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POSTMARSUPIAL DEVELOPMENT AND GROWTH OF *PAGURAPSEUDES LARGOENSIS* MCSWEENY (CRUSTACEA, TANAIDACEA)

Charles G. Messing

ABSTRACT

Postmarsupial development of the gastropod shell-inhabiting tanaidacean *Pagurapseudes largoensis* McSweeny is described and compared with that of *Heterotanais oerstedii* (Krøyer) and *Neotanais micromopher* Gardiner. This is the first such study of an apseudomorphan based on experimentally reared animals. *P. largoensis* is gonochoristic; two manca instars are typical of all tanaidaceans so far investigated. In females, the mancas are followed by two or possibly three juvenile instars (=neutra), one or two preparatory instars characterized by rudimentary oostegites, and a copulatory stage with complete marsupium. Laboratory maintained animals pass through up to three copulatory stages, each separated by a preparatory stage of one or two instars. A preparatory instar, characterized by very small rudimentary oostegites often restricted to thoracopods VI, sometimes occurs between the juvenile and normal preparatory stages. The small number of such field-collected specimens suggests that it is an abnormality. Males develop either directly from the manca 2 instar or from the first juvenile instar. Pleopods and heterochelae either accompany initial appearance of genital cones or appear after one or two additional molts. Males retain a full set of mouthparts, feed, and molt throughout their lives. Variability in the pattern of instar succession may be construed as a primitive trait and supports the position of the Apseudomorpha as least derived of the three tanaidacean suborders. Males alone are heterochelous; the right chela is always major and its growth is allometric with respect to carapace length. Intermolt period increases with age, from a 2-week mean for mancas 1 to about 4 weeks for preparatory and copulatory females and 7 weeks for large males, although minimum intermolt periods are similar for all stages (11–29 days). Longevity is estimated at up to 15 months for males and 9 months for females. The sex ratio for field-collected specimens is about 1:1. Females bear 4–17 offspring per marsupium.

Investigations into the development of the Tanaidacea have treated a very small percentage of the several hundred known species. Most are reconstructions of life histories based on preserved material. Bückle-Ramirez' (1965) experimental rearing of the tanaidomorph *Heterotanais oerstedii* (Krøyer) is the only detailed work based on live animals. The current investigation represents the first study of postmarsupial development of a member of the suborder Apseudomorpha to be based on live animals as well as preserved material.

Pagurapseudes largoensis McSweeny, 1982, belongs to the family Pagurapseudidae Lang, 1970 (see also Gutu, 1972) and occupies vacant gastropod shells as do hermit crabs. It dwells in a variety of shallow, inshore, bottom communities in the Florida Keys but appears to prefer carpets of algae dominated by the red alga *Laurencia poitei* (Lamouroux) that occur in beds of turtle grass (*Thalassia testudinum* König). It is also frequently found clinging to the undersides of tussocks of the calcareous red alga *Jania rubens* (Linnaeus) and to bases of colonies of the inshore finger coral *Porites divaricata* Lesueur, both of which are found in *Thalassia* beds (Messing, 1979).

This tanaidacean has both advantages and disadvantages as an experimental animal. It does not swim and can be kept in open dishes without becoming inextricably and fatally caught in the surface tension, a problem with tanaidaceans that can swim. It appears to be an unspecialized detritivore and is easily maintained in the laboratory. On the other hand, it occupies opaque or, at best, translucent shells that do not permit monitoring of ovarian maturation, egg deposition, copulation, or embryonic development. It is also possible that the adaptations acquired with the occupation of gastropod shells have forced a departure from the basic apseudomorphan developmental pattern. This will be answered only by investigation of other genera and families.

Developmental patterns in the Tanaidacea have recently been reviewed by Gardiner (1975a) and Sieg (1972, 1973, 1978). Briefly, tanaidomorphan and neotanaidomorphan species so far investigated are either gonochoristic or potential protogynous hermaphrodites. The former generally conform to the "normal type" pattern of Bückle-Ramirez (1965) and Sieg (1972, 1973, 1978). In the latter, both gonochoristic (primary) and protogynous (secondary) males exist. Gonochoristic males differ morphologically from males that have passed through an initial female stage; the latter also differ among themselves, depending upon the female stage from which they arise. Lang (1958) reported that in *Sinelobus stanfordi* (Richardson) the females gradually come to resemble the males. In other protogynous species, however, the change occurs in the course of one molt and generally follows the pattern described by Bückle-Ramirez (1965) for *Heterotanais oerstedii* (e.g., *Neotanais micromopher* Gardiner, 1975a; *Leptochelia savignyi* [Krøyer] and *L. forresti* [Stebbing] [personal observations]) as well. I agree with Sieg (1973) that all tanaidomorphan and neotanaidomorphan genera in which the males bear strongly reduced mouthparts will prove to be potential protogynous hermaphrodites.

Two significant differences exist between the pattern described by Bückle-Ramirez (1965) for *Heterotanais oerstedii* (see also Sieg, 1972, 1973, 1978) and that suggested by Gardiner (1975a) for *Neotanais micromopher.* Bückle-Ramirez established experimentally that female *H. oerstedii* pass through a single preparatory instar during which both oostegites and ovaries increase in size. Gardiner's detailed analysis relating oostegite length to oostegite width and to body length revealed a distinctly bimodal distribution in *N. micromopher* (1975a: 91–193) and led him to assume two preparatory female instars. In the second of these two instars, he found the ovary to be extremely swollen, or at least twice as wide as in the first instar. Sieg (1978) referred to the expansion of oostegites in the preparatory female stage of *H. oerstedii* and suggested that Gardiner's data could be explained without having to assume the occurrence of two preparatory instars in *N. micromopher.* Because Gardiner's conclusion was based on preserved material, we cannot be certain of the sequence. However, in addition to the distinct oostegal bimodality, also encountered in *Neotanais persephone* Messing from the Puerto Rico Trench (Messing, 1977), preparatory females of *N. micromopher* exhibit roughly twice the variability in length relative to mean body length than that shown by copulatory females, suggesting that two preparatory instars may be present (see Messing, 1979). Johnson and Attramadal (1982) report three preparatory instars in *Tanais cavolinii* Milne Edwards.

The other difference between the patterns for the two species is that females of *H. oerstedii* retain the empty marsupium until the next molt, whereas females of *N. micromopher* appear to shed it sometime before the next molt. Gardiner based this conclusion on the occurrence of females with "oostegite scars" on the coxae of pereiopods II–V (thoracopods III–VI) and decalcification of the gonoporal region on the coxa of pereiopod V. He compared these to similar scars found by Shiino (1937) in the apseudomorphan *Apseudes nipponicus* Shiino. In *Tanais cavolinii,* offspring are released when the oostegal ovisacs disintegrate prior to molting; after molting, coxal scars may be present (Johnson and Attramadal, 1982). Oostegal ovisacs are also apparently lost in *Sinelobus stanfordi,* although in this case a stub of oostegal cuticle rather than a scar remains (Gardiner, 1975b).

Developmental patterns among apseudomorphan genera are far less certain. As in the Tanaidomorpha and Neotanaidomorpha, gonochorism, protogyny, protandry, and simultaneous hermaphroditism have all been proposed for various taxa. Detailed laboratory studies of living animals are lacking, however, and many reconstructions are based on too little material.

Although Sieg (1972, 1978) suggested that the gonochoristic "normal type" developmental pattern applies as well to the Apseudomorpha, differences apparently exist. Gardiner (1975a: 186–187) reviewed the various ideas. Briefly, Lang (1953a) and Băcescu (1961) reported simultaneous hermaphroditism in *Apseudes hermaphroditicus* Lang (=*A. spectabilis* Studer) and *A. intermedius* Hansen, respectively. Lang also reported copulatory females bearing male genital cones in *Parapseudes latifrons* (Grube) (1966: 551, 564) and *A. grossimanus* Norman and Stebbing (1968: 30). He rejected possible hermaphroditism in the former because of the early appearance and gradual increase with age of chelipedal dimorphism, but suggested possible protogyny in the latter. Lang (1958) stated that protogyny also existed in *Apseudes sarsi* Holthuis (=*A. holthuisi* Băcescu) but gave no details.

Wolff (1956) suggested that protandry existed in *Apseudes* (=*Leiopus*) *galatheae* Wolff and *A.* (=*Leiopus*) *gracillimus* Hansen because the males that he examined fell into a size range between that of the "pre-adults" (=mancas 2) and the "adult females" (preparatory and copulatory females and possibly juveniles). Only 18 specimens were available to him, however.

Gardiner (1973a) found no unequivocal evidence for either protogyny or protandry in *Synapseudes idios* Gardiner. Likewise, neither Lang (1953b) nor Wolff (1956) suggested such patterns for *Apseudes spinosus* M. Sars.

The gonochoristic developmental pattern in the Apseudomorpha approximates that described for the Tanaidomorpha by Bückle-Ramirez (1965) and Sieg (1972, 1973, 1978), but the results obtained for *Pagurapseudes largoensis* discussed below indicate that differences exist. As in the other suborders, some species of apseudomorphans retain the empty marsupium until the next molt (*Pagurapseudes largoensis,* this paper; probably *Apseudes spinosus* and *A. spectabilis,* see Lang, 1953b), while others discard it (*A. nipponicus,* see Shiino, 1937).

MATERIALS AND METHODS

Pagurapseudes largoensis was collected 50–100 m off the southern side of Long Arsenicker Key in Card Sound, southeastern Florida (25°22.4′N, 80°18.0′W), in 1.0–1.75 m of water. Hand-collected samples of loose benthic flora (i.e., clumps of *Laurencia poitei* and dead *Thalassia* blades) were placed in 792 μm nylon mesh bags and washed and sorted in the laboratory.

Collection and laboratory maintenance took place between March 1977 and December 1978. Specimens were maintained in the laboratory in plastic trays of 18 compartments, 3.3 × 3.3 × 2.5 cm, 30 ml each, or in 24-well (3.5 ml each) culture plates, both with their lids removed. These were placed on Plexiglas® stands in 37.85 l, aerated water baths within 1.0 cm of the water surface. The water was maintained between 26 and 28°C and was changed every other week. Extremes of 23 and 34°C were recorded during a few brief episodes of heater malfunction.

The tanaidaceans were provided with fragments of *Laurencia* and *Thalassia* blades and appeared to feed on epiphytes and attached detritus. Fecal material, microalgal films, and detritus were periodically removed by pipetting or swabbing. Some small petri dishes used for holding live specimens for related studies were not monitored as frequently but the resulting accumulated fecal pellets and detritus did not seem to affect the animals. Exuviae and dead specimens were preserved in 70% ethanol or fixed in sea-water Bouin's solution and transferred to 70% ethanol after two washings.

Two major problems arose. On occasion, particularly when an algal film developed in the system, some specimens climbed into adjacent compartments. Specimens that were unequivocally identified were returned to their original compartments. When doubt existed, the specimen(s) in question was either transferred to a new chamber and the record of its development begun anew, or it was eliminated from consideration.

Because materials found in the environment were used as food, organisms such as free-living nematodes, ciliates, foraminiferans, and harpacticoid copepods appeared in culture trays. Small, histophagous ciliates were observed to swarm on and inside recently dead tanaidaceans, but developmental stages remained recognizable. Frequently, however, only the more heavily chitinized and calcified anterior portions of exuviae were recovered from the chambers. In such cases, specific developmental stages often could not be determined. Although both the ubiquitous harpacticoids and the newly molted *Pagurapseudes* themselves are suspected consumers, I have no direct evidence to implicate either.

Drawings of exuviae and sacrificed specimens were made and measurements taken using camera lucida attachments on Wild M20 compound and M5 dissecting microscopes. Posterior curling of *Pagurapseudes* made length measurements particularly difficult. Complete exuviae could be straightened but not without distortion of the posterior pereion and pleon. Measurements were made by juxtaposing the images of a specimen and a ruler with the camera lucida. Dead specimens were held straight, ventral side up, by two fine needles. Straightening occasionally caused ventral separation or tearing of posterior pereionites or pleonites, reducing accuracy of measurement. Therefore, all measurements of total body length (rostrum to pleotelson tip), pereional, and pleonal lengths have been rounded to the nearest 0.1 mm. Length measurements of the carapace and major chela were more precise and have been rounded to the nearest 0.05 mm.

RESULTS

Morphological Variations

Meristic and morphometric growth changes occur gradually in most cases in *Pagurapseudes largoensis* (Figs. 1–8). The abrupt appearance of thoracopod VIII (=pereiopod VII) and the pleopods during the early instars is typical of the entire order. Examples of gradual increases in ornamentation with growth include the number of spines on the second segment of the mandibular palp (Figs. 1G–I, 8), scalelike stubs on the merus and carpus of thoracopods IV–VIII (Fig. 6A–L) and stout, serrate spines on the cutting edges of the chelae, probably similar to the hedgehog hairs of *Homarus americanus* (Derby, 1982) (Fig. 5D–H). Ornamentation does not always increase so regularly, however. The number of carpal spines on thoracopod III (Fig. 5A–C), spatulate spines on the maxillipedal endite (Fig. 4G–I), and segments and aesthetascs on the external antennular flagellum (Figs. 1A–C, 2) are meristic characters that may remain constant through several instars.

The few changes in segmentation that occur with growth are as follows. The external antennular flagellum increases from five to six segments some time after maturity. No uniformity appears; the number may remain constant through several instars (Fig. 2B) or may increase on only one antennule of a pair (Fig. 2C). Although the mancas 1 that I examined have five segments including a small terminal one, I have also seen a mature male with only four (Fig. 2A).

The development of thoracopod VIII is typical. It is absent in the manca 1, present as a straight, unsegmented rudiment with no or few small setae in the manca 2, and completely formed in the following instar (Fig. 6I, J).

Pleopodal form, setation, and time of appearance are all variable. In females maintained in the laboratory, pleopods first appeared in the first copulatory instar. Because not all copulatory females were examined for pleopods, it remains possible that these appendages may first appear at a later instar.

In males, the pleopods usually appear in the fourth instar, the second following the manca 2. The initial form is variable but is generally unisegmented and bears at least two terminal setae (Fig. 6M, P). An indistinctly articulated endopod may be present. A small exopod appears after several molts in the male, although a rudiment may accompany initial appearance of the appendage (Fig. 6N). In females examined, this exopod is absent and the pleopodal setae remain distinctly shorter than in the male. The pleopods illustrated by McSweeny (1982) for this species bear an endopod and exopod of one segment each in both male and female. Our observations may be reconciled by the fact that my figures are taken from


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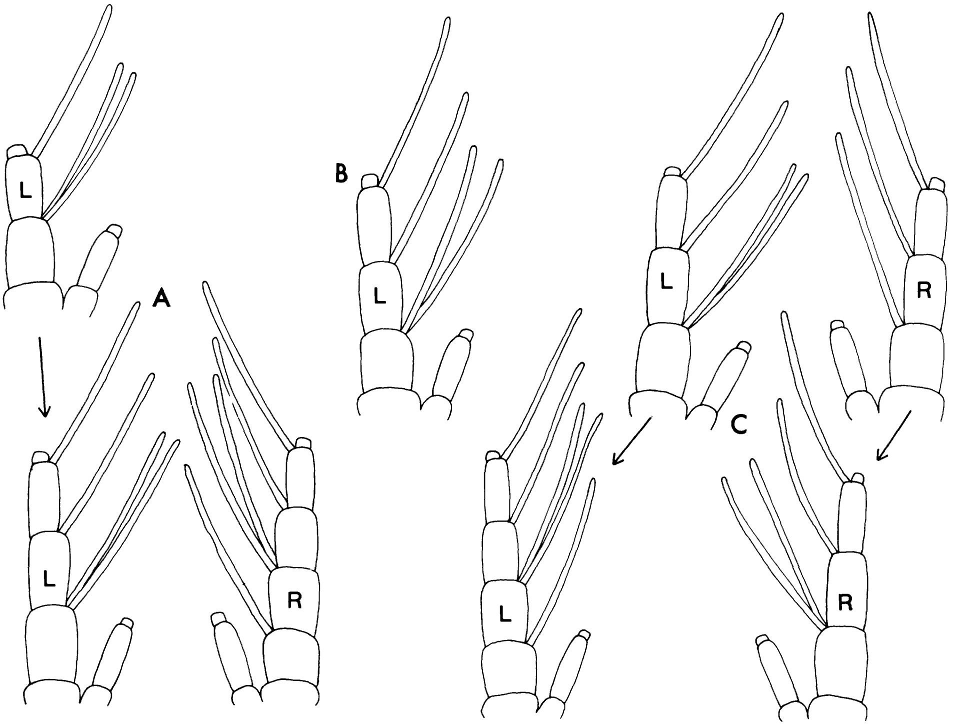

Fig. 2. Variations in the number of segments and aesthetascs of antennular (A1) flagella in three mature males of *Pagurapseudes largoensis*. A, asymmetry and increase in number of flagellar segments and aesthetascs through one molt cycle. Right A1 of earlier exuviae missing; B, specimen that remained unchanged through three molt cycles over 3.5 months; C, asymmetry and increase in number of flagellar segments and aesthetascs through one molt cycle.

exuviae in which segmentation of small appendages is often difficult, if not impossible, to discern (see also uropods, below), Moreover, the lateral pleopodal setae are borne on a distinct shoulder in the female and the larger specimens show a constriction suggestive of segmentation (Fig. 6T, U). In complete specimens that I have examined, the endopod and protopod are distinct segments in both sexes, but I have not seen a well-defined exopod in the female.

The uropodal endopod is usually two-segmented in the manca 1 and three-segmented in other instars. Figure 7H, I, K, and L illustrates the difficulty involved in distinguishing segmentation; although the endopod in 7H appears to be unsegmented, the setae that normally occur along the distal edges of the segments provide an indication of joint placement in 7K and L. McSweeny (1982) figured a two-segmented exopod. By contrast, whole specimens as well as exuviae that I have examined bear a one-segmented exopod, although a few exhibit rudiments of an articulation. Figure 7I, J, and K traces the development through three instars of an aberrant uropod lacking an exopod.

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Fig. 1. *Pagurapseudes largoensis.* A–C, antennule (A1). A, M1, right, dorsal view; B, small male/Juv, left, ventral view; C, large C, right, dorsal view. D, E, antennae (A2). D, M1, left; E, large C, left. F–I, mandibular palp. F, M1; G, first post-M2/Juv; H, P; I, large C. Scales: A–C = 0.2 mm; D–I = 0.1 mm.

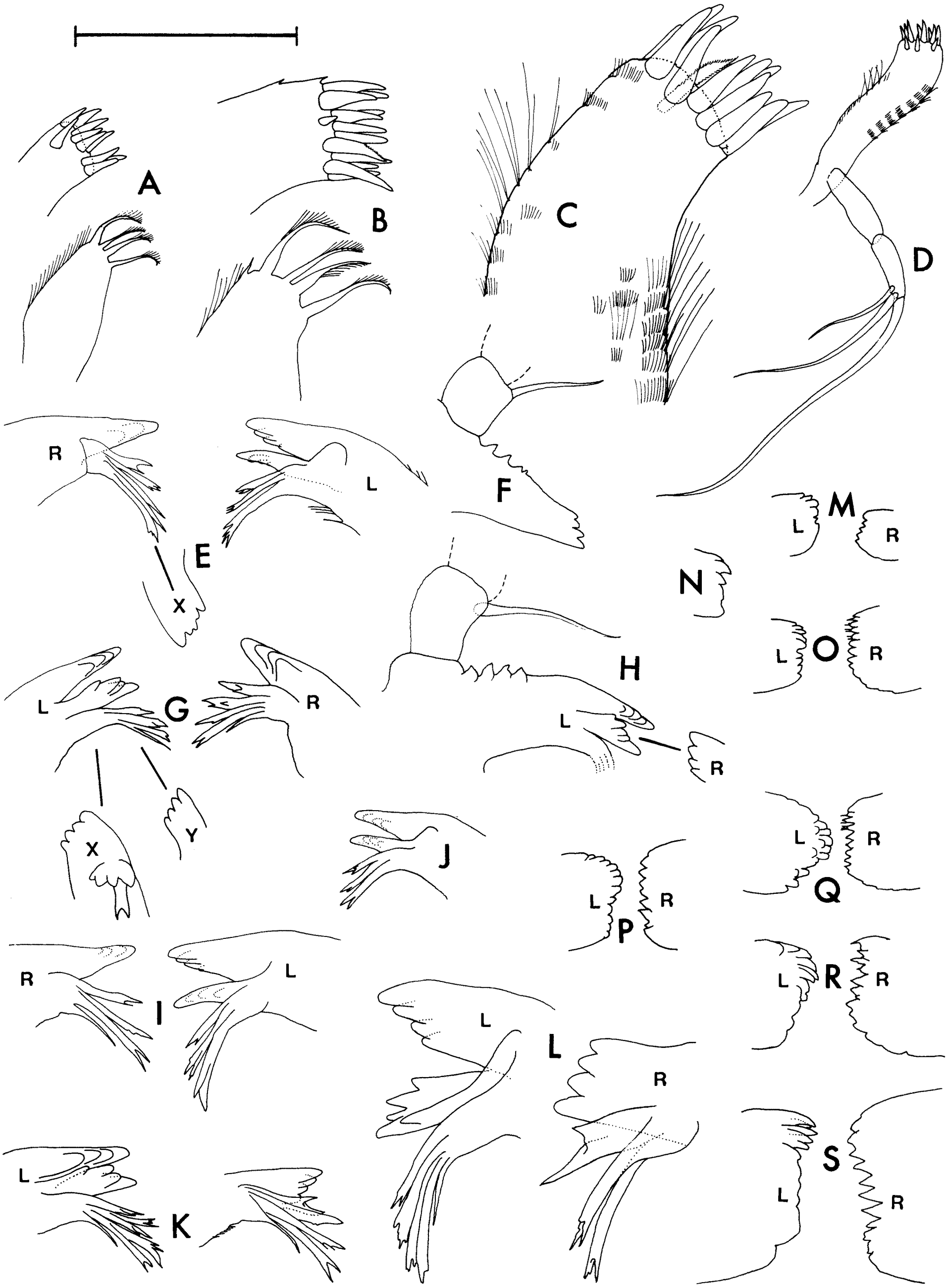

Fig. 3. *Pagurapseudes largoensis.* A–D, maxillule (Mx1). A, distal ends of external and internal endites, M1; B, same, Juv; C, distal end of external endite, large C; D, external endite and 2-segmented palp, P. E–L, mandibles (Md), distal ends. E, M1, posterior view (x = right pars incisiva, ventral view); F, M1, right Md showing teeth adjacent to base of palp; G, M2, anterior view (x = left pars incisiva showing lacinia mobilis and first incisive spine in medial view, y = same, ventral view); H, Juv, left Md showing teeth adjacent to base of palp (R = right pars incisiva, ventral view incisive spines of left broken); I, first post-M2, posterior view; J, second post-M2, left Md posterior view; K,

Appendages that appear in the manca 1 with their definitive number of segments include the antennular peduncle and internal flagellum, second antenna, mandibular and maxillipedal palps, and thoracopods and thoracopodal exopods.

Segmentation of the chelipedal exopod is poorly defined in exuviae through the first few instars and again in a much larger specimen (Fig. 7A–C, F). The constriction that uniformly appears where the second and third segments normally articulate suggests that this appendage is three-segmented at all stages.

Life History

Pagurapseudes largoensis is gonochoristic. No external or functional evidence of protogyny, protandry, or simultaneous hermaphroditism exists. Males retain the full complement of mouthparts and pass through a long series of molts after the secondary sex characteristics appear. No histological analyses were made, however, so it is not known if the rudiments of both male and female gonads are present in the early stages as in some potentially protogynous forms (Gardiner, 1975a) and hermaphroditic species (Lang, 1953a; Băcescu, 1961).

Recent apseudomorphans have diverged less from the theoretical ancestral form envisioned by several authors (Lang, 1956a, b; Gardiner, 1975a) than have the other suborders. Sieg (1980) includes within the Apseudomorpha fossil forms dating to the Permian and relates the suborder, albeit tentatively, to other late Paleozoic forms. The other suborders include no known fossils. The life history of *Pagurapseudes largoensis,* although similar to the "normal type" gonochoristic pattern found in the other suborders, is more variable (Fig. 9). Such variability may be construed as an additional indication of primitivity. The potential protogyny of some tanaidomorph and neotanaidomorph genera appears to be a secondarily acquired, specialized developmental pattern rather than a plesiomorphic one. The development of secondary males with reduced mouthparts from several different female instars cannot be considered a primitive condition. The possibility that some of the variations in the life history of *P. largoensis* may be induced in laboratory-maintained specimens will be discussed below.

Diagnoses and brief descriptions of the various stages in the proposed life history of *P. largoensis* follow. After the mancas, the female sequence is treated, then the male sequence. Figure 9 summarizes the life history. Mouthparts and appendages were examined in detail for three to six specimens of each instar. The numbers accompanying the description of each stage (which may include several instars) are the numbers of field-caught specimens identified to stage or sex (Fig. 10). The number of preparatory females includes all pre- and inter-brood instars bearing rudimentary oostegites. The number of males includes all identifiable instars.

Manca 1.—Pereiopods VII (=thoracopods VIII) and pleopods absent.

Manca 2.—Pereiopods VII unsegmented, short, straight rudiments; pleopods absent.

Juveniles.—All thoracic appendages completely developed; isochelous; pleopods, rudimentary oostegites, and male genital cones absent.

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P, left in anterior and right in posterior views; L, large C, left in posterior and right in anterior views. M–S, mandibular molar teeth. M, M2 (same specimen as G above); N, Juv, left (same as H); O, Juv; P, ♂; Q, P♀; R, P♀ (same as K); S, large C (same as L). Scales : A–C, E, G, I, M, N, Q–S = 0.067 mm; F, G(y), H, J–L, O, P = 0.1 mm; D = 0.2 mm.

Preparatory Females.—Rudimentary oostegites knoblike or paddle-shaped, arising from coxae of one or more thoracopods (almost always III–VI).

Copulatory Females.—Complete marsupium (brood pouch) present.

Males.—Genital cones present on ventrum of last thoracic somite; one pair of pleopods with long setae and right claw larger than left in all but smallest specimens.

Manca 1 (M1).—20 specimens. 1.0–1.3 mm in length. Setation is generally sparse, although the numbers of broom setae on both pairs of antennae closely approach those of mature instars (Fig. 1). On the mandible, the incisive process and spines and lacinia mobilis appear as in the adult. However, only four teeth instead of six are present next to the base of the palp (Fig. 3F) and only a few teeth appear along the anterior edge of the molar process. The carapace is larger in relation to body length than in later stages, accounting for 0.24–0.29 of the total length.

Manca 2 (M2).—20 specimens. All but two specimens examined are 1.3–1.6 mm long (Fig. 10). Setation is generally similar to that of M1. The mandibular molar process still possesses few teeth (Fig. 3M). Thoracopods IV–VII have more scale-like stubs than in M1.

Juveniles (Juv).—41 specimens. Equivalent to the "neutrum" of Bückle-Ramirez (1965) and Sieg (1972, 1973, 1978); 95% of all specimens, both laboratory-maintained and field-collected, are 1.6–2.4 mm long. Laboratory rearing of *Pagurapseudes largoensis* has shown that at least two juvenile instars occur before the preparatory female stage is reached. The wide variation and the roughly bimodal distribution of lengths of field-collected specimens (Fig. 10) also suggest two instars. Males may pass through one such juvenile instar before developing genital cones, pleopods, and heterochelae.

One specimen reared in the laboratory may have passed through three juvenile instars. In this case, the individual passed from M2 (1.4 mm long) to a juvenile 2.4 mm long. The long intermolt period (48 days), relatively large size, and greater ornamentation of the latter suggest that a first juvenile exuviae was lost. Unfor-

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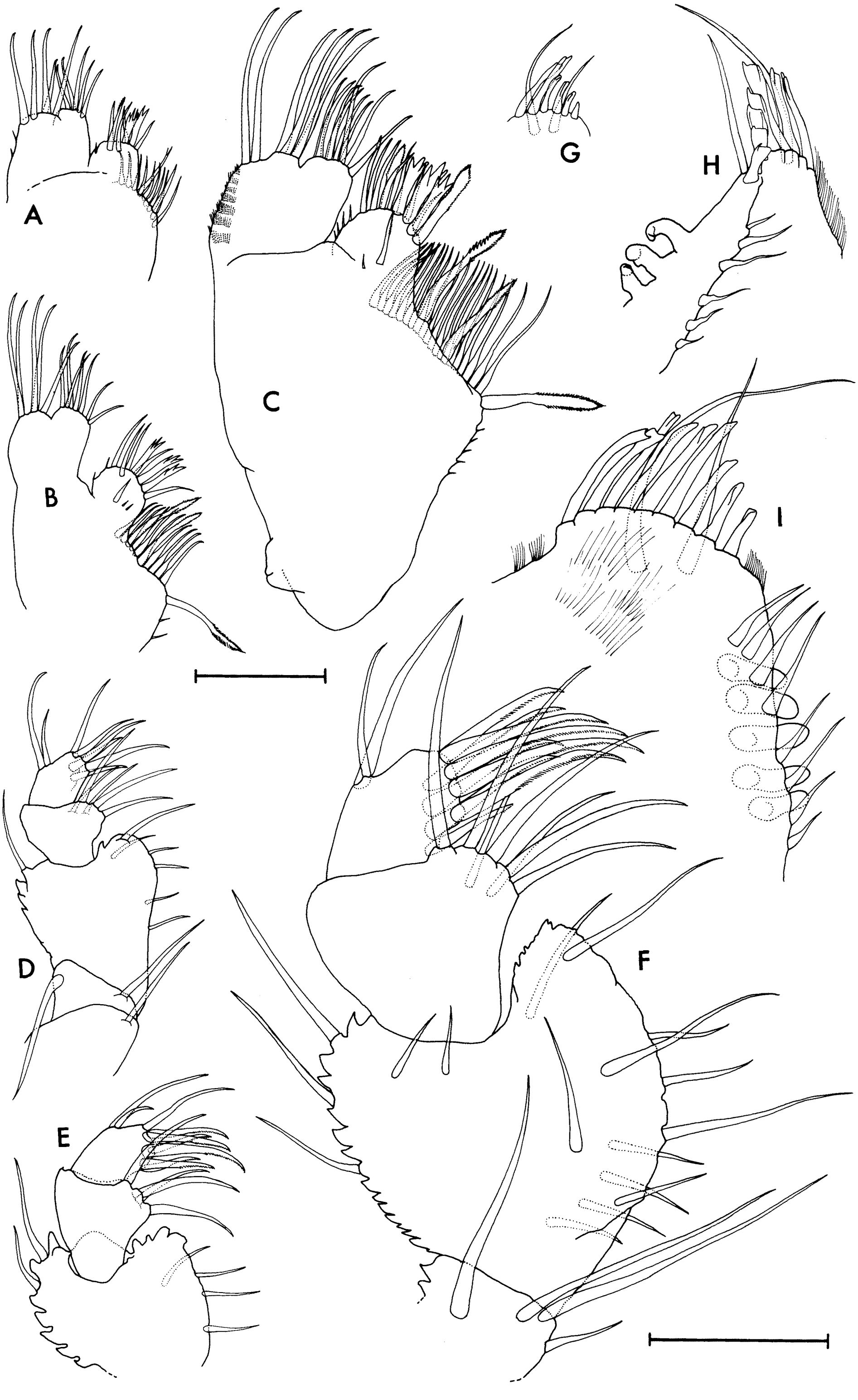
Fig. 4. *Pagurapseudes largoensis.* A–C, maxilla (Mx2). A, M1, right, posterior view; B, first post-M2 ♂, right, posterior view; C, large C♀, right, posterior view. D–F, maxillipedal palp. D, M1, right, posterior view; E, second post-M2 ♂, right, posterior view; F, large C♀, right, posterior view. G–I, maxillipedal endite. G, M1, left, anterior view; H, P♀, right, medial view; I, large C♀, left, anterior view. Scales: upper (A–C, G–I) = 0.05 mm; lower (D–F) = 0.1 mm.

Fig. 5. *Pagurapseudes largoensis.* A–C, thoracopod III (pereiopod II, first walking leg). A, M1, left, exterior view; B, second post-M2 ♂/Juv, right, exterior view; C, large C♀, left, exterior view (oostegite not shown). D–H, chelae. D, M1, left and right, interior view; E, first post-M2 ♂, left and right, exterior view; F, second post-M2 ♂, left and right, exterior view; G, fourth instar ♂, left interior, right exterior view; H, large C♀, right, exterior view. Scales: A–C = 0.2 mm; D–H = 0.1 mm.

Fig. 6. *Pagurapseudes largoensis.* A–E, thoracopod IV (pereiopod III). A, M1, right (showing terminal serrate propodal spine from another specimen); B, M2, right; C, first post-M2 ♂/Juv, right; D, P♀, right (rudimentary oostegite not shown); E, large C♀, left (oostegite not shown). F–H, thoracopod VI. F, M1, right; G, second post-M2 ♂, right; H, large C♀. I–L, thoracopod VIII. I, M2, left; J, first post-M2 ♂, right; K, P♀, left; L, large C♀, left. M–U, pleopods. M, second post-M2 ♂, right; N, fifth instar ♂ (following M2), left and right; O, adult ♂, second pair on pleonite 2; P, second post-M2 ♂; Q, third instar ♂; R, P♀; S, P♀; T, P♀; U, large C♀. Scales: A–F, I, U = 0.1 mm; B–E, G–H, J–T = 0.2 mm.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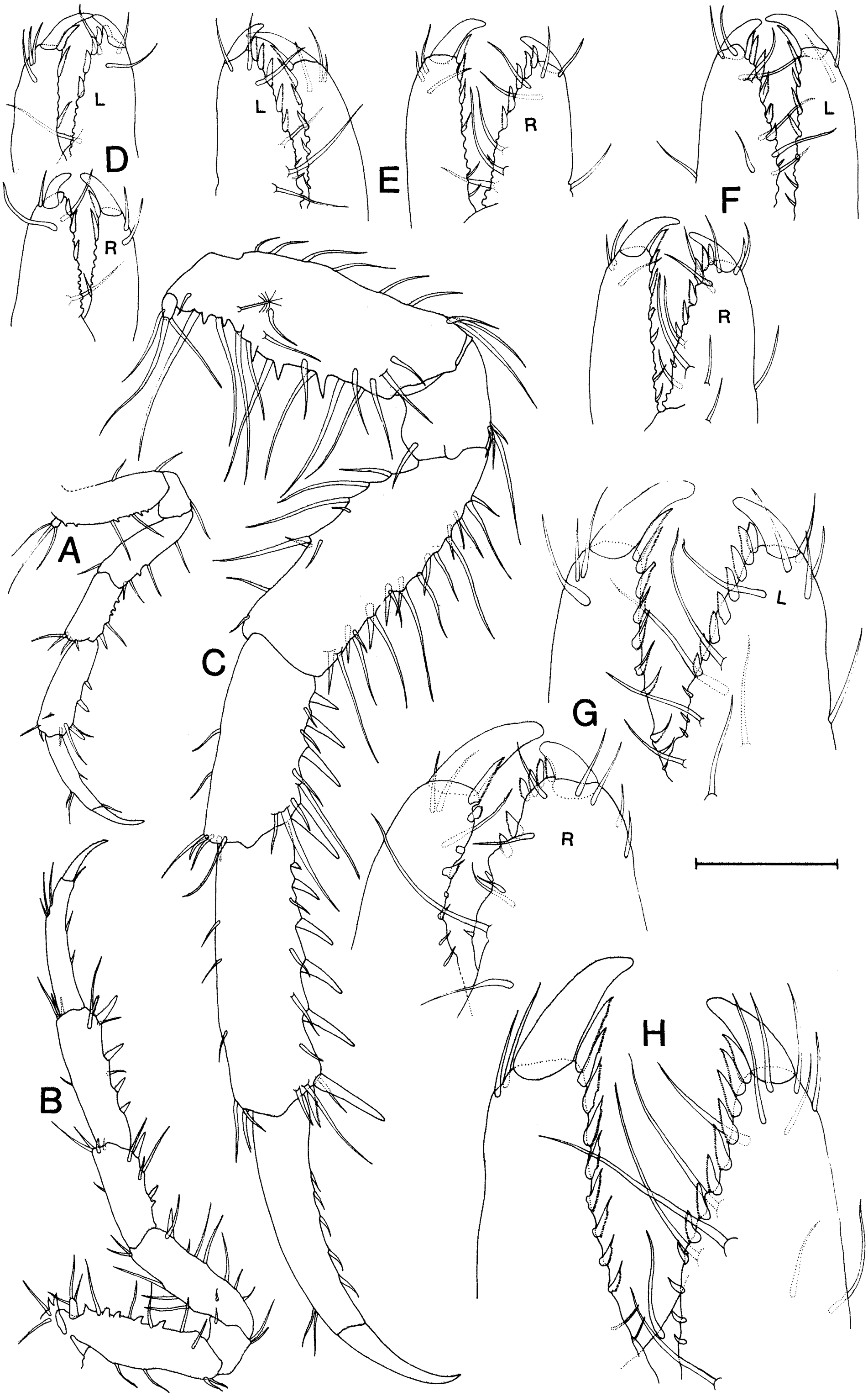
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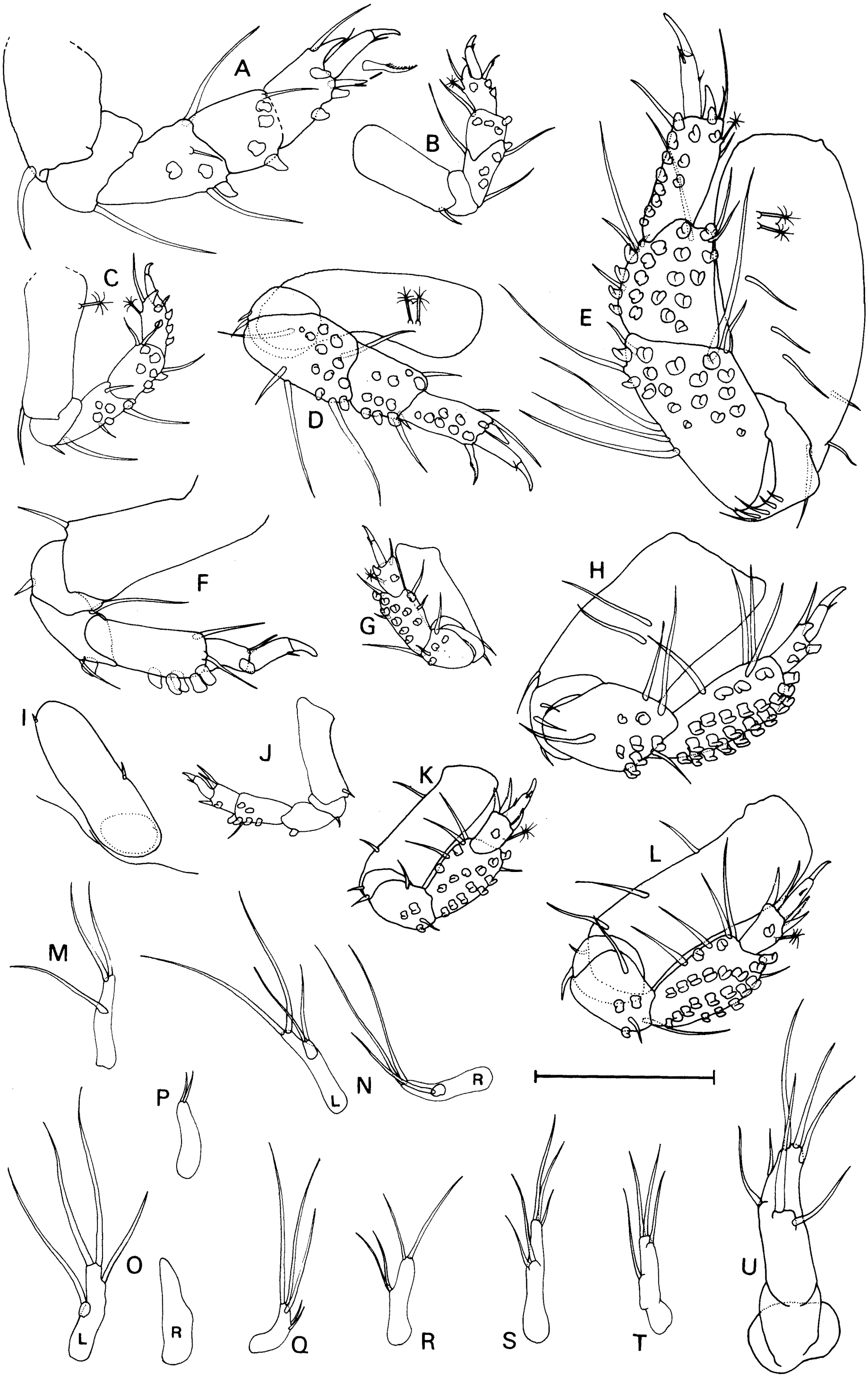
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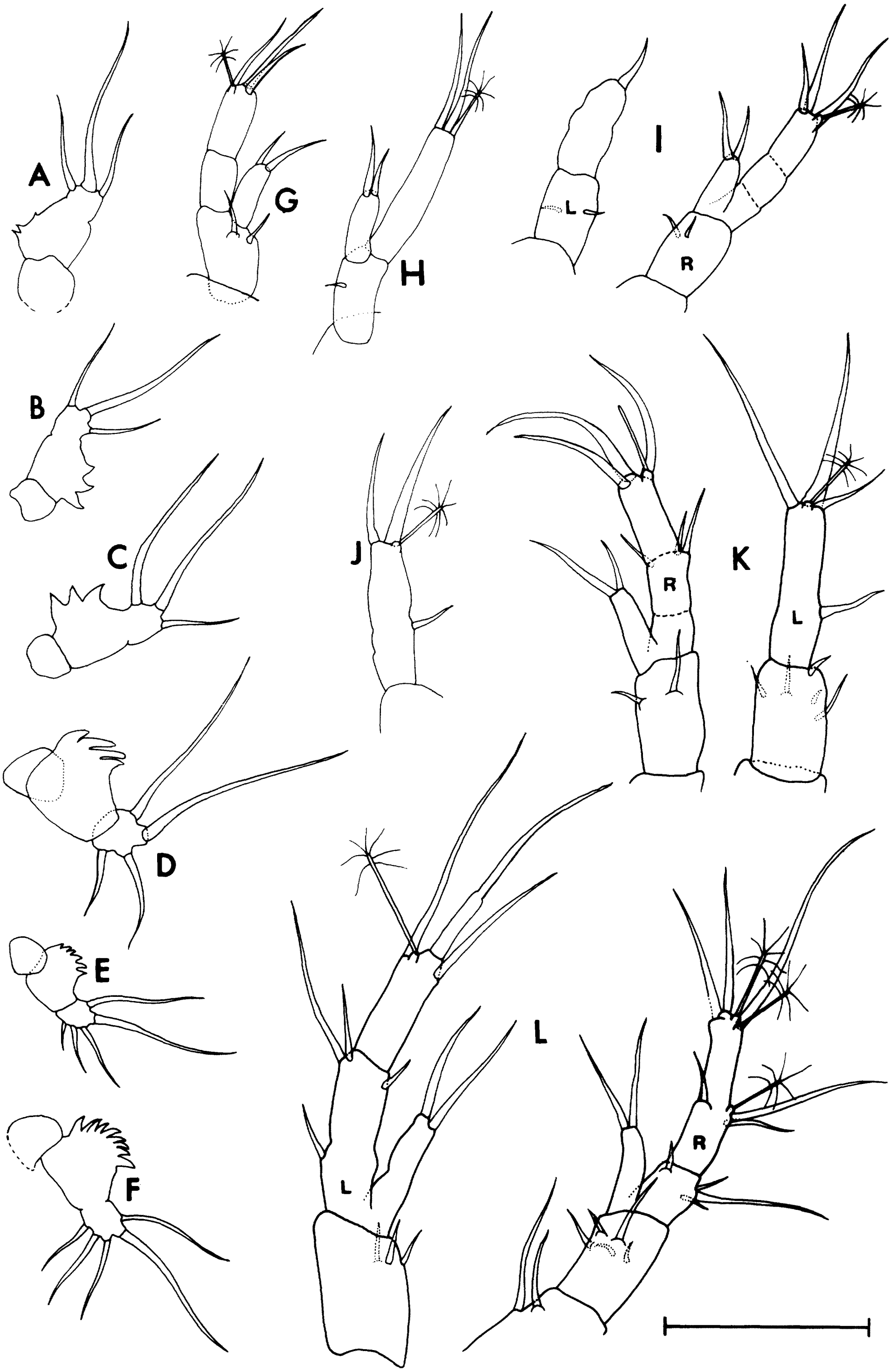
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tunately, the next exuviae was too badly damaged to determine presence or absence of rudimentary oostegites. Subsequently, the specimen passed through two successive preparatory female instars and then a copulatory instar. The badly damaged exuviae probably represented either a third juvenile or what I call an incomplete preparatory female instar.

Incomplete Preparatory Female (P♀i).—Eight specimens. Length range of field-collected specimens 2.1–2.7 mm. This stage is characterized by very small, knob-like, rudimentary oostegites that often appear only on thoracopods VI. The full complement of oostegites is usually not present. The small number of field-collected specimens of this instar suggests that it is either an aberrant form or is passed through very rapidly. This is not a matter of specimens being preserved before the oostegites can expand during an intermolt period, as happens with *Heterotanais oerstedii,* because exuviae of some laboratory-reared animals bear oostegites in this condition. In fact, laboratory-reared specimens bear such oostegites more commonly than expected from the field-collected data. Moreover, the duration of this incomplete preparatory instar is not especially shorter than that of normal preparatory female instars, reducing the likelihood that this instar is passed through rapidly in nature. It is possible that the developmental sequence observed in the laboratory is not a completely accurate reflection of events in nature, however.

These P♀i never give rise directly to copulatory females. One or two typical preparatory instars always intervene.

Preparatory Females (P♀).—100 specimens. Chiefly 2.5–3.6 mm long, range 2.2–4.4 mm (Fig. 10). The anterior three pairs of rudimentary oostegites are short. On thoracopods III, they are usually more than half the length of the basis but are occasionally much shorter. On thoracopods IV and V, they are about as long as or slightly longer than the basis, which is much shorter on these appendages than on thoracopod III (Figs. 5, 6). The rudimentary oostegites on thoracopods VI are the largest and last; they may be flattened or inflated and are often more than twice the length of the basis.

Before the initial copulatory stage, laboratory-reared animals usually passed through two preparatory instars. One specimen, however, passed from a juvenile instar through a P♀i instar and one normal P♀ instar, followed by a copulatory instar. Between successive copulatory instars, a preparatory stage of one or two instars occurs. There is usually little or no increase in oostegal size between two such successive instars, although some enlargement is occasionally observed.

The field-collected data suggest that only a single preparatory instar normally separates successive copulatory stages. If two preparatory instars occurred for every copulatory stage, far more preparatory specimens should have been collected. Intermolt periods observed in the laboratory do not indicate that preparatory instars are passed through much more rapidly than copulatory instars (Fig. 12). Although rearing compartments were occupied for the most part by a female

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Fig. 7. *Pagurapseudes largoensis.* A–F, chelipedal exopod. A, M1; B, M2; C, first post-M2 ♂; D, second post-M2 ♂; E, same, another specimen; F, large C♀. G–M, uropods. G, M1, left, dorsal view; H, M2, right, dorsal view; I, M2, left (deformed) and right, dorsal view; J, first post-M2 ♂ (same specimen as I), left (deformed); K, second post-M2 ♂ (same specimen as I and J), left (deformed) and right, dorsal view; L, P♀, left, dorsal view; M, large C♀, right, dorsal view. Scales: A–D, G–L = 0.1 mm. E, F, M = 0.2 mm.

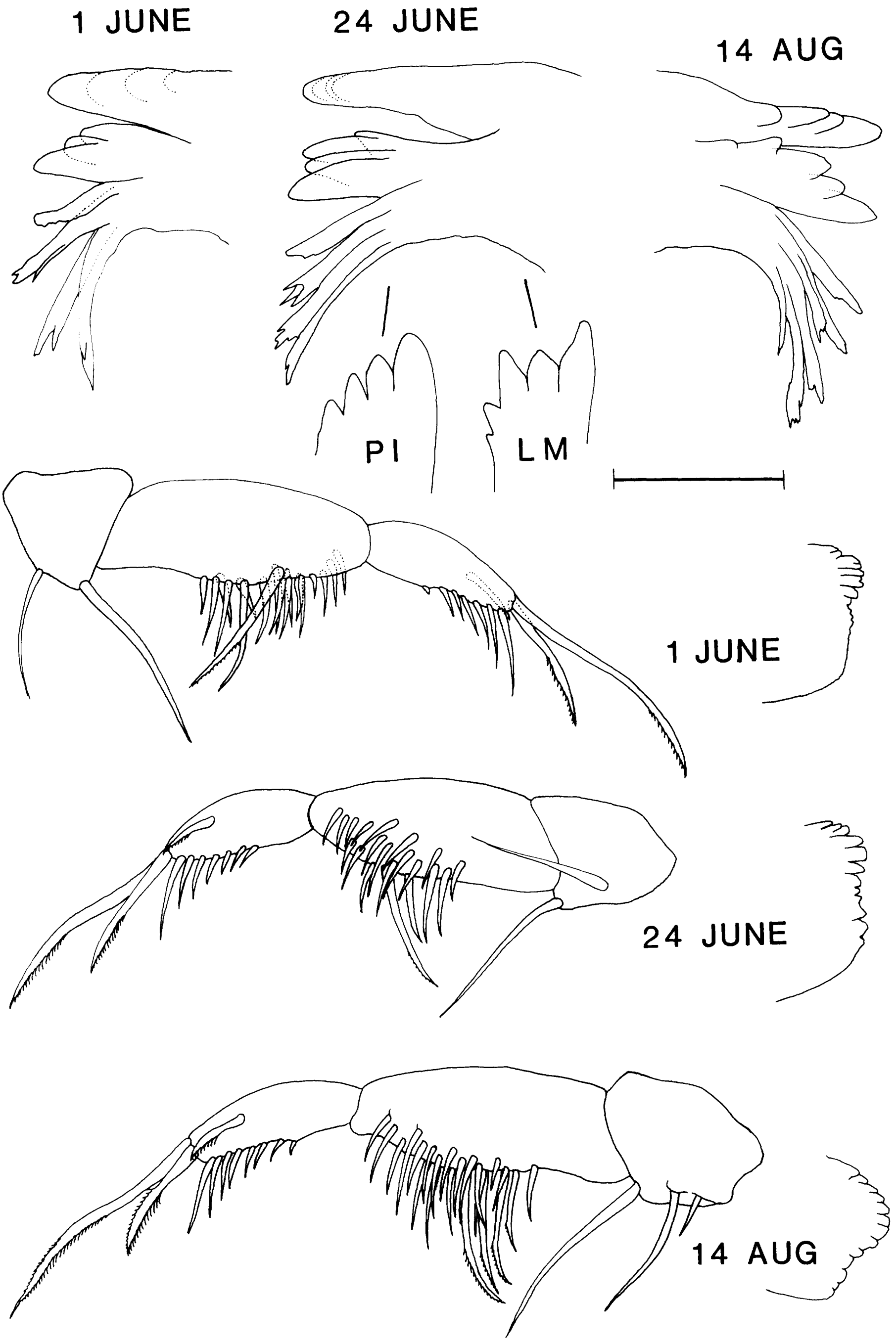

Fig. 8. *Pagurapseudes largoensis*. Growth variations in left mandible of a large male. Top, pars incisiva (PI = distal blade of pars incisiva, LM = lacinia mobilis). Lower left, mandibular palp. Lower right, molar process. Scales: palp = 0.1 mm; pars incisiva and molar process = 0.05 mm.

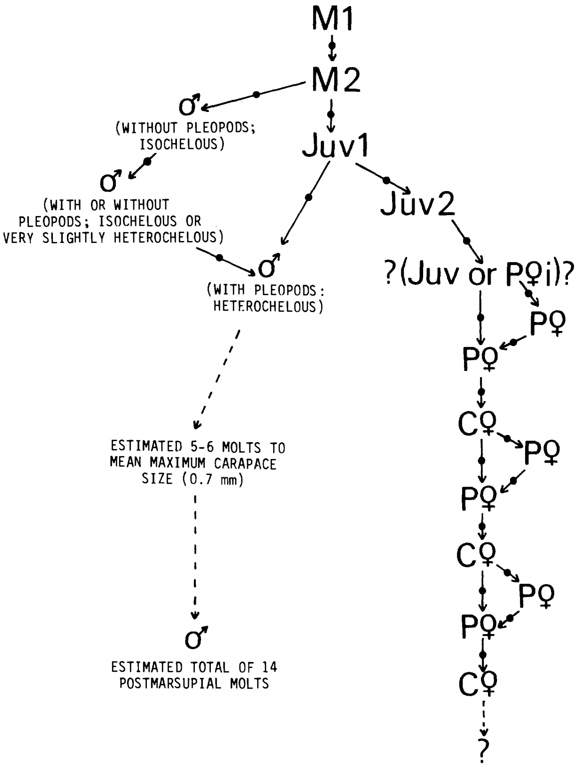

Fig. 9. Proposed life history for *Pagurapseudes largoensis* McSweeny. M = manca, Juv = juvenile, P♀i = incomplete preparatory female, P♀ = preparatory female, C♀ = copulatory female. Each solid arrow with a solid circle represents a single molt.

and an apparently mature male, it is not known if the males possessed mature sperm or were capable of fertilization at all times. Alternatively, less than optimal laboratory conditions may have caused the ovaries to ripen at a slower pace, perhaps necessitating two preparatory instars.

The mature ovaries extend further back into the pleon in *Pagurapseudes* than in other tanaidacean genera for which ovarian placement is known. As a result, the pleon of preparatory females is swollen and is usually longer than in other stages. As mentioned above, pleopods probably appear in the first copulatory instar and persist in preparatory instars thereafter. The great length variation in field-collected preparatory females lacking pleopods may be due to variations in pleonal length. Because of this and because not all copulatory females were examined for pleopods, I hesitate to use the presence of pleopods to differentiate intercopulatory from precopulatory specimens bearing rudimentary oostegites. I have, for the same reasons, chosen not to use Gardiner's (1975a) term "intermediate female" for intercopulatory instars, although such a designation would become perfectly useful if such instars could be distinguished.

Because of pleonal elongation in this stage, the carapace may account for as little as 0.17 per cent of body length, although it usually accounts for 0.19–0.23.

Copulatory Females (C♀). — 140 specimens. Ninety per cent of field-collected specimens are 2.5–3.4 mm long; size range 2.2–4.2 mm (Fig. 10). All specimens possess

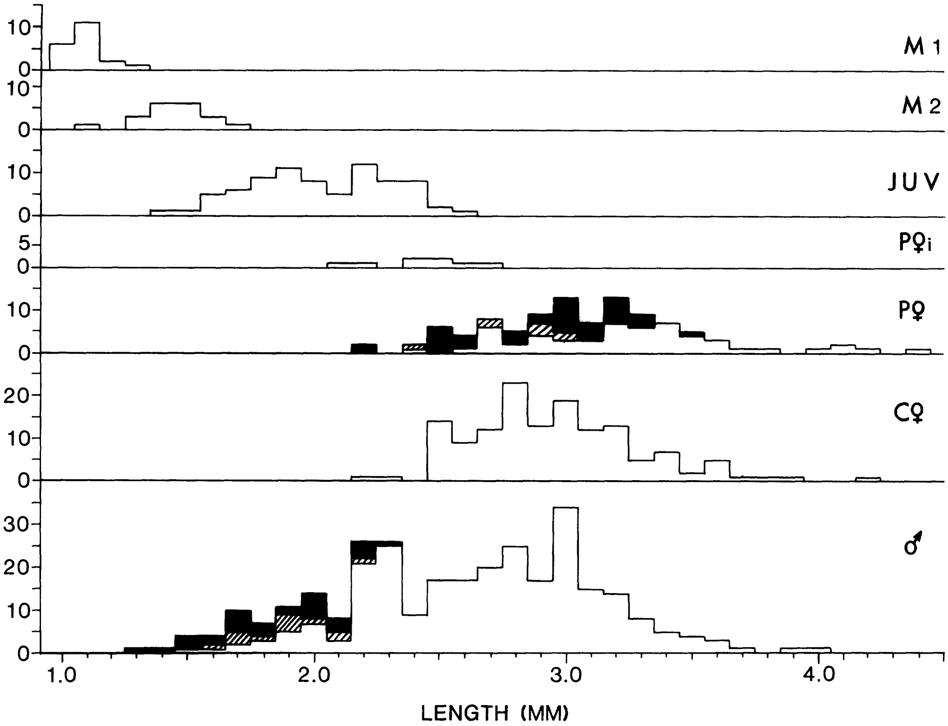

Fig. 10. Number of specimens of *Pagurapseudes largoensis* of all stages collected in the field from July 1977 to September 1978. Under preparatory females (P♀), black areas represent specimens lacking pleopods; hatched areas represent specimens for which presence or absence of pleopods is unknown. Under males, black areas represent isochelous specimens and hatched areas represent specimens lacking the right cheliped. Abbreviations as in Fig. 9.

a completely formed marsupium in which the oostegites fuse together and which is not discarded until the next molt. The large posterior pair of oostegites borne on thoracopods VI form a baglike hind portion which extends posteriorly to the middle of the pleon and curls to conform to the interior of the occupied gastropod shell. This pair of oostegites remains separated posterodorsally, leaving an open slit in the marsupium through which the mancas apparently escape.

In the laboratory, one female passed through three copulatory instars, each separated by a single P♀. Broods of 10 and 12 mancas were produced in the first and third instar, respectively. The second C♀ had a complete marsupium but produced no offspring. There is no reason to doubt that females breed at least three times in the field, particularly if only a single P♀ instar intervenes each time. After spawning, laboratory-maintained females either molted within two days or died. Those that did not molt became sluggish, covered with epiphytes, and lost both chelipeds before dying. Whether these deaths were normal or premature is unknown.

The precise method of release of mancas is still uncertain. If the M1 escape through the rear slit in the marsupium before the mother either molts or changes shells, they may become trapped for a time in the shell spire. While extracting live animals from shells, a manca was more than once observed to leave a shell that had just been vacated by a mature specimen. When the female extends from

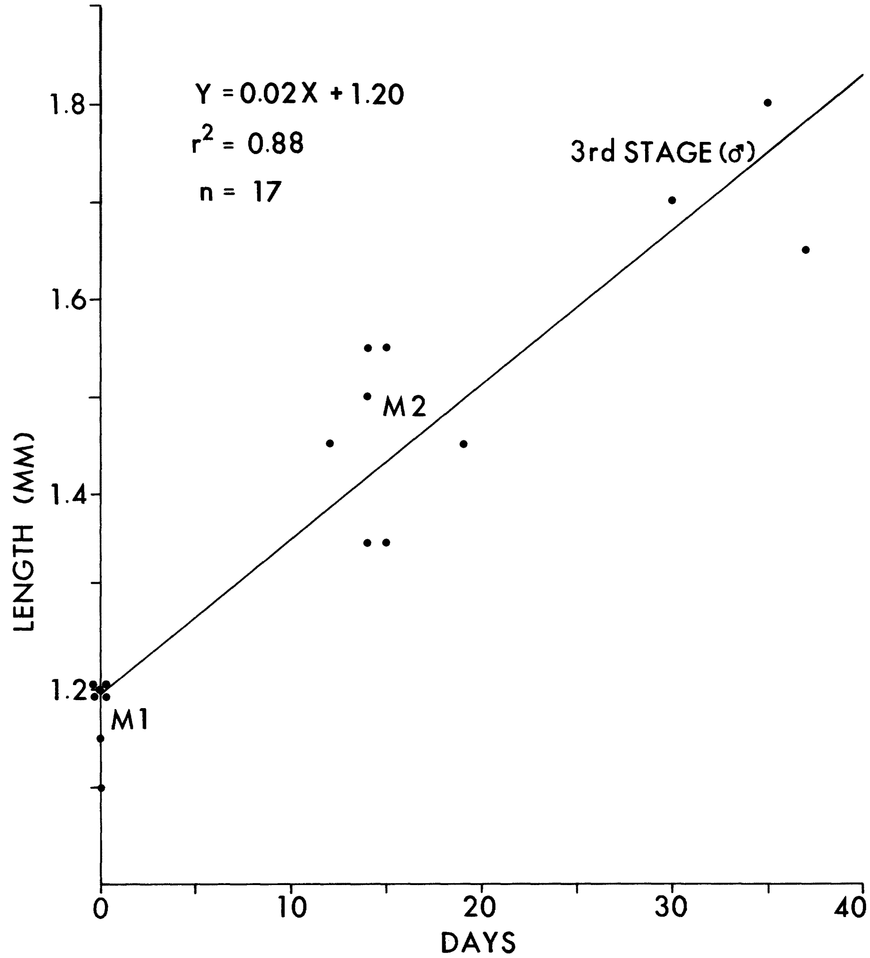

Fig. 11. Growth of first three instars of *Pagurapseudes largoensis* determined from laboratory-reared specimens. Regression of body length in mm (Y) on intermolt period in days (X).

the shell during normal climbing and orientation activities, however, enough room appears to exist for the mancas to escape around her body. On one occasion, three M1 were found alive in the marsupium of a recently cast exuviae.

Setation and spination continue to increase slowly through P♀ and C♀ instars. Figure 3K, L, Q, R, and S shows that mandibular incisive spines and molar processes remain variable even after the animals reach a large size. Figures 1C, E, I, 3C, L, S, 4C, F, I, 5C, H, 6E, H, L, U, 7F and M illustrate the appendages of a particularly large C♀ (approximately 4.4 mm) collected separately from specimens in Fig. 10. With the exception of a few very large, old males, this ornamentation approaches the maximum observed. This stage is always isochelous.

Males (♂).—251 specimens. Ninety-five per cent are 1.5–3.3 mm long; the shortest identifiable male is 1.3 mm and the longest 4.0 mm. The smallest males develop directly from M2; they are isochelous, lack pleopods, have low but usually distinct genital cones, and are less than 2.0 mm long. The following instar may bear or

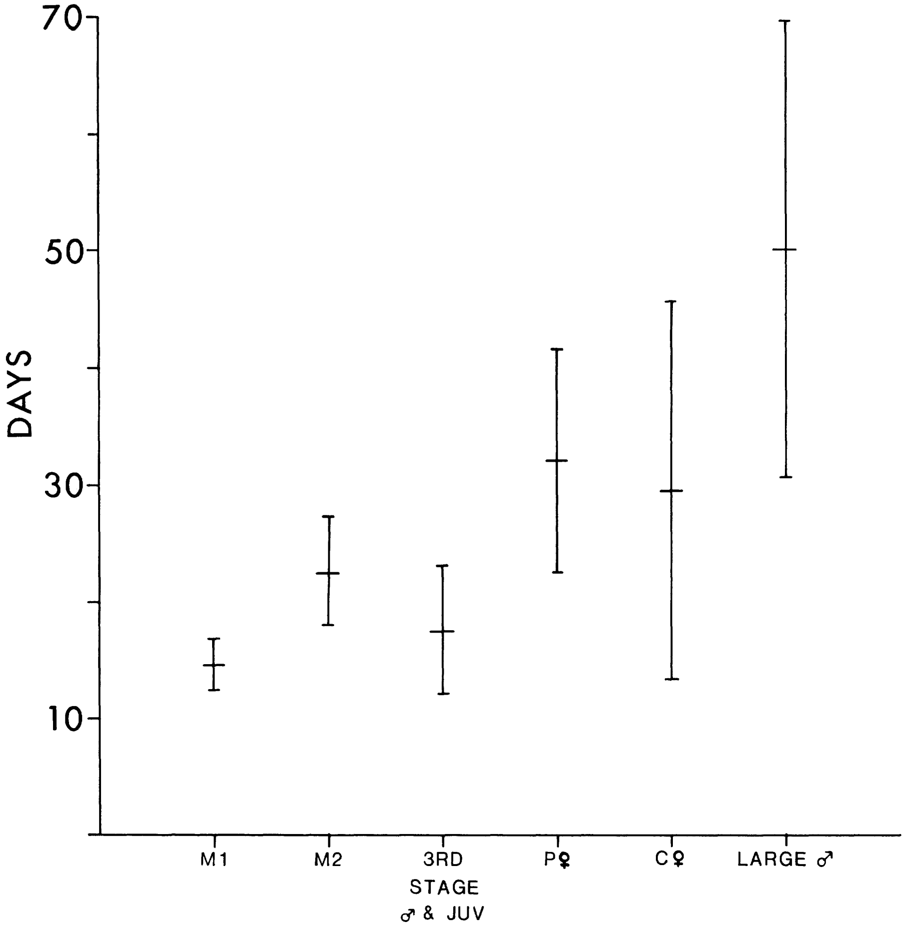

Fig. 12. Relative intermolt periods for different growth stages of *Pagurapseudes largoensis.*

lack pleopods and be isochelous or very slightly heterochelous. In Fig. 10, specimens showing such very slight heterochely are included with the isochelous specimens because differently oriented chelae may appear slightly heterochelous. The third instar following M2 bears pleopods and exhibits definite heterochely.

As mentioned earlier, the first juvenile instar following M2 may also develop into a male. In such cases, the resulting male bears pleopods and distinct heterochelae (Fig. 9). One individual that developed from the M2 and subsequently became a well-defined male, possessed, in the first postmanca instar, extremely weak, almost indistinguishable, male gonopore rudiments.

In subsequent molts, meristic and morphometric changes generally parallel those of females. The primary differences involve the pleopods, pleon, and chelipeds. The pleopods have already been discussed. However, a single specimen with two pairs of pleopods, one on each of the first two pleonites was discovered in the field-collected material. The second pair (Fig. 60) is asymmetric; the right pleopod lacks both setae and an exopod; the left is similar to the first pair.

The pleon in fully grown males is usually much shorter relative to the carapace + pereion length than in other stages; in such males the pleon length/carapace +

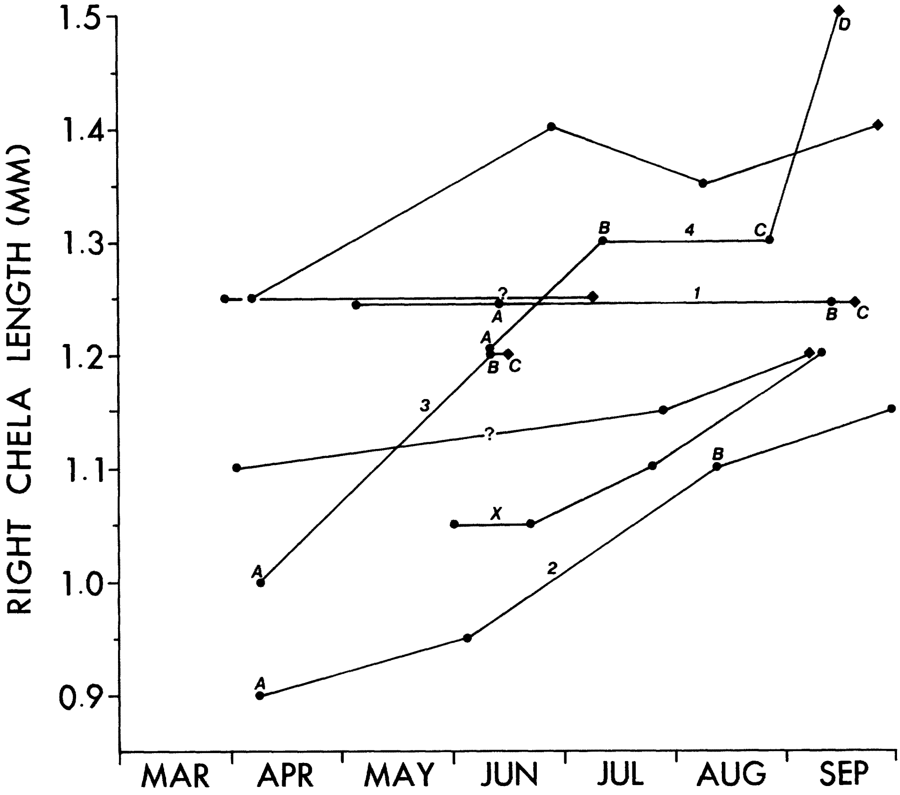

Fig. 13. Growth of major chela in eight large male specimens of *Pagurapseudes largoensis* maintained in the laboratory through several instars. Chelar measurement is the greatest length from the carpo-propodal articulation to the tip of the fixed finger. Solid circles represent molts. Diamonds represent dead specimens. Numbers referring to specimens and letters indicating specific exuviae or dead specimens (with the exception of X, discussed in the text) correspond with those in Fig. 14. Question marks indicate a possible molt, usually evidenced by a very small exoskeletal fragment found in the rearing compartment.

pereion length ratio ranges chiefly from 0.25–0.33 and may be as little as 0.19. In preparatory females, it is usually 0.30 or more and sometimes exceeds 0.40. Considerable overlap exists, however, as does the possibility that the elongate pleon in some males may be due to maturing but eventually abortive oocytes. At least some of the variation in pleon lengths among males is due to complete extension versus overlap of pleonites.

In *Pagurapseudes largoensis,* the males alone are heterochelous and the right chela is always the major one. Growth of the major chela is gradual and apparently continues throughout the life of the animal (Fig. 13). In large, old males, the propodus is extremely big and swollen and reaches 30–40% of the total body length. Allometric growth of the major chela is discussed below.

Growth

Because of damage to and distortion of exuviae, particularly those of older stages, in many cases accurate length measurements could not be made. The following discussion of growth rates centers therefore on the first few instars. Mean

Table 1. Percentage increase in length through first three instars in *Pagurapseudes largoensis* determined from the equation $[(L_2 - L_1)/L_1 \cdot 100\%]$ where L_1 and L_2 are body lengths in mm of successive exuviae.

M1 – M2	M2 – 3rd instar
34.8	16.1
12.5	25.9
29.2	–
25.0	–
20.8	–
20.8	13.8
22.7	–
–	21.4
$N = 7$	4
$\bar{x} = 23.7$	19.3
$s = 7.05$	5.43

body length of field-collected specimens and of exuviae of laboratory-reared specimens are similar: 1.10 + 0.08 mm and 1.18 + 0.04 mm for M1 and 1.45 + 0.14 mm and 1.45 + 0.08 mm for M2, respectively (Figs. 10, 11). Mean body length of the subsequent exuviae of laboratory-reared animals is 1.71 + 0.06. For individuals (two exuviae and one dead specimen) definitely assigned to the fourth instar (Juv2 or second male instar), the lengths are 1.80, 1.95, and 2.10 mm. I did not distinguish between the two juvenile instars or among male instars when measuring field-collected specimens. Although the length data for field-caught juveniles in Fig. 10 is bimodal, the lengths of the laboratory-reared fourth instar specimens suggest that some juveniles contributing to the first peak (1.6–2.0 mm) are second instar juveniles (Juv2). Thus, mean length of field-caught Juvl is probably less than the mean of the first peak (1.83 mm) and approaches that of laboratory-reared Juv1. Males and juveniles can be discussed together in this context because no significant morphometric dimorphism in dimensions of tagmata occurs at these stages.

For the first three instars (M1 to first postmanca), a linear regression of body length on intermolt period gives the equation $Y = 0.02X + 1.2$ (coefficient of determination, $r^2 = 0.88$, $F = 4.00$, 16 *d.f.*, $P < 0.05$) (Fig. 11). The date of spawning is not known for some of the specimens and the day on which the M1 molted was taken as the starting point.

In one brood in which the spawning date was known to within two days, the first postmarsupial molt (M1 to M2) occurred in two to three weeks. In another brood, the three surviving M1 molted in 13 days. In a third, all 11 M1 died in 16 or fewer days without molting. In a fourth, only one of eight M1 had molted in the first month. Percentage increase in body length through the first three postmarsupial instars is shown in Table 1. The difference between the means is not significant.

Intermolt period increases in both duration and variability with age (Fig. 12). Although lengthening of intermolt period with age is well known in crustaceans (Passano, 1960), the minimum period is similar in all stages in *Pagurapseudes largoensis* (11 to about 19 days). Whether the extremely long intermolt periods obtained for some laboratory-maintained P♀, C♀, and large males, that is, greater than 1.5–2.0 months, accurately reflect events in nature is unknown. An intervening exuviae may have been consumed or lost in at least some of the lengthier cases.

Figure 13 shows growth through several instars of the major chela of eight large

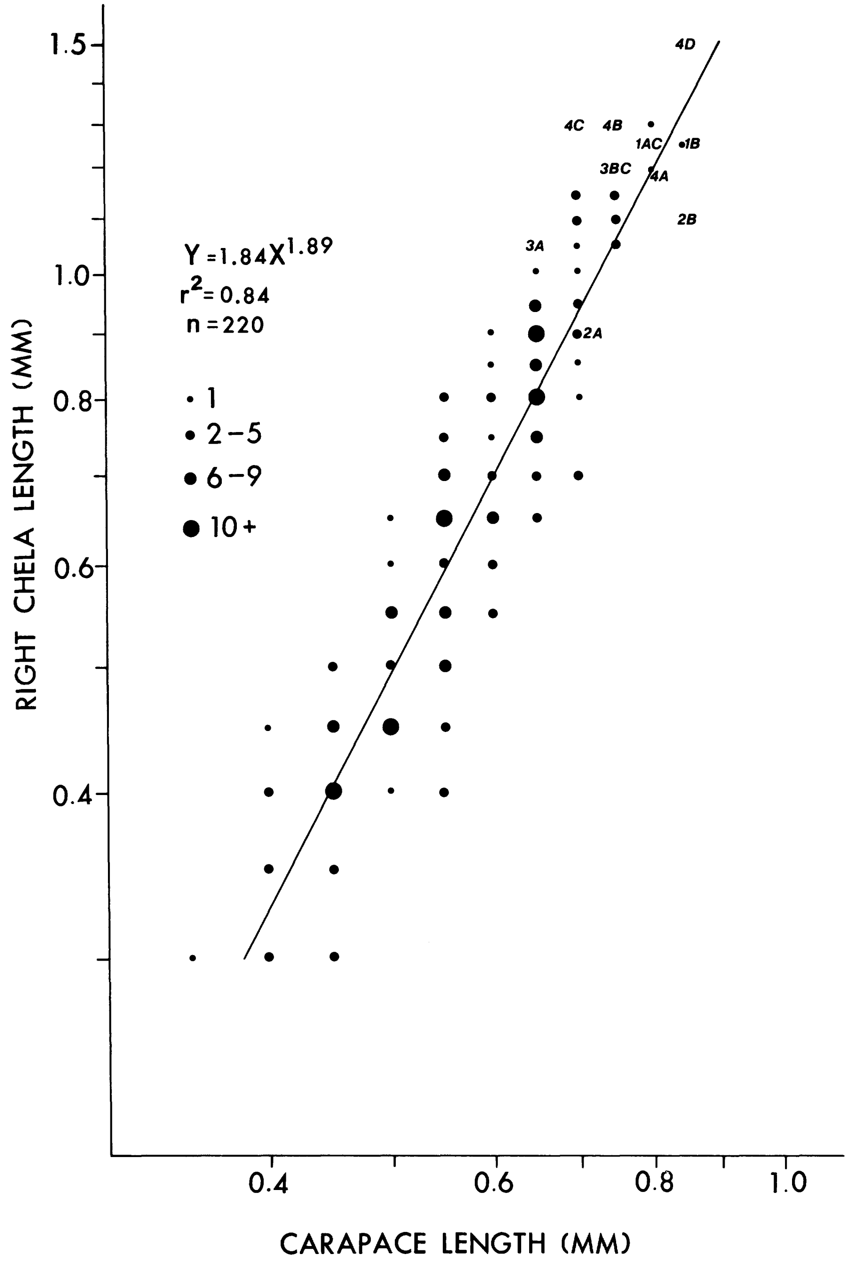

Fig. 14. Regression (log scales) of major chelar length in mm (Y) on carapace length in mm (X). A fitted power curve describes the relationship. Number-letter combinations correspond to those in Fig. 13 and the points that they represent are not included in the calculation of the curve.

males maintained in the laboratory. Measurements represent the greatest length of the propodus from the carpopropodal articulation to the tip of the fixed finger. Several points are of interest here. Two specimens reached chelar lengths (1.35–1.50 mm) greater than found in any field-collected specimen (maximum 1.30 mm; Fig. 14). The specimens with the next largest chelae (1.25 mm) approached the maximum for field-collected specimens, but their major chelae did not increase in length through two to four instars. Carapace length of these specimens could not be determined in many instances due to breakage or loss. Exuviae for which both carapace and chelar lengths were determined are shown as number-letter combinations in Figs. 13 and 14. In some instars, carapace length apparently decreased slightly. Although no breakage was noted in these cases, distortion may have gone unobserved. Points derived from exuviae in Fig. 14 were not included in determination of the regression curve.

The relationship between carapace and major chelar length in male *Pagurapseudes largoensis* is allometric (Fig. 14). Carapace length was chosen as the independent, or reference variable because it could be measured more accurately and was not as variable nor subject to as much distortion as total body length.

A power function was fitted to the fitted least squares regression of major chelar length on carapace length to give the equation $Y = 1.84X^{1.89}$ (coefficient of determination, $r^2 = 0.84$, $t = 0.05$, 218 *d.f.*, $P < 0.05$). Although the fitted power function describes the relationship reasonably well [$P(1.79 \leq B \leq 1.99) = 0.95$], considerable variation in chelar length still exists for any given carapace length, particularly in the middle of the range. Thus, the major chela length of a specimen with carapace length of 0.70 may vary between 0.70 and 1.15 mm. Some variation may be due to regenerating chelae, although laboratory-maintained males never autotomized or otherwise lost appendages.

Variations in carapace length at which heterochely initially appeared coupled with the variability of chelar length for any given carapace length prohibited the recognition of discontinuous regressions representing two or more distinct phases of relative growth similar to those figured by Teissier (1960) and Hartnoll (1978).

Sex Ratio

For the 499 field-collected specimens 2.1 mm or longer (this being the length of the shortest identifiable P♀), the ratio of males to females (both P♀ and C♀) is almost exactly 1:1 (251:248). It is possible that males achieve sexual maturity before reaching 2.1 mm but the maturation molt has not been identified. External male gonopores appear by the second and sometimes the first post-M2 molt (see Life History above) but gonadal development has not been investigated. Even if the smaller males, an additional 52 specimens, are included, the sex ratio only becomes 1.22:1. The ratio could again be balanced by inclusion of juveniles, most of which become females.

Estimated Longevity

When the initial series of rearing experiments was terminated at the end of November 1977, two specimens, a male and a female that were mature when collected in mid-March 1977, were still alive. The female molted twice during this time. The first exuviae was too damaged to identify to stage but was probably a P♀ because the next exuviae, cast 33 days later, bore an empty marsupium. The mean duration of the copulatory instar is 32 days (Fig. 12).

The surviving male molted five times at intervals of 50, 20, 31, and 51 days. The major chela of the first exuviae, although too damaged to measure precisely, was about 1.0 mm long. This chela continued to enlarge during subsequent molt cycles, reaching 1.2 mm by September (X in Fig. 13). Males may thus live at least 7.5 months after reaching a large size.

A young male spawned in the laboratory passed through seven instars in 5.5 months. The seventh exuviae had a carapace length of 0.65 mm and a major chelar length of 0.70 mm, approximately halfway up the curve in Fig. 14. Judging from the growth of chelae shown in Figs. 13 and 14, the specimen would probably have to pass through two more instars before its major chela reached 1.0 mm. Because the intermolt periods for the fifth through seven instars of this and another specimen have a mean of 32 days, the intermolt periods of the next two instars are assumed to be less than the 50 day mean for old, large specimens bearing major chelae longer than 1.0 mm. Using the 32-day mean as a minimum intermolt period for the next two instars, I estimate that a male will reach a carapace length of 0.70–0.75 mm and a major chelar length of about 1.0 mm 7.5 months after release from the marsupium and after passing through about nine postmarsupial instars (including M1 and M2).

Intermolt duration subsequently increases (Figs. 12, 13). As mentioned above, males of this size may lie at least an additional 7.5 months and pass through five more instars. Males may thus live up to 15 months and pass through about 14 instars under suitable laboratory conditions. One or more intermolt periods of two or more months each would, of course, increase this estimate.

The estimated longevity of females is less. Several assumptions must made here, because no individual was reared from M1 beyond the first copulatory stage and because the number of instars appears to be variable. These assumptions are: a two week period from spawning to the first postmarsupial molt (see Growth above); two Juv instars; two P♀ instars before the first copulatory stage but only one between successive broods; three C♀ stages (the maximum recorded in the laboratory) and intermolt periods for the first two P♀ instars of 25 days each. This latter figure is the median between the means for the Juv2 intermolt (17.6 days) and the C♀ intermolt (32.1 days). Though arbitrary, it suffices for this very broad estimate of longevity. Using mean intermolt periods shown in Fig. 12, an estimated nine month lifespan results. Two P♀ instars between successive broods and more than three breeding cycles would increase this estimate by about one month per additional instar. If, on the other hand, the shorter intermolt periods recorded in the laboratory represent events in nature more accurately, then the female lifespan would probably be closer to seven months and that of the male between nine and ten months.

Fecundity

Fecundity was defined as the total offspring spawned per brood per female and was measured by counting all eggs, developing embryos, and unreleased mancas in each marsupium. Figure 15 shows the relationship between fecundity and maternal (C♀) body length. Specimens were preserved in ethanol and could therefore not be weighed accurately. Although specimens in which the marsupium was obviously not full were not included (Bückle-Ramirez observed loss of undersized eggs from the marsupium in *H. oerstedii*), variation in fecundity for any given maternal length was so great that no regression line or curve could reliably be fitted to the data. There is, however, a general increase in fecundity with increasing maternal length. The number of eggs, embryos, and unreleased mancas ranges from 4–17 per marsupium; generally 9 or fewer in females shorter than 3.0 mm, 9 or more in females longer than 3.0 mm, and 12 or more in females 3.5 mm or longer.

Because body length measurements were subject to some inaccuracy, and because pleonal length alone varied considerably, the relationship between fecundity and carapace length was also investigated. Variation at any given length was similarly large. The possibility that interior configuration of the occupied shell may affect the number of eggs deposited was not investigated.

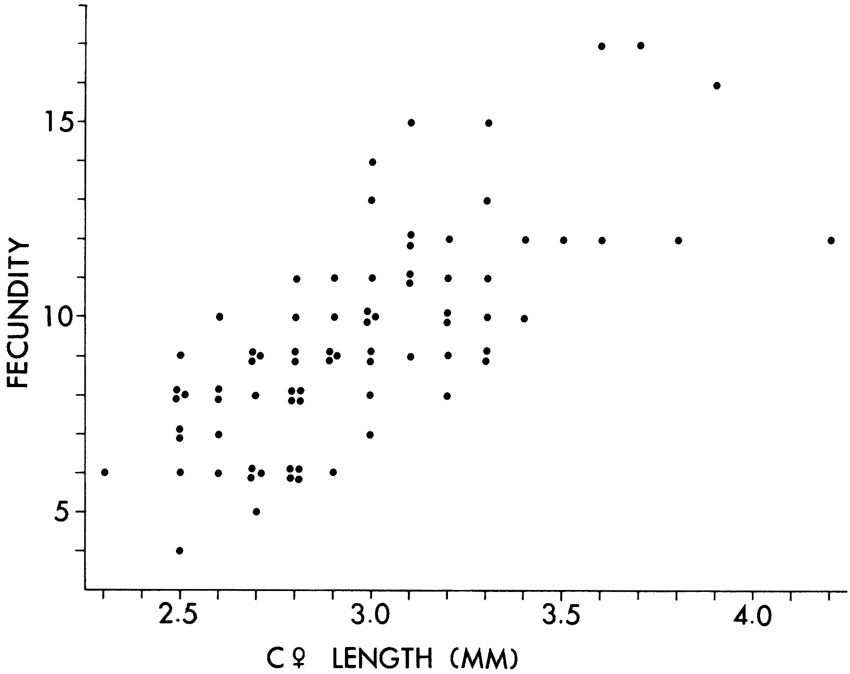

Fig. 15. Fecundity, defined as the number of eggs, developing embryos, or unreleased mancas per marsupium per C♀, plotted against C♀ body length in mm. Individuals in which the marsupium was obviously not full have been omitted.

DISCUSSION

The developmental pattern of *Pagurapseudes largoensis* differs in several important respects from that established for *Heterotanais oerstedii* and *Neotanais micromopher. P. largoensis* is exclusively gonochoristic and no evidence for protogyny exists. Males retain functional mouthparts and continue to molt throughout their lives. Disregarding protogynous aspects, differences remain between the gonochoristic portion of the tanaidomorphan and neotanaidomorphan patterns—the "normal type" of Bückle-Ramirez (1965) and Sieg (1972, 1973, 1978)—and the pattern exhibited by *P. largoensis.* The latter exhibits greater variability, which may reflect a more primitive condition and thus agrees with the concept that the Apseudomorpha have diverged less from the theoretical ancestral tanaidacean than have the other suborders (Lang, 1956a; Gardiner, 1975a; Sieg, 1980).

Female *P. largoensis* pass through two or possibly sometimes three juvenile instars between the M2 and first preparatory instar. *Heterotanais oerstedii* and *Neotanais micromopher,* in contrast, pass through only one. *P. largoensis* passes through two P♀ instars before the first copulatory stage and either one or two between successive copulatory stages. When two P♀ instars occur in laboratory-reared specimens, the successive exuviae often exhibit no enlargement of rudimentary oostegites.

The incomplete preparatory females (P♀i) probably represent a minor developmental abnormality; only eight out of 580 field-collected specimens were of this form. Developmental anomalies have also been reported for *Heterotanais oerstedii.* Jazdzewski (1969) found specimens of this species with chelipeds intermediate between normal male and female forms, with a male carapace and

Table 2. Minimum and maximum intermolt periods recorded for *Heterotanais oerstedii* (Krøyer) reared in the laboratory at 22–23.5°C. Dashes indicate molts. Data from Bückle-Ramirez (1965: 756, Table 3).

Intermolt	Bückle-Ramirez's nomenclature	Duration (days)
M1—M2	(St. II—III)	4–5
M2—Juv	(St. III—NI)	10–15
Juv—P♀	(NI—♀ oo Oos)	7–28
P♀—C♀	(♀ oo Oos—♀ oo M)	14.33
C♀—P♀	(♀ oo M, ♀ oo M, ♀LM, ♀ML–♀ oo Oos)*	22.46

* These five symbols indicate a C♀ with eggs still in the ovary, C♀ with eggs in the marsupium, C♀ with larvae in the marsupium, C♀ with an empty marsupium (mancas released), and a P♀. No molt occurs between any of the first four and the times indicated for each by Bückle-Ramirez have been summed.

female chelipeds and with one male and one female cheliped. He discounted the possibility that these represented transitional forms.

In *H. oerstedii,* one P♀ instar occurs before and after the first C♀. In *N. micromopher,* the two proposed P♀ that occur before the initial C♀ are distinguishable by oostegal size. Gardiner (1975a) suggested that a single instar with rudimentary oostegites, an intermediate female, occurs between copulatory stages. The appearance of two P♀ instars in both *N. micromopher* and *P. largoensis,* one in *Heterotanais,* and three in *Tanais* supports the idea that the neotanaids have diverged least from the Apseudomorpha relative to other tanaidaceans (Lang, 1956a; Lauterbach, 1970; Gardiner, 1975a; Sieg, 1976, 1980).

Pagurapseudes largoensis passes through up to three C♀ stages in the laboratory. Specimens of *H. oerstedii* maintained in isolation in the laboratory passed through an equal number, although they resorbed their eggs and produced no offspring (Bückle-Ramirez, 1965: 757–758). Laboratory animals that were fertilized and produced offspring often turned into secondary males, although Bückle-Ramirez concluded that gonochoristic females could produce several broods per summer in the field. Overwintering females often bred the following spring as well. Gardiner (1975a) indicated that *N. micromopher* probably produces more than one brood.

Male *P. largoensis* develop either directly from the M2 or from the Juv1 instar. In the former case, the first postmanca male instar bears gonopores or gonopore rudiments, is isochelous, and lacks pleopods. Pleopods and a slightly enlarged right chela appear after one or two additional molts. Males that arise from the Juv1 instar are heterochelous and bear pleopods. Because gonadal maturation was not investigated, I cannot say which male instars should properly be called preparatory and which copulatory. Likewise, because males molt repeatedly, feed, and live for relatively long periods, they may not be continuously fertile. Thus all supposedly mature male instars may not correctly be called copulatory.

In both *H. oerstedii* and *N. micromopher,* the primary gonochoristic male instar follows one juvenile and one preparatory male instar, the latter retaining an essentially juvenile external morphology. Both primary gonochoristic and secondary protogynous copulatory males (C♂) of these two species exhibit strong sexual dimorphism that includes reduced mouthparts; they do not feed and they die without molting. The fate of male Tanaidae is less clear because, although protogyny occurs, males retain a full complement of mouthparts.

Mature, laboratory-maintained female (P♀ and C♀) *P. largoensis* molt an average of once a month and large males an average of every seven weeks. Mancas and juveniles molt more frequently, every two or three weeks. This study was carried

Table 3. Fecundity measured as number of eggs, embryos, or unreleased mancas 1 per marsupium for several tanaidacean species.

Species	SOURCE	NUMBER
APSEUDOMORPHA		
Apseudidae Sars		
Apseudes latreillei Milne Edwards	Salvat, 1967	60
Metapseudidae Lang		
Metapseudes aucklandiae Stephensen	Gardiner, 1973a	9
Synapseudes idios Gardiner	Gardiner, 1973a	5–11
Cyclopoapseudes dicenon Gardiner	Gardiner, 1973a	6, 10
Pagurapseudidae Lang		
Pagurapseudes bouryi Bouvier	Bouvier, 1981	7
P. largoensis McSweeny	This study	4–17
Cirratodactylidae Gardiner		
Cirratodactylus floridensis Gardiner	Gardiner, 1973b	12
TANAIDOMORPHA		
Paratanaidae Lang		
Heterotanais oerstedii (Krøyer)	Bückle-Ramirez, 1965	6–16
Tanaidae Sars		
Tanais (now *Sinelobus*) *stanfordi*	Gardiner, 1975b	4–13 (20?)*
Pseudotanaidae Sieg		
Pseudotanais macrocheles Sars	Greve, 1965	6
Cryptocope abbreviata Sars	Greve, 1965	7
Leptognathiidae Sieg		
Leptognathia brevimanu (Lilljeborg)	Greve, 1965	3 (partly empty), 10, 14
L. breviremis (Lilljeborg)	Greve, 1965	3–8
L. dentifera Sars	Greve, 1965	6
L. filiformis (Lilljeborg)	Greve, 1965	3–6
Typhlotanais aequiremis (Lilljeborg)	Greve, 1965	15–18
T. brevicornis (Lilljeborg)	Greve, 1965	2–7

* Sum of eggs in both "ovisacs." "(20?)" derived from total of 10 eggs in single remaining ovisac in one specimen.

out at 26–28°C, between the extremes recorded at the collection site during this period: 20.6°C in January 1978 and 31.9°C in September 1977.

For *H. oerstedii,* the only other tanaidacean for which growth data are available, intermolt periods for laboratory-reared specimens are considerably shorter. Maximum and minimum number of days per intermolt recorded by Bückle-Ramirez are given in Table 2. He performed his experiments at 22–23.5°C, above the range recorded at his field collection site (−1.0–19.3°C). His observed intermolt periods are probably shorter than normal as a result. In addition, his figures do not include overwintering females.

Percentage length increases through the first three postmarsupial instars appear to be greater for *H. oerstedii* than for *P. largoensis.* Bückle-Ramirez (p. 756, Table 3) listed minimum and maximum body lengths for these instars. Because he gave no mean values, percentage length increases were calculated from the median value for each instar using the equation given in Table 1. The resulting values for the M1 to M2 transition and the M2 to juvenile transition are 33% and 31.3%, respectively. The corresponding mean values for *P. largoensis* are 23.7% and 19.3% (Table 1). Again, the results for *H. oerstedii* may be artificially high due to the high temperatures at which the animals were reared relative to field temperatures.

The maximum longevity for *H. oerstedii* appears to be just over a year. Mancas spawned in late June–early July that develop into females may possibly breed twice before males disappear at the end of September. Females that overwinter do not molt again until the spring when they either become secondary males or remain female and spawn again. In either case, individuals spawned the previous year appear to die by the end of July (Bückle-Ramirez, 1965). Laboratory-reared *H. oerstedii* live up to about eight months. In Bückle-Ramirez's experiment 3 (pp. 757–758), a female passed from the juvenile stage through three unfertilized copulatory stages in seven months. From data given in his Table 3, we see that development from marsupial release to the juvenile stage took an additional two or three weeks. As estimated above, laboratory-reared *Pagurapseudes* live somewhat longer, although intermolt durations may have been artificially prolonged by laboratory conditions.

Fecundity, as measured here, ranges from 4–17 potential offspring per brood in *P. largoensis,* which is comparable with that of most other tanaidaceans for which this is known (Table 3). With the exception of *Spelaeogriphus lepidops* Gordon, the single representative of the order Spelaeogriphacea, which has 10–12 eggs per marsupium (Gordon, 1957), the tanaidaceans appear to be the least fecund pericaridans on a per brood basis. Although some members of the other orders produce as few offspring per brood as do tanaidaceans, other species in each order produce far more (even excluding forms with planktonic stages such as bopyrid isopods).

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LITERATURE CITED

Băcescu, M. 1961. Contribution à la connaissance des Tanaidacés de la Méditerranée orientale. 1. Les Apseudidae et Kalliapseudidae des côtes d'Israel.—Bulletin of the Research Council of Israel B. Zool. 10B: 137–170.

Bouvier, E. L. 1918. Sur une petite collection de Crustacés de Cuba offerté au Muséum par M. de Boury.—Bulletin du Muséum National d'Histoire Naturelle 24: 6–15.

Bückle-Ramirez, L. F. 1965. Untersuchungen über die Biologie von *Heterotanais oerstedii* (Krøyer).—Zeitschrift für Morphologie und Ökologie der Tiere 55: 714–782.

Derby, C. D. 1982. Structure and function of cuticular sensilla of the lobster *Homarus americanus.*—Journal of Crustacean Biology 2: 1–21.

Gardiner, L. F. 1973a. New species of the genera *Synapseudes* and *Cyclopoapseudes* with notes on morphological variation, postmarsupial development, and phylogenetic relationships within the family Metapseudidae (Crustacea, Tanaidacea).—Zoological Journal of the Linnean Society 53: 25–58.

———. 1973b. A new species and genus of a new monokonophoran family (Crustacea: Tanaidacea) from southeastern Florida.—Journal of Zoology, London 169: 137–253.

———. 1975a. The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea).—Smithsonian Contributions to Zoology 170: i–iv, 1–265.

———. 1975b. A fresh- and brackish-water tanaidacean, *Tanais stanfordi* Richardson, 1901, from a hypersaline lake in the Galapagos Archipelago with a report on West Indian specimens.—Crustaceana 29: 127–140.

Gordon, I. 1957. On *Spelaeogriphus,* a new cavernicolous crustacean from South Africa.—Bulletin of the British Museum (Natural History), Zoology 5: 31–47.

Greve, L. 1965. The biology of some Tanaidacea from Raunefjorden, western Norway.—Sarsia 20: 43–54.

Gutu, M. 1972. Phylogenetic and systematic considerations upon the Monokonophora (Crustacea-Tanaidacea) with the suggestion of a new family and several new subfamilies.—Revue Roumaine de Biologie et Zoologie 17: 297–305.

Hartnoll, R. G. 1978. The determination of relative growth in Crustacea.—Crustaceana 34: 281–293.

Jazdzewski, K. 1969. Biology of two hermaphroditic Crustacea, *Cyathura carinata* (Krøyer) (Isopoda) and *Heterotanais oerstedii* (Krøyer) (Tanaidacea) in waters of the Polish Baltic Sea.—Zoologica Poloniae 19: 5–25.

Johnson, S. B., and Y. G. Attramadal. 1982. Reproductive behavior and larval development of *Tanais cavolinii* (Crustacea: Tanaidacea).—Marine Biology 71: 11–16.

Lang, K. 1953a. *Apseudes hermaphroditicus* n. sp. A hermaphroditic tanaid from the antarctic.—Arkiv för Zoologi 4: 341–350.

———. 1953b. The postmarsupial development of the Tanaidacea.—Arkiv för Zoologi 4: 409–422.

———. 1956a. Neotanaidae nov. fam., with some remarks on the phylogeny of the Tanaidacea.—Arkiv för Zoologi 9: 469–475.

———. 1956b. Kalliapseudidae, a new family of Tanaidacea.—*In:* K. G. Wingstrand, ed. Bertil Hanstrom, zoological papers in honour of his 65th birthday, Nov. 20th, 1956. Pp. 205–225.

———. 1958. Protogynie bei zwei Tanaidaceen-Arten.—Arkiv för Zoologi 11: 535–540.

———. 1966. Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen. 2. Die Gattung *Parapseudes* G. O. Sars.—Arkiv för Zoologi 18: 549–566.

———. 1968. Deep-sea Tanaidacea.—Galathea Report 9: 23–210.

———. 1970. Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen. 4. Aufteilung der Apseudiden in vier Familien nebst Aufstellung von zwei Gattungen und einer Art der neuen Familie Leiopidae.—Arkiv för Zoologi 22: 595–626.

Lauterbach, K.-E. 1970. Der Cephalothorax von *Tanais cavolinii* Milne-Edwards (Crustacea-Malacostraca), ein Beitrag zur vergleichenden Anatomie und Phylogenie der Tanaidacea.—Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere 87: 94–204.

McSweeny, E. S. 1982. A new *Pagurapseudes* (Crustacea, Tanaidacea) from Florida.—Bulletin of Marine Science 32: 455–466.

Messing, C. G. 1977. *Neotanais persephone,* a new species of hadal tanaidacean (Crustacea, Peracarida).—Bulletin of Marine Science 27: 511–519.

———. 1979. *Pagurapseudes* (Crustacea: Tanaidacea) in southeastern Florida: functional morphology, post-marsupial development, ecology and shell use.—Ph. D. Dissertation. University of Miami, Coral Gables, Florida. Pp. i–xi + 1–242.

Passano, L. M. 1960. Molting and its control.—*In:* T. H. Waterman, ed. The physiology of Crustacea, 1: 473–536. Academic Press, New York.

Salvat, B. 1967. La macrofaune carcinologique endogée des sédiments meuble intertidaux (Tanaidacés, Isopodes et Amphipodes) ethologie, bionomie et cycle biologique.—Mémoires du Muséum National d'Histoire Naturelle 45: 1–275.

Shiino, S. M. 1937. On *Apseudes nipponicus* n. sp. (Crustacea, Tanaidacea).—Annotationes Zoologicae Japonenses 16: 53–62.

Sieg, J. 1972. Untersuchungen über Tanaidaceen. 1. Bemerkungen über die postmarsupiale Entwicklung der Tanaidaceen.—Kieler Meeresforschungen 28: 232–236.

———. 1973. Ein Beitrag zur natürlichen System der Dikonophora Lang (Crustacea, Tanaidacea).—Inaugural Dissertation zur Erlangung der Doktorwürde der Mathematisch-Naturwissenschaftichen Facultat der Christian Albrechts Universität Kiel, Germany. Pp. i–iv + 1–298.

———. 1976. Zum naturlichen System der Dikonophora Lang (Crustacea, Tanaidacea).—Zeitschrift für Zoologische Systematik und Evolutionsforschung 14: 177–198.

———. 1978. Bemerkungen zur Möglichkeit der Bestimmung der Weibchen bei den Dikonophora und der Entwicklung der Tanaidaceen.—Zoologischer Anzeiger 200: 233–241.

———. 1980. Sind die Dikonophora eine polyphyletische Gruppe?—Zoologischer Anzeiger 205: 401–416.

Teissier, G. 1960. Relative Growth.—*In:* T. H. Waterman, ed. The physiology of Crustacea, 1: 537–560. Academic Press, New York.

Wolff, T. 1956. Crustacea Tanaidacea from depths exceeding 6000 m.—Galathea Report 6: 187–241.

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