

Rostrum present, unarmed, about one-third of carapace length; carapace with cervical, post-cervical, branchiocardiac, antennal and gastro-orbital grooves; median dorsal, antennal, branchiostegal, and lateral ridges present; first antennae small, second antennae with large broad scaphocerite; first pereopod large, chelate status unknown; pereopods two through five smaller than first, and two through four subchelate; first pleonic somite short, partially covered by carapace; second pleonic pleura not expanded; apparent pleonic hinges on all pleonic somites; telson broadly subtriangular, unarmed; uropods without diaeresis. This earliest known decapod is a mixture of astacidean and glypheoidean characteristics, and in addition, the antennal scale suggests a 'natantian' affinity. This juxtaposition of characters presents a problem because although most authors consider the dendrobranchiates to be the most primitive decapods, they do not appear in the fossil record until 100 million years after *Palaeopalaemon*. Although we recognize the capricious nature of the fossil record we believe that the available data would indicate that the Dendrobranchiata separated early from the other decapods, a conclusion reached by others. In contrast to most other authors, however, we believe that the origins and relationships of the Caridea and Stenopodidea (and possibly the Procarididea) are to be found among those groups traditionally considered reptants. In this regard our speculations are similar to those of Beurlen & Glaessner (1930), who derive the Caridea from ancestral thalassinoids.

## 8 ACKNOWLEDGEMENTS

We thank the following individuals for assistance, both allowing us access to specimens and commenting on the manuscript: Drs Raymond B. Manning, Robert H. Gore, Frederick R. Schram, Anthony J. Provenzano, Jr, Daryl L. Felder, Dr Sandra Gilchrist, Ms Elizabeth Woodsmall and Mr Kenneth Womble assisted with the graphics. Specimens were kindly provided by the San Diego Museum of Natural History, San Diego, CA, and Scripps Institution of Oceanography, La Jolla, CA. We also wish to thank Dr Anne Thistle for typing and editing the manuscript.

## 9 APPENDIX I

### Material examined

#### Dendrobranchiata

##### Peneidae

*Peneus setiferus* (Linnaeus)

##### Solenoceridae

*Solenocera vioscari* Burkenroad

##### Sergestidae

*Sergestes similis* Hansen

##### Sicyonidae

*Sicyona* sp.

#### Caridea

##### Palaemonidae

*Palaemonetes kadiakensis* Rathbun

*Palaemon floridanus* Chace

*Macrobrachium acanthurus* (Wiegmann)

*Pontonia* sp.

#### Hippolytidae

*Thor floridanus* Kingsley

*Lysmata wurdemani* (Gibbes)

*Hippolyte zostericola* (Smith)

*Tozeuma carolinense* Stimpson

*Saron marmoratus* (Oliver)

#### Atyidae

*Atya innocous* (Herbst)

*Atya margaritacea* A. Milne Edwards

*Micratya poeyi* (Guerin-Meneville)

*Potimirim glabra* (Kingsley)

#### Oplophoridae

*Oplophorus* sp.

*Acathephyra* sp.

#### Alpheidae

- |   |  |
|---|--|
| <p><i>Alpheus lotini</i> Guerin<br/>         Crangonidae<br/> <i>Crangon crangon</i> (Linnaeus)<br/>         Gnathypyllidae<br/> <i>Gnathypyllum</i> sp.<br/>         Pasiphaeidae<br/> <i>Leptocheila bermudensis</i> Bate<br/>         Procaridida<br/>         Procarididae<br/> <i>Procaris ascensionis</i> Chace &amp; Manning<br/> <i>P.hawaiana</i> Holthuis</p> | <p>Stenopodidea<br/>         Stenopodidae<br/> <i>Stenopus hispidus</i> Oliver<br/>         Reptantia<br/>         Cambaridae<br/> <i>Cambarus</i> spp.<br/>         Upogebiidae<br/> <i>Upogebia pugettensis</i> (Dana)<br/>         Axiidae<br/>         axiid sp.</p> |
|---|--|

## 10 APPENDIX II

### List of abbreviations

|     |                     |     |                       |
|-----|---------------------|-----|-----------------------|
| ab  | branchial axis      | m   | mandible              |
| cch | cardiac chamber     | mp  | mandibular palp       |
| cm  | convoluted membrane | mpr | molar process         |
| cpv | cardiopyloric valve | mo  | mesocardiac ossicle   |
| d   | denticles           | mt  | median tooth          |
| e   | esophagus           | p   | ptero-cardiac ossicle |
| ep  | epistome            | pc  | pyloric chamber       |
| epi | epipod              | pf  | pyloric fingerlets    |
| gf  | gland filter        | po  | pyloric ossicle       |
| ip  | incisor process     | sr  | secondary rami        |
| l   | lamellae            | upg | uropyloric groove     |
| la  | labrum              | uo  | urocardiac ossicle    |
| lb  | lateral branch      | upo | uropyloric ossicle    |
| lt  | lateral teeth       | zo  | zygocardiac ossicle   |
| lr  | lateral ramus       |     |                       |

## DISCUSSION

BAUER: You were talking about how some characters in defining carideans, such as the overlap of the second abdominal pleuron of the first and the third, may not be very good. Actually, on the slide you showed of *Glyphocrangon* it looked like the second was overlapping the first. Another point is whether or not there are articulations between the various abdominal segments. For example, in most carideans the hump is caused by the fact there is no articulations between the third and fourth pleura, and that is one of the characters Burkenroad used as a diagnostic feature for the carideans. I have found that in things like *Crangon*, which don't show the caridean hump, they lack that condyle between the third and fourth, whereas the penaeids have a condyle between each of the segments. So that might be a better definition for some of these groups since the pleura, because of other selection pressures, are modified.

ABELE: *Glyphocrangon* does have condyles on the exterior surface of the second and third pleura.

BAUER: No, between the third and the fourth.

ABELE: They have them there as well. They are not as well-developed, but they are present there.

BAUER: Oh.

## REFERENCES

- Abele, L.G. & B.E.Felgenhauer 1982. Eucaridea. In: S.P.Parker (ed.), *Synopsis and classification of living organisms, Vol. 2*: 294-326. New York: McGraw-Hill.
- Balss, H. 1957a. Decapoda, Part VIII: Systematic. In: *H.G.Bronn, Klassen und Ordnungen des Tierreichs* 5(1):7(12):1505-1672. Leipzig: Akademische Verlags.
- Balss, H. 1957b. Decapoda, Part XI: Stammesgeschichte. In: *H.G.Bronn, Klassen und Ordnungen des Tierreichs* 5(1):7(12):1797-1821. Leipzig: Akademische Verlags.
- Bate, C.S. 1888. Report on the Crustacea Macrura collected by HMS Challenger during the years 1873-1876. *Challenger Rept. Zool.* 24:1-942.
- Bauer, R.T. 1976. Mating behaviour and spermatophore transfer in the shrimp *Hepatocarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae). *J. Nat. Hist.* 10:415-440.
- Beurlen, K. & M.F. Glaessner 1930. Systematik der Crustacea Decapoda auf Stammesgeschichtlicher Grundlage. *Zool. Jb. Abt. Syst.* 60:49-84.
- Boas, J.E.V. 1880. Studier over Decapodernes Slaegtskabsforhold. *Vidensk. Selsk. Kristiania, Skrifter* (5)6:25-210.
- Borradaile, L.A. 1907. On the classification of the decapod Crustacea. *Ann. Mag. Nat. Hist. London* (7):19:457-486.
- Bouvier, E.L. 1940. Décapodes marcheurs. *Faune de France* 37:1-399, pls.I-XIV.
- Bowman, T. & L.G.Abele 1982. Classification of the Crustacea. In: L.G.Abele (ed.), *Biology of the Crustacea, Vol. 1*:1-27. New York: Academic Press.
- Brooks, H.K. 1962. The Paleozoic Eumalacostraca of North America. *Bull. Am. Paleontol.* 44:163-280.
- Burkenroad, M.D. 1963. The evolution of the Eucarida (Crustacea, Eumalacostraca) in relation to the fossil record. *Tulane Stud. Geol.* 2:2-17.
- Burkenroad, M.D. 1981. The higher taxonomy and evolution of Decapoda (Crustacea). *Trans. San Diego Soc. Nat. Hist.* 19:251-268.
- Calman, R.T. 1909. Crustacea. In: R.Lankester (ed.), *A Treatise on Zoology, Vol. VII.* Adam & Charles Black, London.
- Chace, F.A. 1976. Shrimps of the pasiphaeid genus *Leptocheila* with descriptions of three new species (Crustacea: Decapoda: Caridea). *Smiths. Contr. Zool.* 222:1-51.
- Chace, F.A. & D.E.Brown 1978. A new polychelate shrimp from the Great Barrier Reef of Australia and its bearing on the family Bresiliidae (Crustacea: Decapoda: Caridea). *Proc. Biol. Soc. Wash.* 91: 756-766.
- Chace, F.A. & L.B.Holthuis 1978. *Psalidopus*: the scissor-foot shrimps (Crustacea: Decapoda: Caridea). *Smiths. Contr. Zool.* 277:1-22.
- Chace, F.A. & R.B.Manning 1972. Two new caridean shrimps, one representing a new family, from marine pools on Ascension Island (Crustacea: Decapoda: Natantia). *Smiths. Contr. Zool.* 131:1-18.
- Coombs, E.F. & J.A.Allen 1978. The functional morphology of the feeding appendages and gut of *Hippolyte varians* (Crustacea: Natantia). *Zool. J. Linn. Soc.* 64:261-282.
- Coutiere, H. 1899. Les 'Alpheidae', morphologie externe et interne, formes larvaires, bionomie. *Ann. Sci. Nat. Zool.* (8)9:1-560.
- Dana, J.D. 1852. Crustacea. *United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, USN Vol. XIII*:1-635.
- Farfante, I.P. 1975. Spermatophores and thelyca of the American white shrimps, genus *Penaeus*, subgenus *Litopenaeus*. *Fish. Bull.* 78:463-486.
- Felgenhauer, B.E. & L.G.Abele (in press). Aspects of mating behavior in the tropical freshwater shrimp *Atya innocuous* (Herbst). *Biotropica*.
- Forest, J. & M.de Saint Laurent 1975. Presence dans la fauna actuelle d'un représentant du groupe mésozoïque des Glypheides: *Neoglyphea inopinata* gen. nov., sp.nov. (Crustacea Decapoda Glypeidae). *C.R. hebd. Seanc. Acad. Sci., Paris (D)*281:155-158.
- Forest, J. & M.de Saint Laurent 1981. La morphologie externe de *Neoglyphea inopinata*, espèce nouvelle de Crustacé Décapode Glyphéide. *Res. Camp. Musorstom. I - Philippines (18-28 Mars 1976) vol.1, Mém. ORSTOM* 91:51-84.
- Forest, J., M.de Saint Laurent & F.A.Chace 1976. *Neoglyphea inopinata*: A crustacean 'living fossil' from the Phillipines. *Science* 192:884.
- Förster, R. 1966. Über die Erymiden, eine alte konservative Familie der mesozoischen Dekapoden. *Paleontographica* 125:61-175.

- Förster, R. 1967. Die reptanten Dekapoden der Trias. *N.J. Geol. Paleontol. Abh.* 128:136-194.
- Glaessner, M.F. 1960. The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. *N.Z. Geol. Survey Paleontol. Bull.* 31:1-63.
- Glaessner, M.F. 1969. Decapoda. In: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology. Arthropoda 4. Part R, Vol. 2*:R399-533. Lawrence: Geol. Soc. Am. & Univ. Kansas Press.
- Guinot, D. 1977. Propositions pour une nouvelle classification des Crustacés Décapodes Brachyours. *C.R. Acad. Sci. Paris (D)*:285-1049-1052.
- Guinot, D. 1979. Problèmes pratiques d'une classification cladistique des Crustacés Décapodes Brachyours. *Bull. Off. Natn. Pêch. Tunisie* 3:33-46.
- Gurney, R. 1924. Crustacea. Part IX – Decapod larvae. *Brit. Antarctic ('Terra Nova') Exped. 1910, Zool.* 8:37-202.
- Gurney, R. 1936. Larvae of decapod Crustacea. Part I: Stenopidea. Part II: Amphionidae. Part III. Phyllosoma. *Discovery Repts.* 12:377-440.
- Gurney, R. 1942. Larvae of decapod crustacea. *Ray Soc. London.*
- Holthuis, L.B. 1946. Biological results of Snellius Expedition. XIV. The Decapoda Macrura of the Snellius Expedition I. The Stenopodidae, Nephropsidae, Scyllaridae and Palinuridae. *Temminckia* 7:1-178.
- Holthuis, L.B. 1951a. The caridean Crustacea of tropical West Africa. *Alantide Rep.* 2:7-187.
- Holthuis, L.B. 1951b. A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. I. The subfamilies Euryrhynchinae and Pontoniinae. *Occ. Paper Allan Hancock Found.* 11:1-332.
- Holthuis, L.B. 1955. The recent genera of the caridean and stenopodidean shrimps (class Crustacea, order Decapoda, supersection Natantia) with keys for their determination. *Zool. Verhand.* 26:1-157.
- Holthuis, L.B. 1971. The Atlantic shrimps of the deep-sea genus *Glyphocrangon* A. Milne Edwards 1881. *Bull. Mar. Sci.* 21:267-373.
- Holthuis, L.B. 1973. Caridean shrimps found in land-locked saltwater pools at four Indo-West Pacific Localities (Sinai Peninsula, Funafuti Atoll, Maui and Hawaiian Islands), with the description of one new genus and four new species. *Zool. Verhandl.* 128:1-48, pls.1-7.
- Huxley, T.H. 1878. On the classification and the distribution of the crayfishes. *Proc. Zool. Soc. London* 1878:752-788.
- Huxley, T.H. 1880. *The crayfish, an introduction to the study of zoology.* London: C.Kegan Paul.
- Kaestner, A. 1970. *Invertebrate zoology. Vol. III. Crustacea.* New York: Interscience.
- Kunze, J. & D.T. Anderson 1979. Functional morphology of the mouthparts and gastric mill in the hermit crabs *Clibanarius taeniatus* (Milne Edwards), *Clibanarius virescens* (Krauss), *Paguristes squamosus* McCulloch and *Dardanus setifer* (Milne Edwards) (Anomura: Paguridae). *Aust. J. Mar. Fresh. Res.* 30:683-722.
- Milne Edwards, H. 1837. *Histoire naturelle générale et particulière des Crustacés et insectes. Tome Troisième.* Paris: Dufart.
- Mocquard, F. 1883. Estomac des crustaceans podophtalmiques. *Ann. Sci. Nat.* 16:1-311.
- Ortmann, A. 1890. Die Decapoden-Krebse de Strassburger Museums mit besonderer Berücksichtigung der von Herrn. Dr Döderlein bei Japan und bei den Lui-Kui-Inseln gesammelten und z. A. im Strassburger Museum aufbewahrten Formen. *Zool. Jb. (Syst.)* 5:437-540.
- Patwardhan, S.S. 1935. On the structure and mechanism of the gastric mill in Decapoda. 5. The structure of the gastric mill in natantous Macrura-Caridea. *Proc. Indian Acad. Sci. (B)*1:693-704.
- Patwardhan, S.S. 1936. On the structure and mechanism of the gastric mill in Decapoda. VI. The structure of the gastric mill in the Natantous Macrura – Penaeida and Stenopidea; conclusion. *Proc. Indian Acad. Sci. (B)*2:155-174.
- Powell, R.R. 1974. The functional morphology of the fore-guts of the thalassinid crustaceans *Callinassa californiensis* and *Upogebia pugettensis*. *Univ. Calif. Pub. Zool.* 102:1-41.
- Powell, R.R. 1976. Two new freshwater shrimps from West Africa: the first euryrhynchinids (Decapoda Palaemonidae) reported from the Old World. *Rev. Zool. Afr.* 90:883-902.
- Powell, R.R. 1977. A revision of the African freshwater shrimp genus *Desmocarid* Solland, with ecological notes and description of a new species (Crustacea Decapoda Palaemonidae). *Rev. Zool. Afr.* 91:649-674.
- Rice, A.L. 1980. Crab zoal morphology and its bearing on the classification of the Brachyura. *Trans. Zool. Soc. London* 35:271-424.



- Saint Laurent, M.de 1979. Vers une nouvelle classification des Crustacés Décapodes Reptantia. *Bull. Off. Natn. Pêch. Tunisie* 3:15-31.
- Saint Laurent, M.de 1980a. Sur la classification et la phylogénie des Crustacés Décapodes Brachyours. I. Podotremata Guinot, 1977, et Eubrachyura sect. no. *C.R. Acad. Sci. Paris (D)*290:1265-1268.
- Saint Laurent, M.de 1980b. Sur la classification et la phylogénie des Crustacés Décapodes Brachyours. II. Heterotremata et Thoracotremata Guinot 1977. *C.R. Acad. Sci. Paris (D)*290:1317-1320.
- Saint Laurent, M.de & R.Cleva 1981. Crustacés décapodes: Stenopodidae. *Res. Camp. Musorstom I. Philippines (18-28 Mars 1976) Vol.1, Mem. ORSTOM* 91:151-188.
- Schaefer, N. 1970. The functional morphology of the foregut of three species of decapod Crustacea: *Cyclograpsus punctatus* Milne-Edwards, *Diogenes brevirostris* Stimpson, and *Upogebia africana* (Ortmann). *Zool. Afr.* 5:309-326.
- Schram, F.R. 1982. The fossil record and evolution of the crustacea. In: L.G.Abele (ed.), *Biology of the Crustacea. Vol.1*:93-147. New York: Academic Press.
- Schram, F.R., R.M.Feldman & M.J.Copeland 1978. The late Devonian Palaeopalaemonidae and the earliest decapod crustaceans. *J. Paleontol.* 52:1375-1387.
- Snodgrass, R.E. 1951. *Comparative studies on the head of mandibulate arthropods*. Ithaca: Comstock Publ.
- Stanton, W. 1975. *The Great United States Exploring Expedition of 1838-1842*. Berkeley: Univ. Calif. Press.
- Williamson, D.I. 1976. Larvae of Stenopodidea (Crustacea, Decapoda) from the Indian Ocean. *J. Nat. Hist.* 10:497-509.
- Williamson, D.I. 1982. Larval morphology and diversity. In: L.G.Abele (ed.), *Biology of the Crustacea, Vol.2*: New York: Academic Press.
- Young, J.H. 1959. Morphology of the white shrimp *Penaeus setiferus* (Linnaeus 1758). *Fish. Bull.* 145: 1-168.

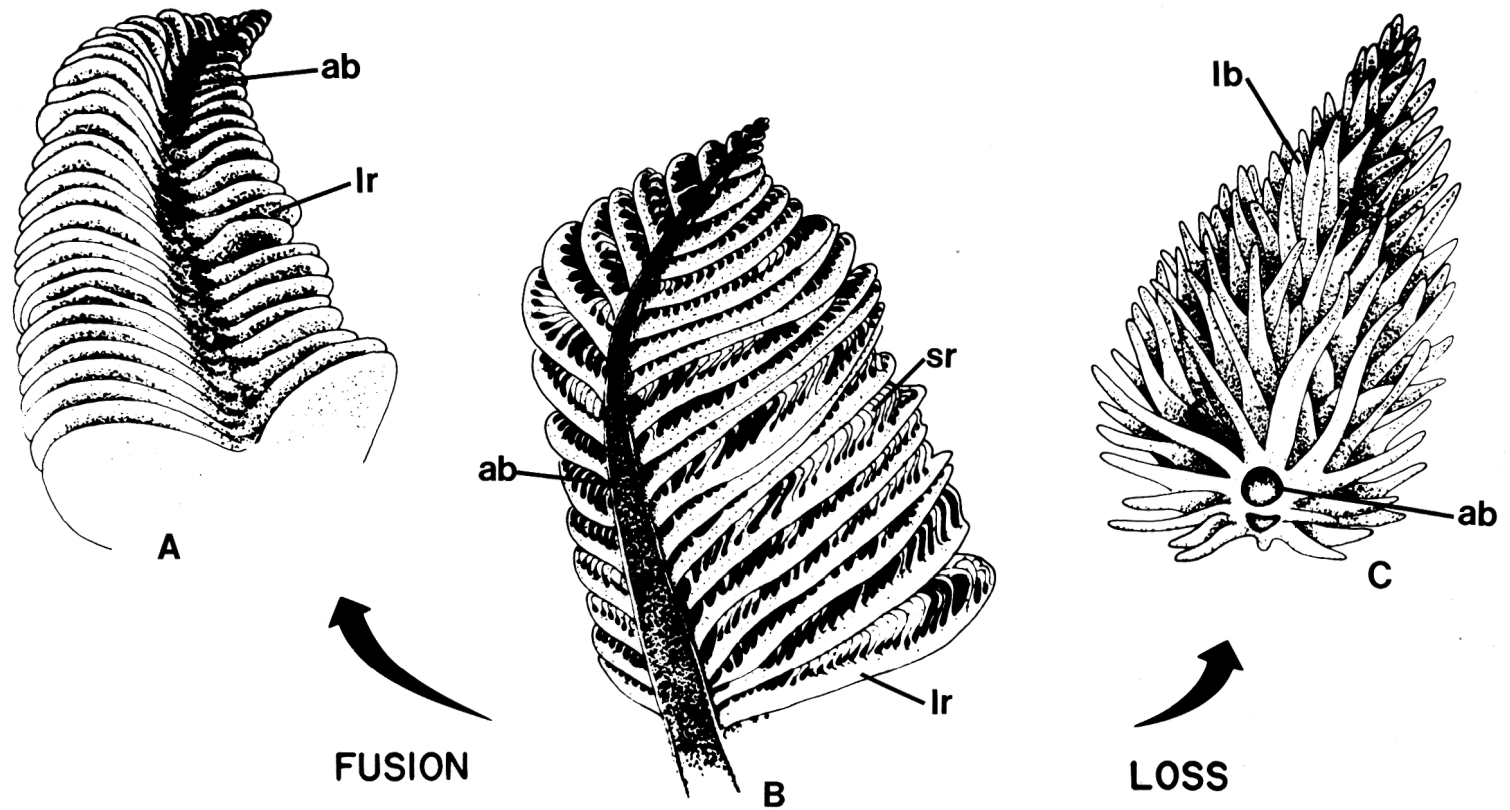


Figure 3. Hypothesis suggested by Boas 1880, and Burkenroad 1981, for the evolution of gill types among the Decapoda. (B) typical dendrobranchiate gill, consisting of lateral branches (lb) extending from the main branchial axis (ab) with a series of subdivided secondary rami (sr) from each lateral branch. Expansion of the lateral branches of the dendrobranchiate type would result in (A) phyllobranchiate gill; whereas loss of the secondary rami (sr) and/or reduction of the lateral branches would give rise to (C) trichobranchiate gill.

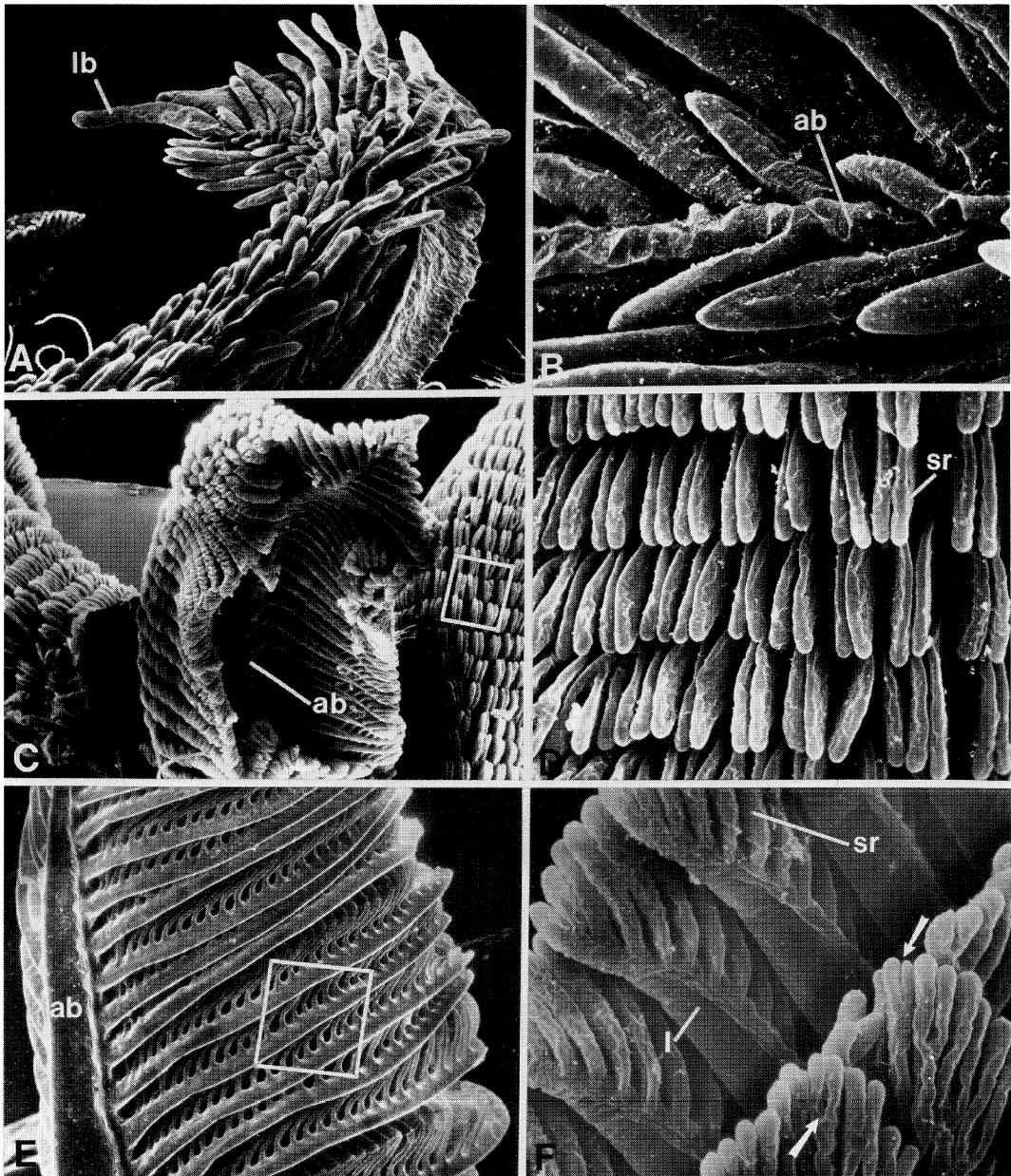


Figure 4. A. Trichobranchiate gill from *Cambarus* sp.; X50. B. Enlargement of trichobranch gill denoting the main branchial axis (ab) with lateral branches (lb) extending from the main gill axis; X100. C. Dendrobranchiate gill from *Peneus setiferus*; note the branchial axis with lateral branches extending from the main branch. The white box indicates the external view of the secondary rami (sr); X50. D. Enlargement of secondary rami (boxed area in C); X200. E. External view of dendrobranchiate gill of *Sergestes similis*; white box indicates branching secondary rami (sr); X60. F. Internal view of *S. similis* gill showing the secondary rami (sr) with white arrows denoting bifurcation of the secondary rami; X200.

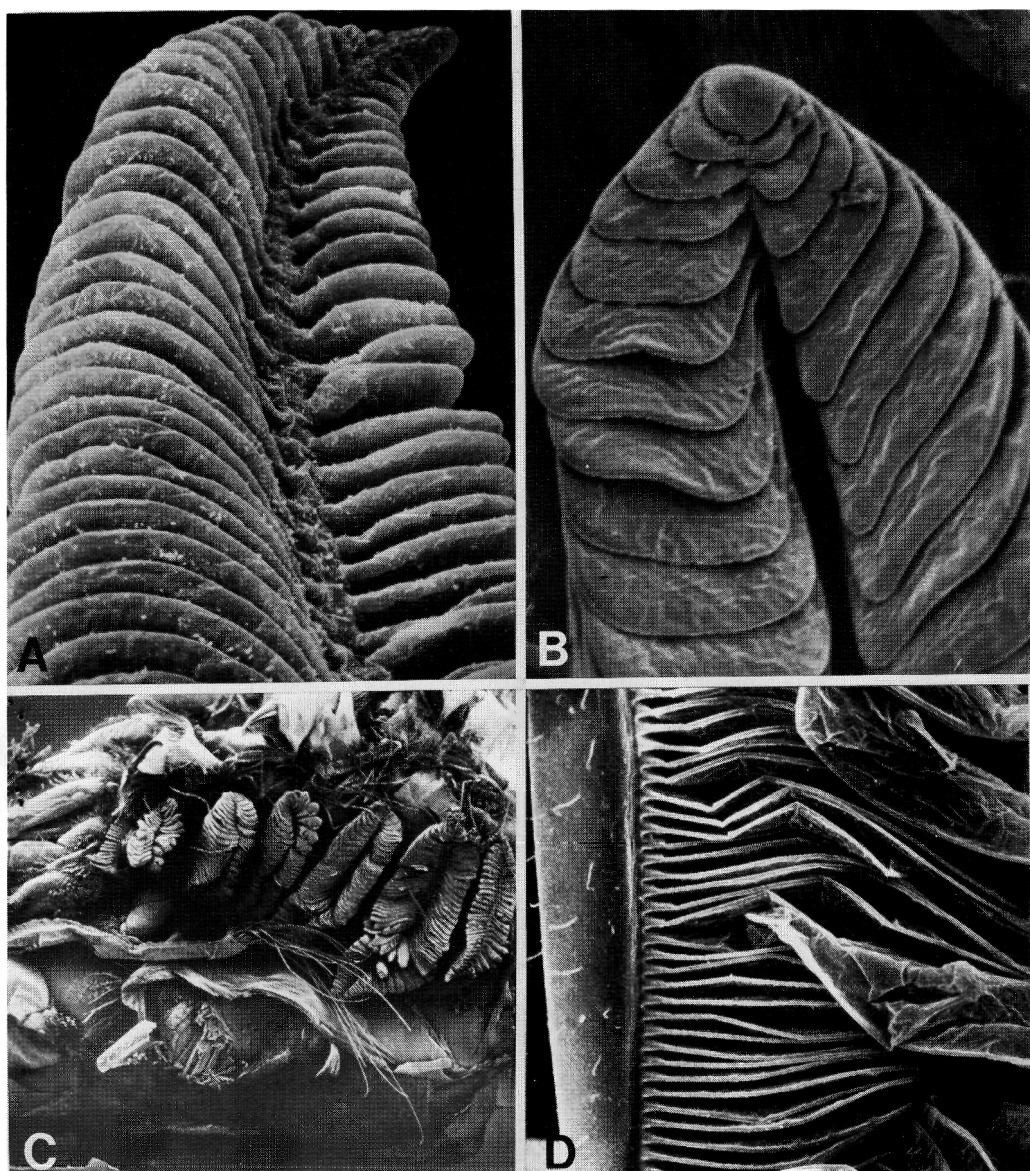
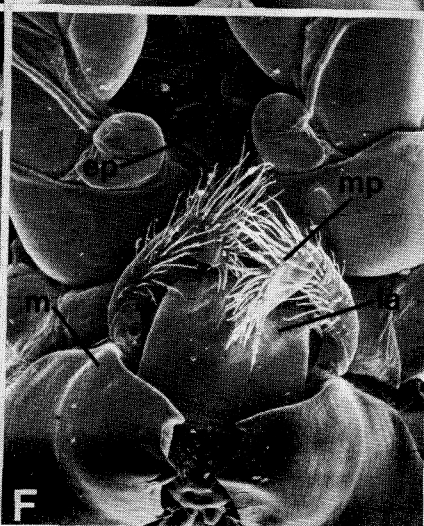
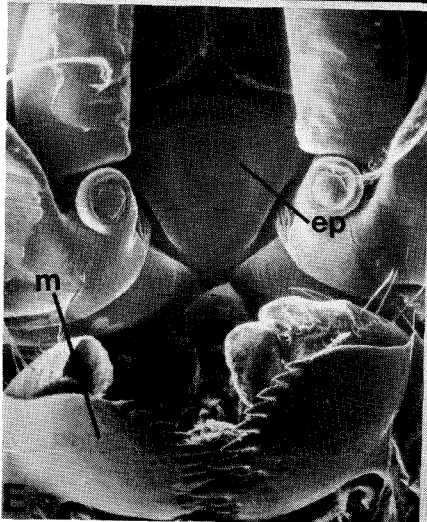
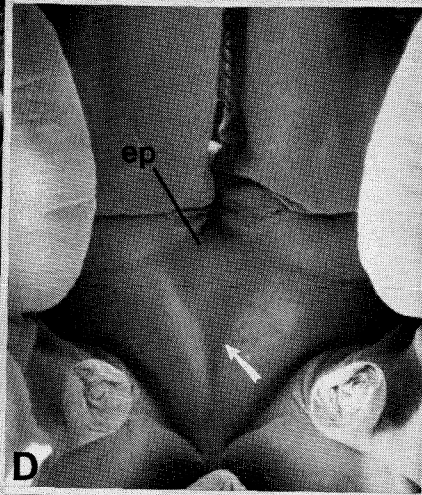
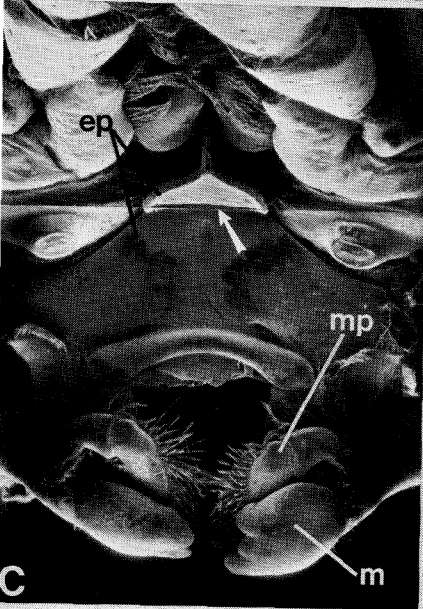
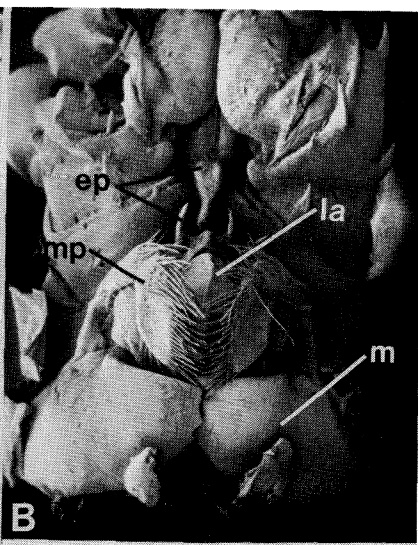
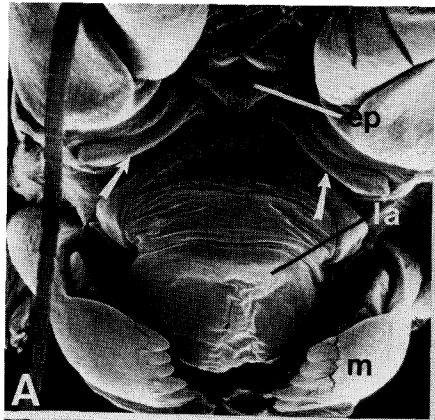


Figure 5. A. Phyllobranchiate gill type from *Palaemonetes kadiakensis*; X60. B. Phyllobranch gill plume of *Atya innocous*, showing the variation seen within this gill type; X80. C. Lateral view of entire gill region of *A. innocous*, indicating the arrangement of the phyllobranch gills; X20. D. Phyllobranch gill of *Oplophorus* sp.; note the thin, plate-like nature of the lateral rami; X50.





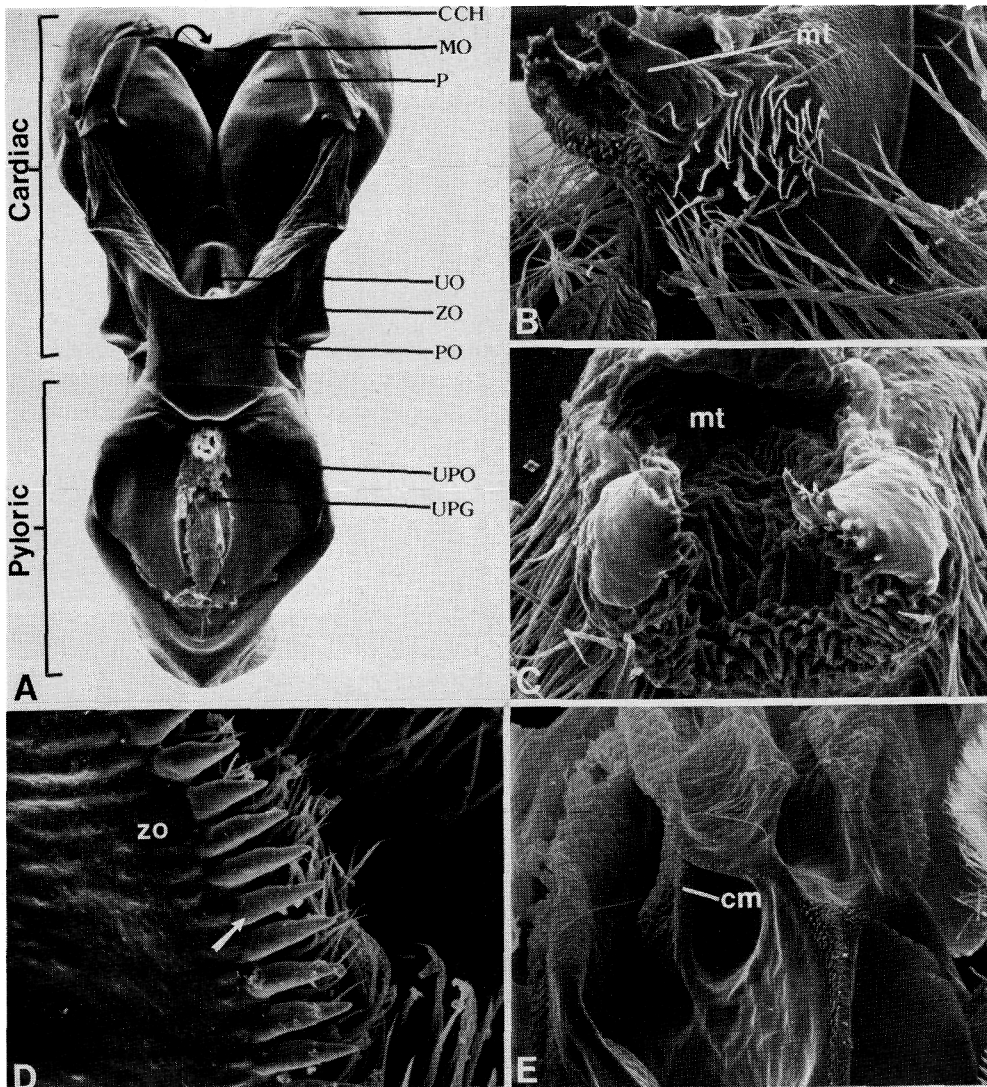


Figure 7. A. Dorsal view of the foregut of *Atya innocuous* (membranes and musculature removed); note the distinct cardiac and pyloric regions along with the distinct chitinous regions (ossicles); X100. B. Lateral view of the bifid median tooth of *A. innocuous* projecting from roof of cardiac chamber; X250. C. Close-up view of the median tooth of *A. innocuous*; note presence of stout denticles on inner portion of tooth; X600. D. Zygocardiac ossicle of *A. innocuous*, arrow indicates the lateral teeth; X600. E. Convoluted membrane (cm) of *Potimirim glabra* located within the pyloric chamber; X170.

Figure 6. A. Ventral view of the protocephalon of *Peneus setiferus*; note condition and location of epistome (ep) between the antennae; white arrow indicate epistomal bar; X25. B. Ventral aspect of protocephalon of *Stenopus hispidus*; note distinctive morphology and location of epistome (ep); X30. C. Protocephalon of *Cambarus* sp.; note location and morphology of the epistome; white arrow indicates membranous connection between anterior and posterior portions of rigid epistome; X20. D. Epistome (ep) of *Palaemonetes kadiakensis* in ventral view; white arrow denotes membranous points of articulation; X70. E. Protocephalon of *Oplophorus* sp.; large labrum has been removed to reveal nature of the epistome (ep); X40. F. Ventral aspect of the protocephalon of *Procaris ascensionis*; note condition and location of the epistome (ep); X40.

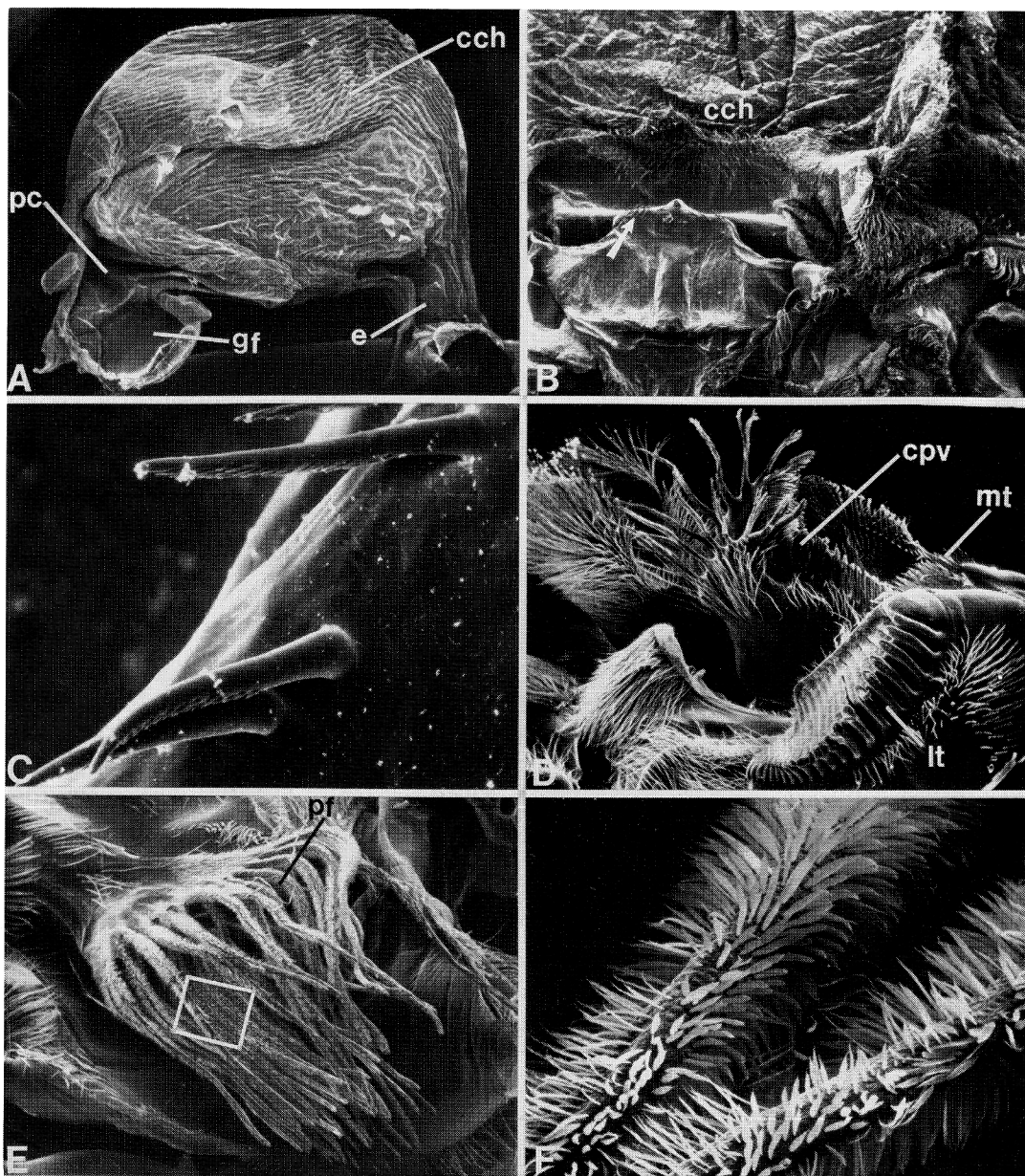


Figure 8. A. Foregut of *Saron marmoratus* (membranes and muscles removed); note lack of chitinized regions (ossicles and reduction of the pyloric chamber (pc); X20. B. Floor of the cardiac chamber (cch) of *Palaemonetes kadiakensis*; note the reduced median tooth (mt) (arrow), and lack of lateral teeth (lt); X1100. D. Lateral view of gastric armature of *Upogebia pugettensis*; note elaborate cardiopyloric valve (cpv); also shown are large lateral teeth (lt) and median tooth (mt) (the median tooth is obscured by the lateral teeth in this micrograph); X25. E. Pyloric fingerlets (pf) within the pyloric chamber of *Upogebia pugettensis*; X25. F. Close-up of pyloric fingerlets; X300.

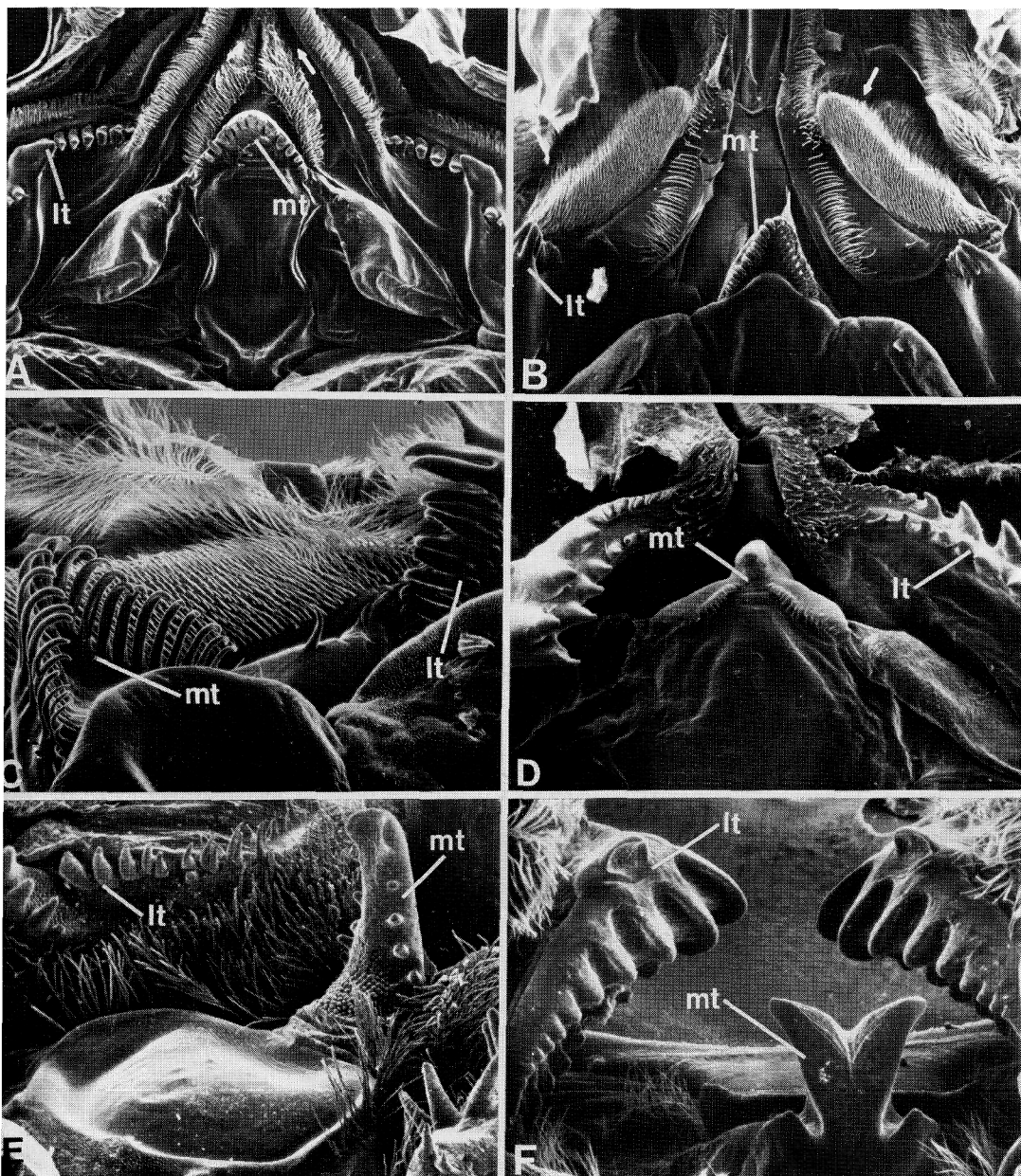


Figure 9. Cardiac chamber of *Peneus setiferus*, showing details of gastric mill; large median tooth is present (mt) flanked by large lateral teeth (lt); note rows of plumose setae anterior to median tooth which direct food to pyloric chamber (arrow); X20. B. Gastric mill of *Solenocera vioscari*; note large median tooth (mt) with robust lateral teeth (lt); dense pads of setae (arrow) direct food to pyloric chamber; X20. C. Lateral view of median tooth of *S. vioscari*; note long teeth borne on median tooth; X80. D. Gastric armature of *Sergestes similis*; note median tooth (mt) and lateral teeth (lt); X40. E. Gastric mill of *Stenopus hispidus*, elongate median tooth present with peg-like spines along its length (mt); lateral teeth also shown (lt); X50. F. Gastric mill of *Cambarus* sp.; note smooth bifid median tooth, massive lateral teeth (lt); X90.