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Some Gastrodelphyid Copepods from the Pacific Coast of North America

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INTRODUCTION

The copepods of the family Gastrodelphyidae are all symbionts of polychaete worms of the family Sabellidae. Although gastrodelphyid copepods have been known for more than one hundred years, only one species has thus far been described from North America [Sabellacheres dalesi Green, 1961, from tentacles of Eudistylia polymorpha (Johnson) at Zuma Beach, California]. All other reports are from Scandinavian, European, and Russian seas and include only those of Michael Sars (1862) for Chonephilus dispar from Chone papillosa Sars [= Euchone papillosa (Sars)] and Sabellacheres gracilis from Myxicola sarsii Kröyer [=Myxicola infundibulum (Rénier)] both from near Tromsø, Norway, Graeffe (1883) for Gastrodelphys clausii from Distylia josephinae Grube [=Bispira volutacornis (Montagu)] collected in the Bay of Muggia near Trieste, List (1890a) for Gastrodelphys myxicolae from Myxicola infundibulum Grube [= Myxicola infundibulum (Rénier)] from the Adriatic Sea near Trieste, and Markewitsch (1940) for Vermiclavella elongata [=Sabellacheres gracilis Sars] from Myxicola sp. at the Murman Coast, Kola Peninsula, Russia.

The present paper is devoted to the details of the external anatomy, life cycle, and biology of gastrodelphyid copepods associated with sabellid polychaetes from the San Juan Archipelago, State of Washington. Two new species are described. Specimens of *Sabellacheres gracilis* from Washing-

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ton and Sabellacheres dalesi from California are treated comparatively, and the males of these species are described for the first time.

It is a pleasure to thank Dr. R. P. Dales for his help in the identification of some polychaete hosts, Mr. Sigurd Olsen for assistance in the translation of some Scandinavian literature relating to the gastrodelphyids, and Mr. J. G. Gonor for specimens of Sabellacheres dalesi. I also wish to express my sincere appreciation to Dr. Robert L. Fernald, Director, University of Washington Marine Laboratories, Friday Harbor, Washington, for the use of laboratory facilities during this work, and to Dr. Paul L. Illg of the University of Washington for his help and inspiring interest in all phases of this study.

The following abbreviations are used to refer to institutions in the present paper:

A.M.N.H., the American Museum of Natural History U.S.N.M., United States National Museum, Smithsonian Institution

SYSTEMATIC ACCOUNT

List (1890a) erected the family Gastrodelphyidae to accommodate his new species, Gastrodelphys myxicolae, and Gastrodelphys clausii Graeffe, which he redescribed. List recognized that Sabellacheres gracilis which Michael Sars described briefly in 1862, but never illustrated, should also be included in this family—an astute observation which has proved to be true on the basis of more modern investigations. Vermiclavella elongata Markewitsch, 1940, is without doubt a synonym of Sabellacheres gracilis Sars.

It is surprising that Chonephilus dispar which was also briefly described by Michael Sars (1862) and which apparently exhibits many features similar to those of Sabellacheres gracilis has never been placed in the family Gastrodelphyidae. Although I propose that Chonephilus dispar shows definite alliance with this group, it must remain an indeterminable species since it has not been rediscovered since the time of the original description and was never illustrated. It is interesting that if the genus Chonephilus should prove to be congeneric with Sabellacheres, it has page priority.

The species Sabellacheres dalesi described by Green (1961) complicates the taxonomic picture of the family, since this species is intermediate in many respects to the species of Sabellacheres and the species of Gastrodelphys. Green, after careful study of his species, recognized that all the previously described forms and his new species might be congeneric and, if so, all would be species of the genus Sabellacheres Sars. It seemed preferable to him, however, to retain the genus Gastrodelphys for species with reduced

swimming legs, and he accordingly placed his species that possesses three pairs of biramous swimming legs in the genus Sabellacheres.

It is my opinion, too, that all the species previously described and the new species that is described below might well ultimately prove to be members of a single broad generic complex. However, there has been so little study of the group that I believe it would be premature to make all the species congeneric at this time. The species of gastrodelphyids do seem to fall into two groups with respect to their habits of life on their particular hosts and to adaptive structural modifications associated with these habits. Adult females and males of Gastrodelphys fernaldi, new species. live simply attached to the tentacles of the sabellid worm by their antennae and rostra and can move about. Adult females of Gastrodelphys clausii Graeffe and Gastrodelphys myxicolae List were also described as attached by their antennae and rostra, and presumably they, too, can change their positions on the tentacular crowns of their polychaete hosts. Adult females of Sabellacheres gracilis Sars and Sabellacheres illgi, new species, are embedded in the tissue of the tentacular base or oral surface of the worm and are essentially sessile. Males and developmental stages of S. gracilis and S. illgi can move about actively on the tentacles, attaching only temporarily. Appendicular modifications associated with the different habits of adult females are discussed below.

Despite the greater development of its swimming legs, Sabellacheres dalesi Green is more closely allied to the species of Gastrodelphys than to the species of Sabellacheres in habitat and in cephalosomic structure, and I, therefore, place the species in the genus Gastrodelphys as Gastrodelphys dalesi (Green). The rationale for this treatment is explored more fully below.

The diagnosis of the family Gastrodelphyidae and a key to the genera and species follow. The familial diagnosis of previous authors is emended to encompass the new species described below. The taxonomic treatment of the sabellid hosts is after Berkeley and Berkeley (1952) and Hartman (1961) for Pacific coast species and after Fauvel (1927) for European species.

FAMILY GASTRODELPHYIDAE LIST, 1890

EMENDED DIAGNOSIS: Symbionts of polychaete worms of the family Sabellidae Malmgren. Body segments obscured in females but well demarcated in males. Females of most species with brood pouch formed by fourth metasomal segment, but one species with pair of external ovisacs dependent from lateral genital openings. Urosomes of females greatly reduced in proportion to bodies. Caudal rami supporting greatly elon-

gated terminal setae. Antennules five-segmented, first two segments flattened and much larger than remaining three segments. Antennae with three or four segments, the last segment bearing one bifid hook and one simple hook. Mandibles small, S-shaped, with flattened, orally directed spinose element articulating on medial surface of proximal curvature. Distal end of mandible consisting of flat denticulate plate. Maxillules short, conical, with terminal trio of setae. Maxillae reduced to pads with medial dorsal processes. Maxillipeds lacking in females, four-segmented with terminal hook process in males. All species with post-oral plate (referred to by previous authors as the "Bauchwirbelkörper" or "sternal plate") projecting from posterior margin of cephalosome and possibly representing intercoxal plate of first thoracic segment. Plate armed with distal teeth in females of some species, but without teeth in some females and never armed with heavy teeth in males. Swimming legs varying according to species. Fifth legs lacking in all males and females.

Key to the Genera and Species of Gastrodelphyidae, Based on Adult Females 1

| | ADULT FEMALES |
|----|---|
| 1. | Antenna with four segments. Cephalosomic post-oral plate armed distally with strong teeth. With internal brood pouch or external ovisacs. Swimming legs variously reduced; third legs never with trimerous rami |
| | |
| | Antenna with three segments. Cephalosomic post-oral plate without large |
| | distal teeth. With internal brood pouch. First three pairs of swimming legs |
| | biramous and with trimerous rami |
| 2. | With external ovisacs. Two pairs of biramous swimming legs with bimerous |
| | rami. Third and fourth legs rudimentary. Maxilla without posteriorly di- |
| | rected ventral processes. Associated with Sabella crassicornis Sars |
| | |
| | With invaginate brood pouch formed by fourth metasomal segment. Maxilla |
| | with at least one posteriorly directed ventral process |
| 3. | First three pairs of swimming legs biramous, fourth legs rudimentary. First |
| | and second legs with trimerous rami, third legs with bimerous rami. Asso- |
| | ciated with Eudistylia polymorpha (Johnson) and Eudistylia vancouveri (Kinberg) |
| | |
| | First two pairs of swimming legs biramous, third and fourth legs rudimentary. |
| | Exopodites of first and second legs trimerous, endopodites unimerous. Asso- |
| | ciated with Bispira volutacornis (Montagu)Gastrodelphys clausii Graeffe |
| | All legs rudimentary, uniramous and unimerous. Associated with Myxicola |
| | infundibulum (Rénier) |
| 4. | Third swimming legs widely separated from the first two. Associated with |
| | Myxicola infundibulum (Rénier) |
| | Third swimming legs not widely separated from the first two pairs. Associated |
| | with Distylidia rugosa (Moore)Sabellacheres illgi, new species |
| | |

¹ The key does not include Chonephilus dispar Sars, indeterminable species.

GENUS GASTRODELPHYS GRAEFFE, 1883

Type Species: Gastrodelphys clausii Graeffe, 1883, Bay of Muggia, Trieste. Type by monotypy. Graeffe's original spelling of the generic name was Gastrodelphis. This original spelling of the name was justifiably emended by List (1890a) to Gastrodelphys.

Gastrodelphys fernaldi, new species

Figures 1-3

Types: Holotype female, A.M.N.H. No. 12440, from Sabella crassicornis Sars, dredged off Blakely Island, Washington, latitude 48° 38.4′ N., longitude 122° 50.5′ W., 31 fathoms, August 24, 1960. Allotype male, A.M.N.H. No. 12441, from Sabella crassicornis Sars, dredged off Blakely Island, Washington, 31 fathoms, August 24, 1960. One female and two male paratypes, A.M.N.H. No. 12442, from Sabella crassicornis Sars, dredged off Blakely Island, Washington, 31 fathoms, August 24, 1960.

ADDITIONAL SPECIMENS EXAMINED: One female, one male from Sabella crassicornis, dredged in Rosario Strait, west side of Clark Island, Washington, 56 fathoms, September 10, 1955. Two females from Sabella crassicornis, dredged off Flat Point, Lopez Island, Washington, latitude 48° 32.6′ N., longitude 122° 55.9′ W., 24 fathoms, June 30, 1956. Six females, five males from Sabella crassicornis, dredged off Blakely Island, Washington, latitude 48° 34.8′ N., longitude 122° 50.5′ W., 31 fathoms, August 24, 1960. Two females, two males from Sabella crassicornis, dredged in Griffin Bay off San Juan Island, Washington, latitude 48° 28.2′ N., 122° 58.8′ W., 16 fathoms, August 4, 1961.

DESCRIPTION OF FEMALE (FIGS. 1A-C, 2A-L): Average total length from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 2.17 mm.

Body (fig. 1A, B) composed of cephalosome, metasome, and urosome. Cephalosome bearing appendages through maxillae and with posterior denticulate post-oral plate. Metasome of two articulated segments bearing the first two pairs of swimming legs and a posterior, elongate, expanded complex of third and fourth segments bearing rudimentary third and fourth legs (fig. 1C). Urosome (fig. 1C) short, four-segmented, much narrower than posterior margin of metasome. Unlike all gastrodelphyids previously described, this species lacking brood pouch and with two long ovisacs dependent from dorsolateral genital openings on first urosomal segment. Entire body somewhat cello-shaped.

Anterior margin of cephalosome prolonged ventrally as deeply incised, bifurcate, crested rostrum.

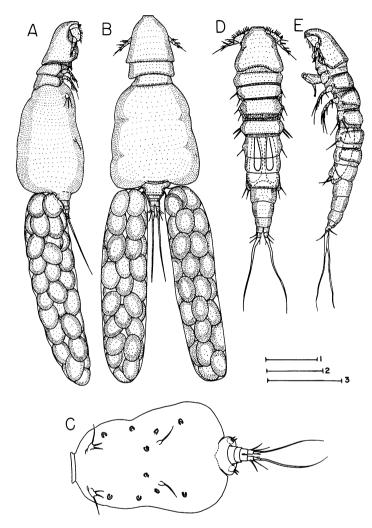


Fig. 1. Gastrodelphys fernaldi, new species. A. Habit of female, lateral view. B. Habit of female, dorsal view. C. Posterior metasome and urosome of female, ventral view. D. Habit of male, dorsal view. E. Habit of male, lateral view. Scale 1 (0.5 mm.) applies to A and B; scale 2 (0.5 mm.), to C; scale 3 (0.5 mm.), to D and E.

Antennule (fig. 2A) composed of five segments. Basal two segments approximately two times wider than distal three segments and making up one-half of appendage. Setal formula as follows: segment I, four setae; II, 14 setae; III, four setae, one aesthete; IV, two setae, one aesthete;

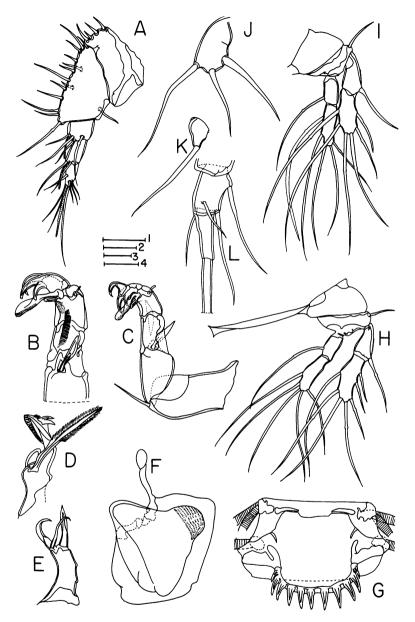


Fig. 2. Female of Gastrodelphys fernaldi, new species. A. Antennule. B. Antenna, distal three segments. C. Antenna. D. Mandible. E. Maxillule. F. Maxilla. G. Post-oral plate. H. First leg with intercoxal lamella. I. Second leg. J. Third leg. K. Fourth leg. L. Caudal ramus. Scale 1 (0.05 mm.) applies to A and C; scale 2 (0.02 mm.), to B, D–F; scale 3 (0.05 mm.), to G and H; scale 4 (0.05 mm.), to I.

V, seven setae, one aesthete. This species lacking acuminate projection at anterior distal corner of second segment. Aesthetes very small.

Antenna (fig. 2B, C) four-segmented, with right-angled flexure between basal and second segments. Basal segment longer than other segments, making up two-fifths of length of appendage. Basal segment with seta at inner distal corner. Second segment with spatulate seta articulating on face near distal margin. Third segment without armature but with comblike row of spinules which crosses articulation with fourth segment and passes onto face of fourth segment. Fourth segment armed with terminal bifid hook and simple hook. All hooks of approximately equal length. Projecting under hooks from distal inner corner of fourth segment a very large, spoon-shaped process ornamented with fine spinules. Below spoon-shaped process a cuticularized projection possibly serving as a support. Fine spinules ornamenting inner margin of fourth segment. Short spatulate seta articulating at outer distal corner of segment.

Mandible (fig. 2D) small, beneath complex labral sclerotization. Appendage S-shaped in basic form, with flattened, anteriorly directed, spinulose process articulating at proximal bend. Distal part of mandible flattened, posteriorly directed, and with heavy serrations on one edge. Opposite edge somewhat triangular and bearing sclerotized serrate patch and finer spinules.

Maxillule (fig. 2E) a lobe with three apical processes. Processes approximately equal in length.

Maxilla (fig. 2F) a triangular lobe with ventral spinulose ornamentation; with spatulate process articulating at anterior dorsal margin and projecting anteriorly under complex labial sclerotization.

Maxilliped lacking in female.

Post-oral process (fig. 2G) projecting from posterior cephalosome almost to intercoxal lamella of first swimming legs. This process heavily sclerotized and with 11 heavy teeth projecting from distal margin.

First two pairs of legs (fig. 2H, I) on first two metasomal segments biramous and with bimerous protopodites, bimerous rami. Protopodites joined by narrow, long, intercoxal lamellae. Setal formula as follows (se, setae; M, medial margin; T, terminal margin; L, lateral margin):

| | Leg l | | | Leg 2 | | | |
|--------------|-------|-----|-----|-------|-----|-----|--|
| | M | T | L | M | T | L | |
| Coxopodite | _ | | | | _ | _ | |
| Basipodite | | | lse | | | lse | |
| Exopodite 1 | _ | _ | lse | | | lse | |
| Exopodite 2 | 2se | 2se | 3se | 2se | 2se | 2se | |
| Endopodite 1 | lse | | | lse | | | |
| Endopodite 2 | 2se | 2se | lse | 2se | 2se | lse | |
| - | | | | | | | |

Third legs (fig. 2J) borne near anterior margin of elongate, fused, terminal, metasomal segment. These legs reduced, each consisting of single flattened plate with three setae equispaced around apex. Most lateral seta the longest. Fourth legs (fig. 2K) smaller than third and consisting of lobe with single terminal seta. These legs borne at approximate middle of terminal, enlarged, metasomal segment. Fifth legs lacking.

Ventral surface of complex terminal metasomal segment characterized by small, spinulose, tongue-shaped projections, these possibly serving in attachment to host (fig. 1C).

First urosomal segment (fig. 1C) with dorsolateral genital openings. Associated with openings are two spines, possibly representing remnants of sixth legs. Second, third, and fourth urosomal segments with no ornamentation or armature.

Caudal rami approximately as long as terminal urosomal segment. Each ramus (fig. 2L) with lateral seta at middle, short dorsal seta at distal fourth, and three terminal setae. Middle terminal seta very stout and greatly elongated, longer than urosome.

Description of Male (figs. 1E-D, 3A-K): Average total length from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 1.60 mm. Body (fig. 1E, D) more cyclopoid in general appearance than that of female, consisting of cephalosome, metasome, and urosome. Cephalosome bearing appendages through maxillipeds. Metasome consisting of two segments bearing functional legs. Major body articulation behind second metasomal segment; urosome, therefore, composed of eight segments.

Rostrum, antennule (fig. 3A), antenna (fig. 3B), mandible (fig. 3C), maxillule (fig. 3D), and maxilla like those of female. Four-segmented maxillipeds present (fig. 3E, F). Basal segment of maxilliped with no armature or ornamentation. Second segment elongate, with short seta at middle of inner margin. Third segment without armature. Fourth segment with subapical seta and elongate, terminal, hook process. Hook process (fig. 3F) with terminal spinulose cup and distal half ornamented with rows of fine spinules.

Post-oral plate (fig. 3G) not nearly so complex as that of female, lacking terminal heavy teeth and consisting of simple pad ornamented with fine spinules.

First two pairs of swimming legs like those of female. Third legs (fig. 3H, K) on first urosomal segment smaller than those of female but also consisting of uniramous, unimerous pads with three setae. Fourth legs (fig. 3I, K) on second urosomal segment consisting of single setae on low projections from ventral surface. Third urosomal segment with no legs

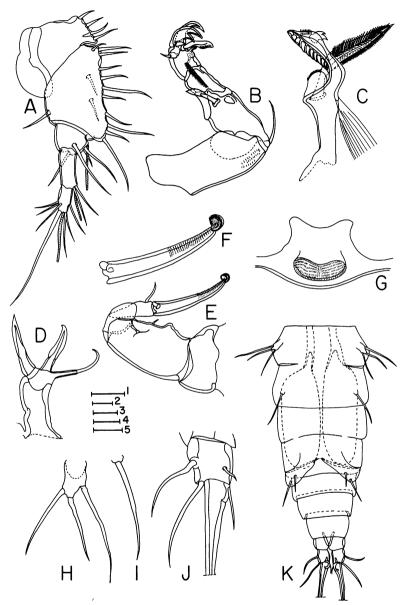


Fig. 3. Male of *Gastrodelphys fernaldi*, new species. A. Antennule. B. Antenna. C. Mandible. D. Maxillule. E. Maxilliped. F. Hook process of maxilliped. G. Post-oral plate. H. Third leg. I. Fourth leg. J. Caudal ramus. K. Urosome. Scale 1 (0.05 mm.) applies to A, F, G; scale 2 (0.02 mm.), to B, J; scale 3 (0.05 mm.), to E; scale 4 (0.02 mm.), to D, C, H, I; scale 5 (0.1 mm.), to K.

or ornamentation, fifth legs absent. Fourth urosomal segment with sixth legs, each consisting of triangular lobe with two subapical setae (fig. 3K). Spermatophore sacs elongate, extending from first to fourth urosomal segment. Fifth through eighth urosomal segments without armature or ornamentation. Caudal rami (fig. 3J, K) similar to those of female.

Remarks: Males and females are opaque white and lack an eye. They are attached temporarily to tentacular filaments by means of rostra and antennae.

Gastrodelphys dalesi (Green), 1961

Figures 4-5

Sabellacheres dalesi Green, 1961, pp. 623-628, figs. 1-14.

ORIGINAL REPORT OF OCCURRENCE (GREEN, 1961): "Five females were found by Dr. R. P. Dales on the branchial crowns of *Eudistylia polymorpha* Johnson (Polychaeta, Sabellidae) which had been sent to him from a collecting station three miles north of Point Dume at the western end of Zuma Beach, near Los Angeles, California. The worms were collected between rocks in water varying in depth from 25–50 feet, in mid August, 1959.

"Dr. Dales noted that the females were capable of active swimming and could detach themselves from the host crown, swim around for a short while, and then reattach themselves."

Specimens Examined for Present Report: Six males, 36 females, developmental stages from tentacular crowns of *Eudistylia vancouveri* (Kinberg) collected intertidally by J. G. Gonor at Tomales Point, Bodega Bay, California, July, 1960.

Redescription of Female (fig. 4A–H): Average total length from anterior end of cephalosome to end of brood pouch, 1.50 mm.; urosome, 0.20 mm. Body (fig. 4A) composed of cephalosome, metasome, and urosome. Cephalosome bearing appendages through maxillae and with heavy-toothed post-oral plate. First three segments of metasome with biramous swimming legs borne closely together. Fourth metasomal segment greatly enlarged, forming brood pouch and bearing reduced fourth legs. Urosome very small, four-segmented, protruding ventrally from approximate middle of fourth metasomal segment.

Anterior end of cephalosome prolonged ventrally as deeply incised, bifurcate rostrum.

Antennule (fig. 4B) of five segments. Basal two segments approximately two and one-half times wider than distal three segments and making up two-thirds of length of appendage. Setal formula as follows: segment I, three setae; II, 15 setae and articulated, pointed projection at distal

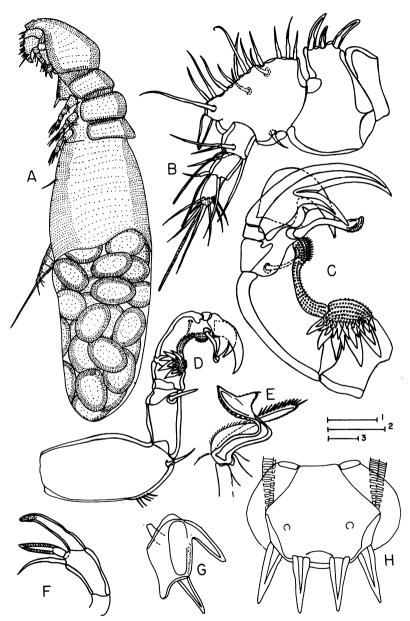


Fig. 4. Female of Gastrodelphys dalesi (Green). A. Habit, lateral view. B. Antennule. C. Antenna. D. Terminal two segments of antenna. E. Mandible. F. Maxillule. G. Maxilla. H. Post-oral plate. Scale 1 (0.2 mm.) applies to A; scale 2 (0.05 mm.), to B, C, G, H; scale 3 (0.02 mm.), to D-F.

anterior corner; III, three setae, one aesthete; IV, two setae, one aesthete; V, seven setae, one aesthete. Aesthetes slender.

Antenna (fig. 4C, D) of four segments, with right-angled flexure between basal and second segments. Basal segment longer than other segments, making up almost half of length of appendage. Basal segment with seta at medial distal margin. Second segment with spatulate seta articulating on posterior face near distal margin. Third segment without armature but with ornamenting patch of heavy spinules which also crosses articulation onto face of fourth segment. Fourth segment armed terminally with bifid hook and simple hook. Parts of bifid hook in proportions of 2/1. Simple hook approximately equal to smaller portion of bifid hook. Projecting under hooks from distal inner corner of fourth segment is a large, spoon-shaped process ornamented terminally with fine spinules. Inner margin of terminal segment also ornamented with rows of fine spinules. Articulating on anterior face near outer distal end of terminal segment is another short, spatulate seta.

Mandible (fig. 4E) small, beneath complex labral sclerotization. Appendage S-shaped in basic form with flattened, anteriorly directed process articulating at proximal bend near spinulose cushion. Distal part of mandible flattened, posteriorly directed. This portion with heavy serrations on one edge. Opposite edge finely serrate and drawn out into triangular process.

Maxillule (fig. 4F) a lobe with three apical setae. Most lateral seta longer than other two setae.

Maxilla (fig. 4G) a shield-shaped lobe bearing two heavy, ventral, spinelike processes which are directed posteriorly. Another process, probably masticatory in function, articulating at anterior dorsal margin and projecting anteriorly under complex labial sclerotization.

Maxillipeds lacking in female.

Post-oral plate (fig. 4H) projecting from posterior cephalosome almost to intercoxal lamella of first legs. This process heavily sclerotized and with four equispaced heavy teeth projecting from distal margin in all specimens examined. Green (1961) found that his specimens had five or six teeth.

First two pairs of swimming legs on first two metaromal segments composed of bimerous protopodites, trimerous rami. Protopodites joined by long, narrow, intercoxal lamellae. Third swimming legs on third metasomal segment set closely to leg 2. Third legs also biramous but with bimerous protopodites, bimerous rami. Armature formula for legs as follows (se, setae; sp, spines; M, medial margin; T, terminal margin; L, lateral margin):

| | | Leg 1 | | | Leg 2 | | | Leg 3 | |
|--------------|-----|---------|--------------|------|---------|------|-----|----------|-----|
| | M | T | \mathbf{L} | M | T | L | M | T | L |
| Coxopodite | _ | | | | | | _ | | _ |
| Basipodite | _ | _ | 1se | | | lse | | | lse |
| Exopodite 1 | _ | | lsp | _ | _ | lsp | | | lsp |
| Exopodite 2 | lse | | lsp | 1 se | | lsp | 2se | lse, lsp | lsp |
| Exopodite 3 | 3se | lse,lsp | 2sp | 4se | lse,1sp | 2sp | | | |
| Endopodite 1 | lse | | _ | 1se | _ | _ | lse | | |
| Endopodite 2 | lse | | _ | 1 se | | **** | lse | 1se | _ |
| Endopodite 3 | 3se | lse,1sp | | 3se | lse,lsp | | | | |

Fourth legs rudimentary, separated from third legs and borne at approximate anterior fifth of greatly expanded and elongate fourth metasomal segment. Each fourth leg consisting of single conical lobe with one seta.

Very large brood pouch in mature female projecting beyond end of urosome, apparently a product of fourth metasomal segment only.

Urosome of four segments. First segment with dorsolateral genital openings discharging ova to brood pouch. Seminal receptacles also situated dorsally on first urosomal segment. Remaining urosomal segments without appendages or ornamentation. Caudal rami short, each with one lateral seta at distal third, dorsal seta at middle, and three terminal setae. Middle terminal seta greatly elongated, approximately equaling urosome in length.

Description of Male (fig. 5A–H): Average total length from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 0.72 mm. Body (fig. 5A) consisting of cephalosome bearing appendages through maxillipeds, metasome of three leg-bearing segments, and urosome of seven segments. Rostrum (fig. 5B), antennule, antenna, mandible, and maxillule like those of female. Maxilla (fig. 5C) similar to that of female but with only one posteriorly directed pointed process on ventral surface.

Four-segmented maxilliped present (fig. 5D). First through third segments unarmed. Second segment the longest of the appendage. Fourth segment with a long seta near apex on inner margin and with elongate, apical, curved, hook process. A short seta articulating at base of hook process on inner margin. Hook slightly serrate at middle of inner margin and with a few terminal spinules.

Post-oral plate (fig. 5E) lacking heavy terminal teeth of post-oral plate of female but ornamented ventrally with papillae and terminally with double rows of heavy spinules.

First swimming legs (fig. 5F), second swimming legs, and third swimming legs (fig. 5G) like those of female.

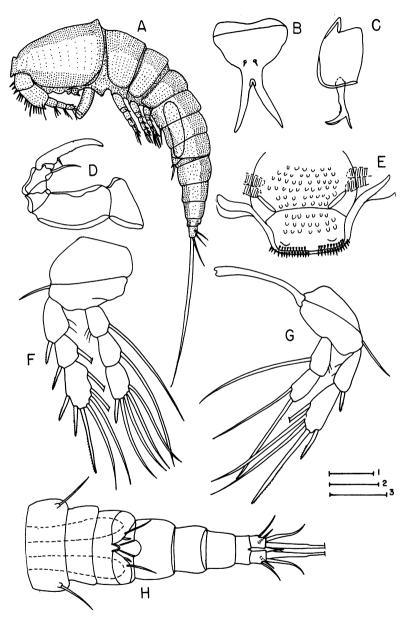


Fig. 5. Male of Gastrodelphys dalesi (Green). A. Habit, lateral view. B. Rostrum. C. Maxilla. D. Maxilliped. E. Post-oral plate. F. First leg. G. Third leg. H. Urosome. Scale 1 (0.1 mm.) applies to A; scale 2 (0.05 mm.), to B-G; scale 3 (0.1 mm.), to H.

Major body articulation between segment of third legs (fourth thoracic segment) and segment of fourth legs (fifth thoracic segment). Urosome (fig. 5H), therefore, seven-segmented. First urosomal segment not inflated as is that of female but bearing fourth legs which are exactly like those of female. Second urosomal segment without appendages, fifth legs absent. Third urosomal segment with subtriangular sixth legs, each bearing a medial subapical spine and a longer seta. Spermatophores elongate, extending from first urosomal segment to spermiducal openings on third urosomal segment. Third urosomal segment also with medial ventral sculpturing between sixth legs. Remaining segments of urosome without appendages or ornamentation. Caudal rami like those of female.

REMARKS: It should be noted that the collector of the specimens of Gastrodelphys dalesi studied here reported them as occurring on the tentacles of Eudistylia vancouveri (Kinberg). No information was given as to the color of the copepods or the yolk of their embryos. No specific notes were given as to the specific locus on the tentacular crown of the host.

The female specimens studied here do show a few differences from the features of G. dalesi from Eudistylia polymorpha (Johnson) described by Green (1961). The post-oral plates of all females examined have only four teeth and do not show variation to five or six teeth as shown by Green's specimens. The lateral apical elements of the armature of the terminal segments of the exopodites of the first through third swimming legs are more spiniform than those shown by Green. These small differences are not considered to be specifically significant.

Gastrodelphys clausii Graffe

Gastrodelphis clausii Graeffe, 1883, pp. 206–214, figs. 1–6. Gastrodelphys clausii Graeffe; List, 1890a, pp. 71–110, pl. 4, figs. 1–18, pl. 5, figs. 19–34. Green, 1961, p. 628.

The description as given in the texts and illustrations of Graeffe (1883) and List (1890a) follows:

HOST AND LOCALITY: Distylia josephinae Grube [=Bispira volutacornis (Montagu)] from the Bay of Muggia, near Trieste.

Locus on Host: Attached to tentacles by rostrum and antennae.

Female: Length, 3.5 to 4.0 mm.; greatest width at posterior end of metasome, 3.0 mm. Body violin-shaped, with brood pouch originating from enlarged fourth metasomal segment. Urosome three-segmented and held at 45-degree angle with metasome in preserved animals. Caudal rami each with one very long seta and three shorter setae. Rostrum deeply forked and with longitudinal suture. Antennules five-segmented. Antennae four-segmented; last segment with three hooks and spoon-

shaped process held in apposition to hooks. Antennae and rostrum used to hold copepod to tentacles of worm. Mandibles S-shaped, flattened, small. Maxillules (?) consisting of lobes with two apical processes. Maxillae ("zweite Maxillarfusspaar") shield-shaped and with toothlike process on inner angle. Maxillipeds absent. Post-oral plate with 12 large teeth on posterior margin. First and second legs set closely together on metasome. These with trimerous exopodites and unimerous endopodites. Third legs separated from first two pairs and each consisting of bimerous, rudimentary ramus. Fourth leg represented by single seta only. Fifth legs absent.

Male: Length, 2.0 mm.; width, 0.4 mm. Body consisting of cephalosome bearing appendages through maxillipeds, metasome of two (?) segments, and urosome of seven (?) segments. Appendages like those of female with following exceptions: three-segmented maxilliped with terminal hook process present on cephalosome; post-oral plate without posterior teeth; large clawed sixth legs associated with posterior ends of elongate spermatophore sacs on fifth urosomal segment.

Gastrodelphys myxicolae List

Gastrodelphys myxicolae List, 1890a, pp. 110-138, pl. 6, figs. 1-18, pl. 7, figs. 19-27; 1890b, p. 329. Green, 1961, p. 628.

The description as given in the text and illustrations of List (1890a) follows:

HOST AND LOCALITY: From Myxicola infundibulum Grube $[=Myxicola\ infundibulum\ (Rénier)]$ from the Adriatic Sea near Trieste.

Locus on Host: Attached by antennae to base of a tentacle, body "floating" between tentacles.

Female: Length, 2.0 mm.; greatest width, approximately 0.7 mm. Outline and form of body much like those of *G. clausii*. Brood pouch somewhat more pointed posteriorly. Rostrum bifurcate but not so massive as that of *G. clausii*. Antennule, antenna, and mandible similar to those of *G. clausii*. Maxillule a plate with three setae, middle seta the longest. Second maxilla with single posteriorly directed ventral hook. Post-oral plate with 13 strong distal teeth. All legs degenerate. First, second, and fourth legs consisting of single conical lobes with single apical seta on each. Third legs represented by single seta on each side. Fifth legs absent. Urosome reported as one-segmented but illustrated as three-segmented. Caudal rami each with one very elongate seta and three shorter setae.

Male: Unknown.

GENUS SABELLACHERES MICHAEL SARS, 1862

Type Species: Sabellacheres gracilis Michael Sars, 1862, near Tromsø, Norway. Type by monotypy.

Sabellacheres gracilis Michael Sars, 1862 Figures 6-7

Sabellacheres gracilis Michael Sars, 1862, pp. 142-143. Levinsen, 1877, p. 352. Green, 1961, p. 627.

Vermiclavella elongata MARKEWITSCH, 1940, pp. 53-57, figs. 1-2.

SPECIMENS EXAMINED: One female from Myxicola infundibulum (Rénier), collected in southeast Alaska by M. H. Pettibone, June 22, 1928, U.S.-N.M. No. 187217. One female from Myxicola infundibulum, dredged off Brown Island, Washington, by M. H. Pettibone, August 11, 1935, U.S.N.M. No. 187217. One female from Myxicola infundibulum, found in haddock stomach, U.S.N.M. No. 188560. One female from Myxicola infundibulum, dredged off Flat Point, Lopez Island, Washington, June 23, 1955. Two females from Myxicola infundibulum, dredged off Frost Island, Washington, July 7, 1956. Two females, two males from Myxicola infundibulum, collected by D. Chase in bay near University of Washington Laboratories, Friday Harbor, Washington, August 7, 1960. One female, one male collected intertidally at Smith Island, Washington, by R. P. Dales, August 8, 1960. One female from Myxicola infundibulum, dredged in "Potato Patch" near Blakely Island, Washington, latitude 48° 34.7' N., 122° 50.5′ W., 31 fathoms, July 26, 1961. One female from Myxicola infundibulum, dredged in "Potato Patch" near Blakely Island, Washington, August 10, 1961.

REDESCRIPTION OF FEMALE (FIG. 6A–O): Females from San Juan Archipelago with average total length from anterior end of cephalosome to end of brood pouch, 2.30 mm.; urosome, 0.20 mm. One specimen from southeast Alaska with total length from anterior end of cephalosome to end of brood pouch, 2.80 mm.; urosome 0.20 mm. Michael Sars (1862) reported his specimens as approximately 5.0 mm. long; Markewitsch (1940), his as 4.6 mm. long.

Body (fig. 6A) very narrow, consisting of cephalosome, metasome, and reduced urosome. Cephalosome bearing appendages through maxillae and with anterior bifurcate rostrum and posterior unarmed cephalosomic post-oral plate. Metasome consisting of four poorly delimited segments. First two segments short and bearing closely spaced first and second legs. Third metasomal segment about two times longer than first two and bearing third legs at posterior limit, these thus widely separated from first and second legs. Fourth metasomal segment about five times longer

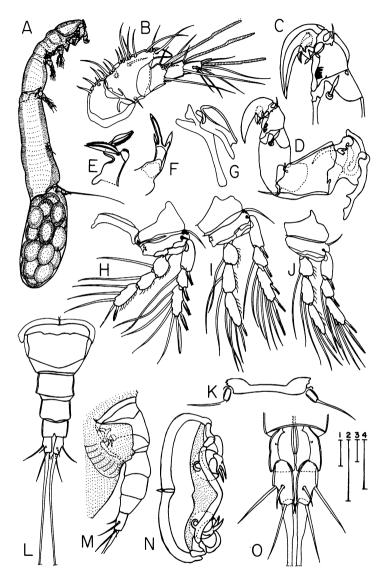


Fig. 6. Female of Sabellacheres gracilis Sars. A. Habit, lateral view. B. Antennule. C. Apex of antenna. D. Antenna. E. Mandible. F. Maxillule. G. Maxilla. H. First leg and intercoxal lamella. I. Second leg. J. Third leg. K. Fourth leg and intercoxal sclerotization. L. Urosome. M. Lateral view of urosome and aperture of brood pouch. N. Genital sclerotization and apertures on first urosomal segment. O. Caudal rami and terminal urosomal segment, dorsal view. Scale 1 (0.2 mm.) applies to A; scale 2 (0.1 mm.), to B, D, G; scale 3 (0.02 mm.), to C, E, F, N, O; scale 4 (0.1 mm.), to H-M.

than third and bearing rudimentary fourth legs at anterior third. Posteriorly, fourth metasomal segment forming elongate brood pouch. Urosome very reduced and projecting at angle with fourth metasomal segment.

Antennule (fig. 6B) of five segments. Appendage short and flattened. Basal two segments approximately two times wider than distal three segments and making up more than half of length of appendage. Setal formula as follows: segment I, four setae; II, 15 setae and pointed unarticulated projection at distal anterior corner; III, four setae, one aesthete; IV, two setae, one aesthete; V, seven setae, one aesthete. Setae relatively short and slender. Aesthetes longer than any of setae and characterized by constriction at distal third.

Antenna (fig. 6C, D) trimerous. Basal articulation extremely complicated. Segments of following proportional lengths, basal to distal: 7/5/2. A right-angled flexure between basal and second segments. A short seta articulating at inner distal corner of basal segment. Second segment with spatulate seta articulating on face of segment near distal margin. Third segment with comblike row of spinules on face near inner margin and an apically directed seta near apex on outer distal margin. Articulating terminally on third segment, a bifid hook and a separate single hook. Parts of bifid hook unequal, outer part approximately as long as terminal segment of appendage and five times longer than inner part. Separate hook slightly less than one-half as long as larger portion of bifid hook. On inner distal margin, associated with apical armature of appendage, is a short, spoon-shaped process, possibly qualifying as an aesthete.

Mandible (fig. 6E) very small, hidden beneath complex labral sclerotizations. Appendage S-shaped in general form, with a flattened ciliated process articulating near middle and directed orally. Lower bend of mandible with ciliated flange. Distal part of appendage somewhat flattened, directed posteriorly. Distal part with one heavily serrate edge, opposite edge with low triangular process, non-serrate.

Maxillule (fig. 6F) a short lobe with three terminal processes. Middle process longer than others.

Maxilla (fig. 6G) a lobe with flattened ventral surface, heavily sclerotized. Spatulate process with finely serrate tip articulating anterodorsally and projecting anteriorly under labial sclerotization.

Maxilliped lacking in female.

Post-oral process projecting from end of cephalosome almost to intercoxal lamella of first swimming legs. Plate rounded posteriorly, lacking heavy posterior teeth but with fine ciliation over entire ventral surface.

First three legs with bimerous protopodites, trimerous rami. Protopodites joined by narrow intercoxal lamella. First two legs (fig. 6H, I) set

closely together on first two metasomal segments. Third legs (fig. 6J) widely separated from second. Armature formula for legs as follows (se, setae; sp, spines; M, medial margin; T, terminal margin; L, lateral margin):

| | | Leg 1 | | | Leg 2 | | | Leg 3 | |
|--------------|-----|----------|-----|-----|---------|-----|-----|----------|-----|
| | M | T | L | M | T | L | M | T | L |
| Coxopodite | | | | | | | | _ | |
| Basipodite | | | lse | - | _ | lse | | _ | lse |
| Exopodite 1 | _ | _ | lsp | _ | | lsp | | _ | lsp |
| Exopodite 2 | lse | | lsp | lse | | lsp | lse | _ | lsp |
| Exopodite 3 | 3se | lse,lsp | 2sp | 4se | lse,1sp | 2sp | 3se | lse, lsp | lsp |
| Endopodite 1 | lse | _ | | lse | _ | | lse | _ ` | |
| Endopodite 2 | lse | _ | _ | 2se | | _ | 2se | _ | _ |
| Endopodite 3 | 3se | lse, lsp | | 3se | 2sp | _ | 2se | lsp | |

Fourth legs (fig. 6K) widely separated from third legs, each consisting of conical lobe with single terminal seta. Intercoxal sclerotization indicated.

Brood pouch large and projecting beyond tip of urosome. Urosome of four segments (fig. 6L, M). First segment (fig. 6N) with dorsolateral genital apertures and complex genital sclerotization. Associated with genital apertures opening to brood pouch are lobes with two spines, possibly representing sixth legs. Remaining urosomal segments non-pedigerous and without ornamentation.

Caudal rami (fig. 6 O) approximately as long as last urosomal segment. Each ramus with one lateral seta and one dorsal seta at middle and three terminal setae. Middle terminal seta greatly elongated, longer than urosome.

Description of Male (fig. 7A–J): Average total length from end of cephalosome to end of urosome, 0.75 mm. Body (fig. 7A) consisting of cephalosome bearing appendages through maxillipeds, metasome of three leg-bearing segments, and urosome of seven segments.

Antennule (fig. 7B) like that of female. Antenna (fig. 7C) like that of female with exception that parts of bifid hook are slightly shorter than in female. Mandible, maxillule (fig. 7D), and maxilla (fig. 7E) like those of female.

Four-segmented maxillipeds present (fig. 7F). Basal segment unarmed. Second segment the longest of the appendage and with a single internal seta. Third segment unarmed. Fourth segment with one long, internal, apical seta and apical hook process. A short seta articulating on base of hook process. Hook with fine spines at middle of inner margin.

First, second, and third swimming legs like those of female but third metasomal segment not elongated as is that of female, so third legs close

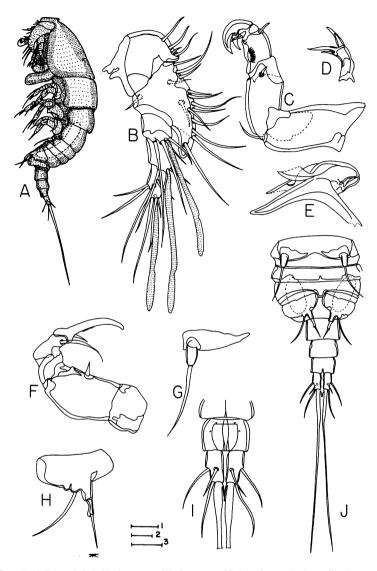


Fig. 7. Male of Sabellacheres gracilis Sars. A. Habit, lateral view. B. Antennule. C. Antenna. D. Maxillule. E. Maxilla. F. Maxilliped. G. Fourth leg. H. Sixth leg. I. Caudal rami and terminal urosomal segment. J. Urosome. Scale 1 (0.1 mm.) applies to A; scale 2 (0.02 mm.), to B-F, I; scale 3 (0.05 mm.), to G, H, J.

to second. Major body articulation between third metasomal segment (fourth thoracic segment) and fourth metasomal segment (fifth thoracic segment). First urosomal segment with fourth legs (fig. 7G), these like

those of female. Second urosomal segment non-pedigerous, fifth legs absent. Third urosomal segment with bilobed sixth legs (fig. 7H). Inner lobe of sixth leg bimerous and bearing a single short, stiffened seta. Outer lobe with single apical seta. Spermatophores elongate, extending from segment of third legs to third segment of urosome. Caudal rami (fig. 7I) like those of female. Fourth through seventh segments of urosome non-pedigerous (fig. 7J).

Remarks: It should be noted that the specimens described here are somewhat smaller than those described by Sars or Markewitsch. The Alaskan specimen is, however, considerably larger than those collected in the San Juan Archipelago. All other features are very consistent with those described by previous authors. All mature adult females were found with their heads embedded in the oral surface of the worm near the reduced ventral collar, the remainder of the body protruding anteriorly between the halves of the tentacular crown. The body of the female and the embryos in the brood pouch are yellowish and completely mimic the color of the worm. The only conspicuous color is the bright red of the eye. Males and immature adult females are free on the tentacles, attaching temporarily by means of their antennae and rostra.

Sabellacheres illgi, new species

Figures 8-10

Types: Holotype female. A.M.N.H. No. 12443, from *Distylidia rugosa* (Moore), dredged in West Sound, Orcas Island, Washington, latitude 48° 36′ N., longitude 122° 58′ W., 22 fathoms, August 24, 1960. Allotype male, A.M.N.H. No. 12444, from *Distylidia rugosa* (Moore), dredged in New Channel off Orcas Island, Washington, by R. L. Fernald, 18 fathoms, July 14, 1956. Three paratype females, A.M.N.H. No. 12445, from *Distylidia rugosa* (Moore), dredged in West Sound, Orcas Island, Washington, latitude 48° 36′ N., longitude 122° 58′ W., 22 fathoms, August 24, 1960. One female paratype, A.M.N.H. No. 12445a, from *Distylidia rugosa* (Moore), dredged off Blakely Island, Washington, latitude 48° 34.7′ N., longitude 122° 50.5′ W., 33 fathoms, June 28, 1963.

ADDITIONAL SPECIMENS EXAMINED: Fifteen females from *Distylidia rugosa*, dredged at mouth of West Sound, Orcas Island, Washington, by P. L. Illg, June 29, 1955. Two females from *Distylidia rugosa*, dredged in New Channel off Orcas Island, Washington, by R. L. Fernald, 18 fathoms, July 14, 1956. Four females, two males from *Distylidia rugosa* dredged in West Sound, Orcas Island, Washington, latitude 48° 36′ N., 122° 58′ W., 22 fathoms, August 24, 1960. Six females from *Distylidia rugosa*, dredged in Griffin Bay, San Juan Island, Washington, latitude 48° 28.2′ N.,

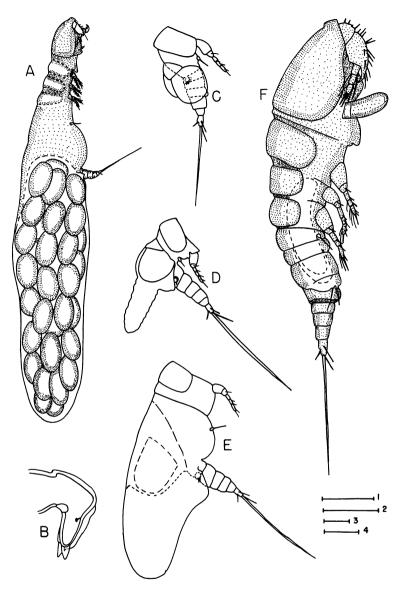


Fig. 8. Sabellacheres illgi, new species. A. Habit of female, lateral view. B. Rostrum of female, lateral view. C. Posterior metasome and urosome of very young immature adult, female with protrusion of brood pouch not yet initiated. D. Posterior metasome and urosome of immature adult female, showing initial stage of protrusion of brood pouch. E. Posterior metasome and urosome of immature adult female, showing intermediate stage in protrusion and enlargement of brood pouch. F. Habit of male, lateral view. Scale 1 (0.5 mm.) applies to A; scale 2 (0.1 mm.), to B; scale 3 (0.1 mm.), to C–E; scale 4 (0.1 mm.), to F.

122° 58.8' W., 16 fathoms, August 4, 1961. One male from Distylidia rugosa, dredged in West Sound, Orcas Island, Washington, latitude 48° 36′ N., longitude 122° 58′ W., 20 fathoms, August 4, 1961. Eight females from Distylidia rugosa, dredged in Griffin Bay, San Juan Island, Washington, latitude 48° 28.2′ N., longitude 122° 58.8′ W., 16 fathoms, June 28, 1963. Five females from Distylidia rugosa, dredged off Blakely Island, Washington, latitude 48° 34.7′ N., longitude 122° 50.5′ W., 33 fathoms, June 28, 1963. One female from Distylidia rugosa, collected intertidally at Turn Island, Washington, July 8, 1963. One female from Distylidia rugosa, dredged in Griffin Bay, San Juan Island, Washington, by D. L. Ray, July 10, 1963. Two males, five immature adult females from Pseudopotamilla occelata Moore, dredged off Upright Head, Lopez Island, Washington, 31 fathoms, July 26, 1961. Four males, three immature adult females from Pseudopotamilla occelata, dredged in West Sound, Orcas Island, Washington, latitude 48° 36.3′ N., longitude 122° 58.1′ W., 15 fathoms, July 26, 1961. Four males, seven immature adult females from Pseudopotamilla occelata, dredged off Bald Bluff, Blakely Island, Washington, latitude 48° 33.3′ N., longitude 122° 50.2′ W., 20–23 fathoms, August 4, 1961. Nine immature adult females, 15 males from Pseudopotamilla occelata, dredged in West Sound, Orcas Island, Washington, latitude 48° 36' N., longitude 122° 58' W., 20 fathoms, August 10, 1961. Six males, one immature adult female from Pseudopotamilla occelata, dredged in West Sound, Orcas Island, Washington, latitude 48° 36' N., longitude 122° 58′ W., 22 fathoms, August 24, 1960. Five males, four immature adult females from Branchiomma burrardum Berkeley, dredged in West Sound, Orcas Island, Washington, latitude 48° 36' N., 122° 58' W., 20 fathoms, August 4, 1961. One immature adult female from Branchiomma burrardum, dredged in West Sound, Orcas Island, Washington, latitude 48° 36′ N., longitude 122° 58′ W., 20 fathoms, August 10, 1961.

Description of Female (figs. 8A–E, 9A–K): Average total length of fully mature females measured from anterior end of cephalosome to end of brood pouch, 4.0 mm.; urosome, 0.25 mm. Body (fig. 8A) elongate, stout, composed of cephalosome, metasome, and urosome. Cephalosome with appendages through maxillae. Anterior end prolonged ventrally into crested bifurcate rostrum (fig. 8B) and posteriorly with unarmed post-oral plate. Metasome of three narrow, closely set, and poorly delimited segments bearing first three legs and one greatly elongated fourth segment bearing rudimentary fourth legs at anterior thirteenth. Fourth segment forming a very long brood pouch. Reduced five-segmented urosome protruding ventrally at anterior limit of brood pouch. Brood pouch formed by invagination and posterior protrusion of fourth meta-

somal segment. Figure 8C–E illustrates formation of brood pouch by allometric growth of fourth metasomal segment of immature adult female. Allometric growth without molting has been observed occurring in living animals in culture.

Antennule (fig. 9A) of five segments. Basal two segments approximately two and one-half times wider than distal three segments and making up two-thirds of length of appendage. Setal formula as follows: segment I, four setae; II, 15 setae and pointed unarticulated projection at anterior distal corner; III, four setae, one aesthete; IV, two setae, one aesthete; V, seven setae, one aesthete. Aesthetes longer than any setae of appendage, characterized by constriction at distal third.

Antenna (fig. 9B) trimerous, with right-angled flexure between basal and second segments. Basal segment with seta at inner distal corner. Second segment with spatulate seta articulating on face near distal margin. Third segment with patch of graduated spinules on inner margin, small spoon-shaped process at inner distal corner, and small seta at outer distal margin. Articulating apically on third segment are a large bifid hook with parts in proportions of 2.5/1.0 and a separate single hook approximately equal in length to smaller portion of bifid hook.

Mandible (fig. 9C) small, beneath complex labral sclerotization. Appendage S-shaped in general form, with flattened, anteriorly directed spinulose process articulating at proximal bend. Proximal bend with ciliated cushion. Distal part of mandible flattened, with heavy serrations on one edge, fine spinules on opposite edge.

Maxillule (fig. 9D) a lobe with three apical processes. Processes approximately equal in length but lateral process much heavier than two medial processes.

Maxilla (fig. 9E) a lobe with flattened ventral surface. Edges heavily sclerotized and with fine spinulose ornamentation. Finely toothed process articulating anteriorly and projecting under labial sclerotizations.

Maxilliped lacking in females.

Post-oral plate extending from end of cephalosome almost to intercoxal lamella of first legs. Plate not armed with heavy teeth but covered ventrally with fine spinules.

First legs (fig. 9F), second legs (fig. 9G) and third legs (fig. 9H) with bimerous protopodites, trimerous rami. Protopodites joined by intercoxal lamella. All three legs set closely together on faintly indicated first three segments of metasome. Armature formula for legs as follows (se, setae; sp, spines; M, medial margin; T, terminal margin; L, lateral margin):

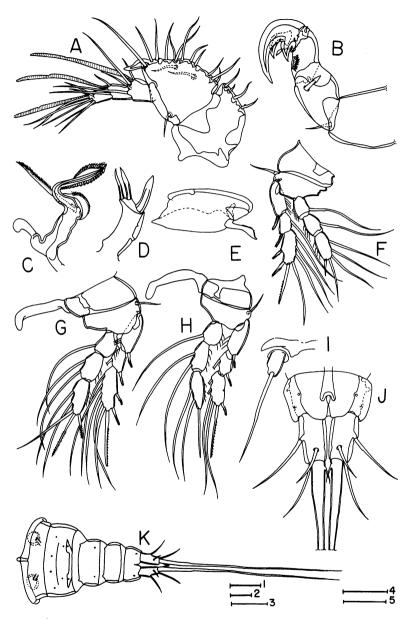


Fig. 9. Female of Sabellacheres illgi, new species. A. Antennule. B. Antenna. C. Mandible. D. Maxillule. E. Maxilla. F. First leg. G. Second leg. H. Third leg. I. Fourth leg. J. Caudal rami and last urosomal segment, dorsal view. K. Urosome. Scale 1 (0.05 mm.) applies to A; scale 2 (0.02 mm.), to B; scale 3 (0.02 mm.), to C; scale 4 (0.05 mm.), to D, F, K; scale 5 (0.05 mm.), to E, G-J.

| | | Leg 1 | | | Leg 2 | | | Leg 3 | |
|--------------|-----|----------|------|-----|----------|-----|-----|---------|-----|
| | M | T | L | M | T | L | M | T | L |
| Coxopodite | | | | | _ | _ | | | |
| Basipodite | _ | | l se | | | lse | | | lse |
| Exopodite 1 | | | lsp | _ | | lsp | | | lsp |
| Exopodite 2 | lse | | lsp | lse | | lsp | lse | | lsp |
| Exopodite 3 | 3se | lse, lsp | 2sp | 4se | lse, lsp | 2sp | 3se | lse,lsp | lsp |
| Endopodite 1 | lse | | | lse | | | lse | | |
| Endopodite 2 | lse | | | 2se | | | 2se | | |
| Endopodite 3 | 3se | lse,lsp | | 3se | 2sp | | 2se | lsp | |

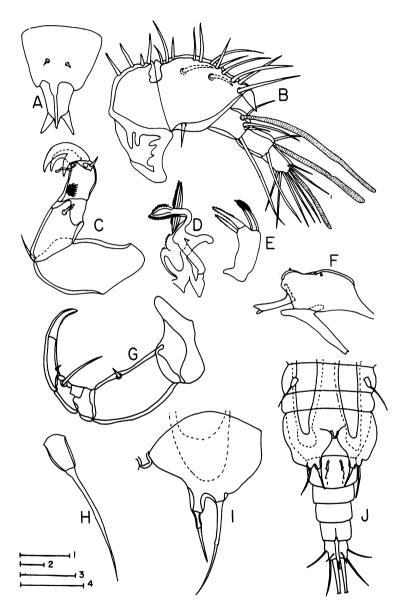
Fourth legs (fig. 9I) separated from third, each consisting of conical lobe with single terminal seta. Intercoxal sclerotization indicated.

Very large brood pouch in mature female projecting beyond tip of very small urosome. Urosome (fig. 9K) of five segments. First segment with dorsolateral genital openings and complex genital sclerotization. Openings to seminal receptacles also situated dorsally. Associated with genital apertures which open to brood pouch are lobes with two spines, these possibly representing sixth legs. Remaining urosomal segments without appendages.

Each caudal ramus (fig. 9J) with one lateral seta at middle, short dorsal seta at distal third, and three terminal setae. Middle terminal seta greatly elongated, longer than urosome.

DESCRIPTION OF MALE (FIGS. 8F, 10A-I): Average total length from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 0.93 mm. Body (fig. 8F) consisting of cephalosome bearing appendages through maxillipeds, metasome of three leg-bearing segments, and urosome of seven segments. Rostrum (fig. 10A) and antennule (fig. 10B) like those of female. Antenna (fig. 10C) like that of female, with exception that major part of bifid terminal hook shorter and minor part of hook longer than those of female. Proportions of parts of bifid hook 1.5/1. Mandible (fig. 10D), maxillule (fig. 10E), and maxilla (fig. 10F) like those of female, with slight differences shown in illustrations. Foursegmented maxilliped present (fig. 10G). First segment unarmed. Second segment the longest of the appendage and armed with a single short seta on middle of inner margin. Third segment unarmed. Fourth segment with a single long internal seta near apex and a terminal hook process. A short seta articulating at base of hook process. Hook armed with a few spinules near tip.

Swimming legs on first three metasomal segments like those of female. Major body articulation between third metasomal segment (fourth thoracic segment) and first urosomal segment (fifth thoracic segment). First urosomal segment with rudimentary fourth legs (fig. 10H). Fourth



1964

Fig. 10. Male of Sabellacheres illgi, new species. A. Rostrum. B. Antennule. C. Antenna. D. Mandible. E. Maxillule. F. Maxilla. G. Maxilliped. H. Fourth leg. I. Sixth leg. J. Urosome. Scale 1 (0.05 mm.) applies to A–C, F, G; scale 2 (0.02 mm.), to D, E; scale 3 (0.1 mm.), to H, I; scale 4 (0.1 mm.), to J.

legs like those of female. Second urosomal segment non-pedigerous, fifth legs absent. Third urosomal segment with bilobed sixth legs (fig. 10 I). Inner lobe of sixth leg bimerous and with single, short, stiffened apical seta. Outer lobe single and with one apical seta. Spermatophores very long, extending from second metasomal segment to spermiducal openings on third urosomal segment. Fourth urosomal segment with medial ventral sculpturing. Remaining segments of urosome without appendages and without ornamentation (fig. 10J). Caudal rami like those of female.

Remarks: Most fully mature females are found with their cephalosomes embedded in the medial portions of the coiled tentacular base of Distylidia rugosa (Moore). The remainder of the body extends anteriorly, mimicking a tentacle in the tentacular coil. In one case only, a female was found embedded in the ventral collar of the worm. The area where the copepod was embedded was swollen and had a pink coloration which was not seen in the rest of the oral area of the worm or in uninfected worms. Immature adult females and males are found on the tentacles of Distylidia rugosa, Pseudopotamilla occelata, or Branchiomma burrardum. These are attached temporarily by their antennae and rostra but can swim very rapidly when disturbed. Adult females have a general orange-pink coloration and a bright red eye. Eggs in the ovary are pink, and embryos in the brood pouch are pinkish orange. Males and immature females are pink.

DEVELOPMENT

The study of development is incomplete because the gastrodelphyids have proved rather refractory to attempts to culture them under artificial conditions. Since there have been only two incomplete reports of naupliar structure (Green, 1961; List, 1890a), however, it is considered important to add some details of development here which were obtained in the present study.

All the gastrodelphyids studied have free-living lecithotrophic nauplii. Gastrodelphys fernaldi appears to have only two naupliar stages, while Sabellacheres illgi and Sabellacheres gracilis have at least four nauplii. The first copepodid has been obtained in culture only for S. gracilis and S. illgi, and it is the first stage of S. illgi to be found on sabellid worms. It is postulated, therefore, that the first copepodid is the infective stage in the gastrodelphyid copepods. There are six symbiotic copepodid stages found on the sabellid hosts in S. illgi. First through fifth symbiotic copepodids of S. gracilis and G. fernaldi have not been discovered on polychaete hosts.

In successful cultures of S. gracilis, the first copepodid stage was reached

in approximately 36 hours after the nauplii were released from the brood pouch and hatched, and there were about four naupliar stages. In S. illgi, the naupliar time span and the number of molts were as in S. gracilis, but the first copepodids were unsuccessful in emerging completely from the last naupliar exuviae and were removed by dissection. In G. fernaldi, second nauplii were approaching a molt to first copepodid at 24 hours after the first nauplii hatched, but no cultures of this species were successful, and no first copepodids were obtained.

Nauplii of the Gastrodelphyidae Figure 11

NAUPLII OF Gastrodelphys fernaldi: In first nauplius, antennule (fig. 11A) bimerous. Basal segment with one short ventral seta at distal third and one seta at ventral distal margin. Apex of second segment with one long ventral seta, one short dorsal seta. Aesthete associated with base of longer apical seta. In second nauplius, basal segment of antennule like that in first nauplius. Terminal segment adds six short setae to distal half of dorsal margin and two short setae to distal ventral margin.

Antenna (fig. 11B) of first nauplius with obscurely bimerous protopodite, trimerous exopodite, unimerous endopodite. Basipodite J-shaped, outer projection with one long seta at distal medial margin. Two basal segments of exopodite each with one long seta on distal medial margin. Terminal segment with one short medial seta, one longer apical seta. Endopodite with short seta at middle of medial margin and two long terminal setae. Antenna showing no changes in second nauplius with exception that medial seta of endopodite reduced to tiny point.

Mandible (fig. 11C) with bimerous protopodite, trimerous exopodite, bimerous endopodite. Coxopodite with no armature. Basipodite J-shaped, longer lateral arm equivalent to basal segment of exopodite in other species, bearing one long medial seta. Three segments of exopodite each with one long seta. Basal segment of endopodite with no armature. Terminal segment with two long apical setae. Mandible showing no changes at second naupliar stage.

The first nauplius is 0.229 mm. long. The general ectoderm is an opaque white, and the midgut contains brownish yellow yolk. The nauplius lacks an eye. The exuvia of the first nauplius (fig. 11D) is oval, with a hemispherical oral plate at the anterior ventral third. The cuticular lining of the stomodaeum is shed with the exuvia. At the posterior end of the exuvia are two abdominal setae.

The second nauplius shows a very slight increase in length. The general coloration of the body and the yolk are like those in the first nauplius, and

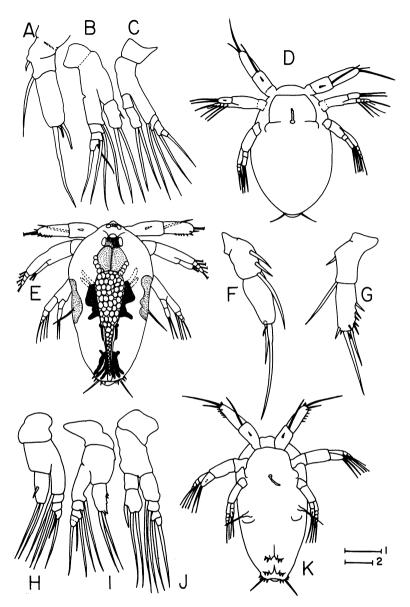


Fig. 11. Gastrodelphyid nauplii. A-D. Gastrodelphys fernaldi. A. Antennule of first nauplius. B. Antenna of first nauplius. C. Mandible of first nauplius. D. Exuvia of first nauplius. E-K. Sabellacheres illgi. E. Habit of second nauplius, dorsal view. F. Antennule of first nauplius. G. Antennule of last nauplius. H. Antenna of first nauplius. I. Antenna of last nauplius. J. Mandible of first nauplius. K. Exuvia of last nauplius, ventral view. Scale 1 (0.05 mm.) applies to A-C, F-J; scale 2 (0.05 mm.), to D, E, K.

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the second nauplius also lacks an eye. The postmandibular appendages show great development at this stage to approach the form of the appendages of the copepodid. The cuticular covering of the second nauplius shows changes in the primitive appendages noted above. In addition, a setiferous lobe on each side just below the mandible indicates the maxillule, lines indicate the margins of the maxillae, and denticulate sacs show the terminal outlines of the first and second swimming legs. Eight setules are added to the terminal end of the abdomen.

NAUPLII OF Sabellacheres gracilis AND Sabellacheres illgi: Antennule of first nauplius (fig. 11F) bimerous. Basal segment with two setules on ventral surface beyond proximal third and one long seta at distal ventral margin. Terminal segment with apical armature of one elongate ventral seta and one short dorsal seta. Aesthete associated with base of long seta. In second and later nauplii, basal segment of antennule (fig. 11G) with only one short ventral seta and one long distal seta. One setule of basal segment lost. Terminal segment adds six short dorsal setae and two short distal ventral setae, these setae showing an increase in length during naupliar stages.

Antenna of first nauplius (fig. 11H) with bimerous protopodite, trimerous exopodite, unimerous endopodite. Coxopodite without armature. Basipodite J-shaped, outer projection with elongate seta at medial distal corner. First two segments of exopodite with long seta at distal medial corner. Terminal segment of exopodite with one short medial seta, one long terminal seta. Endopodite with one short seta at middle of medial margin and two longer terminal setae. Antenna of second and subsequent nauplii (fig. 11 I) with no changes in segmental composition. Protopodite and exopodite like those of first nauplius. Endopodite showing changes as follows: medial seta reduced in length to tiny point and four new setose projections added to medial and medial terminal margins.

Mandible (fig. 11J) with bimerous protopodite, tetramerous exopodite, bimerous endopodite. Protopodite unarmed. Each of four segments of exopodite with one long seta. Basal segment of endopodite unarmed. Terminal segment with short stout seta on medial margin at distal third and two long terminal setae. Mandible showing no changes in second nauplius or later nauplii.

The nauplii of S. gracilis and S. illgi are very similar in general structure and show differences only in size and in coloration of body and yolk. The first nauplius of S. gracilis averages 0.188 mm. in total length, with an increase at the second nauplius to 0.194 mm. The first nauplius of S. illgi is 0.233 mm. long, with an increase at the second nauplius to 0.250 mm. The nauplii of S. gracilis have a general yellowish color and a bright

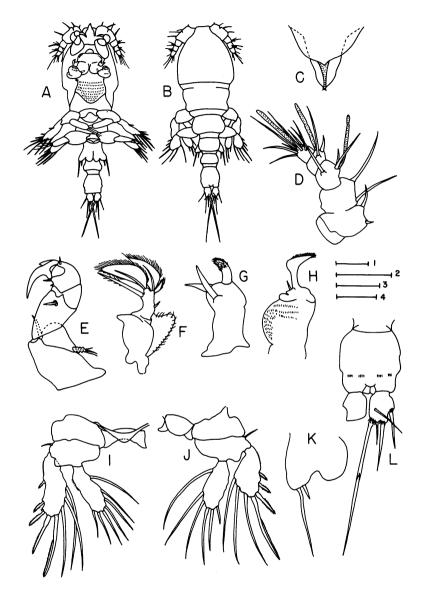


Fig. 12. First copepodid of Sabellacheres illgi. A. Habit, ventral view. B. Habit, dorsal view. C. Rostrum. D. Antennule. E. Antenna. F. Mandible. G. Maxillule. H. Maxilla. I. First leg. J. Second leg. K. Third leg. L. Caudal rami and terminal segment of urosome. Scale 1 (0.1 mm.) applies to A, B; scale 2 (0.05 mm.), to C–E, K, L; scale 3 (0.02 mm.), to F–H; scale 4 (0.05 mm.), to I, J.

red eye. The yolk in the midgut is orange. In S. illgi (fig. 11E), the tripartite eye is bright orange-red, the yolk is yellow, the general body ectoderm is pinkish, and there are secondary concentrations of bright orange-red granular pigment around the gut and near the bases of the mandibles and the maxillules. A bilobed protocerebrum is seen dorsally between the eye and the midgut.

The first naupliar exuvia in S. illgi and S. gracilis is similar to that of G. fernaldi, with some differences in the primitive appendages as noted above. The exuviae of the second nauplius and subsequent nauplii (fig. 11K) show external indications of maxillules as setiferous lobes, lines for maxillae, and denticulate sacs which indicate the terminal outlines of the first and second legs. The terminal end of the abdomen has 10 setae rather than two setae as in the first exuvia. The appendicular outlines become more pronounced on the exuviae of later nauplii, and the terminal setae of the abdomen are lengthened.

COPEPODIDS OF THE GASTRODELPHYIDAE

Figures 12-16

The first through fifth symbiotic copepodids have been found only for Sabellacheres illgi. It is interesting that the younger copepodids of this species (first through fourth copepodids and male fifth copepodids) are found only on Pseudopotamilla occelata Moore. Female fifth copepodids, adult males, and immature adult females are found on Pseudopotamilla occelata, Branchiomma burrardum Berkeley, and on the definitive host, Distylidia rugosa (Moore). Mature adult females with protruding brood pouches have been found only on Distylidia rugosa. It would appear that the younger stages find existence more favorable on a worm other than the definitive host. Migration to the definitive host probably occurs during the fifth copepodid stage. All the worms noted as hosts for the various stages can be dredged in the same locality.

It is possible that younger copepodids of Gastrodelphys fernaldi and Sabellacheres gracilis are also found on a worm or other animal different from the definitive hosts, which may explain my inability to find them.

FIRST COPEPODID OF Sabellacheres illgi

Figure 12

Specimens Examined: One from *Pseudopotamilla occelata*, dredged off Upright Head, Lopez Island, Washington, 31 fathoms, July 26, 1961. One from *Pseudopotamilla occelata*, dredged in Griffin Bay, San Juan Island, Washington, latitude 48° 28.2′ N., longitude 122° 58.8′ W., 16

| TABLE 1 | |
|--|----------|
| SETAL FORMULAS FOR ANTENNULE OF COPEPODIDS 1-5 OF Sabellache | es illgi |

| Segment | Cl | C2 | C3 | C4 | C 5 |
|---------|--------|---------|------------|-------------|------------|
| I | 2se | 2se | 3se | 3se | 4se |
| II | 2se | 6se | 7se,2sl,1p | llse,lsl,lp | 15se, 1p |
| III | 3se,1a | 3se,1a | 4se, la | 4se,la | 4se, la |
| IV | 2se,1a | 2se,1a | 2se,1a | 2se,la | 2se,1a |
| V | 7se,1a | 7se, la | 7se, la | 7se,la | 7se,la |

I-V, segments of antennule, proximal to distal.

fathoms, August 4, 1961. Seven from culture. Adult female used in culture from *Distylidia rugosa* (Moore), dredged in Griffin Bay, San Juan Island, Washington, 16 fathoms, August 4, 1961. Nauplii hatched on August 8, 1961. First copepodids removed by dissection from last naupliar exuvia on August 10, 1961.

DESCRIPTION: Average total length from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 0.525 mm. Body (fig. 12A, B) composed of cephalosome bearing appendages through maxillae, metasome of two leg-bearing segments, and urosome of three segments and terminal caudal rami. Rostrum (fig. 12C) a ventrally directed lobe with median crest. Antennule (fig. 12D) obscurely five-segmented, basal segment only partially articulated with second segment. Setal formula in table 1. Large aesthetes on third, fourth, and fifth segments. Antenna (fig. 12E) with protopodite, bimerous endopodite, and vestigial, saccular exopodite. Protopodite with seta at distal medial corner. Basal segment of endopodite with seta on anterior surface. Terminal segment of endopodite with apical hook and apical flange precursory to secondary simple hook of later stages. Posteriorly directed seta at base of hook on lateral margin, medially directed seta at base of hook on medial margin. Mandible (fig. 12F) minute, functioning under complex labral sclerotization and consisting of lobe with three apical, flattened, fringed blades, one apical seta, and one lateral seta. Maxillule (fig. 12G) a lobe armed terminally with spinulated element and two medially directed setae. Maxilla (fig. 12H) a lobe ornamented ventrally with rows of spinules and continued anteriorly as a serrate projection functioning under labrum. Maxillipeds absent at this stage. Large post-oral plate bearing rows of spinules and projecting

C1-C5, first through fifth copepodid stages.

se, setae.

sl, setules.

p, anterior projection.

a, aesthetes.

 $\begin{tabular}{ll} TABLE & 2 \\ Armature & Formulas for Legs & 1-3 of Copepodids & 1-5 of Sabellacheres illgi \\ \end{tabular}$

| | Leg 1 | | | Leg 2 | | | Leg 3 | | |
|--------------|-------|----------|-----|-------|----------|-----|-------|-----------|----------|
| | M | T | L | M | T | L | M | T | L |
| Copepodid 1 | | | | | | | | | |
| Coxopodite | _ | _ | | _ | _ | _ | Ruc | limentary | with 2se |
| Basipodite | _ | | lse | _ | | lse | | | |
| Exopodite 1 | 3se | 2sp | 3sp | 2se | lse, lsp | 3sp | | | |
| Endopodite 1 | 4se | 2se | lse | 3se | 2se | lse | | | |
| Copepodid 2 | | | | | | | | | |
| Coxopodite | | _ | | | | _ | Ruc | limentary | with 2se |
| Basipodite | | _ | lse | | | lse | | | |
| Exopodite 1 | _ | _ | lsp | | | lsp | | | |
| Exopodite 2 | 3se | 2sp | 2sp | 2se | lse, lsp | 2sp | | | |
| Endopodite 1 | lse | _ | | lse | | | | | |
| Endopodite 2 | 4se | 2se | _ | 3se | 2se | _ | | | |
| Copepodid 3 | | | | | | | | | |
| Coxopodite | _ | _ | _ | _ | | | | _ | _ |
| Basipodite | _ | _ | lse | _ | _ | lse | _ | | _ |
| Exopodite 1 | _ | | lsp | _ | | lsp | _ | | lsp |
| Exopodite 2 | 3se | 2sp | 2sp | 2se | lse, lsp | 2sp | _ | 2se | |
| Endopodite l | lse | | | 1se | | _ | _ | | |
| Endopodite 2 | 4se | 2se | | 3se | 2se | | _ | _ | _ |
| Copepodid 4 | | | | | | | | | |
| Coxopodite | _ | | _ | | | | _ | | - |
| Basipodite | | | lse | | _ | lse | _ | | lse |
| Exopodite 1 | _ | _ | lsp | _ | _ | lsp | _ | | lsp |
| Exopodite 2 | 3se | lse, lsp | 2sp | 4se | lse, lsp | 2sp | 4se | lsp | lsp |
| Endopodite 1 | 1se | _ ` | | lse | | | lse | | |
| Endopodite 2 | 4se | 2se | | 4se | 2se | | 3se | lsp | _ |
| Copepodid 5 | | | | | | | | = | |
| Coxopodite | | | _ | | | | _ | | _ |
| Basipodite | | _ | lse | | _ | lse | | _ | lse |
| Exopodite 1 | | _ | lsp | | _ | lsp | _ | | lsp |
| Exopodite 2 | lse | | lsp | lse | | lsp | lse | | lsp |
| Exopodite 3 | 3se | lse, lsp | 2sp | 4se | lse, lsp | 2sp | 3se | lse, lsp | lsp |
| Endopodite 1 | lse | _ ` ' | | lse | _ ` | _ | lse | | |
| Endopodite 2 | lse | | | 2se | _ | | 2se | _ | |
| Endopodite 3 | 3se | 2sp | _ | 3se | 2sp | | 2se | lsp | |

M, medial margin of segment.

T, terminal margin of segment.

L, lateral margin of segment.

se, setae.

sp, spines.

from posterior margin of cephalosome almost to first legs. First swimming legs (fig. 12 I) and second swimming legs (fig. 12 J) with bimerous protopodites, unimerous rami. Protopodites joined by articulated intercoxal lamellae. Formula for armature of swimming legs in table 2. Third legs (fig. 12K) on first segment of urosome. These legs rudimentary, consisting of terminally bilobed protuberances; lateral lobe with two setae. Second and third urosomal segments non-pedigerous. Third urosomal segment with some ventral spinulose ornamentation (fig. 12L). Caudal ramus (fig. 12L) with lateral seta near middle, dorsal seta at posterior third, and three terminal setae. Medial seta the longest of the terminal trio, about four times length of ramus.

Remarks: With the exception of its smaller size, 0.476 mm., the first copepodid of *Sabellacheres gracilis* obtained by ecdyses of the last nauplii in culture agrees exactly with the description of *S. illgi* above.

SECOND COPEPODID OF Sabellacheres illgi

Figure 13

Specimens Examined: Three from *Pseudopotamilla occelata*, dredged off Upright Head, Lopez Island, Washington, 31 fathoms, July 26, 1961. One from *Pseudopotamilla occelata*, dredged in Griffin Bay, San Juan Island, Washington, 16 fathoms, August 4, 1961. One from *Pseudopotamilla occelata*, dredged in West Sound, Orcas Island, Washington, 20 fathoms, August 10, 1961.

DESCRIPTION: Average total length from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 0.543 mm. Body (fig. 13A, B) composed of cephalosome, metasome of two leg-bearing segments, urosome of four segments and caudal rami. Rostrum like that in first copepodid. Antennule (fig. 13C) obscurely five-segmented. Setal formula in table 1. Aesthetes on third, fourth, and fifth segments proportionately much smaller than in first copepodid. Antenna (fig. 13D) with protopodite and bimerous endopodite, exopodite lost at this stage. Protopodite with seta at distal medial corner. Basal endopodite segment with seta on anterior surface near articulation with second segment. Apical segment with patch of spinules on anterior surface and with lateral apical seta, minute apical medial seta, and terminal bifid hook and separate single hook. Terminal armature of antenna of definitive form at this stage. Mandible (fig. 13E) minute and nearly of definitive form. Appendage consisting of major S-shaped piece, distal portion flattened and with heavy serrations. An anteriorly directed, flattened spine articulating at proximal bend near finely serrate flange. Maxillule (fig. 13F) like that in first

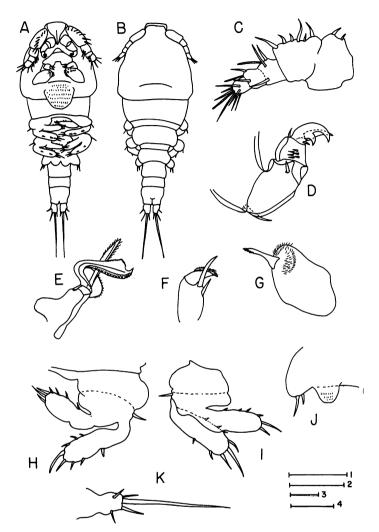


Fig. 13. Second copepodid of Sabellacheres illgi. A. Habit, ventral view. B. Habit, dorsal view. C. Antennule. D. Antenna. E. Mandible. F. Maxillule. G. Maxilla. H. First leg. I. Second leg. J. Third leg. K. Caudal ramus. Scale 1 (0.1 mm.) applies to A, B; scale 2 (0.05 mm.), to C, H-K; scale 3 (0.02 mm.), to D, G; scale 4 (0.02 mm.), to E, F.

copepodid. Maxilla (fig. 13G) similar to that of first copepodid but anterior projection somewhat reduced. Maxillipeds absent. Post-oral plate large, projecting from posterior margin of cephalosome almost to intercoxal lamella of first legs. First legs (fig. 13H) and second legs (fig. 13I)

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showing segmental fusion and shortening of elements of armature from condition in first copepodids. Legs consisting of obscurely bimerous protopodites joined by intercoxal lamellae and obscurely bimerous rami. Armature formula for legs in table 2. Third legs on first segment of urosome (fig. 13J) similar to those of first copepodid. Remaining three segments of urosome non-pedigerous. Caudal ramus (fig. 13K) with lateral seta near middle, dorsal seta at posterior third, and three terminal setae. Middle seta of terminal trio the longest, its length about four times the length of ramus.

THIRD COPEPODID OF Sabellacheres illgi

Figure 14

Specimens Examined: Two male third copepodids and one female third copepodid from *Pseudopotamilla occelata*, dredged off Upright Head, Lopez Island, Washington, 31 fathoms, July 26, 1961. One male third copepodid and two female third copepodids from *Pseudopotamilla occelata*, dredged in West Sound, Orcas Island, Washington, 20 fathoms, August 10, 1961.

DESCRIPTION: Average total length from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 0.653 mm. Sexes first distinguishable at this stage. Body of male copepodid (fig. 14A, B) composed of cephalosome bearing appendages through rudimentary maxillipeds, metasome of two leg-bearing segments, and urosome of four segments and caudal rami. Body of female copepodid (fig. 14C) with cephalosome bearing appendages through maxillae, metasome of two leg-bearing segments, and urosome of five segments. Antennule (fig. 14D) obscurely five-segmented, aesthetes small. Setal formula in table 1. Antenna (fig. 14E) similar to that of second copepodid, but elements of armature of terminal segment proportionately larger and spinules on anterior face of terminal segment arranged as a comb. Mandible, maxillule, and maxilla (fig. 14F) like those in second copepodid. Maxillipeds lacking in female copepodids but present in male copepodids as lobes on each side of postoral plate. This appendage (fig. 14G) with tiny apical points. First legs (fig. 14H) and second legs (fig. 14I) with obscurely bimerous protopodites, obscurely bimerous rami. Protopodites joined by intercoxal lamellae. Armature formula for legs in table 2. Third legs on first urosomal segment (fig. 14J) still rudimentary and consisting of unimerous protopodite, obscurely bimerous rami. Exopodite with setiform spine at middle of lateral margin and two terminal elements, endopodite unarmed. Second segment of urosome of male copepodid with two minute setae at posterior margin, these probably representing rudimentary fourth legs. Second

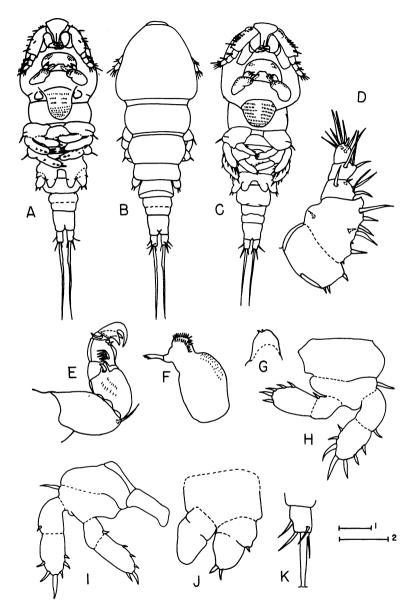


Fig. 14. Third copepodids of Sabellacheres illgi. A. Habit of male third copepodid, ventral view. B. Habit of male third copepodid, dorsal view. C. Habit of female third copepodid, ventral view. D. Antennule. E. Antenna. F. Maxilla. G. Maxilliped. H. First leg. I. Second leg. J. Third leg. K. Caudal ramus. Scale 1 (0.1 mm.) applies to A–C; scale 2 (0.05 mm.), to D–K.

segment of urosome of female copepodid unarmed. Third segment of urosome of male copepodid with constriction in middle, this segment corresponding to third and fourth urosomal segments in female copepodid. Caudal ramus (fig. 14K) like that of second copepodid, but medial terminal setae longer.

FOURTH COPEPODID OF Sabellacheres illgi

Figure 15

Specimens Examined: Four male fourth copepodids and five female fourth copepodids from *Pseudopotamilla occelata*, dredged off Upright Head, Lopez Island, Washington, 31 fathoms, July 26, 1961. Two female fourth copepodids from *Pseudopotamilla occelata*, dredged in West Sound, Orcas Island, Washington, 15 fathoms, July 26, 1961. One male fourth copepodid from *Pseudopotamilla occelata*, dredged in West Sound, Orcas Island, Washington, 20 fathoms, August 10, 1961. One female fourth copepodid from *Pseudopotamilla occelata*, dredged in West Sound, Orcas Island, Washington, August 24, 1961.

DESCRIPTION: Male fourth copepodid with average total length from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 0.672 mm. Female fourth copepodid with average total length of 0.705 mm. Male fourth copepodid with body (fig. 15A) composed of cephalosome bearing appendages through maxillipeds, metasome of three leg-bearing segments, and urosome of four segments and caudal rami. Body of female fourth copepodid (fig. 15B, C) composed of cephalosome bearing appendages through maxillae, metasome of three leg-bearing segments, and urosome of four segments and caudal rami. Antennule (fig. 15D) five-segmented. Setal formula in table 1. Antenna (fig. 15E), mandible (fig. 15F), maxillule, and maxilla (fig. 15G) like those in third copepodids. Maxilliped lacking in female copepodid. In male copepodid, maxilliped (fig. 15H, I) composed of bimerous lobe, with single seta on basal segment and terminal button and setule on second segment. Postoral plate large, similar to that of earlier copepodids. First legs (fig. 15J) and second legs (fig. 15K) with bimerous protopodites, obscurely bimerous rami. Third legs (fig. 15L) functional for first time at this stage and consisting of unimerous protopodite, obscurely bimerous rami. Armature formula for legs in table 2. Rudimentary fourth legs present in both sexes as unisetiferous lobes on first urosomal segment (fig. 15M, N). Second urosomal segment in male copepodid (fig. 15M) with central indentation and sixth leg rudiments as pointed lobes at posterior margin. In female copepodid, second urosomal segment (fig. 15N) showing only some lateral

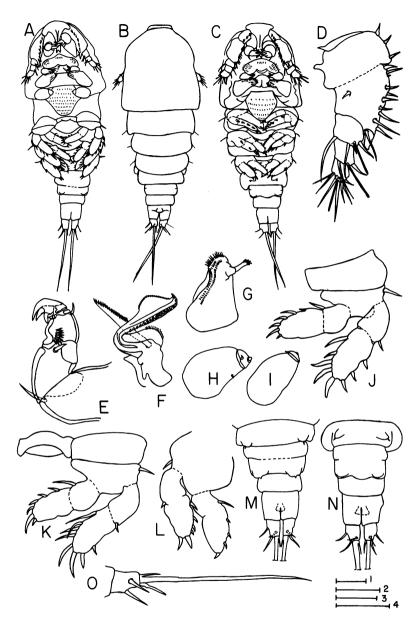


Fig. 15. Fourth copepodids of Sabellacheres illgi. A. Habit of male fourth copepodid, ventral view. B. Habit of female fourth copepodid, dorsal view. C. Habit of female fourth copepodid, ventral view. D. Antennule. E. Antenna. F. Mandible. G. Maxilla. H, I. Maxillipeds. J. First leg. K. Second leg. L. Third leg. M. Urosome of male fourth copepodid. N. Urosome of female fourth copepodid. O. Caudal ramus. Scale 1 (0.1 mm.) applies to A–C; scale 2 (0.05 mm.), to D, E, G–L, O; scale 3 (0.02 mm.), to F; scale 4 (0.1 mm.), to M, N.

indentation and with simple lobes at posterior margin, possibly representing sixth legs. Remaining urosomal segments non-pedigerous. Caudal ramus (fig. 15 O) like that of third copepodid.

FIFTH COPEPODID OF Sabellacheres illgi

Figure 16

Specimens Examined: One male fifth copepodid and one female fifth copepodid from *Pseudopotamilla occelata*, dredged off Upright Head, Lopez Island, Washington, 31 fathoms, July 26, 1961. Two male fifth copepodids and one female fifth copepodid from *Pseudopotamilla occelata*, dredged in West Sound, Orcas Island, Washington, 15 fathoms, July 26, 1961. Seven male fifth copepodids and seven female fifth copepodids from *Pseudopotamilla occelata*, dredged in West Sound, Orcas Island, Washington, 20 fathoms, August 10, 1961. Three male fifth copepodids and three female fifth copepodids from *Pseudopotamilla occelata*, dredged in West Sound, Orcas Island, Washington, August 24, 1960. One female fifth copepodid from *Branchiomma burrardum*, dredged in West Sound, Orcas Island, Washington, 20 fathoms, August 4, 1961. One female fifth copepodid from *Distylidia rugosa*, dredged in West Sound, Orcas Island, Washington, 20 fathoms, August 4, 1961.

Description: Average total length of male fifth copepodid from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 0.763 mm. Average total length of female fifth copepodid from anterior end of cephalosome to end of caudal rami, exclusive of caudal setae, 0.875 mm. Body of female copepodid (fig. 16A) consisting of cephalosome bearing appendages through maxillae, metasome of four segments, and urosome of four segments and caudal rami. Tergal plate of fourth metasomal segment projecting posteriorly and laterally over first urosomal segment. Body of male copepodid (fig. 16B) composed of cephalosome bearing appendages through maxillipeds, metasome of three leg-bearing segments, and urosome of six segments and caudal rami. Rostrum (fig. 16C) bifurcate, with medial crest. Antennule (fig. 16D) obscurely five-segmented. Setal formula in table 1. Antenna (fig. 16E) trimerous with armature like that in fourth copepodid. Apical hooks of antenna of male copepodid more slender than those in female copepodid. Mandible, maxillule (fig. 16F), and maxilla like those in fourth copepodids. Maxilliped lacking in female copepodid. In male copepodid, maxilliped trimerous (fig. 16G). Basal segment with single setule, middle segment unarmed, and terminal segment with small apical hook and apical medial setule. Post-oral plate large, extending from level of maxillipeds to intercoxal lamella of first swimming legs. Plate ornamented ventrally with

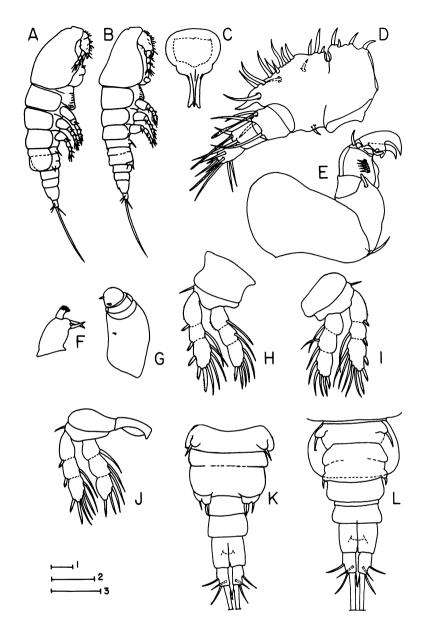


Fig. 16. Fifth copepodids of Sabellacheres illgi. A. Habit of female fifth copepodid, lateral view. B. Habit of male fifth copepodid, lateral view. C. Rostrum. D. Antennule. E. Antenna. F. Maxillule. G. Maxilliped. H. First leg. I. Second leg. J. Third leg. K. Urosome of male fifth copepodid. L. Urosome of female fifth copepodid. Scale 1 (0.1 mm.) applies to A, B; scale 2 (0.05 mm.), to C–G; scale 3 (0.1 mm.), to H–L.

rows of spinules. First swimming legs (fig. 16H), second swimming legs (fig. 16I), and third swimming legs (fig. 16J) with bimerous protopodites joined by intercoxal lamella and obscurely trimerous rami. Armature formula for legs in table 2. Fourth legs on first urosomal segment of male copepodid and on last metasomal segment of female copepodid consisting of single lobes, each with a single terminal seta (fig. 16K, L). Second urosomal segment of male unarmed, third segment with bilobed sixth legs, each lobe with a seta (fig. 16K). First urosomal segment of female copepodid equivalent to second and third urosomal segments of male copepodid. In female copepodid, first urosomal segment with sixth legs at posterior margin consisting of unisetiferous lobes (fig. 16L). Genital openings not patent at this stage. Remaining urosomal segments non-pedigerous. Caudal rami like those in second through fourth copepodids. Middle terminal setae of caudal rami much longer than are those in earlier stages.

DISCUSSION

Some important specific characters of the adult females of the six known species of gastrodelphyid copepods can be compared as follows: In size, Gastrodelphys dalesi is 1.5 mm. long; Gastrodelphys fernaldi, 2.2 mm.; Gastrodelphys myxicolae, 2.0 mm.; Sabellacheres gracilis, 2.3–5.0 mm.; and Sabellacheres illgi, 4.0 mm.

In the armature of the two basal segments of the antennule, Gastro-delphys dalesi has: I, three setae; II, 15 setae and an anterior projection; Gastrodelphys fernaldi has: I, four setae; II, 14 setae and projection lacking; Gastrodelphys clausii has: I, four setae; II, 13 setae and projection lacking; Sabellacheres gracilis has: I, four setae; II, 15 setae and an anterior projection; and Sabellacheres illgi has: I, four setae; II, 15 setae and an anterior projection.

The antenna is tetramerous in Gastrodelphys dalesi, Gastrodelphys fernaldi, Gastrodelphys clausii, and Gastrodelphys myxicolae. This appendage is trimerous in the two species of Sabellacheres.

The maxilla possesses posteriorly directed processes on the ventral surface in Gastrodelphys dalesi, Gastrodelphys clausii, and Gastrodelphys myxicolae. Ventral processes are lacking in Gastrodelphys fernaldi, Sabellacheres gracilis, and Sabellacheres illgi.

The cephalosomic post-oral plate is armed with four to six teeth in Gastrodelphys dalesi, 11 teeth in Gastrodelphys fernaldi, 12 teeth in Gastrodelphys clausii, and 13 teeth in Gastrodelphys myxicolae. This plate is unarmed in Sabellacheres gracilis and Sabellacheres illgi.

All the legs are represented by papillae, and none is functional in Gastrodelphys myxicolae. In Gastrodelphys fernaldi, the first two pairs of legs are biramous with bimerous rami, but the third and fourth legs are rudimentary. In Gastrodelphys clausii, the first two legs are biramous with trimerous exopodites and unimerous endopodites, and the third and fourth legs are rudimentary. The first three pairs of legs are biramous in Gastrodelphys dalesi, but the first two legs have trimerous rami, while the third legs have bimerous rami. The fourth legs are rudimentary in Gastrodelphys dalesi. In the two species of Sabellacheres, the first three pairs of legs are biramous and have trimerous rami. The fourth legs are rudimentary.

It can be seen that these six species show much intergradation in the features listed above. If the genus Gastrodelphys and the genus Sabellacheres are both to be retained, it is apparent that the species Sabellacheres dalesi Green must be placed in the genus Gastrodelphys as Gastrodelphys dalesi (Green) since it shares more characters of antennule, antenna, maxilla, and post-oral plate with the species of Gastrodelphys than with the species of Sabellacheres. I consider that these features, which are adaptive for recognition and fixation to hosts, and similarities in the habit of life on the tentacles of the worm, are more important in showing relationship than are the similarities which Gastrodelphys dalesi shows with species of Sabellacheres in the development of biramous third legs. Gastrodelphys fernaldi and the species of Sabellacheres show distinct differences in their naupliar stages, and a more complete study of the nauplii of Gastrodelphys dalesi than that given by Green (1961) may help further to resolve the problem of the taxonomic alignment of this species.

The gastrodelphyids and their polychaete hosts do not appear to have followed coincident trends of evolution. As an example, the adult gastrodelphyid copepods that I consider to be most closely related (Sabellacheres gracilis and Sabellacheres illgi) live on hosts of different subfamilies (Myxicola infundibulum of the subfamily Myxicolinae and Distylidia rugosa of the subfamily Sabellinae, respectively). On the other hand, the most distantly related gastrodelphyids, Sabellacheres gracilis and Gastrodelphys myxicolae, both live on the cosmopolitan sabellid species Myxicola infundibulum (Rénier), although not simultaneously, since S. gracilis is a cold-water form and G. myxicolae has been found only in the Adriatic Sea.

Mature adult females do seem to be associated with particular worms at the specific level, with the exception of *G. dalesi* which is specific to hosts at the generic level. The copepodid stages, adult males, and immature adult females of *Sabellacheres illgi*, however, exhibit some peregrination among worms of different genera and species, although all worms serving as hosts of these stages can be dredged at the same area. It is im-

portant that some selection is evidenced, however, since other sabellid worms collected in the same areas, such as *Demonax medius* (Bush) and *Schizobranchia insignis* Bush, have consistently failed to yield any gastro-delphyid developmental stages or adults. Other sabellids collected in the intertidal zone, such as *Chone infundibuliformis* Kröyer and *Eudistylia vancouveri* (Kinberg) from Washington, have also lacked gastrodelphyid associates.

A few inferences on the biology of the gastrodelphyids have been gained in this study. Adult females and males of the species of Gastrodelphys and males, immature females, and copepodids of the species of Sabellacheres attach to the tentacles of their hosts by protruding the bifurcate rostrum into a tentacular filament and then clasping the filament against the rostrum with the antennae. Adults of Gastrodelphys fernaldipresented with isolated tentacles of miscellaneous species of sabellid worms consistently choose those of their normal host, Sabella crassicornis.

It would appear that the gastrodelphyid copepods are commensals and feed on the food material carried in mucus by ciliary tracts of the tentacles of the worm. The nutritional relationships of the adult females of species of *Sabellacheres*, which are embedded in the tissue of their hosts, are still enigmatic, although the similarity in the color of the yolk of the embryos of these gastrodelphyids and the color of the tissues of their hosts might indicate that the pigments have been derived from the hosts. Chemical analyses and histochemical studies will be necessary to prove this point.

It is important here to consider the relationship of the family Gastro-delphyidae and other groups of copepods. Michael Sars (1862) was of the opinion that Sabellacheres gracilis was a representative of the Siphonostomata of Latreille, but he could not relate this species to any particular family then known. He also noted a possible alliance with the genus Notodelphys because of the possession of "a single dorsal egg sac" (=brood pouch) in both genera. Levinsen (1877) listed all copepod associates of annelids known at that time but gave no conclusions as to their relationship. Graeffe (1883) and List (1890a) both believed that the gastro-delphyids were intermediate to the siphonostomes and the notodelphyids. Markewitsch (1940) placed his Vermiclavella elongata [=Sabellacheres gracilis] in the suborder Notodelphyoida.

There is no evidence of a close relationship of the poecilostomous Gastrodelphyidae and the gnathostomous Notodelphyidae in either development or morphology. The possession of incubatory pouches in both groups formed by the invagination and protrusion of a metasomal segment appears to be a convergent modification in two separate evolutionary

lines rather than a true evidence of alliance. One gastrodelphyid, Gastro-delphys fernaldi, possesses external ovisacs rather than a brood pouch, and it is quite possible that other such species will be found as the group is more extensively studied.

It is my opinion that the family Gastrodelphyidae is a highly specialized and separate group of poecilostome cyclopoids that shares some characteristics with copepods of the family Lichomolgidae. The group also shows a more distant relationship with copepods of the nereicoliform group, particularly the family Clausidiidae (Gooding, 1960, MS).

The gastrodelphyids particularly show some resemblance to Sabelliphilus elongatus Sars (Michael Sars, 1862; George O. Sars, 1917), a lichomolgid that also lives on sabellid worms and that I have collected at Naples on Spirographis spallanzanii Viviani. Sabelliphilus elongatus is not nearly so modified a copepod as any representative of the Gastrodelphyidae, since it has four pairs of swimming legs and reduced fifth legs, and the females have maxillipeds. Resemblances are as follows: the antennule, although seven-segmented, has an armature on the terminal three segments exactly like that in the gastrodelphyids, and the two basal segments show some enlargement and flattening; the antenna is tetramerous and bears three terminal hooks as in the Gastrodelphyidae, but an additional hook on the third segment and so many setae are not found in the gastrodelphyids; the mandible of Sabelliphilus is simpler, while the maxillule is of similar form but bears more setae; the maxilla has many similarities to that of Sabellacheres; and the maxilliped of the male is very similar to that of the male gastrodelphyid. It seems quite possible that the Gastrodelphyidae may have diverged from the lichomolgids via a form such as Sabelliphilus.

Gooding (MS) has defined a nereicoliform family group which includes the families Clausididae, Clausididae, Nereicolidae, Eunicicolidae, Synaptiphilidae and Catiniidae as follows: "Body segmented to partially sacciform. Basal antennulomeres not expanded. Four antennomeres. Maxillipeds may be secondarily reduced or lost in female. Mandible bearing four-? one terminal elements, none a flat, triangular, uniarticulated blade. At least two pairs of legs. Leg five, when best developed, with four elements on terminal podomere." This author noted that a number of factors could implicate the family Gastrodelphyidae as a relative or member of this familial complex. The definition above, particularly with respect to the antennulomeres and the fifth leg would exclude the Gastrodelphyidae, but there is no doubt that the gastrodelphyids do show some distant relationship with this group. Gooding has pointed out the importance of the study of first copepodids in relating the poecilostomous

copepods. Examination of the description of the first copepodid of Sabellacheres illgi will show some definite similarities to species of Hemicyclops (George O. Sars, 1917; Gooding, 1960, MS), particularly in the form of the mandible at this stage. Gooding is of the opinion that Hemicyclops is the most primitive of the poecilostomes, and the similarities shown by the gastrodelphyids may be only relict features and not evidences of close relationship.

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