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A REVIEW OF THE COPEPOD GENUS PARANTHESSIUS CLAUS

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The problem of arriving at a natural classification of the copepods has been in no small measure complicated by the repeated appearance within the group of the parasitic and commensal habit. In the cyclopoids, two sections, the Poecilostoma and the Siphonostoma, have been established and remain well differentiated on the basis of the specialization of mouth appendages correlated with parasitic and semiparasitic existence. Unfortunately for the systematist, these copepods seem to exhibit the widest tolerance in the selection of hosts. From the records, any phylum above the Protozoa which is represented to any conspicuous degree in the marine fauna is likely to appear in the roster of hosts of cyclopoid symbionts. This diversity of occurrence, in addition to small size, inconspicuous appearance, and remarkable agility in eluding usual methods of capture, has resulted in a scattered and fragmentary representation of this group in museum collections and consequently in the literature on copepods. The most extensive reports to date either have been surveys of the faunas of fairly limited localities or have been compendia of the symbionts of some particular category of host, with the emphasis of interest frequently tending toward the host rather than toward the copepod.

Probably a high degree of artificiality has been introduced into the classification because of this history. One of the major groups of the copepods is now found defined in numerous publications as an assemblage of parasites and commensals of ascidians. This reference is, of course, to the Notodelphyoida, which in such broad interpretation includes many degenerate parasites. The actual affinities of many of these may very well prove to be with several of the main stocks of the copepods when more emphasis is placed upon the details of structure rather than upon the fortuities of ecological distribution.

The copepods here considered are cyclopoids that show a tendency to reduction of mouth appendages; this character defines the section Poecilostoma. In these copepods the traits unifying the group are the very features that provide the most vexing of technical difficulties to the investigator. It is essential for any coherent presentation of the relations of the poecilostomes to establish the details of structure of the mandibles, maxillules, maxillae, and maxillipeds. These appendages are simplified in construction, reduced in size to minute proportions, closely appressed, and wedged into a very small area with closely impinged surrounding structures, such as a labrum which envelops a great part of the oral space. Dissection is the only satisfactory means of elucidating these features, because the normal arrangement of the mouth parts is such that most are held somewhat perpendicular to the axis of the body and even the best *toto* views often lead only to confusion of the details.

The present collection comprises symbionts of pelecypod mollusks. They were obtained, however, as a portion of a series of poecilostomes collected in association with a diverse array of invertebrates from the Pacific coast of North America. The forms are all assigned to the genus *Paranthessius* Claus, according to the definition to be established here. Noteworthy is the fact that congeners of these commensals of mollusks have been described as living in association with coelenterates, holothurians, and ascidians, evidencing the tendency in the poecilostomes to diversity of host organisms.

The genus *Paranthessius* is perhaps one of the most generalized of all the diverse copepod types customarily assigned to the family Lichomolgidae. In the structure of the mouth parts there is found as simplified and basic a plan as is encountered elsewhere in the family. The arrangement of the swimming legs of some of the representatives is possibly the least specialized among lichomolgids. I refer here to species in which the armature of the fourth endopodite retains on the terminal segment five outgrowths (setae or spines). A prominent character of most of the species of the genus is the tendency to suppression of the ornamentation of the fourth endopodite. In the extreme condition of this modification, existing in several *Paranthessius* species, the armature of the terminal segment of the fourth endopod is reduced to two outgrowths.

The subdivision of the Lichomolgidae proposed by Gurney (1927) into Sabelliphilinae and Lichomolginae would place *Paranthessius* in the former subfamily. This separation does not, I feel, follow a strongly characterized natural tendency of the group but, rather, cuts across a well-discernible trend. Consideration of species of *Anthessius* Della Valle (synonym: *Pseudomolgus* Sars, Wilson, etc.) as typical lichomolgids has perhaps contributed to this viewpoint. I suggest that a more significant subdivision would set aside *Anthessius*, *Rhinomolgus* Sars, perhaps *Panaietis* Stebbing, and other genera, as well distinguished froim the Lichomolgidae proper, either as a family or subfamily. The forms retained in the *Lichomolgus*-line follow, without necessity of subdivision, several trends which may or may not be of generic value but are hardly of familial or subfamilial importance. Such trends all seem to have strong foreshadowing in the genus *Paranthessius*. A conspicuous example would be the series exhibiting suppression of the fourth endopodite, as discussed above. Again, a series may be selected in which is traced the progressive transfer of the prehensile function from the terminal podomere of the antenna to the penultimate segment. Suggestions of various trends of modification of the rostrum are apparent. Such species as *P. saxidomae*, *P. robustus*, and *P. serendibicus* perhaps anticipate the great circular expansion in outline of the anterior body region, seen characteristically in the *Stellicola* section of *Lichomolgus*. *P. columbiae*, particularly in the adult female, shows the tendency of elongation and narrowing of the body in the direction of vermiform construction found in some of the most aberrant of the parasitic copepods. This trend is further suggestive of significance when it is noted than an accompanying phenomenon is the extension of the ovarian (or oviducal?) structure out into the full extent of the abdomen.

Family LICHOMOLGIDAE Claus

Genus PARANTHESSIUS Claus

Paranthessius Claus, 1889, pp. 342–343 (type, *P. anemoniae* Claus, 1889).—Canu, 1891, p. 479; 1892, p. 236; 1894, p. 137; 1898, pp. 413–415.—Zulueta, 1912, p. 12.—Monod and Dollfus, 1932, pp. 143–146.—Wilson, 1932, p. 587.—Atkins, 1934, p. 674.—Leigh-Sharpe, 1935, pp. 47–48.—Nicholls, 1944, p. 53. (Not *Paranthessius* T. Scott, 1903, p. 130.)

Diogenidium Edwards, 1891, pp. 89, 93 (type, *D. nasutum* Edwards, 1891).—Canu, 1891, p. 479; 1892, p. 236.—Wilson, 1932, p. 587.

Herrmannella Canu, 1891, pp. 479–480 (type, *H. rostrata* Canu, 1891); 1892, pp. 235–236.—T. Scott, 1894, p. 259.—Canu, 1899, p. 73.—Norman and Scott, 1905, p. 299.—T. Scott, 1906, p. 354 (part).—Pelseneer, 1929, pp. 35, 43.—Fraser, 1932, p. 279.

Hermannella Canu, 1891, p. 436; 1894, pp. 3, 10.—Thompson and Scott, 1903, pp. 282–283 (part).—Norman and Scott, 1906, p. 199 (part).—Sars, 1918, pp. 174–175 (part).—Brian, 1924, p. 5.—Wilson, 1932, p. 586.—Heegaard, 1944, pp. 361, 365.

Herrmanella T. Scott, 1903, p. 28.—Pelseneer, 1929, p. 45.

Lichomolgus (part) T. SCOTT, 1892, pp. 266–267.—T. and A. SCOTT, 1892, pp. 201–203.—HERDMAN, 1893, pp. 83, 135.—THOMPSON, 1893, pp. 177, 207–208.

Pseudolichomolgus THOMPSON, 1897, cited in Herdman, 1897, p. 87 (type, *P. columbiae Thompson*, 1897).—WILSON, 1932, p. 591.

Pseudolichomolgus PESTA (*not* Thompson), 1909, pp. 263–265 (type, *P. pectinis* Pesta, 1909).—PELSENEER, 1929, pp. 35, 44.

Pestalichomolgus WILSON, 1932, p. 587 (new name for *Pseudolichomolgus* Pesta; type, *P. pectinis* (Pesta, 1909)).

Diagnosis.—Body shape cyclopoid. Segmentation somewhat variable; metasome 4- or 5-segmented; urosome of female 5-segmented, that of male 6-segmented. Rostrum well developed with obvious prehensile function. Antennule 7-segmented. Antenna of four segments, second always longest. Labrum deeply divided in the midline. Mandible constructed on simplest lichomolgid type, elongated, with tapering flat blade arising from a fairly stoutly chitinized base, with no articulation. Edges of mandible serrate, finely dentate or ciliate. Maxillule, inserted directly on head rather than on mandible, consists of flat palplike appendage; terminal armature various, comprising two or three setae. Maxilla 2-segmented, base very large and conspicuous. Two setae typically present on second segment, the more distal usually with a row of spinules or cilia on its medial margin; proximal seta not thus ornamented. Maxilliped of female considerably reduced, its segmentation varying among the species. Terminal podomere a pointed, spinelike segment, or bluntly rounded. Male maxilliped 3-jointed, prehensile. Swimming legs all biramous, trimerous, with characteristic modification of fourth endopodite. Fifth leg a single free segment, base represented only by a slight expansion of the body proper, basal seta present, borne on dorsal side of appropriate body segment. Armature of free segment two members, usually a conspicuously heavy spine and a seta.

Genotype.—*Paranthessius anemoniae* Claus.

Remarks.—The wide definition of *Paranthessius* as here offered presents some difficulties in the possibility of inclusion of *Modiolicola* Aurivillius and *Sabelliphilus* Sars. The latter genus stands fairly well alone by virtue of the following characters: The rostrum (bifid); the antennule (proximal two segments expanded); the antenna (prehensile hooks on both third and fourth segments); and the ornamentation of the maxilla (fairly spinous). Its remaining appendages would fit with no difficulties in the normal variations of the species of *Paranthessius*. Many years of usage make it most desirable to retain the generic distinction. *Modiolicola* presents even less strong separation, and it is possible that a further broadening of the definition of *Paranthessius* to include the forms now placed in *Modiolicola* may become desirable. However, as I am convinced that the number of undescribed species of lichomolgids is greater than the number now known to science, I consider it is entirely probable that generic limits will be subjected to review and revision on future occasions. The group *Modiolicola*, therefore, serves for the present to set aside obviously related, well-characterized species which differ principally from those of *Paranthessius* as follows: Absence of a rostrum; possession of the highly characteristic antenna, with very much shortened second segment, accompanied by elongation of the third and fourth segments, and lack of armature on the third segment; and the reduction of the armature of the maxilla to a single unornamented seta.

There is a notable tendency to grouping of the species of *Paranthessius* within the limits set forth above. Subgeneric division is hardly justified because of the existence of transitional species. In six species the armature of the distal segment of the fourth endopodite, consisting of some combination of setae or spines to the total number of four or five, is developed. In the forms with four spines or setae, further, the outline of the segment characteristic of the full armature of five persists. In all these species there is reduction of the prehensile function of the terminal antennal segment, the usual strong claw being replaced by a group, typically three, of long setae, or weakly clawed slim spines. In some of these examples, but not all, the prehensile function is transferred to the penultimate antennal segment and the terminal joint then reduced to palplike dimensions.

The remaining species form a fairly coherent group characterized by reduction of the distal segment of the fourth endopodite, both in general outline, and in its armature, which is reduced to two or three spines or setae. In all but one of these species the terminal antennal segment bears a heavy prehensile claw, and the penultimate segment is the shortest and least developed. *Paranthessius parvus* (Norman and Scott) bridges the distinction between these groups, however; in that species, the prehensile function of the terminal segment is lost, although the terminal endopodite segment of the fourth leg has the spine complement reduced to two.

In its body outline *Paranthessius* is characteristically cyclopoid, or better, lichomolgid. An oval-shaped forebody is typical; in some species there is a tendency to elongation, and in others toward inflation of the outline of this region to an approximate circle.

The segment of the first swimming leg (the second thoracic segment—almost invariably called first segment by earlier authors) in some species is joined to the cephalothorax, in others is a free segment like the other pedigerous somites. The metasome then possesses three or four free segments posterior to the cephalothorax. Thoracic segment 5 is much the smallest of all. Frequently the greatest width of the metasome is at the first free segment.

The conspicuous rostrum of *Paranthessius* is bent downward and backward as a strong, pointed beak or hook, and, from the arrangement of the supporting structures, obviously enjoys considerable freedom of movement. It thus becomes an important prehensile structure in this genus. The chitinous bars and articulating masses on the ventral surface of the head which support the rostrum include in close association bars that are related to the bases of the antennules and antennae. Running backward in the midline as far as the upper lip is a broad straplike plate of chitin which, at its anterior end, is rounded to form a very mobile articulation with the beak proper (fig. 34, F). Curiously, Scott and Scott (1892) in their description of *Lichomolgus agilis* Scott (not Leydig) [=*Paranthessius rostratus* (Canu)] interpreted the rostrum as a "short trumpet-shaped siphon, capable of being extended or depressed * * *" Canu, in his monograph, illustrated the rostrum very well (Canu, 1892, pl. 24, fig. 3).

The antennules are 7-segmented. The third segment is usually the shortest; often it exhibits a great tendency to fusion with the adjacent segments. An apparent trend is the stressing of the articulation between segments 4 and 5, with the formation of a basal group (actually inflated in some species) and with the terminal segments arranged as a slenderer, more freely movable unit.

The antennae are 4-segmented and there is a highly complicated articulation with the ventral surface of the head. In some dissections a considerable mass of the articulating region may come free with the appendage, suggesting a fifth, basal segment. In the descriptions of various of the species a 5-segmented antenna is mentioned or depicted, and I suggest that this interpretation is due to such an artifact. The four terminal segments are similar, in any case. The first (basal) segment is short; the second is the longest of all, frequently somewhat flattened in a plane parallel to the body axis (in the normal orientation of the appendage) and at the same time expanded mediolaterally. The arrangement and ornamentation of the two terminal segments follow various trends, as has been described above.

The original description of *Paranthessius* Claus, 1889, was based upon one of the most aberrant representatives of the genus, and as a result, to the present, no satisfactory, complete resolution of the subsequent multiplication of synonyms has been brought forward.

The lichomolgid nature of *Paranthessius* was emphasized by its author, and very properly so, since, as has been pointed out above, reference to the amplified characters of the genus will show it to exhibit in most fundamental arrangement the defining structures of this much-abused family. A "Lichomolgus-like" body shape is typical of *Paranthessius* in Claus' sense. Further characters of his definition to which we must still adhere would be the rostrum, antennule, antenna (although it is rather at the extreme of one of the trends of modification pointed out above), mandible, maxillule, maxillipeds of the two sexes, and the remaining thoracic limbs (although here the exceptional armature of the second segment of the fourth endopodite remains unique).

In *P. anemoniae* Claus some features that distinguish it markedly from most members of the genus were included in the generic diagnosis. The maxilla is unique, the more distal of the two setae of the terminal joint being enlarged to equal in dimension and arrangement of ornamentation the terminal prolongation of the main mass of the segment proper, which, further, has the appearance of being jointed basally. It is very difficult to reconcile this structure with the usual condition in lichomolgids, but Claus' description is supported by an account of Canu (1898), which is accompanied by a figure comparable to that presented with the original description. The armature of the fourth endopodite of *P. anemoniae* also sets this form apart from all others of the genus; indeed, is remarkable among the members of the family Lichomolgidae. The first segment (basal) bears the usual seta distally placed on the medial margin. The second segment bears two medial setae. All other species referred in the present treatment to *Paranthessius* bear a single seta on this segment, and this last condition is typical also of members of *Lichomolgus*, *Modiolicola*, and *Sabelliphilus*, genera perhaps most closely related to *Paranthessius*. All members of the genus *Anthessius* have the setae in question exactly like those of *P. anemoniae*, but in my estimation *Anthessius* is so distinct from typical lichomolgids that I incline to the establishment of a family, or at least a subfamily, for this genus and its allies. In all other characteristics, *P. anemoniae* is a lichomolgid without question, and I should consider it a dubious benefit to single out the species for generic status. Moreover, the unusually wide range of variability among the representatives of the genus should provide latitude for the reception of Claus' species.

Diogenidium Edwards, 1891, was instituted apparently without knowledge of the description of *Paranthessius*, although the author acknowledges consultation with Claus on systematic points dealing with other copepods described in the same paper. *D. nasutum* conforms well to the generalized characteristics of *Paranthessius* in its present sense. Various details were not included in the description; the mouth parts, for example, were dismissed as like those of *Lichomolgus*. One slight inconsistency occurred—the generic diagnosis cites an 8-segmented antennule, but the species description and the illustrations present the antennule as 7-jointed. The characteristic rostrum is present and well developed. The segmentation of the fourth endopod is typical, and the character of three outgrowths on the terminal segment is shared with several more recently described species.

Herrmannella was established by Canu, 1891. Its distinction from *Paranthessius* was implied by the author's statements and *Diogenidium* was represented as differing generically by the configuration of the mid-region of the body and the nature of the mouth parts. In its particulars his characterization of *Herrmannella* and his species *H. rostrata* is a description of a generalized *Paranthessius.* His claimed differentation from *Diogenidium* is not supportable, and any treatment that removed *P. anemoniae* Claus to separate rank would have to admit the priority of *Diogenidium* over *Herrmannella.*

Canu, in his impressive monograph of 1892, republished his diagnosis of *H. rostrata*, amplified and illustrated, and stated specifically his bases for separation of the genus from *Paranthessius*—the antennule, maxilla, and the fourth endopodite. He repeated here his vague differentiation from *Diogenidium*, admitting the close relationship of the genera, the situation paralleling, in his statement, the resemblance of *Paranthessius* to *Anthessius.*

The subsequent synonymy of *Paranthessius* involves a number of obvious misinterpretations, most of the authors usually bringing forward subsequent corrections. One feature lending a certain flavor to this synonymy is the variety of lapses in transcription of *Herrmannella*, its author himself leading off the distinguished procession of those dropping out one or another of the improbable-appearing doubled consonants.

Most of the species described for the genus have been instituted under *Herrmannella* (Scott, Thompson and Scott, Sars). In these treatments a frequent error was the inclusion in the generic concept of species more properly assignable to *Anthessius.* This error probably was due to the condition of the fourth endopodite, the segmentation, as we have seen, being the same in the two genera.

The name *Pseudolichomolgus* was proposed twice for representatives of *Paranthessius.* I am convinced that specimens in my collection are either identical with *Pseudolichomolgus columbiae* Thompson (which was an immature stage) or are representatives of an exceedingly closely related species. In the adult condition these specimens can be assigned without question to *Paranthessius* (see further discussion under species).

Sars' concept (1918) of *Hermannella* (sic) would apply, in general, from evidence of species considered, to *Paranthessius* as here defined, except for his mention, in discussion only, of *H. maxima* (Thompson), a synonym of *Modiolicola inermis* Canu. Sars had never seen specimens of this species. His generic diagnosis is very superficial, hardly serving more than to establish the genus in the Lichomolgidae and to differentiate it weakly from *Modiolicola* (*M. insignis* Aurivillius). He claimed importance for the rostrum as a generic character but did not describe or illustrate the structure for any of the five species that he otherwise completely depicted with his customary meticulous care.

The most important synthesis of the scattered synonymy of *Paranthessius* was offered by Monod and Dollfus (1932) in their survey of the parasites of mollusks. They (pp. 143–146) refuted Canu's differentiation of *Herrmannella* from *Paranthesius*, pointing out parallel extremes of variation in *Lichomolgus* and further demonstrating that inclusion of Sars' *Herrmannella* species in the concept of the genus broadens it amply to receive *P. anemoniae.* They also added *Pseudolichomolgus* Pesta, 1909, to the synonymy of *Paranthessius.*

The interpretations of Heegaard (1944) require comment with reference to *Paranthessius.* This author's *Scambicornus* exhibits many traits which come within the defined limits of *Paranthessius.* Unfortunately, the types were not dissected, and the lack of information about the mouth parts requires assigning the form as a *genus incerta sedis* among the Lichomolgidae, if it belongs in that family, as the author claims. As they are illustrated, admittedly somewhat indefinitely, the mandible and maxilla of *Scambicornus* are not like those typical for the family Lichomolgidae. The fourth endopodite, as depicted in the illustrations, has an armature that does not appear elsewhere among lichomolgids. If these features could be clarified, it seems possible that *Scambicornus* may be related to *Paranthessius.*

More pertinent to present considerations on *Paranthessius* is the invoking by Heegaard of the structure of the antenna of *Herrmannella prehensilis* Sars, as figured by its author, in support of Heegaard's proposition that such an antenna is a biramous appendage bearing an exopodite and an endopodite. Sars' *H. prehensilis* has patently an antenna in which the prehensile function has been transferred from the stout claw typically borne on the terminal segment to a correspondingly developed hooked spine on the penultimate segment, with the end segment undergoing reduction to a short, palplike, setiferous member. The illustrations in the original descriptions of *H. serendibica* and *H. robusta* of Thompson and Scott (1903) are in agreement with Sars' presentation. There seems to be no advantage in departing from the traditional concept of the uniramous structure of the antenna. The genus *Paranthessius* offers an array of species in which may be traced very fully the tendency of transfer of prehensile function from the ultimate segment to the penultimate. A further support to the accepted view may be found in the condition of the antenna in the family Clausidiidae where an expanded third segment with fairly profuse ornamentation ordinarily dominates in size the more palplike terminal segment.

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KEY TO THE SPECIES OF PARANTHESSIUS

(Based on characters of females)

1. Armature of terminal endopodite segment of fourth leg consisting of 2 spines or setae or a spine and a seta ____ 2
   Armature of this segment consisting of 3 spines or 2 spines and a seta ____ 10
   Armature of this segment consisting of 4 spines or setae ____ 12
   Armature of this segment consisting of 5 spines or setae ____ 13
2. Terminal antennal segment bearing heavy prehensile claw ____ 3
   Terminal antennal segment without usual heavy claw, bearing instead 3 jointed setae of about equal size ____ parvus (Norman and Scott)
3. Caudal rami 2 or more times as long as wide ____ 4
   Caudal rami no more than one and one-half times as long as wide. validus (Sars)
4. Rostrum a strongly curved, posteriorly directed, heavily chitinized beak ____ 5
   Rostrum replaced by a gently curved, short prominence accompanied by a bifurcate, weakly chitinized accessory structure. perplexus, new species
5. Fifth leg the usual slightly modified cylinder, or with base expanded ____ 6
   Fifth leg characteristically shaped: in outline an inverse truncated cone, the squared-off terminal surface about twice as wide as base. cynthiae (Brian)
6. Length of longest antennal segment much more than twice width ____ 7
   Length of longest antennal segment less than twice width ____ pectinis (Pesta)
7. Margins of fifth leg roughly parallel ____ 8
   Free segment of fifth leg expanded basally ____ 9
8. Ventral surface of last abdominal somite with a pair of rows of long slender spinules ____ columbiae (Thompson)
   No ornamentation on last abdominal somite ____ rostratus (Canu)
9. Lateral margin of terminal segment of fourth endopodite bearing 2 spinous processes ____ tivelae, new species
   Lateral margin of this segment without processes ____ saxidomi, new species
10. Second segment of fourth endopodite with a single seta ____ 11
    Second segment of fourth endopodite bears 2 setae on medial surface. anemoniae Claus
11. Terminal segment of fourth endopodite with 3 spines ____ panopeae, new species
    Terminal segment of fourth endopodite with 2 spines and a ciliated seta. nasutum (Edwards)
12. Length of caudal rami twice width ____ robustus (Thompson and Scott)
    Length of caudal rami at least 4 times width. serendibicus (Thompson and Scott)
13. Terminal antennal segment longer than penultimate segment ____ 14
    Terminal antennal segment much smaller than penultimate. prehensilis (Sars)
14. Third antennal segment bearing only setae ____ 15
    Third antennal segment with a heavy spine on the distal ectal corner. propinquus Nicholls
15. Length of caudal rami 4 times width ____ finmarchicus (Scott)
    Length of caudal rami 10 times width ____ tenuicaudis (Sars)

PARANTHESSIUS ANEMONIAE Claus, 1889

Paranthessius anemoniae Claus, 1889, p. 343, figs. 8–15 (Trieste; host: *Anemonia* sp.).—Canu, 1894, p. 137 (Îles Chausey, France); 1898, pp. 413–415, pl. 10.—Zulueta, 1912, p. 12.—Monod and Dollfus, 1932, pp. 143, 145–146.

PARANTHESSIUS CYNTHIAE (Brian, 1924)

Hermannella cynthiae BRIAN, 1924, pp. 5–7, figs. 1–4 (Mauritania; host: *Cynthia* sp.).

PARANTHESSIUS FINMARCHICUS (T. Scott, 1903)

Herrmannella finmarchica T. SCOTT, 1903, pp. 28–30, pl. 4, figs. 14–19 (Bog Fjord, Finmark).
Hermannella finmarchica SARS, 1918, pp. 179–180, pl. 101 (west and south coasts of Norway).

PARANTHESSIUS NASUTUM (Edwards, 1891)

Diogenidium nasutum EDWARDS, 1891, pp. 89–93, pl. 4, figs. 12–19 (Bahama Islands; host: *Mülleria agassizii* Selenka).

PARANTHESSIUS PARVUS (Norman and Scott, 1905)

Herrmannella parva NORMAN and SCOTT, 1905, pp. 299–300 (Plymouth Sound, England; "among Hydrozoa, etc., near low-water").
Hermannella parva NORMAN and SCOTT, 1906, p. 199, pl. 13, fig. 15, pl. 15, figs. 7–10, pl. 16, fig. 12, pl. 19, fig. 5.—SARS, 1918, pp. 176–177, pl. 99 (west and south coasts of Norway; free-swimming at moderate depths).

PARANTHESSIUS PECTINIS (Pesta, 1909)

Pseudolichomolgus pectinis PESTA, 1909, pp. 263–265, pl. 2, figs. 8–10, pl. 3, figs. 11–16 (Barcola Canal, near Trieste; host: *Pecten glaber* [Linnaeus]).—PELSENEER, 1929, pp. 35, 44.
Paranthessius pectinis MONOD and DOLLFUS, 1932, pp. 148, 194.

PARANTHESSIUS PREHENSILIS (Sars, 1918)

Hermannella prehensilis SARS, 1918, p. 178, pl. 100 (Skjerjehavn, outside Sogn Fjord, Norway; free-swimming, about 20 fathoms depth).

PARANTHESSIUS PROPINQUUS Nicholls, 1944

Paranthessius propinquus NICHOLLS, 1944, pp. 53–54, figs. 23–24 (Sellick Reef, South Australia).

PARANTHESSIUS ROBUSTUS (Thompson and Scott, 1903)

Hermannella robusta THOMPSON and SCOTT, 1903, p. 282, pl. 17, figs. 1–8 (Gulf of Manaar, Ceylon; from washings of invertebrates).

PARANTHESSIUS ROSTRATUS (Canu, 1891)

Herrmannella rostrata CANU, 1891, p. 480 (sand banks, Pointe aux Oies, Wimereux, France; host: *Mactra stultorum*).
Hermannella rostrata CANU, 1891, p. 436 (Étaples, France; host: *Pecten opercularis* Linnaeus).
Herrmannella rostrata CANU, 1892, pp. 236–237, pl. 24, figs. 1–13 (Baie d'Authie, France; host: *Cardium edule* Linnaeus).
Lichomolgus agilis T. SCOTT (not Leydig), 1892, pp. 266–267 (Morecambe Bay, England; Firth of Forth; host: *Cardium edule* Linnaeus).—T. and A. SCOTT, 1892, pp. 201–203, pl. 15, figs. 1–14.—HERDMAN, 1893, p. 83 (Liverpool Bay); 1893, p. 135.—THOMPSON, 1893, pp. 177, 207–208, pl. 25, figs. 4, 8d.
Hermannella rostrata CANU, 1894, pp. 3, 10.
Herrmannella rostrata T. SCOTT, 1894, p. 259.—CANU, 1899, p. 73.— T. SCOTT, 1906, p. 354.
Hermannella rostrata SARS, 1918, pp. 175, 180.

Herrmannella rostrata PELSENEER, 1929, p. 43.—FRASER, 1932, p. 279 (Morecambe Bay; nettings of plankton over beds of *Cardium edule* Linnaeus).
Paranthessius rostratus MONOD and DOLLFUS, 1932, pp. 147–148, 194–195.—ATKINS, 1934, p. 674 (Plymouth).—LEIGH-SHARPE, 1935, pp. 47–48 (Plymouth; hosts: *Cardium edule* Linnaeus, *Chlamys opercularis* [Linnaeus], *Paphia pullastra* [Montagu]).

PARANTHESSIUS SERENDIBICUS (Thompson and Scott, 1903)

Hermannella serendibica THOMPSON and SCOTT, 1903, pp. 282–283, pl. 17, figs. 9–11 (Gulf of Manaar, Ceylon; washings of sponges).

PARANTHESSIUS TENUICAUDIS (Sars, 1918)

Hermanella tenuicaudis SARS, 1918, pp. 180–181, pl. 102 (west coast of Norway).

PARANTHESSIUS VALIDUS (Sars, 1918)

Hermannella valida SARS, 1918, pp. 175–176, pl. 98 (Stavanger Fjord, Norway; among dredged material from about 50 fathoms).

PARANTHESSIUS COLUMBIAE (Thompson, 1897)

FIGURES 33, 34

Pseudolichomolgus columbiae THOMPSON, *in* Herdman, Thompson, and Scott, 1897, pp. 87–88, pl. 8, figs. 1–10 (Puget Sound; plankton).

Specimens examined.—One lot of specimens from several examples of *Schizothaerus nuttallii* (Conrad), collected at Tomales Bay, Marin County, Calif., May 23, 1943, by P. L. Illg. Eleven adult females, 6 adult males, 50 immature specimens. (Selected specimens constitute U. S. N. M. No. 85348.)

Washings (formalin in sea water) of the red algal tuft on the siphon plates of an example of *Schizothaerus nuttallii* (Conrad), Tomales Bay, Marin County, Calif., May 23, 1943, P. L. Illg. One male of the fifth copepodid stadium. The alga was collected during the period of outgoing tide and was awash in several inches of water.

From one specimen of several examples of *Protothaca tenerrima* (Carpenter), Tomales Bay, Marin County, Calif., May 23, 1943, P. L. Illg, collector. Two adult females.

From several examples of *Schizothaerus nuttallii* (Conrad), Bodega Lagoon, Sonoma County, Calif., January 23, 1944. Collector K. A. Hok. Six adult females, five adult males, three immature specimens.

It is probably significant that every adult specimen of *S. nuttallii* examined on both the recorded occasions yielded examples of the copepod.

Distribution.—Puget Sound; Tomales Bay and Bodega Bay, Calif.

Description.—FEMALE: The body is elongated and slender; the habit is unique among the members of the genus (fig. 33, A). The

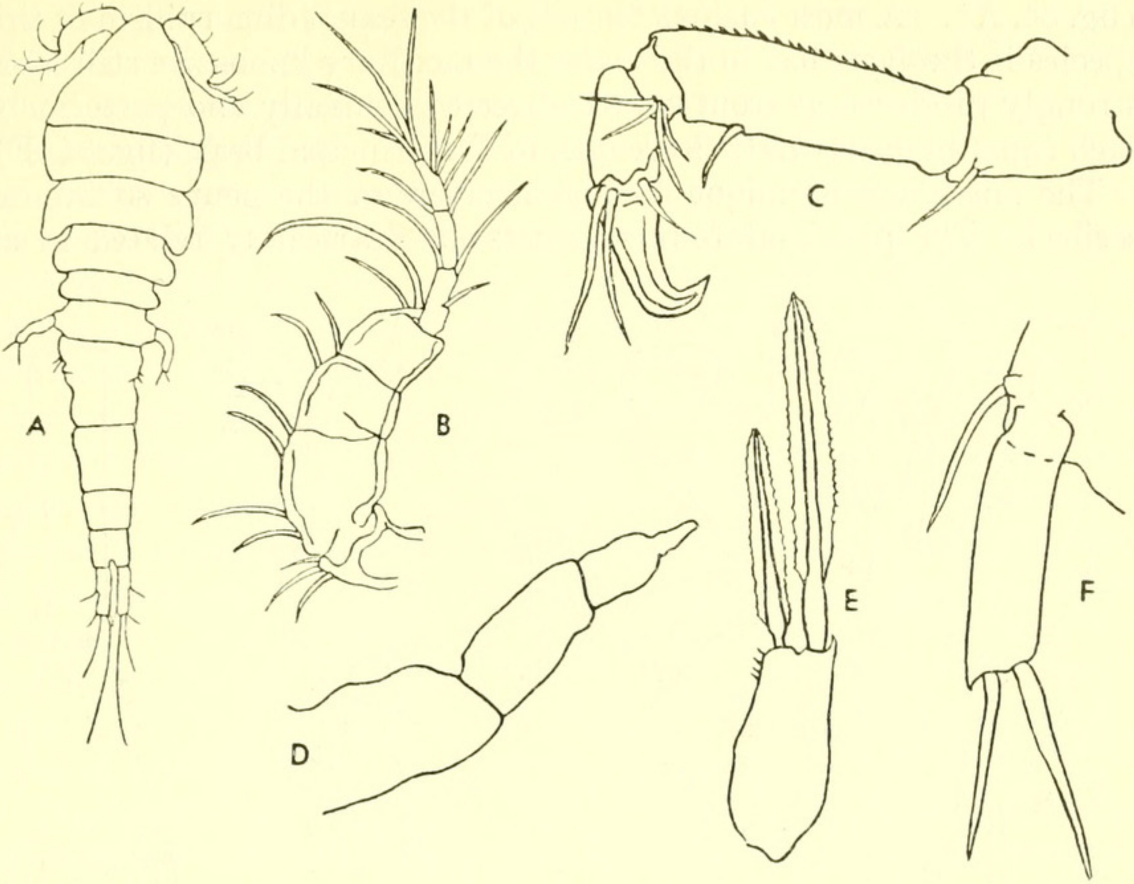

FIGURE 33.—*Paranthessius columbiae* (Thompson): FEMALE, A, body outline (× 28); B, antennule (× 114); C, antenna (× 240); D, maxilliped (× 707); E, terminal segment of fourth endopodite (× 240); F, fifth leg (× 240).

somite of the first swimming leg (the second thoracic somite) is separated from the cephalothorax and is the longest pedigerous segment. The articulation with the cephalothorax is very distinct both dorsally and ventrally. The legs are placed far back on the ventral side of the segment, and so the space between the mouth parts and the swimming legs is of considerable extent. The third thoracic segment is slightly shorter than the second and is the only metasome segment exhibiting posterior prolongation of its lateral margins. The fifth thoracic segment is the terminal segment of the metasome and is much the shortest and narrowest of these segments. The urosome is slightly longer than the metasome. It consists of the segment of the fifth legs, the genital segment and three free abdominal segments. The ovisacs are held closely appressed to the body and they extend slightly beyond the tips of the caudal rami. An estimate based on a typical ovisac would indicate as the usual contents approximately 120 small eggs.

The rostrum is highly characteristic. It is the well-developed prehensile organ typical of the genus, with the unique feature that the anterior, baselike structure of the beak is produced laterally in wide expansions, the extremes of which exhibit further ventral prolongation, so that the principal beak is accompanied by two auxiliary knobs (fig. 34, A). A most curious feature of the sexual dimorphism of this species is the fact that in the males the auxiliary knobs are still more strongly produced as stout spines, directed ventrally and posteriorly, each equal to nearly half the length of the principal beak (fig. 34, F).

The antennule is unique among members of the genus so far described. The proximal four segments are intricately related in an

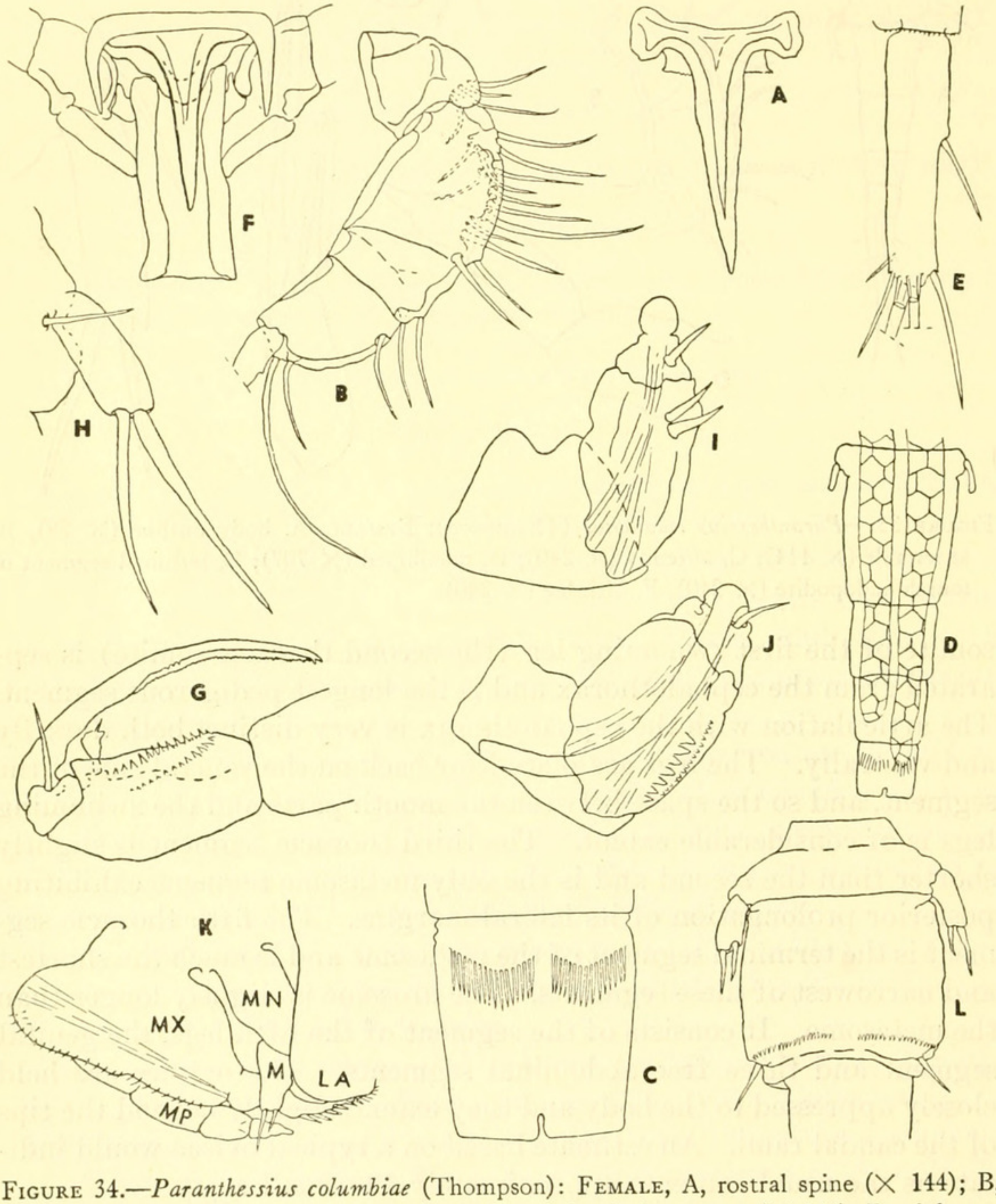

FIGURE 34.—*Paranthessius columbiae* (Thompson): FEMALE, A, rostral spine (× 144); B, basal segments of antennule (× 296); C, last abdominal segment (× 144); D, abdomen (× 42); E, caudal ramus (× 144). MALE, F, rostrum and bases of antennules (× 144); G, maxilliped (× 144); H, fifth leg (× 424). FIFTH COPEPODID, male, I, maxilliped of young example (× 296); J, maxilliped of individual about to molt (× 296). FOURTH COPEPODID, K, mouth parts (× 296; *LA*, upper lip; *MN*, base of mandible; *M*, maxillule; *MX*, maxilla; *MP*, maxilliped); L, sixth and seventh thoracic somites (× 144).

expanded, arched plate with highly chitinized margins (fig. 34, B). The distal three segments constitute a terminal whip, much narrower, more cylindrical, and with less departure from the usual lichomolgid structure (fig. 33, B). The first segment has a very mobile articulation with the second, which as usual is the longest segment of the antennule. The limit between the second and third segments is traceable by distinct but incomplete sutures, and a considerable partial fusion unites them. The articulation between the third and fourth segments is a complete one. The first segment bears four setae on the anterolateral corner. The second segment bears 13 setae arranged as a fairly dense row along the anterolateral margin. The third segment bears two setae on the distolateral corner. The fourth segment bears three setae on the anterolateral margin, one proximal, the others at the distal corner. The most distal of these is the longest seta of the antennule. The fifth segment, which is the longest of the distal trio, bears three setae. The sixth segment, just slightly shorter than the fifth, bears two setae. The short seventh segment bears four apical setae and four in a subapical position.

The antenna is 4-segmented. The second segment is much longer than the others and is somewhat flattened dorsoventrally, expanded mediolaterally. The heavy claw borne on the terminal segment is so oriented with the antenna that the dissected appendage takes a position which presents a deceptive narrowness of the second segment (fig. 33, C). The first and second segments each bear a single seta. The third segment bears four setae. The terminal segment, in addition to its large claw, has three setae, all placed at the base of the claw.

The mandible is the characteristic flat blade, tapering to a pointed flexible tip, with ciliate margins (as seen in the illustrated mandible of *Paranthessius tivelae*, fig. 36, I). The maxillule bears two terminally placed setae. Figure 34, K, presents the mouth parts of an immature individual in which there is complete correspondence to the adult female.

The maxilla is 2-segmented. The base is very large; its posterior margin bears a row of spinules. The terminal joint bears an unornamented proximal seta and a more distal, larger seta with cilia arranged along its posteromedial margin.

The maxilliped is very reduced, consisting of three simple segments, the terminal segment the shortest (fig. 33, D).

The swimming legs conform to the characteristic pattern for the genus. The arrangement of spines and setae on the segments of the rami follows:

First leg, exopodite: First segment (basal) bears a lateral spine; second segment bears a lateral spine and a medial seta; third segment (terminal) bears four spines and four setae. Endopodite: First segment—medial seta; second segment—medial seta; third segment—one spine and four setae.

Second leg, exopodite: First segment—lateral spine; second segment—lateral spine and medial seta; third segment—four spines and five setae. Endopodite: first segment—medial seta; second segment—two medial setae; third segment—three spines and three setae.

Third leg, exopodite: First segment—lateral spine; second segment—lateral spine, medial seta; third segment—four spines and five setae, Endopodite: first segment—medial seta; second segment—two medial setae; third segment—three spines and two setae.

Fourth leg, exopodite: First segment—lateral spine; second segment—lateral spine, medial seta; third segment—three spines and five setae. Endopodite: first segment—medial seta; second segment—medial seta; third segment—two terminal spines, the lateral about three-fifths of the length of the medial (fig. 33, E).

In all the pairs of swimming legs, the distal margins of the basipodites are set with very close-set, long, fine spinules which form a conspicuous fringe. The basis in each leg bears a small lateral seta just proximal to the articulation of the exopodite with the basis. The coxa bears a large ciliated seta at its medial distal corner. The margins of the rami are ciliated to varying degrees.

The fifth leg possesses a very elongate free segment (length three or more times the width), which is directed somewhat posteriorly. A dorsal seta, set on the body somite proper, represents the basis of the fifth leg. The terminal armature of the free segment comprises a shorter, lateral setiform member and a slightly longer, much stouter, medial spine (fig. 33, F).

The urosome is elongate, exceeding slightly the metasome. The urosome comprises the sixth thoracic segment (which bears the fifth legs); the genital segment, a fused composite of the seventh thoracic segment and the first abdominal somite; and three free abdominal segments. In all these, the posterior margins are entire, lacking the spinous serrations characteristics of some other species. The terminal segment exhibits an unique form of ornamentation. About midway in length of the segment is placed across the ventral surface a pair of rows of slender, elongate spinules, in fringe arrangement. The rows do not meet at the midline, and they form arches across the ventral surface nearly to its lateral extent. The number of spinules per row in specimens examined has varied from approximately 15 to 20 in each row (fig. 34, C).

Perhaps a significant anticipation of the encroachment of the whole body by reproductive structures in the most degenerate parasitic copepods is provided in this species where the ovarian (or oviducal) tubes of the two sides of the body extend into the abdomen, on one side, at least, usually penetrating the terminal segment (fig. 34, D).

The state of preservation of my specimens is not favorable for determining details of internal anatomy, so the exact identity of the oviferous bands has not been established. The typical position of the ovaries and oviducts in lichomolgids is in the thoracic segments, with no extension posterior to the apertures of the oviducts on the genital segment.

The caudal rami are about four times as long as wide (fig. 34, E). The proximal lateral seta is placed relatively far posteriorly, at about two-fifths the length of the ramus. The external seta is longer than the internal. The two longest central setae of the tip of the ramus are jointed at their bases; the longer is about two and one-half times the length of the caudal ramus.

Length of the body, exclusive of the setae of the caudal rami, is 2 mm.

Male: The body habit retains the tendency to elongation of the female, but not in such extreme form; there is therefore little departure from the facies of the typical lichomolgid male. The segmentation of the metasome is the same in the two sexes. In the urosome, the genital thoracic segment of the male is a free somite and bears well-developed sixth legs. The separation of the first abdominal somite from the genital segment results in a urosome of six segments. The more extreme development of the rostrum of the male in comparison to the condition in the female has been described above (fig. 34, F). The antennule is alike in the two sexes.

The antenna bears out a tendency in the dimorphism of the species of *Paranthessius* I have seen toward an increase in number and size of spinous protuberances of the appendages. The second segment of the male antennule bears a row of spinules which are much stouter and longer than those seen in the female. The mandibles, maxillules, and maxillae do not exhibit dimorphism.

The maxilliped is one of the diagnostic structures of the male (fig. 34, G). The appendage is the largest and most conspicuous of the mouth parts. Of the three segments, the basal one is the shortest. The second segment is stout and long, its length about double the width. The terminal segment is parallel with and appressed to the second segment and, by a complicated articulation, forms a subchelate appendage with that segment. The terminal segment is a long narrow blade, about one and one-half times the length of the second segment. A seta, of curiously modified character, is borne on the second segment. A long seta is borne on the basal portion of the terminal segment. Stout spinules, set in rows, ornament the medial surface of the second joint.

In the swimming legs the sex of adults might be determined by the more spinous ornamentation of the limbs of the males. The fringes

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of the basipodites are of heavier, more spinulelike members, particularly in the first three legs. The fourth pair is more like that of the female. A further feature of the first three legs is the prolongation of the distal medial corner of the second segment of the endopodite into a long, stout spinous process. This is not a true spine, as it lacks an articulation at the base and is therefore a direct extension of the integument of the podomere proper. These spinous processes are equivalent in size to the true, articulated spines, however. The contrast between these structures in the male and female is illustrated (fig. 36, C, F) for *Paranthessius panopeae*, the species in which the dimorphism is seen most strikingly. In the original description of *Pseudolichomolgus pectinis* Pesta, the illustrations show spines on the two proximal segments of all the endopodites. If these were movable spines, this would represent an unique condition among lichomolgids. The illustrations do show a somewhat subtle differentiation of these outgrowths from the truly articulated spines in the usual positions, and I suggest that they be interpreted as spinous processes comparable to those seen in the males described here.

The male fifth leg is reduced, much shorter in proportion to width than in the female, and the outgrowths are less robust, more setiform (fig. 34, H). The lateral seta is longer than the medial.

The seventh thoracic segment of the male is much modified because of a pair of chambers containing the sperm masses. The ventral portion of the segment is prolonged posteriorly on each side, and at the lateral limit of this prolongation is the slight prominence bearing two setae that constitutes the sixth leg. The posterior border of the prolonged region is further ornamented by spinules set in row formation parallel to the margin. In the present species there are two such rows of spinules on each side, parallel to each other, the count of spinules for one side being 24 in the anterior row, 16 in the posterior row. Figure 35, G, shows the arrangement of this segment and leg for *Paranthessius panopeae*.

The terminal abdominal segment bears the rows of spinules characteristic of the species in both sexes, and there is no notable dimorphism of the caudal rami. The body length is about 1.7 mm.

Immature forms: The several specimens available of late developmental stages at first presented a puzzling complex of resemblances and differences. As will be presented in detail below, sufficient features were established to conclude that a portion of these represented the females and males of the final larval stadium (the fifth copepodid) and the remainder were of the fourth copepodid stage, in which no basis for differentiation of the sexes was discovered in the small sample considered.

Fifth copepodid. Female: The rostrum is very conspicuously developed in the 3-pronged pattern of the adult male. The lateral spines are equal to two-thirds of the length of the central beak. The appendages of the head all are identical with the adult condition. The thoracic appendages of the metasome are all identical with those of the adult. The small maxilliped establishes the specimen as a female, since the adult condition of the swimming legs is taken to be conclusive indication that this stadium is the ultimate larval copepodid.

In the urosome the characters depart from those of the adult. The fifth leg, however, approaches closely to the adult condition, although it is perhaps slightly less elongate. It is, in actual measurement, at least twice the bulk of the fifth leg of the adult male. Further, the terminal armature presents the stout medial spine, longer than the lateral seta. In the male, both adult and of this stadium, the longer member of these outgrowths is the lateral, and neither attains spinelike dimensions.

The urosome is 5-jointed, but it represents different segments from those present in the adult urosome of the same number of somites. The first segment is the sixth thoracic somite, bearing the fifth legs. The second segment is the seventh thoracic somite; it is thus established by the presence at its posterior margin of a spinule row and one seta, comparing incompletely but satisfactorily to the sixth leg armature of the adult male. The adult male, and also that of the fifth copepodid stadium, show two setae for this member. In this subadult female, the spinule row is but a single set of about 20 spinules on each side as compared to the pair of double rows of the corresponding male.

Three abdominal somites complete the urosome. Of these, the terminal one is the longest. This segment bears the characteristic pair of rows of spinules, exhibiting but eleven spinules on either side in the specimen examined. The proportion of length of segments is significant as it indicates clearly the rearrangement of segmentation of the urosome that takes place during the final molt. The result of this molt is a urosome in which the terminal thoracic segment and the first abdominal somite are fused into the very long genital segment. In this modification, all the ornamentation of the sixth leg disappears (except perhaps a reduced seta or two very inconspicuously placed at the openings of the oviducts). In the adult, the most proximal of the three abdominal segments is the longest, and this fact indicates that the terminal segment of the fifth copepodid is subdivided in the final molt.

The caudal rami of the fifth copepodid are stubbier than those of the adult. The proportion of length to width is about 3.3. The length of the body measures 1.4 mm.

Fifth copepodid. Male: The subadult condition of this male is patent in the 5-segmented urosome, which conforms in proportion and arrangement exactly to that of the female of the same stadium.

The fifth leg is comparable to that of the adult male. The longer of the terminal setae is lateral. The structures of the seventh thoracic somite are the two setae of the sixth leg and two pairs of rows of spinules, as in the adult.

The metasome of the subadult male exhibits some diagnostic features. The maxillipeds, while they are by far the most developed of the mouth parts, lack the free, subcheliform terminal segment of the adult. Two such maxillipeds (fig. 34, I, J) show the sequence of development of this appendage at an early stage and a later period within the same stadium. In the early copepodid of stage five, there is no indication of the elongate terminal claw (fig. 34, I). A globose end segment is the forerunner of the claw, however, as is seen in the second example where, under the cuticle, can be made out the features of the adult condition, about to be uncovered by the imminent final molt.

In the swimming legs the spinous processes of the distal medial corners of the second endopodite segments to be seen in the adult are here lacking. The segmentation of the rami and the complement of spines and setae are identical with those of the adult.

Length, exclusive of setae of the caudal rami, is about 1.4 mm.

Fourth copepodid. The metasome has the degree of segmentation seen in the adult. The rostrum shows very great development of the lateral spines, these being equal to more than three-fourths of the length of the central beak. The antennules, antennae, and mouth parts are as in the adult female. Figure 34, K, shows the arrangement of the mouth parts, the very large basal segment of the maxilla nearly obscuring the much reduced maxillipeds.

The swimming legs are 2-jointed and the complement of spines and setae of the adult is not attained, as the following representation of the armature of these appendages demonstrates:

First leg, exopodite: First segment—lateral spine; second segment—four spines, four setae. Endopodite: first segment—medial seta; second segment—one spine, six setae.

Second leg, exopodite: First segment—lateral spine; second segment—four spines, five setae. Endopodite: first segment—medial seta; second segment—three spines, five setae.

Third leg, exopodite: First segment—lateral spine; second segment—four spines, five setae. Endopodite: first segment—medial seta; second segment—three spines, three setae.

Fourth leg, exopodite: First segment—lateral spine; second segment—four spines, five setae. Endopodite: first segment—medial seta; second segment—two spines, one seta.

It will be noted that, while the full armature of the adult limb is not present in this larval state, there are included in the complement of the terminal segment spines or setae which finally appear, in the adult stadium, on the second segment.

The urosome is 4-segmented, composed of the sixth and seventh thoracic segments and two abdominal somites. Of these latter, the terminal segment is the longer. The fifth legs are short, the length equalling about one and one-half times the width. Of the terminal setae, the lateral is much the longer. The sixth leg is represented by a single seta. The single pair of spinule rows of the seventh thoracic segment comprise about twenty spinules on each side (fig. 34, L).

The caudal rami are relatively short and wide; the ratio of length to width is about 2.6. Total body length, exclusive of setae of caudal rami, is about 0.9 mm. No characters for differentiation of the sexes were found.

Remarks.—The single specimen upon which this species was founded was taken swimming in the plankton in the Puget Sound region. It was diagnosed as a male in the original description, with, however, one lapse where it was referred to as female in the legend for the illustrations (p. 90). The character that convinced the describer of the generic distinctness of the species was the 2-segmented rami of the swimming legs. This feature, together with the spine shown on the genital segment and the general configuration of the rostrum in the figures of the type, I find ample evidence to identify Thompson's specimen with the fourth copepodid developmental stage, as borne out by the series of specimens available to me which I consider to represent the same species. Additional information from my series serves to explain some other apparently anomalous features of Thompson's description.

The following are the characters in which Thompson's description and figures agree with my specimens:

The rostrum and antennules are alike in these two instances and are unique for the genus *Paranthessius*. The antennae, mandibles, maxillules, and the terminal portions of the maxillae correspond reasonably well. The maxilliped described by Thompson and illustrated as his figure 8 resembles no such structure known among the lichomolgids. However, reference to the mouth parts figured here as figure 34, K, may serve to explain this appendage. The base of the maxilla, with its very obvious muscle band, if the terminal portion were torn away and the line of this disruption misinterpreted as part of the natural boundary, might very well be delineated in exactly the appearance of Thompson's figure. Also, the maxillipeds are so inconspicuous and so overshadowed by these enlarged maxillae that it would be very easy to overlook them in a single dissection.

The first and fourth swimming legs are figured by Thompson and, in segmentation and arrangement of ornamentation, conform exactly to my description above.

The fifth feet present a discrepancy, Thompson's figure depicting a longer medial terminal seta. Whether great pains were taken to depict this feature exactly in an illustration (Thompson, fig. 1) obviously designed to present the body habit of the copepod rather than details of its anatomy might be subject to question.

Three abdominal segments are shown in Thompson's illustration (fig. 1), with a row of spines depicted along the boundary of the second and third segments. I suggest that the spinules present on the undivided terminal segment in my specimens could be readily so misinterpreted in casual observation. The seta of the sixth leg corresponds in the two instances.

The length (1.98 mm.) given by Thompson is greatly at variance with my specimens. He does not state whether the caudal setae are included in the measurement, but these structures are much less than half the body length in extent and could not account for the discrepancy seen. It may be that Thompson studied a specimen of a species different from my examples, but there are so many points by which I can reconcile these with his description that I do not deem it advisable to add a new name for representatives of this genus.

The specimens I have examined, including ovigerous females, adult males, and immature stages were taken as commensals or parasites upon the gills of clams. I have specimens collected from the mudflats near the mouth of Tomales Bay, Marin County, Calif., and additional examples from the similar situation nearby, Bodega Bay, Sonoma County, Calif. Further information as to the extent of occurrence of the copepod and the seasonal fluctuation of incidence and abundance would be of considerable interest. The thorough work of MacGinitie (1935) on the population of Elkhorn Slough, Monterey County, Calif., did not discover the presence of *Paranthessius columbiae*, although the abundantly occurring principal host was sufficiently scrutinized to bring forth numerous records of the encysted larvae of tapeworms. Even so inconspicuous a copepod could not have eluded such search. From observation of the living animals *in situ* upon the host, I can attest the great transparency and nearly complete invisibility of this copepod. Even under close scrutiny of the gills of the mollusk no more than a minute dark thread of about a millimeter or two in length betrays the parasite. This thread is the gut, which has a heavy wall. Whether the dark color is pigmentation of the wall itself or a property of the contents of the gut, I did not determine upon living copepods, and in preserved specimens the coloration rapidly disappeared.

The occurrence of Thompson's specimen in the plankton is not difficult of explanation. It is a frequent phenomenon for lichomolgids to leave the host for varying periods, and numerous species have been described that have never been taken in association with another organism. Several records of *Paranthessius rostratus* are derived from collections of plankton from waters above cockle beds where the mollusks are infested by this species. In the case of *Paranthessius columbiae* I have recovered a male individual of the fifth copepodid stadium from washings of the red alga, which almost invariably occurs as dense tufts on the heavy siphon plates of *Schizothaerus nuttallii* of Tomales Bay. The amount of migration of the adults and the relative wanderings of the larval stages would be interesting details to supply in a complete biological investigation of this copepod. Large scale surveys of the mollusk fauna of a given locality should provide information of great interest in regard to the limits of specific infestation of given hosts.

PARANTHESSIUS PANOPEAE, new species

FIGURES 35, 36

Specimens examined.—Fourteen adult females, nine adult males, one female of the fifth copepodid stadium, from a single specimen of *Panope generosa* Gould, collected in Tomales Bay, Marin County, Calif., May 23, 1943, P. L. Illg, collector.

Types have been assigned the following United States National Museum catalog numbers: Holotypic female, 85343; allotypic male, 85344.

Description.—FEMALE: The body is elongated although not so extremely as in *P. columbiae.* The metasome consists of five somites. The cephalothorax is the longest segment. The relative lengths of the succeeding somites are in the order of their arrangement, as are also their relative widths. The somite of the first swimming legs is the widest somite of the metasome (fig. 35, A).

The urosome is 5-segmented, consisting of the sixth thoracic somite, the genital somite, and three free abdominal segments. The ovisacs are narrow, closely appressed to the abdomen, and elongate, reaching to the ends of the caudal rami. The eggs are small; a single ovisac contains a hundred or more eggs.

The rostrum is a long, pointed beak, directed posteriorly. It is movable, and the supporting structures on the head are associated with the bases of the antennules and antennae. There are no lateral auxiliary projections (fig. 36, A).

The antennule (fig. 36, A) is long and slender; it comprises seven segments. The second segment is the longest. The setal armature is as follows: First segment—four setae; second segment—nine setae; third segment—four setae; fourth segment—three setae; fifth seg-

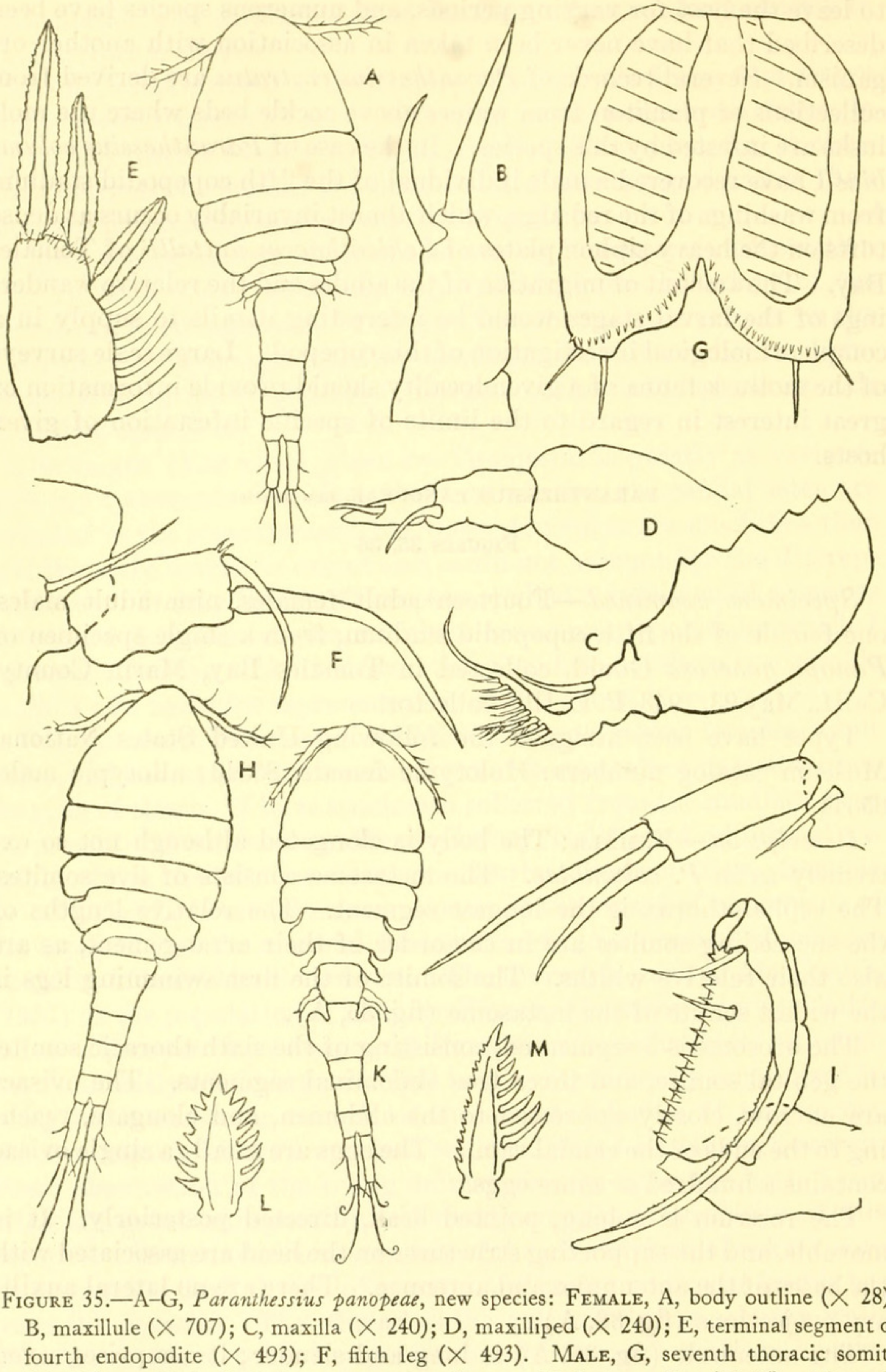

FIGURE 35.—A–G, *Paranthessius panopeae*, new species: FEMALE, A, body outline (× 28); B, maxillule (× 707); C, maxilla (× 240); D, maxilliped (× 240); E, terminal segment of fourth endopodite (× 493); F, fifth leg (× 493). MALE, G, seventh thoracic somite (× 167). H–J, *P. tivelae*, new species: FEMALE, H, body outline (× 45). MALE, I, maxilliped (× 240); J, fifth leg (× 707). K–M, *P. perplexus*, new species: FEMALE, K, body outline (× 43); L, spine of basal segment of first exopodite (× 424); M, spine of second segment of first exopodite (× 424).

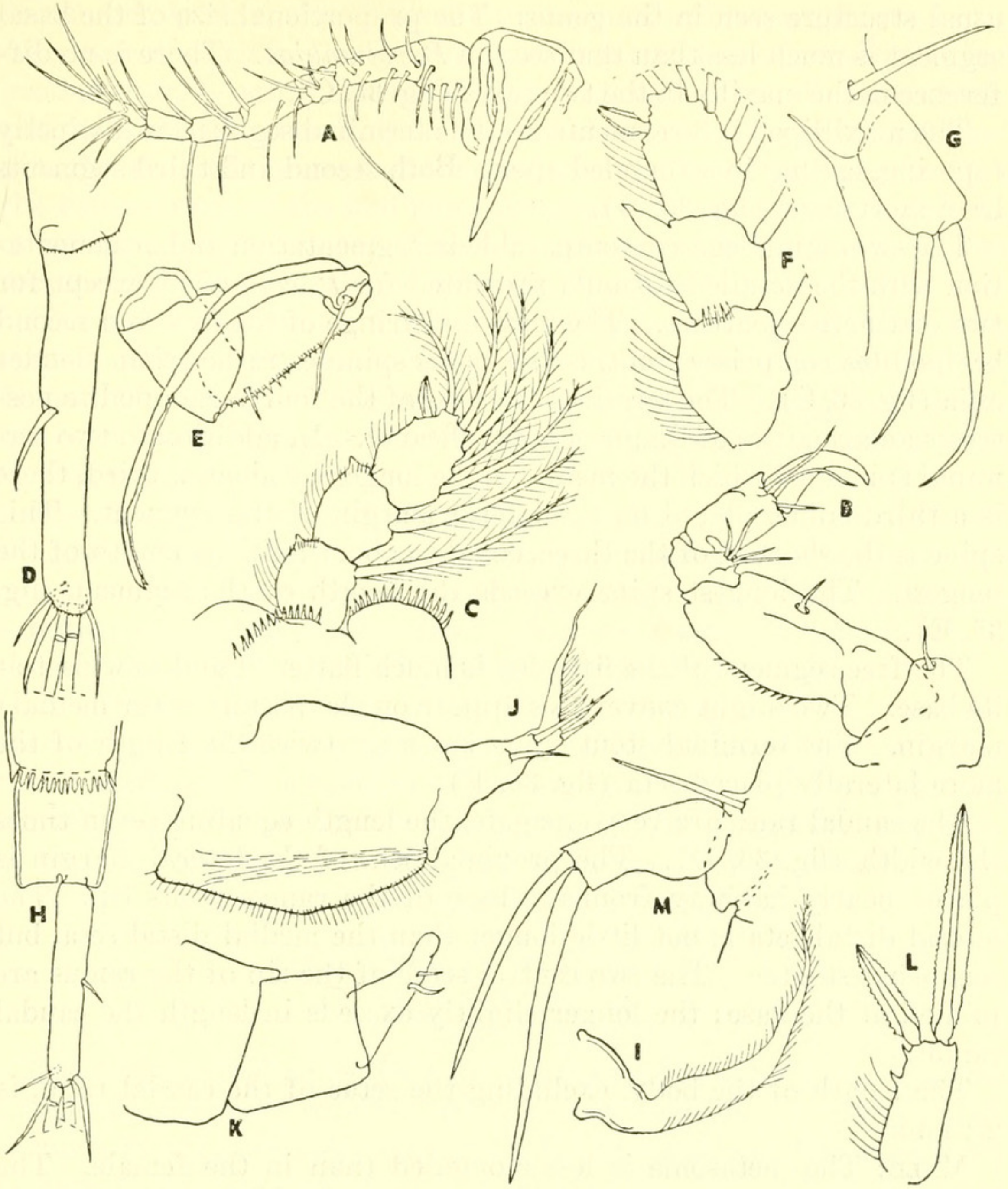

FIGURE 36.—A–G, *Paranthessius panopeae*, new species: FEMALE, A, rostrum and antennule (× 100); B, antenna (× 144); C, first leg (× 296); D, caudal ramus (× 296). MALE, E, maxilliped (× 144); F, first leg (× 296); G, fifth leg (× 424). H–M, *P. tivelae*, new species: FEMALE, H, last abdominal somite and caudal ramus (× 144); I, mandible (× 424); J, maxilla (× 424); K, maxilliped (× 424); L, terminal segment of fourth endopodite (× 296); M, fifth leg (× 424).

ment—four setae; sixth segment—three setae; seventh segment—eight setae.

The antenna is very stout, 4-segmented. The relations of its parts are better presented by figure than by description (fig. 36, B).

The mandible is like that of the other species described here. The maxillule is a single, flattened segment, bearing two stout, spiniform setae terminally (fig. 35, B). The maxilla does not depart from the usual structure seen in the genus. The proportional size of the basal segment is much less than that seen in *P. columbiae*. There is no difference in the maxilla in the two sexes (fig. 35, C).

The maxilliped is 3-segmented. The terminal segment is distinctly tapering, ending in a rounded apex. Both second and third segments bear short setae (fig. 35, D).

The swimming legs are comparable in segmentation and ornamentation with the detailed formula presented for *P. columbiae* except for two distinctive features. The marginal fringe of the first and second basipodites comprises stout, conspicuous spinules rather than slender cilia (fig. 36, C). The terminal segment of the fourth endopodite possesses an armature of diagnostic significance. In addition to two terminal spines, of which the medial is the longer by about a third, there is a third spine, placed on the lateral margin of the segment. This spine is the shortest of the three, equal to about half the length of the longest. The longest spine exceeds the length of the segment (fig. 35, E).

The free segment of the fifth leg is much flattened and is widest at its base. Two slight convexities appear on the posterior (or medial) margin. The terminal stout spine is nearly twice the length of the more laterally placed seta (fig. 35, F).

The caudal rami are very elongate, the length equaling seven times the width (fig. 36, D). The proximal seta of the lateral margin is placed nearly halfway from the base of the ramus to its tip. The lateral distal seta is but little longer than the medial distal seta, but somewhat stouter. The two central setae of the tip of the ramus are jointed at the base; the longer slightly exceeds in length the caudal ramus.

The length of the body, excluding the setae of the caudal rami, is 2.1 mm.

Male: The metasome is less elongated than in the female. The urosome is 6-segmented. The rostrum, antennule, antennae, and cephalic mouth parts are just as in the female. The maxillipeds are of the characteristic male subcheliform construction. The basal segment is very wide. The second segment is less than twice as long as wide. It bears a seta and a row of spines along the medial surface. The terminal segment is the usual slender arc, its length exceeding twice that of the second segment (fig. 36, E).

The first three pairs of swimming legs exhibit on the distal lateral corner of the second segment of the exopodite a great prolongation of the integument into a large spinous process, which is differentiated from a true spine by its lack of a joint or articulation with the main body of the podomere. On the first leg this process equals in dimension the articulated spine of the distal segment (fig. 36, F). On the fourth endopodite, this tendency to the production of spinous processes is less extreme, the appropriate corner in this appendage being produced only into a short, thornlike denticle of small dimensions. Somewhat similar, small, thornlike denticles occur on the lateral margin of the distal segment of this ramus, one placed just proximal to the base of each of the two more proximal spines. A further slight deviation in this podomere from the female condition is seen in the relatively greater length and slenderness of its spines.

The usual dimorphism of the lichomolgid fifth leg is seen in this species. The free segment is shorter and narrower than that of the female (fig. 36, G). The terminal armature is strikingly different, the setae being subequal in proportions with the lateral one slightly the longer.

The ornamentation of the seventh thoracic segment is typical for the genus (fig. 35, G). The pair of rows of spinules exhibit about 18 spinules on each side. The armature of the sixth leg comprises two subequal setae. The caudal rami differ in no essential from those of the female. The total length of the body is about 1.8 mm.

Immature stage: Female of the fifth copepodid stadium. A single specimen of this stage was available and it was not subjected to detailed study, as it presented the diagnostic features of the species, slightly modified by the characteristics of the developmental state, as has been described here in detail in the cases of *P. columbiae* and *P. tivelae*. The length of the specimen is 1.6 mm.

PARANTHESSIUS TIVELAE, new species

Figures 35, 36

Specimens examined.—Nine adult females, one adult male, thirteen immature specimens obtained from a single specimen of *Tivela stultorum* (Mawe), collected at La Selva Beach, Monterey Bay, Monterey County, Calif., June 13, 1943, P. L. Illg.

Types have been assigned the following United States National Museum catalog numbers: Holotypic female, 85346; allotypic male, 85345.

Description.—Female: The proportions of the metasome conform fairly closely to the oval configuration of the typical cyclopoid (fig. 35, H). The cephalothorax includes the segment of the maxillipeds; the somites of the four swimming legs comprise the remainder of the 5-segmented metasome. The lateral portions of the segments of the swimming legs are produced posteriorly as rounded lobes.

The urosome is of the usual five segments. Distinctive of the species are the coarsely serrate posterior margins of the abdominal segments, with the exception of the terminal segment. These serrations comprise very long toothlike shreds of the integument, arranged roughly as alternate wide and narrow spinules (fig. 36, H).

The egg sacs are elongate in this species, reaching to the caudal rami. The eggs are large. Each ovisac contains about 30 eggs.

The rostrum and antennules conform very closely to the condition figured for *P. panopeae*. The terminal segments of the antennule exhibit a slight degree of specific differentiation, however; in *P. tivelae* the sixth segment is longer than the fifth; in *P. panopeae* the proportion is reversed.

The antenna conforms almost exactly in proportions to that of *P. columbiae*.

The mandible is a very generalized one, its gradual taper and very simplified ornamentation of marginal cilia suiting it to exemplification as the typical form of the appendage for the genus or even for the family (fig. 36, I). The maxillule differs only in subtle and insignificant particulars of outline from that already illustrated for *P. columbiae*. It is a simplified, flat, tapering plate with two terminal setae. The maxilla, like the mandible, may be considered as generalized in construction (fig. 36, J). The well-developed base does not show the extreme enlargement that characterizes this appendage in *P. columbiae*. In the present species, the length of the basal segment but little exceeds its width. The terminal segment differs from the other species in the present collection by the lack of ornamentation of the more distal of the setae on the anterior surface. In the other species there are fine spinules or cilia arranged along one or both margins of the seta. Such simple setae are found in this position in some other members of the genus. In all the species, the more proximal of the two setae of this segment is always without ornamentation.

The maxilliped is distinctive in *P. tivelae* (fig. 36, K). The articulation with the head is so complicated that it is impossible from my preparations to say with certainty whether the appendage is 2- or 3-segmented. The terminal segment is conical, with pronounced rounding of the tip. This segment bears two minute setae. The segment next proximal (basal segment?) is subquadrate, of very great width in proportion to its length.

The swimming legs are all by generic definition 3-jointed in both rami. The number and distribution of the spines and setae are exactly those presented above for *P. columbiae*. Characteristic minor features of these limbs for the species are the following, however: The basipodite of the first legs bears a marginal fringe of very stout spinules (as illustrated for the male of *P. panopeae*). On the bases of all the other legs, this fringe is comprised of well-developed cilia, much more slender and delicate in configuration than the robust spinules, although of about equal length. Very stoutly developed spinous processes of the integument are placed on the distal lateral corners of the middle segments of the endopodites of the first and second legs. These processes are nearly as highly developed as those described for the males of the other species of the present collection. In the third and fourth endopodites, there are thornlike, short, spinous projections in the corresponding position, but these do not show the prolongation into long outgrowths like those of the first two legs. The terminal segment of the fourth endopodite is an identifying structure in this species (fig. 36, L). The edges of the segment are nearly parallel. Two small thornlike processes (spinules or denticles) on the lateral margin are characteristic. The more proximal spinule is placed at a point two-thirds the length of the margin from the base of the segment. The distal spinule is at the base of the terminal spine.

The fifth leg bears a resemblance to that of *P. saxidomi* in the inflation of the posterior proximal margin of the free segment. However, the terminal spine of this species is twice the length of the segment (in *P. saxidomi* the spine is little more than one and one-half times the length of the segment). As in the other species, the spine is the more posterior outgrowth of the free segment. This spine of *P. tivelae*, further, exceeds the accompanying seta by one sixth of its own length (fig. 36, M).

The caudal rami are about five and one-half times as long as wide (fig. 36, H). The lateral proximal seta is inserted slightly short of half the distance from the base to the tip of the ramus. The most medial terminal seta is longer than the lateral apical seta. The two central setae of the four at the tip of the ramus are jointed at their bases. The longer of these two is about two and one-half times the length of the ramus. No seta of the caudal rami exhibits ciliation of its margins. The total length of the body, excluding the caudal setae, is 1.3 mm.

Male: The shape of the body and the segmentation present the usual dimorphism characteristic of this group of copepods. The cephalic appendages correspond to those of the female. The basal segment of the prehensile maxilliped bears a weakly produced spinous projection at the posterior medial corner. The length of the second segment is roughly twice the width. A simple row of conspicuous spinules forms a border along the medial margin of the segment. The long claw comprising the terminal joint is twice the length of the second segment (fig. 35, I).

The swimming legs conform more closely to the female type than is usually the case in the other species in the present collection. There is an accentuation of the spinous nature of the marginal fringes of the basipodites and the spinous processes of the endopodites are somewhat longer and more robust.

The margins of the free segment of the fifth leg are parallel. Both terminal outgrowths are setiform; of these, the posterior is much the shorter (fig. 35, J). The sixth legs are represented only by two setae. The ornamentation of the last thoracic segment is a pair of rows of spinules, about thirty spinules comprising the row on either side. The heavily spinous serrations of the posterior margins of the abdominal somites are like those in the female. There is no feature of the caudal rami exhibiting any considerable dimorphism. The total length of the body, exclusive of the setae of the caudal rami, is about 1.1 mm.

Immature stage: Female copepodid of the fifth stadium. The metasome presents no point of difference in its contours or its complement of appendages from the condition of the adult female, except its slightly smaller size. The urosome is very different from the adult condition. The five segments comprise the last two thoracic segments and three abdominal segments. Of these latter, the terminal segment is the longest. This proportion anticipates the final molt in which the first abdominal segment becomes fused to the last thoracic segment and a subdivision of the terminal somite restores the number of free abdominal segments to three. The two anterior abdominal segments present have the coarse serration of the posterior margins which is characteristic of the adults of the species. The caudal rami are not so long in proportion to width as is the case in the adult, but the general aspect of arrangement of the ornamentation shows no significant difference.

The fifth legs are just like those of the adult male. This is a strong contrast to the condition in *P. columbiae*, where in the fifth copepodid this appendage is recognizable as of the female type. The proportion of the length to width of the free segment of the fifth leg is about that seen in the male. The more posterior (medial) of the terminal setae is much shorter than the anterior (lateral) seta. The terminal thoracic segment bears a small seta at each posterior lateral corner of the ventral side, representing the reduced sixth leg. An additional ornamentation of the segment is a pair of rows of fine, short spinules extending across the ventral surface parallel with and close to the posterior ventral margin of the segment.

The total length of the body, exclusive of the caudal setae, is 1 mm.

PARANTHESSIUS SAXIDOMI, new species

Figure 37

Specimens examined.—Six adult females, three adult males, twenty-two copepodids of the fourth and fifth stadia obtained from several specimens of *Saxidomus nuttallii* Conrad, collected in Tomales Bay, Marin County, Calif., May 23, 1943, P. L. Illg.

Types have been assigned the following United States National Museum catalog numbers: Holotypic female, 85341; allotypic male, 85342.

Description.—Female: The metasome is very wide in proportion to its length, presenting a suborbicular outline (fig. 37, A). The

Figure 37.—A–H, *Paranthessius saxidomi*, new species: Female, A, body outline (× 25); B, antenna (× 144); C, maxilliped (× 684); D, terminal segment of fourth endopodite (× 296); E, fifth leg (× 296); F, caudal ramus (× 144). Male, G, maxilliped (× 296); H, fifth leg (× 684). I–P, *P. perplexus*, new species: Female, I, rostrum (× 296); J, antennule (× 144); K, antenna (× 144); L, mandible (× 424); M, maxilliped (× 296); N, terminal segment of fourth endopodite (× 296); O, fifth leg (× 296); P, caudal ramus (× 144).

greatest width is seen in the second segment of the metasome, which segment is that of the first swimming legs. The third metasome segment has the posterior lateral margins strongly produced caudad as rounded lobes. The urosome is 5-segmented, with no ornamentation of spinules. The metasome slightly exceeds the urosome in length.

The rostrum is distinctive in this species. At the anterior limit of the structure, there is great lateral expansion, equivalent to that seen in *P. columbiae*. There is here, however, no further production of the structure into auxiliary knobs or spines like those seen in the previously described form.

The antennules are of generalized structure, departing only in insignificant details from the appendage as described and figured above for *P. panopeae*. In the present species, there is a heavier chitinization of the anterior and posterior margins of the more proximal segments.

The distinction of the antenna from that of the species described above must be principally on subtle variations of the proportions of the component segments. A pronounced proximal constriction of the second segment produces a distinctive club-shaped contour (fig. 37, B).

The mouth parts resemble those in the species heretofore described. The most notable feature is the extreme reduction of the maxilliped. It retains the usual three segments (fig. 37, C), but the size is reduced so greatly that the sum of the lengths of the three segments is less than half the length of the basal segment of the maxilla. The basal segment is expanded and articulates with a complex set of very heavily chitinized ridges on the ventral surface of the head.

The rami of the swimming legs are all 3-segmented. The complement of spines and setae is exactly that presented in detail above for *P. columbiae*. The ornamentation of the terminal segment of the fourth endopodite is distinctive. The very long medial spine is nearly two and one-half times longer than the lateral spine (fig. 37, D). The basipodites of the first three pairs of swimming legs bear the usual marginal fringes, but they are composed in this species of exceptionally stout, numerous spinules. The fourth basipodite is fringed by sparsely distributed, short, fine cilia.

The outline of the fifth leg presents a rounded expansion at the base (fig. 37, E). The terminal outgrowths are relatively short, subequal, the more posterior (medial) stouter and more spinelike.

The caudal rami are of moderate length (fig. 37, F). The ratio of length to greatest width is about 3.5. The proximal lateral seta is articulated at a point well short of half the length of the ramus. The two elongate, central apical setae are jointed at their bases. The longer of the two is more than three times the length of the ramus. None of the setae of the caudal ramus is ciliated.

The total length of the body, exclusive of the terminal setae of the caudal rami, measures about 1.7 mm.

MALE: The metasome is not so inflated in outline as that of the female. The segmentation (five joints) is the same in the two sexes. As is usual, the urosome of the male is 6-segmented. The rostrum, antennules, and cephalic mouth parts are not distinctly different in the two sexes. The maxillipeds present the most conspicuous ornamentation among the species considered here (fig. 37, G). A large posteriorly and medially directed spinous process forms a prolongation of the basal segment. The second segment bears a modified seta, recalling that seen in *P. columbiae*. Unusually stout and numerous spinules ornament the medial margin of the second segment (several rows of small spinules on the ventral surface of that segment are not depicted in the illustration because of the confusion of detail that would result).

In the swimming legs there is the same development of spinous processes on the endopodites of the first three legs as in the preceding species.

The fifth leg is much reduced by comparison to the female structure. The basal portion of the free segment is constricted somewhat. No preparation was obtained which preserved both the terminal setae. That observed and figured (fig. 37, H) is the more posterior, and it is a fairly stout and notably shortened spinelike outgrowth.

The sixth legs are represented by the usual two setae. On the flaplike extension of the body somite are borne two pairs of rows of spinules (recalling *P. columbiae*). The more anterior row comprises about 22 spinules on each side, the posterior row about 15 spinules on each side.

The abdomen, except for its characteristically male segmentation, exhibits no other features differentiating it from that of the female. The total length of the body is 1.2 mm.

PARANTHESSIUS PERPLEXUS, new species

FIGURES 35, 37

Specimens examined.—Two adult females, from gills of *Saxidomus nuttallii* Conrad, in association with numerous specimens of *P. saxidomi*. Collected at Tomales Bay, Marin County, Calif., May 23, 1943, P. L. Illg.

The holotypic female has been designated U. S. N. M. No. 85347.

Description.—FEMALE: The body configuration is distinctive (fig. 35, K). The 5-segmented metasome is not exceptional, its narrowly oval contour being of the generalized cyclopoid facies. The urosome is of the usual five segments. The contour of the genital segment is characteristic for the species. An ellipsoid process, with free rounded anterior extremity, is extended laterally from each side, the lobes thus produced each nearly equaling in width the central portion of the segment. The width of the segment, by this lateral extension, considerably exceeds its length. The urosome is slightly shorter than the metasome. The margins of the abdominal somites are entire, exhibiting no denticulation or spinous serration.

The rostrum and associated structures are exceptional, unique in form among members of the genus that I have seen (fig. 37, I). The usual beaklike spine is absent; the front of the head is produced ventrally and somewhat posteriorly in a rounded lobe. The usual basal chitinous plate extending posteriorly between the bases of the antennules and antennae presents a remarkable modification. At a level just back of the bases of the antennules, this structure is produced ventrally as an elongate, terminally bifurcate projection. The aspect is of rather soft and flexible consistency of the thin chitinous integument. The usual chitinous bars of this region are represented posterior to this bilobed structure as a narrow bar, divergent posteriorly in the shape of an inverted Y.

The antennules are 7-segmented. The margins are rather irregular in outline and show no indication of the chitinous reinforcements seen in some of the species described above. The sixth and seventh segments are unusually short in proportion to their width. All the details of setal armature that could be made out on the two available specimens are presented in the accompanying figure (fig. 37, J).

The antennae are very stocky in general aspect by comparison with the other species described here. The length of the second segment is considerably less than twice the greatest width. In the other species seen the ratio of length to width of this segment is much greater than 2. In the details of ornamentation the appendage does not differ significantly from that of the other species (fig. 37, K).

The mandibles exhibit an expansion of the basal portion of the flat ciliated blade that approaches in appearance the mandible of some of the species of *Lichomolgus* (fig. 37, L). This contour is the only such instance among the members of *Paranthessius* that I have seen, but its significance can be hardly more than a verification of the rather close systematic relationship of the genera. The maxillule is like that of the other species described above. The maxilla is of generalized appearance, sufficiently resembling that of *P. tivelae* to require no separate illustration. However, in *P. perplexus* the more distal of the two setae of the terminal segment of the maxilla bears the usual fringe of fairly heavy cilia along its distal margin as in the remainder of the species treated here.

The maxilliped is developed to a degree remarkable among the members of the genus. Here it is the most conspicuous of the mouth parts, very considerably exceeding in its dimensions the maxilla, which is usually the most prominent oral appendage. The basal segment is long and is expanded basally in its complicated articulation with the surface of the head. The exact proximal limit of the appendage could not be made out. The second segment is the longest. It has rather irregular contours with a slight inflation of outline toward its center. A single minute seta is borne slightly distal to the center. The distal segment is a short cone bearing at its apex a small, articulated hook. It would be a matter of opinion to interpret the hook as a dactylar segment or, alternatively, as a process of the usual 3-jointed appendage (fig. 37, M).

The swimming legs have the same distribution of spines and setae as has been given above for *P. columbiae.* A most distinctive feature of the first legs is the modification of the more proximal spines of the exopodite. The spine of the first joint of this ramus is expanded and flattened in the plane of the appendage and both margins consist of rows of elongate, highly developed, secondary denticles (fig. 35, L). The spine of the second segment and the three more proximal spines of the terminal segment all exhibit the same flattening. In these spines, however, the pectinate denticles are restricted to the more proximal margin (fig. 35, M). The distal margins of these spines exhibit the coarsely serrated, almost transparent laminae that are seen on the spines of all the species of *Paranthessius* considered here.

The apical segment of the fourth endopodite bears terminally two subequal spines. The medial spine exceeds the lateral one by about one-sixth of its own length. Both spines are very stout (fig. 37, N).

The fifth leg is peculiar to the species. The free segment is inflated and larger basally than distally. At about one-third of the length of the segment from the base there is a pronounced constriction. Of the terminal outgrowths, the more anterior is the stouter and longer (fig. 37, O).

The abdominal somites exhibit no spinous ornamentation. The caudal rami are about six times as long as wide (fig. 37, P). The proximal lateral seta is inserted just midway on the lateral margin. Of the four terminal setae, the more lateral is longer than the medial seta. The two central setae are jointed basally. At the distal extremity these two setae tend to curl into loose spirals. The longest seta is about one and one-half times the length of the ramus. None of the setae bears ciliation. The length of the body, exclusive of the caudal setae, is 1.3 mm.

No male was found.

SUMMARY

The genus *Paranthessius* Claus, 1889, is reviewed and redefined to include species formerly assigned to *Diogenidium* Edwards, *Herrmannella* Canu, *Lichomolgus* Thorell (part), *Pseudolichomolgus* Thompson, *Pseudolichomolgus* Pesta, and *Pestalichomolgus* Wilson. A key to the 18 species is presented, with synonymies and a compilation of the published distribution.

Representatives of the genus have been found in semiparasitic or commensal association with a number of common clams of the Pacific coast. *Paranthessius columbiae* (Thompson) was taken from the gaper clam, *Schizothaerus nuttallii* (Conrad), and from *Protothaca tenerrima* (Carpenter).

New species are *Paranthessius panopeae*, from the geoduck, *Panope generosa* Gould; *P. tivelae* from the pismo clam, *Tivela stultorum* (Mawe); and *P. saxidomi* and *P. perplexus* from the Washington clam, *Saxidomus nuttallii* Conrad.

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