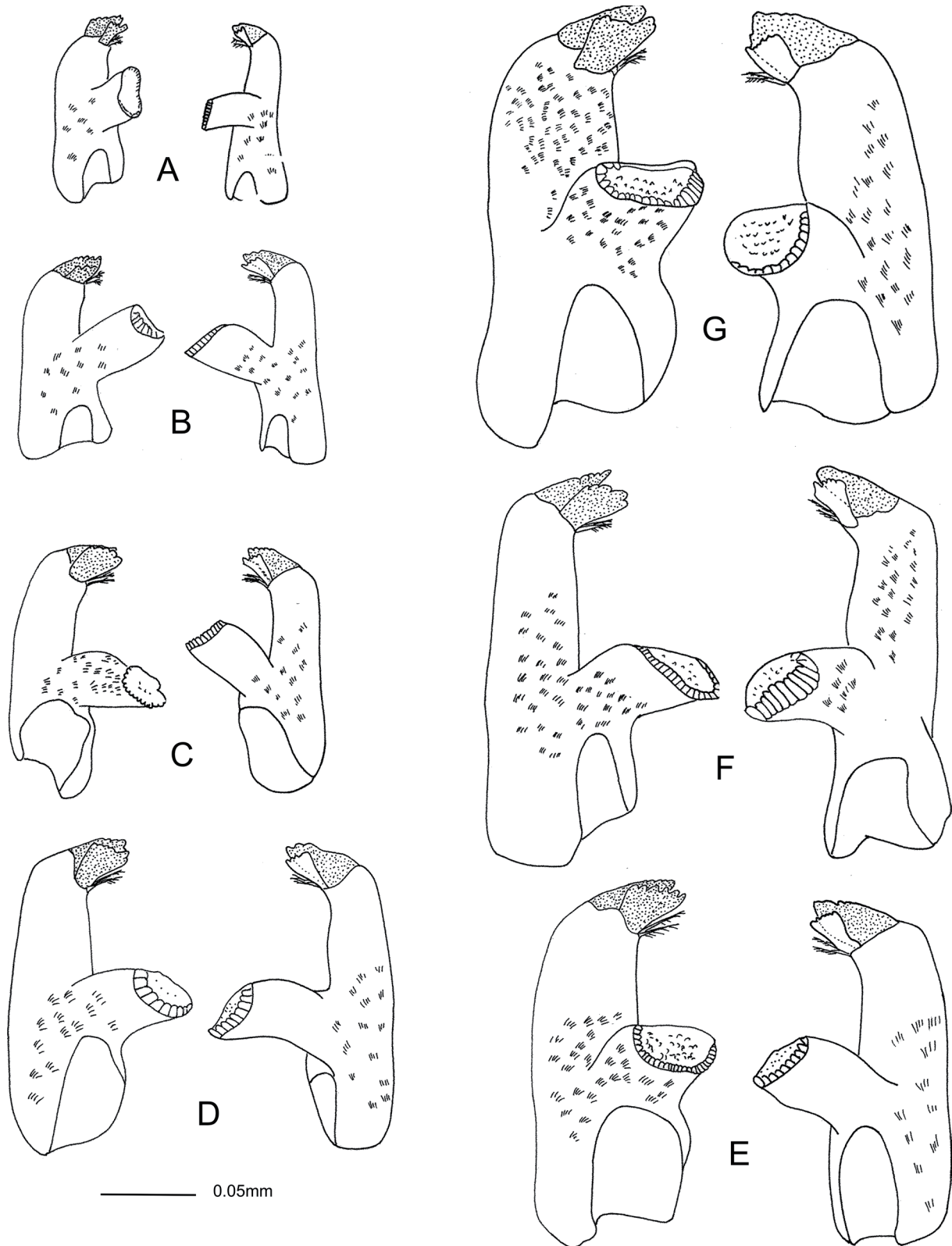
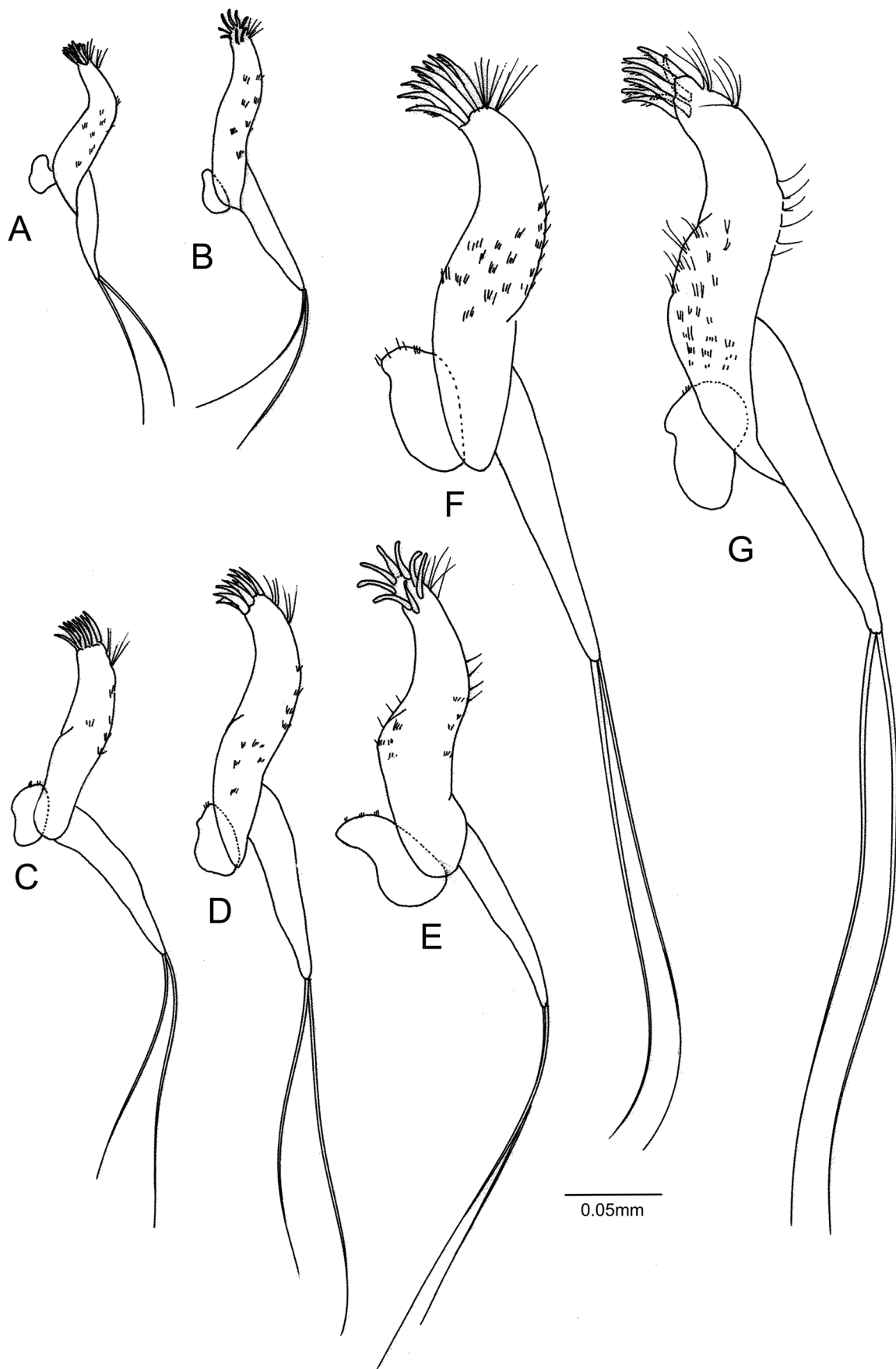


Figure 8. *Sinelobus stanfordi*. A-G, left and right mandibles, dorsal view. A, MII; B, MIII; C, ♂JUVI; D, ♀JUVII; E, ♂COPII; F, ♂COPIII; G, ♂COPIV.



**Figure 9.** *Sinelobus stanfordi*. A-G, maxillule and maxilla, ventral view. A, MII; B, MIII; C, ♂JUVI; D, ♀JUVII; E, ♂COPII; F, ♂COPIII; G, ♂COPIV.

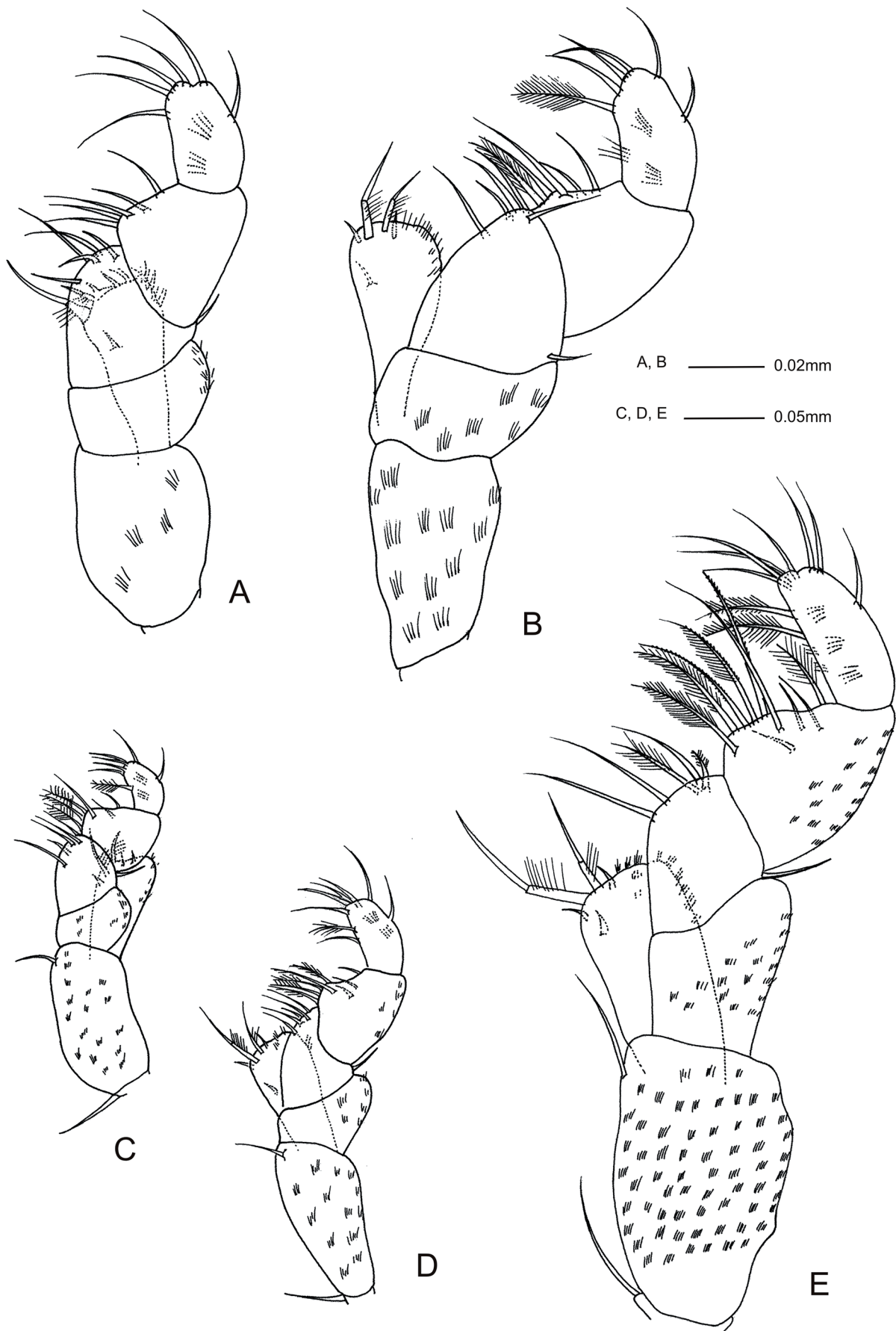
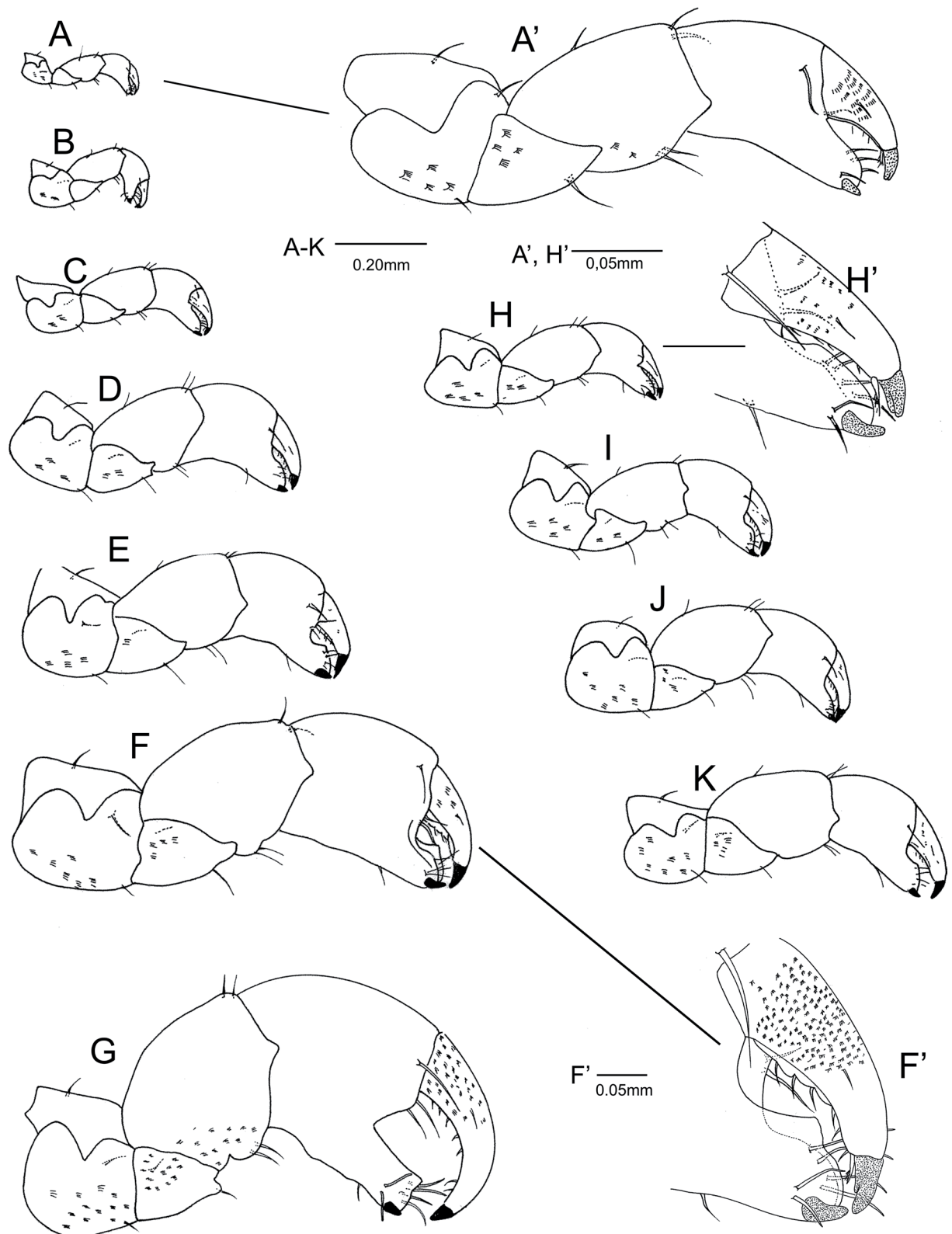


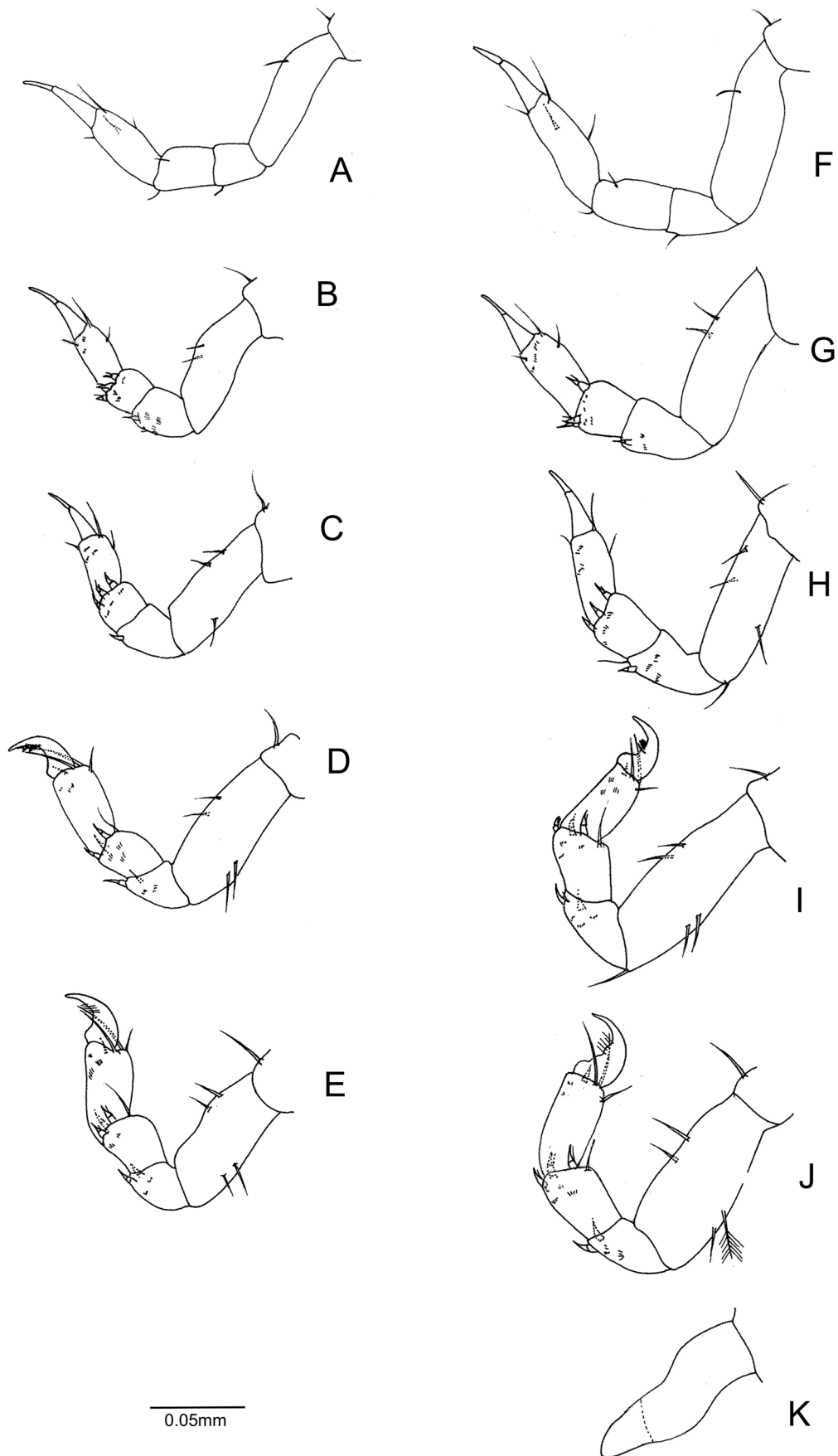
Figure 10. *Sinelobus stanfordi*. A-E, maxilliped, ventral view. A, MIII; B, MIII; C, ♂JUVI; D, ♀JUVII; E, ♂COPIV.

gan the construction of continuous tubes at both ends of the glass tube, that were attached to the substratum. These entirely natural sections had, at

least, one third of the total glass tube length, and they functioned as anchorage points of the whole tube complex. The anchorage process was delayed



**Figure 11.** *Sinelobus stanfordi*. A-K, left cheliped, inner view; F', H', cheliped tips, inner view. A, A', MII; B, MIII; C, ♂JUVI; D, ♂COPI; E, ♂COPII; F, F', ♂COPIII; G, ♂COPIV; H, H', ♀JUVII; I, ♀PREI; J, ♀COPI; K, ♀PREII.



**Figure 12.** *Sinelobus stanfordi*. A-E, MII left pereopods 1-5, outer view; F-K, MIII left pereopods 1-6, outer view. A, Pr-1; B, Pr-2; C, Pr-3; D, Pr-4; E, Pr-5; F, Pr-1; G, Pr-2; H, Pr-3; I, Pr-4; J, Pr-5, K, Pr-6.



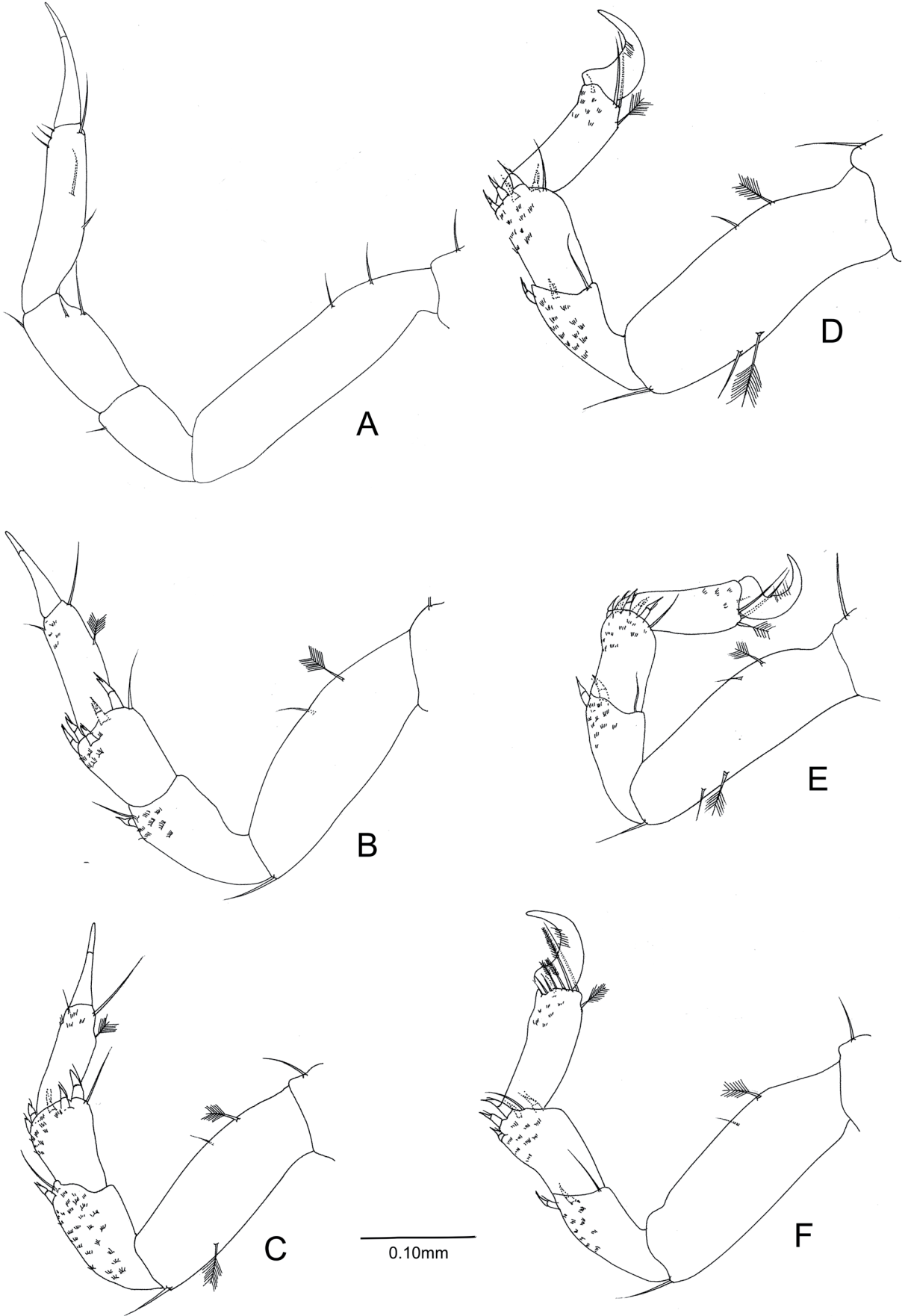


Figure 13. *Sinelobus stanfordi*. A-F, ♂COPIII left pereopods 1-6, outer view. A, Pr-1; B, Pr-2; C, Pr-3; D, Pr-4; E, Pr-5; F, Pr-6.

**Table I.** *Sinelobus stanfordi*. Number or presence (\*) of simple seta(e), plumose seta(e), spine(s), combs and row of fine spines (f.s.r.) in each of six articles of Pereopod 1-6, from manca to adult stages. Claw=dactylus+ unguis; M=Manca, JUV=Juvenile, COP=Copulatory, PRE=Preparatory.

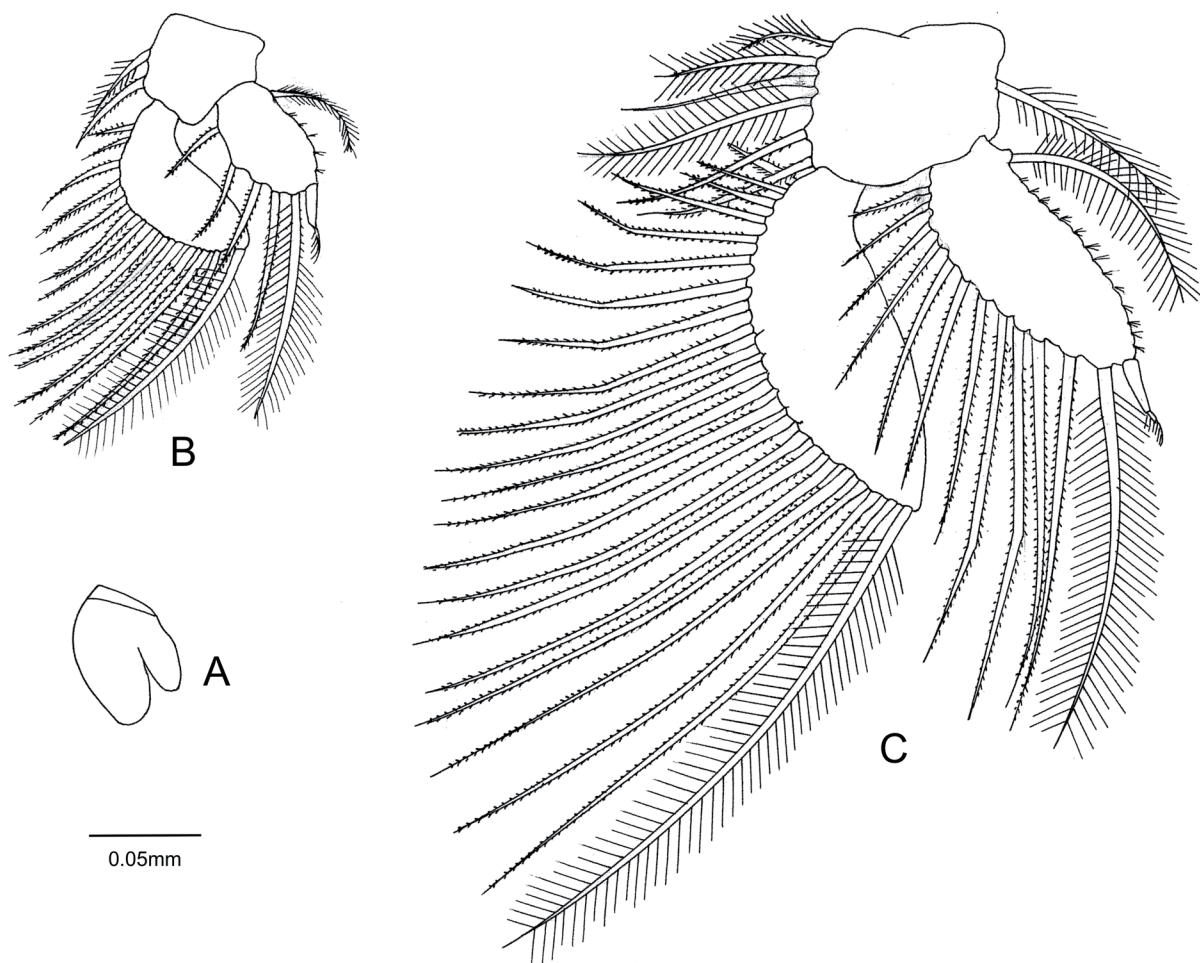
	STAGE/SETA	coxa		basis		merus			carpus			propodus			claw
		simple	plumose	simple	spine	combs	simple	spine	combs	simple	plumose	combs	f.s.r.		
Pereopod 1	MII, MIII, JUVI	1	1		1		*	2		*	4		*		
	♂COPI, JUVII	1	2		1		*	2		*	4		*		
	♂COPII, ♀PREI	1	2		1		*	3		*	5		*		
	♂COPIII, ♀COPI	1	2		1		*	3		*	6		*		
	♂COPIV, ♀PREII	1	2		1		*	3		*	6		*		
Pereopod 2	MII, MIII		2			1	*		3	*	3		*		
	JUVI		1	1	1	1	*		3	*	2	1	*		
	♂COPI, JUVII		2	1	1	1	*	1	4	*	2	1	*		
	♂COPII, ♀PREI		2	1	2	2	*	1	5	*	2	1	*		
	♂COPIII, ♀COPI		2	1	2	2	*	1	5	*	2	1	*		
	♂COPIV, ♀PREII		2	1	2	2	*	1	5	*	2	1	*		
Pereopod 3	MII	1	3			1	*		3	*			*		
	MIII	1	4		1	1	*		3	*			*		
	JUVI	1	2	2	1	1	*		3	*	2	1	*		
	♂COPI, JUVII	1	2	2	1	1	*	1	5	*	2	1	*		
	♂COPII, ♀PREI	1	2	2	1	1	*	1	5	*	2	1	*		
	♂COPIII, ♀COPI	1	2	2	1	1	*	1	5	*	2	1	*		
	♂COPIV, ♀PREII	1	2	2	1	1	*	1	5	*	2	1	*		
Pereopod 4	MII	1	4			2	*	1	3	*	4		*	*	
	MIII	1	5			2	*	1	3	*	5		*	*	
	JUVI	1	3	2		2	*	1	4	*	5	1	*	*	
	♂COPI, JUVII	1	3	2	1	2	*	1	5	*	5	1	*	*	
	♂COPII, ♀PREI	1	3	2	1	2	*	1	5	*	5	1	*	*	
	♂COPIII, ♀COPI	1	3	2	1	2	*	1	5	*	5	1	*	*	
	♂COPIV, ♀PREII	1	3	2	1	2	*	1	5	*	5	1	*	*	
Pereopod 5	MII	1	4			2	*	1	3	*	4		*	*	
	MIII	1	3	1		2	*	1	3	*	4		*	*	
	JUVI	1	4	2		2	*	2	4	*	3	1	*	*	
	♂COPI, JUVII	1	4	2	1	2	*	2	4	*	3	1	*	*	
	♂COPII, ♀PREI	1	4	2	1	2	*	2	5	*	3	1	*	*	
	♂COPIII, ♀COPI	1	4	2	1	2	*	2	5	*	3	1	*	*	
	♂COPIV, ♀PREII	1	4	2	1	2	*	2	5	*	3	1	*	*	
Pereopod 6	MII (absent)														
	MIII (uniarticulated)														
	JUVI	1	4			2	*	1	4	*	5		*	*	
	♂COPI, JUVII	1	4	1	1	2	*	1	4	*	4	1	*	*	
	♂COPII, ♀PREI	1	4	1	1	2	*	1	5	*	5	4	*	*	
	♂COPIII, ♀COPI	1	4	1	1	2	*	1	5	*	6	4	*	*	
	♂COPIV, ♀PREII	1	4	1	1	2	*	1	5	*	6	4	*	*	

if no mush was provided, because the mucus was the only material for the construction of natural tubes. In latter condition, most animals abandoned the tube. The diameter of the glass capillarity was also a critical factor for the acceptance by tanaids: with few exceptions, glass tubes with proportional diameter to the animals' were quickly inhabited. Animals that were maintained in natural tubes also began to secrete mucus, soon after they had been transferred to the culture recipients; in the case of partial damage of the tube, it was restored. They used any available particle for the tube construction or restoration: food, feces, pie-

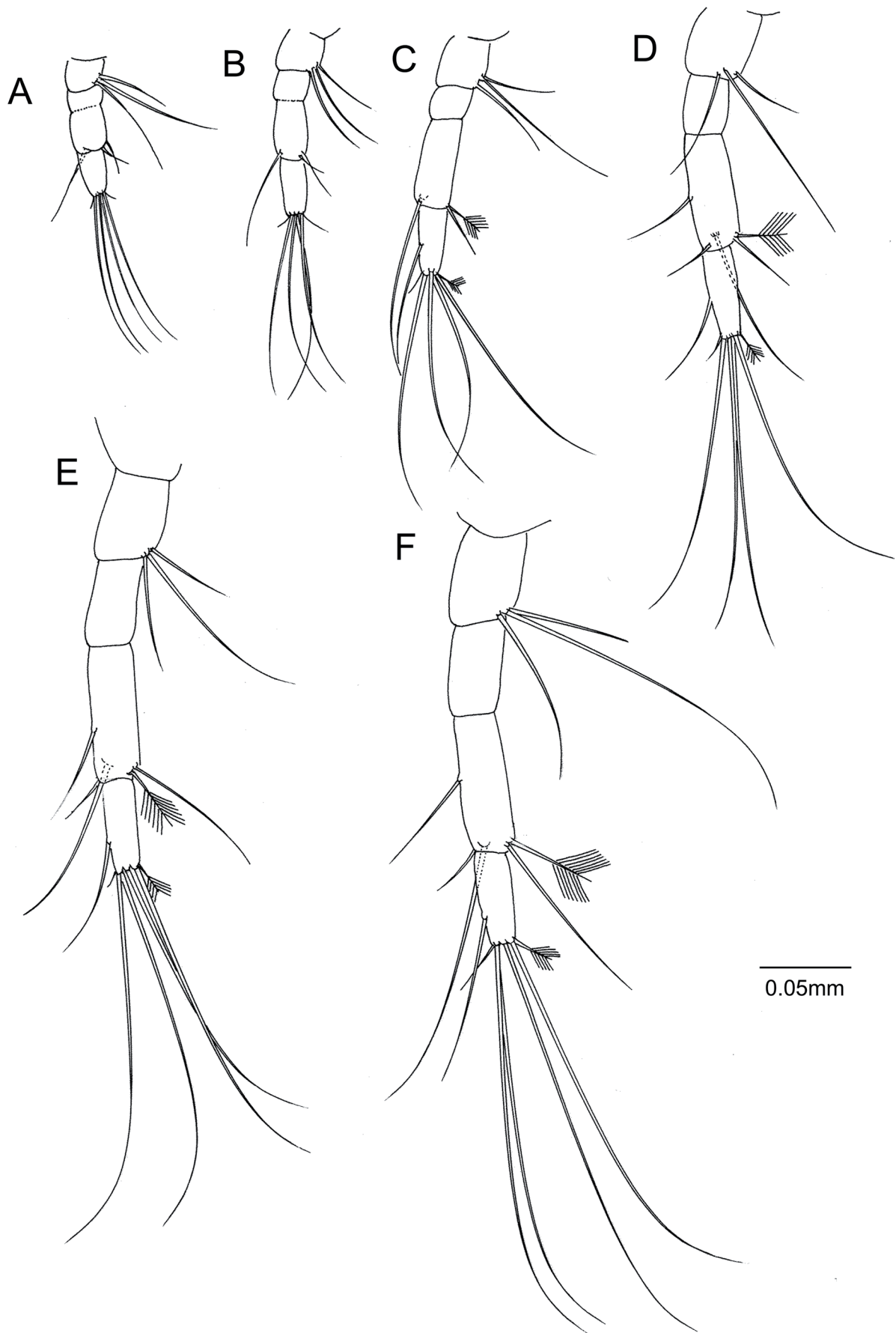
ces of exuvies or calcareous shells. These particles were placed close to the extremity of the tube with chelipeds and soon embedded into the tube with the mucus. In contrast, animals maintained in glass tubes did not take advantage of those particles, as the lining mesh tube was exclusively made of mucus. Particles that occasionally entered into the tube and had stuck to this mesh were expelled by the water current produced by pleopods that were beating alternately. The lining mesh tube also had a role of holding the animal inside the glass tube, mainly for the newborn ones that anchored to it with chelipeds: it avoided they had dragged by the

**Table II.** *Sinelobus stanfordi*. Setal formula (maximum number) for pleopod articles.

	STAGE(S)/ARTICLE	basal article	endopod	exopod
Pleopod 1	MII (absent)			
	MIII	0, 0	0, 0, 0, 0	0
	JUVI	0, 2	1, 5, 1, 4	14
	♂COPI, JUVII	0, 2	1, 5, 1, 5	14
	♂COPII, ♀PREI	1, 5	1, 14, 1, 9	14
	♂COPIII, ♀COPI	1, 5	1, 14, 1, 9	17
	♂COPIV, ♀PREII	1, 6	1, 14, 1, 11	22
Pleopod 2	MII (absent)			
	MIII	0, 0	0, 0, 0, 0	0
	JUVI	0, 2	1, 5, 1, 5	14
	♂COPI, JUVII	0, 2	1, 7, 1, 5	14
	♂COPII, ♀PREI	1, 4	1, 8, 1, 7	19
	♂COPIII, ♀COPI	1, 5	1, 14, 1, 10	23
	♂COPIV, ♀PREII	1, 6	1, 14, 1, 11	23
Pleopod 3	MII (absent)			
	MIII	0, 0	0, 0, 0, 0	0
	JUVI	0, 2	1, 5, 1, 5	13
	♂COPI, JUVII	0, 2	1, 5, 1, 5	13
	♂COPII, ♀PREI	1, 3	1, 8, 1, 9	18
	♂COPIII, ♀COPI	1, 3	1, 9, 1, 9	19
	♂COPIV, ♀PREII	1, 4	1, 14, 1, 11	21

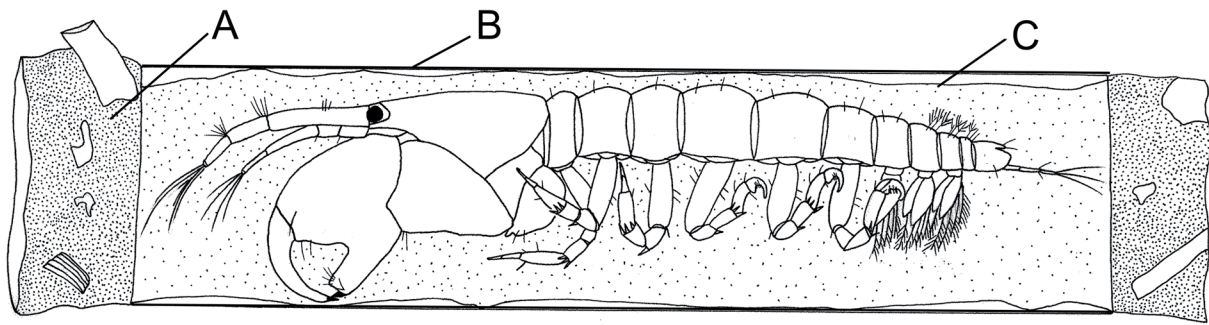


**Figure 14.** *Sinelobus stanfordi*. A-C, left pleopod 2, posterior view. A, MIII; B, ♂JUVI; C, ♀PREII.



*Nauplius*

Figure 15. *Sinelobus stanfordi*. A-F, right uropod, dorsal view. A, MII; B, MIII; C, ♂ JUVI; D, ♀ JUVII; E, ♂ COPII; F, ♂ COPIII.



**Figure 16.** *Sinelobus stanfordi*. Habitus, lateral view, Copulatory Male IV inside the glass tube. A, natural section; B, glass tube; C, fine mesh lining the glass tube wove by the tanaid.

water current produced by mother appendages. In the case of competition for a glass tube by two tanaids, the largest one always took it. **FEEDING.** When larvae were already developed, a yellowish substance similar to the yolk was produced inside the female marsupium that indicated the hatch was coming. This “yolk” constituted the first meal for these larvae, as newly hatched manca had their intestine plenty of this yellowish food. Larvae that did not feed this “yolk” did not survive. After few hours from hatching, mancas began to ingest particles from outside, such as mother’s feces and those brought by the water current. Tanaids in Manca and Juvenile stages ate their own exuvies with higher frequency than adults, certainly, to supply their requirements of calcium carbonate in these intensive growth phases. *S. stanfordi* did not select food in the omnivorous or detritivorous way: any particle within chelipeds’ reach was taken and ingested, including pieces of activated coal that were experimentally offered. Hard particles such as mollusk shells were not ingested, but these were utilized for the construction of tubes. Oviparous females usually fed during the egg incubation period. Cannibalism was not observed in this species; even brooding females never fed eggs that did not hatch, nor larvae that were weakened or dead soon after hatching; these were taken away the tube by the water current. Females continued feeding normally until the next ecdysis. In copulatory females that were not fecundated, eggs were reabsorbed and a new brood was produced in the next ecdysis. **BREATHING, BODY CLEANING AND ECDYSIS.** Epipodites of maxillipeds were appendages that beat rhythmically and constantly and produced a continuous water current throughout the branchial chambers for the animal bre-

athing. In weakened animals, this movement was slow. Oviparous females oxygenated her eggs by pressing the marsupium with a regular movement of pereopods IV to VI, that produced a small position changing of eggs and a water renewing inside the marsupium. Particles or dust that were stuck among setae of antennules, antennas and maxillipeds, were removed by the aid of chelipeds. On the other hand, the cleaning of pleopod setae was performed with the aid of dactyl spines of pereopods 5 and 6; the animal bent ventrally the pleon against the pereon for this purpose. Weakened animals did not clean neither the body nor appendages, and they died by an accumulation of particles on the whole body surface. In the pre-ecdysis period, tanaids suppressed the feeding and their body took a whitish coloration. After brooding up the suture located between the carapace and the 1<sup>st</sup> pereonite, the animal liberated, firstly, the new carapace and, after, the remainder of the body. Old exuvies were dragged outside of the tube by the power of the water current produced by pleopods. **NUPTIAL COURTS AND REPRODUCTIVE ACTIVITIES.** As tanaids attained juvenile stage when the secondary sexual differentiation took place, some began a random migration to neighbor compartments. In most cases, the migrant juveniles stopped their journey when met an individual of the opposite sex, probably after a number of unsuccessful visits to previous compartments.

The copulation always happened in the female’s tube, in spite of her resistance against the male intrusion: she attacked him with her chelipeds and tried to obstruct the male’s passage throughout the tube, by bending the carapace against the pereon. But this aggressive behavior lasted for a short time and the male has been accepted

soon after. In the sequence, the male touched female antennules with his own, in a performance that could be considered as nuptial court. The direct observation of the copulation act was not possible, because the partners were unfastened by the slightest disturbance such as observer proximity or change in the light intensity of the optic equipment. However, couples were observed in copulation position, that is to say, with the ventral side in close contact. The copulation position occurred only between animals of similar size, or between female larger than male; no copulation position was observed in the inverse arrangement. After the fecundation, most males stayed in the females' tube during a period of time from few hours to many days. Some males took five days to fecundate females and others did it only after an ecdysis. Some males fecundated two females in a short period of time (until one day) but they were not able to fecundate a third one soon after: only after some days or after an ecdysis. Females intensified pleopod beatings during the manca delivery. Simultaneously, the marsupium was completely disintegrated, but cuticle remains produced scars at the base of pereopods 4. Newly hatched mancas had a tendency to abandon the maternal tube but, when this happened, the mother picked them up with its chelipeds and brought them near the brood, that was always concentrated in the middle of the tube. Only in the second day after hatching, they left the maternal tube and began to build their own tubes directly on the bottom of the cultivation recipient; these were finer and more transparent than those produced by tanaids of later stages, and were constructed close, far away or over the maternal tube. Mancas II that were not moved to glass tubes secreted natural tubes, suiting them to the body size and, at each ecdysis, tanaids built new tubes.

#### Duration of developmental stages

The egg incubation period was longer in the winter culture (9-12 days after fecundation) than in the autumn (8-10 days) or summer one (6-8 days). The development from MII to ♀COPII lasted 35 days after larva hatching in summer, 42 days in autumn and 61 days in winter culture. Mortality rates

were quite different in these cultures, but the highest one occurred in the ecdysis from MII to MIII (18.5% in summer, 24.4% in autumn and 26.3% in winter). The most advance the developmental stage, the longest the intermolt period (Fig. 17).

#### Discussion

The absence of external evidence of protandry, protogyny or hermaphroditism among native and cultivated populations in the present study leads to consider *S. stanfordi* as a gonochoristic species. Surely, anatomical analysis will confirm this sexual category.

Lang (1958) inferred the occurrence of protogynic hermaphroditism in *Tanais* (now *Sinelobus stanfordi* f. *sylviae*) based on the shape of the carapace, antennules and chelipeds, and on a superficial histological analysis. He found that some phenotypically defined females would have ovotestis, with the ovarian part extending from 2<sup>nd</sup> to 4<sup>th</sup> somites and the testis occupying the remaining pereon. As this histological analysis was incomplete, the hermaphroditism in this species is doubtful. In spite of the Lang's (1958) affirmation that environmental variables can induce sex reversion, this event does not seem to occur in *S. stanfordi* from Parana-gua Bay, as native population has not any evidence of hermaphroditism.

The cuticle coloration soon after the molting has a normal pattern of the species in *S. stanfordi*, whereas in *H. oerstedii*, it is white (Bückle-Ramirez 1965). In this last species, if a female had a blue coloration before the ecdysis, it will change the sex. The only white coloration observed in *S. stanfordi* before ecdysis can be related to the gonochoristic nature of the species.

The following results of the present research brought out evidences that thwart the observations of Lang (1958) about *S. stanfordi*: 1. The sexual dimorphism is evident as early as JUVI, when individuals bearing tiny genital cones will develop to males and those lacking them, to females. Messing (1983) also found genital cones in a juvenile of gonochoristic *Pagurapseudes largoensis* reared in laboratory. 2. The reduction of males' mouthparts is not a general rule for Tanaidacea, and in gonochoristic species, the sexual ratio will not

be unbalanced in function of the feeding inability of males. 3. The secondary sexual dimorphism in antennules, antennae, chelipeds and carapace arises gradually in the developmental sequence, and not abruptly after a single molt. According to Sieg (1984), in Tanaidae with sexual dimorphism, its differentiation occurs gradually in gonochoristic

species, while in hermaphroditic species, the animal acquires characteristics of the opposite sex through an ecdysis. He considers that other information regarding these differentiations, including the Lang's, is interpretation mistake.

According to Sieg (1983b), the sexual dimorphism is a characteristic of primitive Tanaidacea,

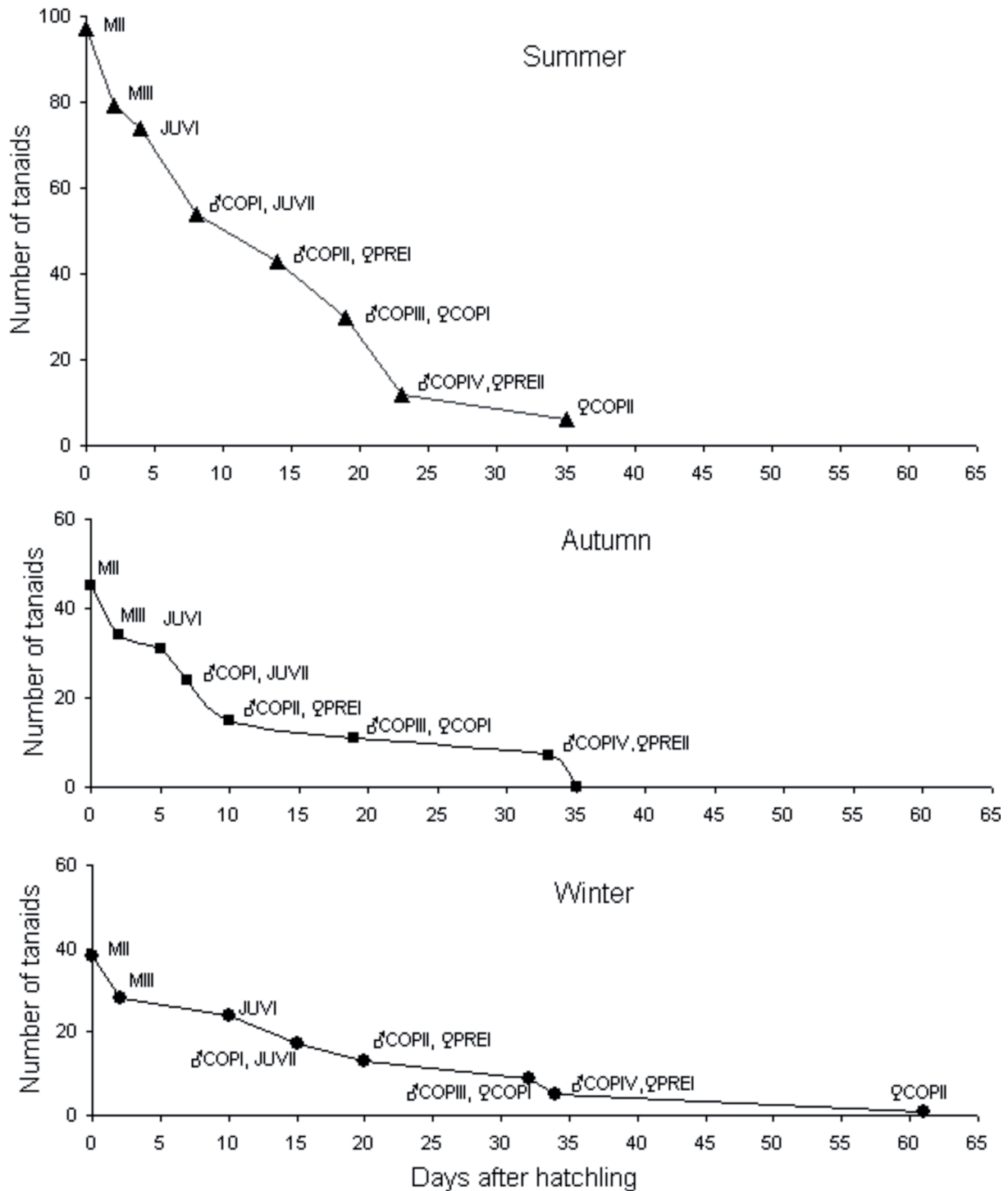


Figure 17. *Sinelobus stanfordi*. Duration of developmental stages and survival from MII to ♀COPII, in summer and winter cultures.

among which members of the family Tanaidae are included. He pointed out that the first indication of sexual dimorphism is the faster growth of males' chelipeds than females', that would secondarily induce the sexually diversified growth of antennules and antennae. Additionally, certain families as Neotanaidae and other belonging to Tanaidomorpha (excluding Tanaidae), adult males present reduced mouthparts. This reduction would shorten the life and the number of males in comparison to females', which would cause an unbalanced sexual ratio and consequent difficulties in fertilization. The protogynic hermaphroditism would have appeared in order to lessen this unbalance through the increment of secondary males (Sieg 1983b). As males of *S. stanfordi* do not reduce mouthparts during the development, their number is relatively high even in adult stages without any demanding of hermaphroditism strategies; the gonochoristic nature of this species corroborates above assumption.

Bückle-Ramirez (1965), Gardiner (1975b), Masunari and Sieg (1980), Johnson and Attramadal (1982b), Messing (1983), Hamers and Franke (2000) and Schmidt *et al.* (2002) have demonstrated that, each Tanaidacea family has its own pattern of postmarsupial development. Actually, these patterns are species-specific, as it was found for *Tanais dulongii* (described by Johnson and Attramadal 1982b and Hamers and Franke 2000) and for *S. stanfordi* (present paper), both species belonging to the family Tanaidae, which life cycles were described based on the laboratory cultures. Additionally, the same species can have different number of Neutrum (without sexual differentiation) stages in populations coming from different localities, as the case of *T. cavolinii* reported by Johnson and Attramadal (1982a) from Bergen area, Norway, and by Hamers and Franke (2000) from Isle of Helgoland, German. Thus, even within the same species, these patterns can be diversified between populations living in distinct places.

Sieg (1983b, 1984) stated that, in Tanaidae and Neotanaidae, females do not pass through stage JUVII. However, in *S. stanfordi*, this stage is evident and, it is clearly distinguished from the corresponding male (♂COPI) through the simple observation of the relative size of the carapace, antennules, antennae and chelipeds.

In spite of variable number, it seems that preparatory stages for females are very important event during the tanaid life cycle, as oostegites need to be expanded before the copulation activity. Gardiner (1975b) found a positive correlation between dimensions of oostegites and the body length in preserved females of *Neotanais micromorpher* (Gardiner, 1975), and suggested two preparatory stages in this species, within which oostegites increase in size. Three preparatory stages were registered in *T. dulongii* from European waters by Johnson and Attramadal (1982b) and Hammers and Franke (2000), and in *A. hirsutus* from Magellanic waters by Schmidt *et al.* (2002). On the other hand, *S. stanfordi* always passed only once by the preparatory stage, but the second copulatory females can be preceded or not by second preparatory stage (see Fig. 1). Surely, water temperature can influence the number of preparatory females.

Some characters like the change of the natural position of pereopods 2-6, which articulations make them uprighed, and the presence of setae on dorsal surface of antennules in *S. stanfordi*, are believed to be an adaptation to the life inside a tubular habitat as mentioned by Johnson and Attramadal (1982a) who studied *T. cavolinii*. This life style also influences the carapace pigmentation pattern of these tubiculous species: the anterior part of the body, that is more often extruded from the tube for feeding purpose, is exposed to the light for a longer time, and consequently, it is more strongly pigmented than the remainder body (see Fig. 2 and 3).

According to above authors, the body lengthening and the relative shortening of antennae and antennules through the developmental stages in *T. cavolinii* are also adaptations for the tubiculous life. This statement is also true for *S. stanfordi*, considering that pereon and pleon somites increased in the proportion length/width from JUVI to adult stages. Furthermore, the anterior narrowing of the male carapace is inversely related to the widening of its chelipeds. This morphological strategy seems to make comfortable the tanaid accommodation along the tube diameter that is almost uniform.

Sieg (1980) included in the diagnosis of *S. stanfordi* the presence of two rows of long and abundant plumose setae in a semi-circle distribu-



tion on the surface of the 1<sup>st</sup> and 2<sup>nd</sup> pleonites. This character was observed in native specimens larger than 3.5 cm long, but among individuals reared in laboratory, these setae were less abundant and their distribution was almost irregular, independently of the sex. In *T. cavolinii*, these setae rows together with pleopods function as a barrier against the water recirculation inside of the tube, and as a way for retaining food particles to be ingested by MII (Johnson and Attramadal 1982a). This strategy probably occurs in *S. stanfordi*, at least in native populations.

The functions of pereopods 1-3 observed in *S. stanfordi* are also shared with *H. oerstedii*: three pair of spinning legs, among which, two last ones also perform locomotion (Bückle-Ramirez 1965). In contrast, *T. cavolinii* has only a pair of spinneret legs (pereopods 1) that do not participate in the locomotion (Johnson and Attramadal, 1982a). This tendency to the specialization of thoracic appendages in this last species can be considered as a step in the evolution within Tanaidae.

The variation in the number of setae, spines and denticles combs on appendages observed in *S. stanfordi* was also reported by Messing (1983) in *P. largoensis*: variations within a certain pair of appendages and/or among individuals of a same stage. However, the most notable aspect in the morphology of *S. stanfordi* is the constancy of the article number in its appendages during all developmental stages, with the exception of pereopods 6 in manca stages. Among Tanaidacea species which developmental stages are known, alterations in the article number of antennules, pleopods and uropods are registered in *P. largoensis* by Messing (1983), and the increase in the article number of uropods is described by Gardiner (1975b) in *N. micromopher*, in *Z. coralensis* by Masunari and Sieg (1980) and in *L. savignyi* by Masunari (1983b). In these last three species, the first developmental stage can be recognized by simple counting of uropods articles.

Unlike the description of Sieg (1980), both mandibles of *S. stanfordi* bear two plumose setae, instead just one, issuing from the base of each lacinia mobilis. In a later publication, Sieg (1984) rectified this description and considered the presence of these two setae as a characteristic of the family Tanaidae.

The morphology of maxilla, labrum and labium observed in the present work is in accordance to the Sieg's (1980). However, three short and basally wide setae on the terminal surface of the maxilliped endite found in all developmental stages from Paranagua Bay specimens are not mentioned by above author. Furthermore, the long seta in the ventral distal corner in the first four articles of pereopod 1 described by Sieg did not occur in *S. stanfordi* in the present research. Flattened setae in the distal margin of the propodus of pereopods 6 (Sieg 1980) were not observed in the present paper, but only simple and plumose setae as in Sieg (1976). The setae disposition in uropods is a little different from the description of Sieg (1980), but it is identical to the Stephensen's (1936) who studied specimens coming from Kurile Islands. These variations can be considered as a consequence of the wide geographical distribution of this species.

Like *T. cavolinii* studied by Johnson and Attramadal (1982a), the presence of short setae in maxillipeds of *S. stanfordi* confirms the detritivorous feeding habit of these species, when compared with filter feeding species which bear long setae in those appendages (Sieg 1984). On the other hand, the increase of plumose setae number in pleopods during the development is probably related to increased demand of the water circulation control inside of the tube.

Klepal and Kaestner (1980) found denticles combs in the pereopods of *T. cavolinii* and they considered that these non-sensorial structures can be useful to increase the adherence with the tube wall. However, the presence of these combs in the appendages that are not in direct contact with tube wall, like pleopods of *T. cavolinii* (Klepal and Kaestner 1980) and mouthparts in *S. stanfordi* (present paper), weakens this hypothesis.

The interruption of the feeding before the ecdysis observed in *S. stanfordi* seems to be common behavior among tanaid species; it has been reported for *T. cavolinii* by Johnson and Attramadal (1982b) and for *H. oerstedii* by Bückle-Ramirez (1965).

The oxygenation of eggs inside of the marsupium is done through distinct strategies among tanuids: while in *S. stanfordi* it is performed by the movement of pereopods 4-6, in *H. oerstedii* it is done by oostegites movement, as in this species,

the marsupium is composed of overlapping oostegites. By the way, in females with this type of marsupium, some eggs or embryos are easily lost which are usually eaten by the tanaid mother, as observed by Bückle-Ramirez (1965). In contrast, in *S. stanfordi* these losses never occur as its brood pouch is closed: even in the case of an unsuccessful fecundation, eggs are reabsorbed and not eaten.

After the manca hatchling, females of *H. oerstedii* keep their marsupium empty until the next molting (Bückle-Ramirez 1965), but marsupium disintegration with scar remaining as observed in *T. stanfordi* is also reported by Gardiner (1975a) for the same species. This species-specific difference seems to be related to more complex interaction between tanaid broods and the marsupium disintegration. Johnson and Attramadal (1982b) observed in *T. cavolinii* that the marsupium disintegrated only after mancas have been fed on yolk. They inferred that, these mancas could have secreted an enzyme that dissolved the marsupium. Some evidences that corroborate this hypothesis were observed in *S. stanfordi*: 1. in the natural way, mancas were usually delivered through the marsupium disintegration. 2. a marsupium still containing mancas that had been accidentally removed from the mother pereon did not disintegrate. Two mancas picked up from this miscarried marsupium got to survive. Probably, the secretion of the above mentioned enzyme is a function of the mancas' maturation.

The competitive behavior between two tanaids for the same tube in *S. stanfordi* is similar to described for *H. oerstedii* by Bückle-Ramirez (1965). However, the aggressiveness of females in the last species is stronger than observed in former one: while the female allowed the male to stay inside her tube up to three days after the copulation in the former species, the male was expelled soon after the sperms transference has been happened in last species. Besides, the sexual intercourse in *H. oerstedii* can last, at most, for 11 hours while in *S. stanfordi*, up to 24 hours. Even the size selection of males by females is least rigorous in *S. stanfordi*, as in *H. oerstedii*, the copulation do not take place between tanaids of different sizes.

In *S. stanfordi*, males are not always ready for copulation and it seems that the spermatozoon

maturation occurs intermittently: some of them delayed to fecundate females and others had to pass by an ecdysis before the fecundation. On the other hand, some males fecundated two females in a same day. Messing (1983) also could not elucidate if males of *P. largoensis* are able to fertilize females without interruption.

In a general way, the behavior of *S. stanfordi* in the culture condition reminds that of *T. cavolinii* reported by Johnson and Attramadal (1982b), in spite of the striking aggressiveness of females of the later species.

Notwithstanding the water temperature control in the culture aquarium, the difference in the intermolt duration between summer, autumn and winter cultures obtained in the present research is notable (see Fig. 17). Probably, this fact can be related to endogenous rhythm of the species or/and to distinct quality of the natural food provided to these tanaids. In the last case, winter hydroid mush would have low quantity and variety of food items and consequently low energetic contents to support a shorter intermolt period than summer one. In extreme condition of low temperature and food shortage in natural habitats, tanaids hibernate as reported by Bückle-Ramirez (1965) for *H. oerstedii* from temperate region. The natural water temperature in winter of Paranagua Bay do not seems to be low enough to induce *S. stanfordi* for a hibernation: only a lengthening of the intermolt duration.

The tendency to a progressively larger duration in most advanced stages observed in culture of *S. stanfordi* (see Fig. 17) is also reported for *P. largoensis* by Messing (1983:400). It seems a general characteristic of the development of tanaids.

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