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The study of the Epicaridea suborder of the Isopoda on the west coast of the United States has not been extensive, with the result that there is much to be learned about the distribution, the life histories, and the genera present. In order to attempt an investigation of the Bopyridae in this obscure but interesting suborder, it was necessary to review the pertinent literature covering at least the past century, and to determine the status of the eastern Pacific forms in relation to members from the rest of the world.

Workers in other nations, notably England, France, India, Italy, Japan, Norway and Russia have written voluminously on the epicarids, and from this the author compiled a listing of the known genera and species comprising the Bopyridae family of the world. Despite similarities in latitude and temperature with bopyrid-rich areas elsewhere, the western United States marine waters seem to support remarkably few parasitic isopods. It is assumed therefore, that the isopod fauna might actually be quite

plentiful, and that the apparent paucity is due only to a lack of field work.

Collecting was done in Canada, Washington, Oregon, California and Hawaii. In the last locale, a new form (as yet unnamed) was obtained.

By experimentation carried out in aquaria, it was determined that copepods (particularly Calanus) were the intermediate host of the west coast bopyrid Argeia pugettensis Dana. Further, it was found that isopod infection of the host Crago nigromaculata (Lockington) occurred at late (or immediately post-) larval stages of the shrimp.

Other experiments were conducted to test various aspects of the life cycle, infectivity, praemunition, and effect upon the host. A restudy was made of two specimens from the Smithsonian Institute. Theories on sex-determination, life cycles, host sterilization, and classification were compared. Some changes were suggested in the general epicarid taxonomy.

BOPYRIDIAN (CRUSTACEA, ISOPODA) PARASITES FOUND IN THE EASTERN PACIFIC OF THE UNITED STATES

by

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Charles G. Danforth

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1. POSITION OF THE BOPYRIDAE

Although the Isopoda order is well known to biologists, a knowledge of its extent and diversity is not universal. There are parasitic isopods found throughout the group, but the Epicaridea suborder is exclusively parasitic, and it is with one of the constituent families that this paper deals.

In general, the members of the Bopyridae are ectoparasites on decapods, and have become greatly altered in comparison with the typical isopod appearance. The female develops into what is essentially only a brood pouch, with the male living as a diminutive "parasite" upon her. Due to its existence on or under the host's carapace, the female also usually has considerable lateral distortion to her body.

A study of the distribution of the Bopyridae has indicated that there is no major area of the world in which bopyrids have not been found in marine environments. Forms have been reported from the ocean shores of every continent, from the Arctic and the Antarctic, from oceanic islands, from inland seas, and apparently at all depths of the oceans from which decapods have been collected. Surprisingly enough, bopyrids are also occasionally reported from fresh water and estuarine locations (21), and there are records of these parasites from streams at elevations up to 4,000 feet (12, p. 541) (63, p. 416). Considering the fact that not many research workers interest themselves in the Bopyridae, the large number of reports indicates the apparent ubiquity of representatives of this family.

As might be expected, details of classification will vary depending upon the authority consulted. However, the following seems to be in general use:

ARTHROPODA (phylum)
CRUSTACEA (class)
MALACOSTRACA (subclass)
EUMALACOSTRACA (series)
PERACARIDA (division)
ISOPODA (order)
  (synonomy of the Isopoda):
  Polygonata Fabricius 1798 (excl. of Monoculus)
  Tetracera Latreille 1810
  Isopoda Latreille 1817
  Equisopoda Kossmann 1881
ANTHURIDEA (suborder)
ASELLOTA (suborder)
FLABELLIFERA (suborder)
GNATHIDEA (suborder)
ONISCOIDEA (suborder)
PHREATOICIDEA (suborder)
VALVIFERA (suborder)
EPICARIDEA (suborder)

(synonomy of the Epicaridea):
Epicarides Latreille 1825
Epicaridea Latreille 1931
"Isopodes Sedéntaire" (pt.) Edwards 1840
Epicarida G. L. Sars 1882
Epicaridea Stebbing 1893
Epicarida G. O. Sars 1899
Bopyroidea Richardson 1902
Epicaridea Richardson 1905
Epicarides Gilson 1909

CRYPTONISCIDAE (family)
DAJIDAE (family)
ENTONISCIDAE (family)
BOPYRIDAE (family)

(synonomy of the Bopyridae):
Bopyridae Dana 1853
Bopyridae Bate and Westwood 1867
'Bopyriens' Giard and Bonnier 1887
Bopyridae Stebbing 1893
'Bopiridi' Nobili 1906

The group called the "Edriophthalma," which was once given ordinal status, was composed of the Isopoda, Chelifera and Amphipoda.

Within the Epicaridea, the families are often separated on the basis of the type of parasitism demonstrated:

Bopyridae -- usually parasites of the branchial chamber of crabs and shrimps. Some forms may attach to the abdomen of the host.
Cryptoniscidae -- usually visceral parasites of amphipods, isopods, ostracods, mysids and rhizocephalans.
Dajidae -- usually superficial parasites of the dorsum and the branchial region of the Mysidacea and Euphausidacea.
Entoniscidae -- usually visceral parasites of the Brachyura.

A classification approach (omitting the "Microniscidae") which is favored by many is that proposed by

Bonnier (2, p. 178-233):

Cryptoniscinae	Bopyrinae
Asconiscidae	Bopyridae
Cabiropsidae	Dajidae
Crinoniscidae	Entoniscidae
Cyproniscidae	Phryxidae
Hemioniscidae	
Liriopsidae	
Podasconidae	

Many workers, in particular Caullery (11, p. 65-85), use a taxonomic subdivision of the Epicaridea in which there is less separation of the groups:

Bopyridae
Cryptoniscidae (having 7 subdivisions as given in the foregoing list by Bonnier)
Dajidae
Entoniscidae
Phryxidae

It is obvious that there is considerable variation among authors as to the best method of separating the apparently dissimilar members of the Epicaridea. Consequently, genera and families have been erected on the basis of hosts, external morphology, or anatomy -- points which at the time might have seemed adequate criteria, but which today are not considered to be critical. Therefore the literature must be studied with the point of view of the author in mind, as well as with a knowledge of the epicarids.

In regard to the geologic history of the Isopoda order, there is much more data than one might expect. According to Zittel (72, p. 757, 758) isopods were first found in the Devonian period; the specific form being Oxyuropoda ligioides Carpenter and Swain. The palaeontological work by Piveteau (43, p. 322-326) supports this, giving the British Isles as the site of the specimen; and also adds the Devonian genera Praearcturus Woodward, and Amphipeltis Salter. Going further back in time, Raymond (45, p. 201-203) indicated that Mollisonia gracilis (which he renamed as Houghtonites gracilis) from the mid-Cambrian of British Columbia, might be an isopod. He suggested placing Houghtonites in a group between the trilobites and isopods, for which he proposed the name "Protisopoda." If this interpretation is correct, it means that isopods have occurred on earch since the beginning of the Palaeozoic era.

Since fossilization is a rather rare occurrence, one might anticipate that the possibilities of preservation of a host that was parasitized by an isopod would be extremely slight. Nevertheless, evidence of bopyrid parasitism on Mesozoic forms has been found. Branchial bulges on the carapaces of fossil decapods have been recorded for the following genera (43, p. 322-326): Cyclothyreus, Galatheites, Gastrosacus, Pithonoton (from the Jurassic); and Notopocorystes, Palaeocorystes (from the Cretaceous).

In view of the many authors, the diverse areas of the world that are involved, the large span of time encompassed, and the fact that there is no coordinating body for the collation of material about the Bopyridae, it is extremely difficult to ascertain the status of forms mentioned in the literature. For this reason, the following tabulation has been developed as an aid to research on the bopyrids.

List of the Bopyrid Genera and Species of the World, Arranged Alphabetically

Anacepon sibogae
Anathelges mulleri
Anisarthrus pelseneeri
Anomophryxus deformatus
Apocepon pulcher
Apopenaeon japonicum
  j. hiraiwai
  richardsonae
Apophrixus philippinensis
Aporobopyrina lamellata
Aporobopyroides upogebiae
Aporobopyrus aduliticus
  curtatus
  gracilis
  johannis
  oviformis
Argeia calmani
  lowisi
  nierstraszi
  pauperata
  pugettensis
Athelges (=Athelge=Athelgue?)
  aniculi
  bilobus
  cardonae
  caudalis
  cladophora
  fullode (=paguri?)
  guitarre
  intermedia
  japonicus
  lacertosi
  lorifera
  paguri
  pelagosae
  prideauxii
  takanoshimensis
  t. tenuibranchiatus
  tenuicaudis
Atypocepon intermedium
Bathygyge grandis
Bonnieria indica
Bopyrella alphei
  angusta

asymmetrica
barnardi
bonnieri
choprai
deformans indica (=Syn-
synella deformans?)
distincta
harmopleon
hodgarti
inoi
Bopyrella intermedia
lata
megatelson
mortenseni
nierstraszi
nitescens
pacifica
palaemonis
richardsonae
thomasi
thompsoni
Bopyrina abbreviata
andamanica
brachytelson
choprae
cochinensis
crangona
giardi
gigas
gracilis
hippolytes
kossmanni
latreuticola
nitescens
ocellata
sewelli
striata
thorii
urocaridia
virbii
Bopyrinella albida
antilensis
a. nipponica
stricticauda
Bopyrinina dorsimaculata

Bopyriscus calmani
Bopyrissa magellanica
Bopyro choprae
Bopyroides acutimarginatus
hippolytes
sarsi
wood-masoni
Bopyrosa phryxiformis
Bopyrus alphei
fougerouxii (=squillarum?)
helleri
palaemonis
rathkei
squillarum
s. bimaculatus
stebbingi
Bopyrus treillianus
xiphias
Botryllofer (=Athelges?)
Cancricepon elegans
kossmanni
pilula
Capitetragonia aspero-
tibialis
Cardiocepon pteroides
Cataphryxus (=Epiphrixus)
primus
Cepon distortus
elegans
halimi
messoris
naxiae
pilula
portuni
typus
Colypurus (a bopyrid?)
Crassione aristaei
Cryptione bakeri
elongata
laevis
Dactylocepon catoptri
richardsoni
Dactylokepon (Dactylocepon)
Diplophryxus alphei
jordani

kempi
richardsoni
synalphei
Duplorbis smithi (probably a rhizocephalan)
Entophilus omnitectus
Eophrixus shojii
Epicepon indicum
japonicum
Epipenaeon elegans
grande
ingens
japonica
nobili
oviforme
pestai
Epiphrixus adriaticus
primus (=Cataphryxus primus)
Ergyne cervicornis (=Portunicepon portuni=P. shojii?)
hendersoni
savignyi
Gigantione bouvieri
giardi
ishigakiensis
Gigantione moebii
rathbunae
sagamiensis
Grapsicepon choprae
edwardsii
fritzii
magnum
messoris
rotundum
Grapsion cavolinii
Gyge arcassonensis
branchialis
galatheae
Hemiarthrus (=Phryxus)
abdominalis
brevicauda
cranchii
filiformis
f. attenuata
nigrocinctus
pelseneeri
schmitti
subcaudalis
typtonis
virbii
Heptalobus paradoxus (a cryptoniscan?)
Heterocepon marginatus
Hyperphryxus tattersalli
Hypocepon ovale
Hypohyperphrixus latilamellaris
Hypophryxus yusakiensis
Ione brevicauda
cornuta
gebiae
thompsoni
thoracica
vicina
Ionella agassizii
Jone (=Ione)
Kepon (=Cepon)
Leidya bimini
distorta
Lobocepon grapsi
Lobosaccus (questionable)
Megacepon choprae
Merocepon xanthi
Mesocepon tosizimensis
Metabopyrus ovalis
Metacepon leidya
Metaphryxus caroli
Metathelges mülleri
Microniscus (invalid, a larval stage)
Munidion laterale
parvum
princeps
Onychocepon giardi
harpax
resupinum
Oosaccus (questionable)
Orbimorphus constrictus
lamellosus

Orbione angusta
  bonnieri
  halipori
  h. libera
  incerta
  kempi
  penaei
  thielemanni
Pagurion tuberculata
Palaegyge abhoyae
  affinis
  alcocki
  bengalensis
  bonnieri
  borrei
  brachysoma
  brevipes
  buitendijki
  de mani
  fluviatilis
  godaveriensis
  hoylei
  incerta
  insignis
  marina
  meeki
  pica
  plesionikae
  prashadi
  weberi
Parabopyrus kiiensis
Paracepon stebbingi
Paragigantione papillosa
Parapagurion calcinicola
Parapenaeon bonnieri
  consolidata
  c. richardsonae
  secundum
  tertium
Parapenaeonella distincta
Paraphryxus adriaticus
Parapleurocrypta alphei
Parapseudione dubia
  lata
Parargeia ornata
Parathelges aniculi
  racovitzai
  weberi
  whiteleggei
Parione lamellata
  paucisecta
Parionella decidens
  elegans
  richardsonae
Parionina chinensis
  pacifica
Parioninella astridae
  obovata
Pauperella rotunda
Phryxus (=Hemiarthrus)
  abdominalis
  cladophorus
  distortus
  misanthropus
  nematrocarcini
  paguri
  resupinatus
  subcaudalis
Phyllocturus (=Phyllodurus?)
Phyllodurus abdominalis
  robustus
Pleurocrypta balearica
  galatheae
  hendersoni
  hessei
  intermedia
  keiensis
  langi
  longibranchiata
  macrocephala
  marginata
  microbranchiata
  nexa
  perezi
  porcellanae
  strigosa
  yatsui
Pleurocryptella formosa
  indica
  infecta

Pleurocryptosa megacephalon
Portunicepon cervicornis
goeticii
hendersoni
portuni
rissoi
savignyi
tiariniae
Probopyrinella latreuticola
Probopyrus aberrans
alcocki
alphei
annandalei
ascendens
bengalensis
bithynis
b. gigas
creaseri
dubius
floridensis
gangeticus
giardi
latilamellaris
latreuticola
oviformis
palaemoneticola
panamensis
pandalicola
papaloapanensis
semperi
Procepon insolitum
Propseudione rhombicosoma
Prosthete cannelee
Prosynsynella deformans
indica
Pseudione affinis
asymmetrica
brandaoi
calcinii
callianassae
chapini
clibanarticola
confusa
crenulata
curtata
diogeni
dohrni
dubia (=hyndmanni?)
elongata
e. normalis
euxinica
filicaudata
fimbriata
fraisei
furcata
galacanthae
giardi
hanseni
hayi
hoylei
hyndmanni
incerta
indica
insignis
intermedia
japanensis
kossmanni
laevis
latilamellaris
lenticeps
longicauda
magna
minimo-crenulata
nephropsi
nobilii
orientalis
paucisecta
petrolistheae
proxima
retrorsa
sagamiensis
subcrenulata
tattersalli
trilobata
tuberculata
upogebiae
Pseudionella attenuata
pyriforma
Pseudostegias hapalogasteri
setoensis

Rhabdocheirus incertus (probably not a bopyrid)
Rhopalione pelseneeri
  uromyzon
Syracepon hawaiiensis
  quadrihamatum
  tuberculosa
Stegias andoronopholos
  (=andronophoros?)
  angusta
  clibanarii
Stegoalpheon kempi
Stegophryxus hyptius
  resupinatus
  thompsoni
Synsynella (=Bopyrella?)
  deformans
Trapezicepon amicorum
Tylokepon bonnieri
Upogebiophilus rhadames
Urobopyrus processae
Zeuxo (=cryptoniscids?)
  alphei
  porcellanae

2. SUMMARY OF THE MAJOR LITERATURE

History. References to animals which might have been isopods may be found in early written records, but the first conclusively bopyridian citation seems to have been one reported by Stebbing (63, p. 392). In this, Stebbing states that a, "M. Deslandes" in 1722 "scientifically supported" the idea of early French fishermen that bopyri in prawns were young flat fish. Calman (4, p. 220) indicated that the "Peter's Stone" of Icelandic folklore was probably the hardened blood-engorged gut of the fish blood-sucking isopod Aega. It was not until the last half of the eighteenth century that scientists such as Linné, Pennant and Fabricius put any particular emphasis on the isopod group. However, this work must not have been well disseminated, since Stebbing (63, p. 415) reported that Leach's 1814 "Crustaceology" gave Bopyrus in the Vermes class.

Early work was subsequently enlarged by the great amount of oceanographic studies carried out in the nineteenth century; but in the United States, research upon the Epicaridea is far behind that published by other major countries today.

Any listing of the better-known names in bopyrid research would probably be incomplete by another's standards; however, the following seem to be the major contributors within the past few years. Barnard (Africa), Brender à Brandis (Netherlands), Caroli (Italy), Caullery (France), Chopra (India), Dahl (Norway), Hiraiwa (Japan), Nierstrasz (Netherlands), Pearse (United States), Pike (England), Reinhard (United States), Reverberi (Italy), and Shiino (Japan).

Today, most major countries are reporting work done on the Bopyridae -- probably more as an aspect of the greatly heightened interest in oceanography than through the importance of the isopods per se. Undoubtedly there will be many new records, and perhaps a long overdue evaluation of the older records, when the multi-nation oceanographic survey of the Indian Ocean is complete.

Hosts of the Bopyridae. Although nearly 150 genera of arthropods (involving approximately 535 species) have been indicated in the literature for the world as being hosts of the Bopyridae, most would not be found in the coastal waters of western United States. (The known hosts for this area are given later in this section.)

The general groups which are parasitized by bopyrids are relatively few, and all are crustaceans. Most are decapods. Anomurans, brachyurans and carideans comprise the great bulk of the hosts; although about 10 genera of peneids and one genus of astacuran (62, p. 32-36) have been found for other parts of the world.

Two major exceptions to the foregoing are important. Apparently bopyrids may parasitize other members of the Bopyridae. To date, the only verifiable case is that reported by Caroli (7), wherein *Pseudione euxinica* lives on *Gyge branchialis*, which in turn parasitizes *Upogebia littoralis*. When *Gyge* dies, *Pseudione* directly parasitizes *Upogebia*.

Although Stebbing (64, p. 114) indicated that *Lobosaccus* parasitized the bopyrids *Palaegyge* and *Trapezicepon*, there is considerable question as to whether *Lobosaccus* is a member of the Bopyridae.

The second exception relates to intermediate, rather than to definitive hosts. Much of the literature on the Bopyridae indicates that copepods are required as temporary hosts of the bopyrids during their development. However, authors are not in full agreement on this point, and it may be that bopyridian life cycles are not uniform throughout the family.

There are some references to hosts other than the foregoing, but these have not been borne out. Dahl (13, p. 16) cites the case of Phryxus having been reported by a "J. Grieg" as parasitizing the amphipod Gammaracanthus loricatus. Dahl examined Grieg's original amphipod specimens, and found no indication of any parasitism. Müller (37, p. 57-60) reported a Bopyrus resupinatus found on the roots of Sacculina purpurea or Peltogaster socialis, which in turn was on a hermit crab in South America. Since this occurrence has not been substantiated by later workers, and since this situation is known for cryptoniscids, the record has little value.

Nierstrasz and Brender à Brandis (38, p. 116, 117) list the "bopyrid" Duplorbis smithi as parasitizing bopyrids Parathelges, Pleurocrypta and Pseudione, as well as the anthurid isopod Calathura. However, other taxonomists indicate that Duplorbis is not a bopyrid but a rhizocephalan (27, p. 95).

Parasite Location and Effect Upon the Host. Since the Bopyridae as interpreted by this paper includes the "Phryxidae" of some authors, the location of the parasite upon the host will be both branchial and abdominal. There are four major sites.

The most common position (Plate 3, Figure 1) is immediately under the host's branchiostegite, which causes a pronounced swelling of the carapace over the gills. Although many records seem to indicate that if any preference for one side or the other exists, it is slight; there are a few reports where definite selection seems to have occurred. Rayner (46, p. 237) found that Pseudione galacanthae was present in the right branchial area of Munida gregaria and M. subrugosa in over 90% of the infected cases. Conversely, Shiino (61, p. 263-278) reported that Pseudione clibanaricola is found only in the left gill chamber of Clibanarius bimaculatus, whereas Pseudione asymmetrica is found only in the right branchial area of the same crab. Thus there may be bilateral infection. Many other authors have indicated that both gill chambers of a host have been occupied by bopyrids. The female parasite is always positioned with her head ventrally and posteriorly-directed with respect to the host; and the isopod's dorsum is pressed against the host gills -- thus the marsupium faces outwards. The above stipulations of this diagonal position are met whether the parasite is on the host's left or right side.

The second most frequent location (Plate 3, Figure 2) is on the ventral abdomen. In this, the female isopod holds onto the host's pleopods near the anterior abdomen, and thereby creates an obvious protrusion. The ventral aspect of the parasite is facing outward, thus the marsupium is free to release the embryos directly to the water. The head of the female is directed towards the host's posterior.

A third position of the parasite is on the dorsal abdomen of hermit crabs. The same conditions prevail -- namely that the head of the isopod is towards the host's tail, and the marsupium is upward. Although the drawing of Stegophryxus appears to show the marsupium against the host, the text of the article by Thompson (68) indicates that the parasite's back is against the crab.

The fourth position (Plate 3, Figure 3) is unique, and restricted to Entophilus omnitectus from the deep-water channels of the Hawaiian Islands. The parasite lies under the mid-dorsal carapace of the host, Munida normani, so that it is actually visceral. It might be assumed that this was an aberrant situation, were it not that a great many specimens have been obtained. The writer was privileged to study two of the hosts originally collected by Richardson and now in the possession of the Smithsonian

Institution (Catalogue No. 28966, U.S. National Museum), and his conclusion was that although Entophilus is definitely not in the branchial chamber of Munida, it is not as far removed as the words "visceral" parasite (56, p. 681) connote. Apparently the isopod lies with the marsupium towards the host carapace, and causes a small but obvious bulge. No information is available as to whether the bopyrid's head faces towards the posterior of the host, as is the case for the other positions described.

There are records of bopyrids in other than their "normal" location, such as Orbione being found on the abdomen of its host instead of in the branchial region (2, p. 282). Cattley (8) reported an Athelges paguri which was found in the branchial region instead of on the abdomen of Eupagurus bernhardus.

The incidence of infection seems to vary greatly with the parasite, the season, and the area under consideration. A great many authors report that female hosts are more common than male hosts, a point which has led to considerable speculation. Perhaps hosts are feminized by the bopyrid, thus leading to misidentification of the true sex. Reverberi (49, p. 56-70) covered sexual changes found on various hosts when parasitized by rhizocephalans and bopyrids, and concluded that males were not castrated, but were feminized; concurrently there was an atrophy of the ovaries in the female. However, Hiraiwa and Sato (30, p. 115-122) found that for the prawn Penaeopsis akayebi there was no feminization of the male, but rather a general retardation of the secondary sexual characteristics in both sexes. This retardation also extended to the gonads of both sexes, and it was found that males became normal upon removal of the epicarid. It was pointed out that the forms used by Reverberi and others in the Mediterranian were sexually quite labile, and therefore this might explain the different results obtained by various workers.

The writer has noted many Crago females that were in berry despite both single and double bopyrid infestation of long standing.

Data upon the percentage of incidence of bopyrids on their hosts would be biased by the size of the sample, unless large hauls were available. Chopra (12, p. 411-415) discussed hosts, locales and incidence of bopyrids, and stated, ". . . almost all the species of caridean prawns generally available in the Calcutta markets are infected with them." This indicates horizontal, but not vertical density for the family in India; whereas an infection rate of 70% was reported in part of Japan (30, p. 105); an incidence of infection of from 7 to 18% for certain forms from Great Britain (41, p. 243-245); and a 3 to 24% figure for forms in California (24, p. 13-14). It is the experience of the writer that the epicaridization is highest in mid-summer, and lowest in late winter. This closely parallels the findings of Gifford (24, Table 3) for *Argeia pauperata* in San Francisco Bay.

There is little or no evidence of praemunition, inasmuch as multiple infection is quite common, and even parasitization by different taxonomic forms is known. This latter was reported by Reinhard and Buckeridge (48), wherein the bopyrid *Stegophryxus hyptius* was known to occur simultaneously with the entoniscid *Paguritherium alatum* on the host *Pagurus longicarpus*. Yet Reinhard, in a previous publication (47, p. 26) had indicated that there should be expected only one bopyrid couple per host. As mentioned earlier, Caroli (7) described one genus parasitic upon a second genus of the Bopyridae, and both were then parasitizing the decapod host.

The mode of nutrition of the bopyrids has not been satisfactorily determined. Tucker (69), in discussing the branchial forms, pointed out that the female's mouth is away from the host's viscera and against the branchiostegite. He therefore assumed that whatever nutrition was necessary was obtained from eating the inner membrane of the branchiostegite. For the male, Tucker said that since it is even more isolated from the host, it is strange that the mouthparts and gut are usually well developed. Certainly no great amount of damage to the host has been ascertained, regardless of whether the bopyrid is branchial or abdominal.

There is a dearth of specific literature concerning the total effect of epicaridization upon the decapod, although as previously stated, study has been made on the changes in secondary sexual characteristics. Pike (41, p. 245) reported that parasitized Pandalus bonnieri did not reach the larger sizes of the non-parasitized forms, which would indicate that the presence of the bopyrid (Pseudione affinis) inhibited growth -- a point apparently disproved by others -- or that the bopyrid caused premature death of the Pandalus. He also found that 18% of the infected hosts outlived their parasites. At the same time, a problem arose concerning the time of infection of the host. Since many reports indicate that original infection occurs during the host larval or immediately post-larval stages, there was no explanation for the fact that the incidence of infection for the second year of the host's life was almost double that for the first year.

Bopyrid Life Cycles. Early work was confused by errors of many sorts, some of which still affect current research. In one isopod group, the male was identified as the genus *Anceus*, the female as the genus *Gnathia*, and the larvae as the genus *Praniza*. According to Stebbing (63, p. 414) when Risso named the epicarid *Ergyne cervicornis* in 1816, he mistook the tail for the head, and felt that the pleon appendages were plumose antennae. However, the most extensive error was initiated by the eminent French carcinologists Giard and Bonnier. In all of their early works, they believed that parasitic isopods were specific for each host (23). As a consequence, they gave different generic names to the same parasites merely because the host was not the same. This "one kind of isopod per host genus (or species)" led to widespread confusion in taxonomy, some of which still exists.

A life cycle study involves several major issues, and these will be taken up sequentially. Such as: larval forms, intermediate hosts if any, host specificity, life span of the parasite, and sex determination of the bopyrid.

There apparently are no copulatory devices in the Bopyridae, and the male must therefore be nearby when the eggs are released into the marsupium of the female. These eggs (Plate 2, Figure 1) develop by superficial cleavage (29, p. 102), and the length of time between egg-laying cycles seems to vary according to the species and genus being studied. Reinhard (47, p. 19) noted that two weeks after egg-laying, the larvae were released, and the cycle was initiated again after five days. Pike (42, p. 227) found the incubation period to be 32 days, with a three day interval before the next egg laying.

Due to the cyclic nature of the laying and to the external fertilization, all embryos are at the same stage of development. The first larval stage is the epicaridian (Plate 2, Figure 2), which can be described broadly as:

Oval, free-swimming; usually seeking the water surface.
Piercing mouthparts with a styliform mandible in a suctorial oral cone formed by the upper and lower lips.
Short, 3-part antennules; 2-part antennae.
First maxillae absent; second maxillae vestigial.
6 subchelate thoracic appendages, hooked.
6 abdominal segments, with 5 pairs of pleopods and one pair of uropods.
General proportions of 270 X 150 X 120 mu.

When the epicaridians are released from the marsupium, they are strong swimmers, and usually positively phototropic (24, p. 12). Most authors state that the epicaridian becomes a microniscan (Plate 2, Figure 3), although some writers indicate that this form has not been observed (24, p. 17) (29, p. 125). Where the microniscan forms are commonly reported, they are found attached to the dorsum of a copepod. This gave rise to the erection of a Microniscidae family of the Epicarida tribe by Giard and Bonnier, which Sars (53, p. 193, 194) strongly deplored, and which is not generally accepted today.

The microniscan stage was described by Tucker (70, p. 5) as:

> Soft integument
> No definite segmentation of the appendages.
> Musculature atrophys.
> Pleopods lose their setae.

While this microniscan is attached to the copepod (if one is part of the life cycle), it moults several times, and becomes a cryptoniscan larva (Plate 2, Figure 4). The length of time on the copepod has been reported variously as one month (41, p. 246) to one week (6). The cryptoniscan then leaves the copepod, and has a much more "isopod" appearance than did its predecessor:

> Piercing and sucking mouthparts.
> Rigid chitin.
> 7 pairs of thoracic legs, all similar.

All appendages regular and fully segmented.
Adapted for pelagic life.
6 pairs of uniramous natatory pleopods.
One pair of biramous uropods.
An average length of about 680 mu.

Why there is any intermediate host is not known, because no appreciable effect on the copepod is evident. If the copepod is used merely for transportation, it would seem unnecessary in view of the swimming ability of the bopyrid. If it is used for food, why is there not more evidence of damage? Among the writers who raised the foregoing questions were Marshall and Orr (36, p. 142-154) who reported that it was usually the female copepod which became the parasite host, and that attachment was normally at copepodite stage V or adulthood (although some of the stage III and IV were parasitized). The microniscus usually lies with its head towards the front of the host, and the body is diagonal to the copepod midline. A red dot may be observed at the point of attachment, but even that is a result of accumulation of the copepod's own pigments. Their conclusion was that the host's chitin was pierced for sustenance.

If a biochemical change in the bopyrid is brought about by ingestion of small amounts of a copepod, thus permitting moulting and subsequent attachment to the definitive host (50, p. 122-125), how can this be reconciled with other reports such as those of Hirawai (29, p. 125-127) wherein the microniscan stage and the copepod parasitization are missing?

After leaving the copepod, the cryptoniscan larva is apparently capable of infecting the final host. This too is done in different ways, judging from diverse reports. There may be an immediate entrance into the gill chamber of the new host at some early development phase of that host; or the bopyrid has been observed attaching to the last pleopods of the host, moulting, and then migrating to its dorsal abdominal position (47, p. 22). Pike (41, p. 245) found that Hemiarthrus first entered the gill chamber of Spirontocaris, and later migrated to its definitive ventral abdominal position. But in all cases it would seem that the host must be in a larval or immediately post-larval stage. Rayner (46, p. 237) found cryptoniscan forms on the grimothea stage of Munida; Pike (42, p. 228) found cryptoniscans on the megalopa stage of Pagurus; and many other reports seem to bear out this assumption.

Once in place on the host, the cryptoniscan moults to form the adult or bopyridium stage. This becomes the final phase in the case of the male, but for the female, great growth and distortion must still occur. The differences between the male and female are shown in Plates 4 through 14, and a general description of a bopyridium is:

Reduced antennules.
Reduced antennae.
Abortion of the eyes (not true for all cases).
Shortened thoracic limbs.
Reduced pleopods.
Loss of natatory setae of the pleopods.
The male is sexually mature.
The female continues to grow and modify.

With respect to the intermediate hosts, there seems to be a great deal of latitude as to exactly which copepods are utilized. Gnanamuthu and Krishnaswamy (25) found 12 "microniscus" in 24,000 specimens of Acartia erythraea, Acrocalanus longicornis, and Eucalanus crassus from the Indian Ocean. Many writers state that Acartia and Calanus are the most used intermediate hosts. Naturally, one wonders what forms would be used by fresh-water bopyrids, such as Probopyrus and Palaegyge; or if an intermediate host is employed in non-marine environments. Caullery (9) found that Acartia clausii and A. discandata were favored by isopods in preference to Euterpe, Centropages and Cyclopina hosts. Pike (42, p. 227) found that for larvae of Athelges, the copepods preferred were Pseudocalanus, Acartia, Temora and Centropages in that order, but that only the parasites on Pseudocalanus continued their development. Calanus was not used at all. Yet he also found (41, p. 248) that Pseudione affinis would accept only Calanus finmarchicus as a host in the laboratory. Gifford (24, p. 17) was unable to find any parasitized copepods in connection with his study of Argeia pauperata in San Francisco Bay.

Knowledge of the specificity for the definitive host is likewise inconclusive, judging from the literature. Apparently it is possible to find a fair to good correlation between hosts and their bopyrids for certain areas -- which may have led to Giard and Bonnier's original concept of a different parasite for each different host. For instance, Davis (17) noted that Phyllodurus abdominalis was found only on hippolytid shrimp; and that hippolytids were also preferred by Argeia and Bopyroides. Pike (41, p. 242) found that Hemiarthrus parasitized the Hippolytidae more than three times as often as it did the Pandalidae. However, many writers feel that selection of a host may be more a matter of timing and availability than of specificity.

The life span of parasitic isopods has not been worked out in most cases. Tucker (70, p. 13) found that Gyge, which parasitizes Upogebia, had the same life span as did the host, which in this case was approximately three years. Pike (41, p. 250) stated that the normal length of life for Pseudione affinis and Hemiarthrus abdominalis is about 18 months.

If it were assumed that a female bopyrid were to live for two years, and during that time have from two to five broods a year, then if each brood was approximately 200, this one female would release over 2,000 larvae during her lifetime. This is probably quite conservative.

The matter of sex determination in the Epicaridea is at present far from clear. Caullery (10) pointed out that the major question was whether the sex was determined "ab ovo," or by direct or indirect parasitism of the host. To test this, he took a "complemental male" from the marsupium of the female isopod, and placed it into an unparasitized normal host. Due to technical difficulties, the result was not conclusive. He also (11, p. 65-85) indicated a belief that sex determination was related to the food supply of the parasite -- thus the bopyridium existing directly on the host became a female, while the one existing on the female would become a male. Certainly there must be a close relationship between the female and the host, since he reported that moulting occurs simultaneously.

This "first arrival becomes a female" concept seems to be well accepted in the literature (70, p. 6). Therefore, second and successive parasites to arrive on the host become the male or "complementary" males, and are thought to stay as males because they may receive an inhibitory hormone from the female on which they are located. Nevertheless, several questions still are unanswered. According to this hypothesis, how would it be possible to obtain male <u>Phyllodurus abdominalis</u>, inasmuch as this particular male lives separately from the female on the <u>Gebia</u> host? And how can an ovarian effect suppress further male growth when, as pointed out by Carlisle and Knowles (5, p. 97) the reverse should be true, since the testes exert an effect similar to the androgenic gland in converting implanted ovary into testes, or in causing the ovary to change to testes if the gland is implanted into the female. This was further expanded by Waterman (71, p. 420-441) when he stressed that if an androgenic gland were transplanted to a female (which has none), yolk inhibition and external masculinization occurred, and sperm could even be found in the ovary.

Reinhard (47, p. 24) carried out an experiment wherein he took the first cryptoniscan larva (which would normally have become a female) from a host, and placed it into the marsupium of an adult female. It became a male. However, he was unable to take a second cryptoniscan (which would be expected to become a male) from a different host, and by putting it on a new host, thereby obtain a female. Just what would bring another larva to a host already parasitized by a female bopyridium is questionable. Perhaps it is due only to the large numbers of isopod larvae, although Reverberi and Pitotti (50, p. 131) stated that _Ione_ gives off a diffusing substance which attracts cryptoniscan larvae.

Bopyrids Recorded From the Eastern Pacific Area. In the compilation of the following list, a great deal of difficulty was encountered in determining geographical locations mentioned in the literature. Consequently the names of political locales which have been frequently employed in references are included as an aid to subsequent workers.

Alaska:

Auke Bay	Point Barrow
Bering Sea	Yes Bay

British Columbia:

- Boundary Bay
- Cape Beale
- Cowichan Gap
- Crescent Beach
- Departure Bay
- Esquimalt Harbor
- Fort Rupert
- Hecate Strait
- Nanaimo
- Nanoose Bay
- Queen Charlotte Strait
- Ruxton Pass
- Strait of Georgia
- Sydney
- Vancouver Island
- Victoria

Washington:

- Admiralty Inlet
- Alki Point
- Anacortes
- Brown Island
- Cape Johnson
- Carkeek Park
- Crane Island
- Destruction Island
- Flattery Rocks
- Friday Harbor
- Gray's Harbor
- Griffin Bay
- Haro Strait
- Hood Canal
- Lopez Island
- Maury Island
- Orcas Island
- Peavine Pass
- Port Townsend
- Puget Sound
- Rocky Bay
- Rosario Strait
- San Juan Island
- Seattle
- Shipman Bay
- Strait of Juan de Fuca
- Wasp Passage
- Yahwhitt Head

Oregon:

- Cape Arago
- Cape Perpetua
- Charleston
- Columbia River mouth
- Heceta Bank
- Newport Bay
- Tillamook Head
- Yaquina Head

California:

- Ano Nuevo Point
- Farallones
- Goleta
- Humboldt Bay
- Laguna
- La Jolla
- Monterey Bay
- Point Arena
- San Diego
- San Francisco Bay
- San Luis Obispo Bay
- San Nicolas Island
- San Simeon Bay
- Santa Barbara
- Santa Barbara Island
- Tomales Bay

Mexico:

- Acapulco
- Guadalajara
- Gulf of California
- Lower California

Hawaii:

- Diamond Head
- Main Island
- Maui
- Molokai
- Oahu
- Pailolo Channel

The heading of "Puget Sound" in the subsequent tabulation will refer to the whole northwest Washington region, which is an area about 140 miles long. This technique is not without precedent, inasmuch as Richardson (54, p. 869) indicated the collection region for Bathygyge grandis as being Acapulco, whereas Hansen actually collected it (26, p. 122, 124) at 21 degrees 15 minutes North and 106 degrees 23 minutes West -- an airline difference of over 400 miles.

In the designation of the hosts, the names used are those employed by the original authors. However, it seems obvious that there is a great deal of redundancy. Even though Argis is clearly equivalent to Nectocrangon, there is considerable question as to whether Eualis = Heptacarpus = Hippolyte = Spirontocaris in every case. Similarly, Crago is interchanged with Crangon (54, p. 868), (57, p. 551); and Callianassa longimana seems to be superceded by C. gigas. Eupagurus is being replaced by Pagurus, and Gebia by Upogebia; thus indicating the still present taxonomic confusion mentioned by Rathbun (44).

The isopod taxonomy is equally uncertain. Therefore, it must be assumed that Ione brevicauda = I. cornuta, according to Fee (20, p. 25). Also, according to synonomy and statements by Richardson (57, p. 545, 568), it is understood that *Argeia calmani* = *A*. *pugettensis*, and *Bopyroides acutimarginatus* = *B*. *hippolytes*. As indicated later in this paper, *Hemiarthrus* is preferred to *Phryxus*.

For each bopyrid, the following sequence will be used:

a - the genus and species, alphabetized for the Eastern Pacific of the U.S., extending from 72 to 15 degrees north latitude.
b - the hosts, alphabetized for each parasite.
c - the areas, listed from north to south for each host.
d - the major reference(s), arranged chronologically.

ARGEIA Dana 1853 *CALMANI* Bonnier 1900. See *A*. *pugettensis*.

ARGEIA Dana 1853 *PAUPERATA* (Stimpson 1857). (Plate 4).
Argeia pauperata Stimpson 1857
Argeia depauperata Stebbing 1893
Argeia depauperata Richardson 1899
Argeia pauperata Bonnier 1900
Argeia depauperata Richardson 1904
Argeia pauperata Richardson 1905

Crago communis (Rathbun)	Puget Sound	Dunn 1949
C. *franciscorum* (Stimpson)	S. F. Bay	Gifford 1934
C. *nigromaculata* (Lockington)	S. F. Bay	Gifford 1934
Crangon franciscorum Stimpson	S. F. Bay	Stimpson 1857 Richardson 1905

This is a branchial parasite, and to date has been reported only from the San Francisco Bay area in any numbers. It is very similar to *Argeia pugettensis*, except that the head is bilobate, smaller and more tumid; the marsupium is more extensive; and the antennae and antennules each have 3 segments. The segments of the abdomen of the male are fused. Approximately 9 by 6 mm in size for the adult female.

ARGEIA Dana 1853 *PUGETTENSIS* Dana 1853. (Plate 4).
Argeia pugettensis Dana 1853
Argeia sp? Calman 1898
Argeia pugettensis Richardson 1899
Argeia calmani Bonnier 1900

Argeia pugettensis Bonnier 1900

Argis alascensis Kingsley	Destruction I.	Hatch 1947
	Gray's Harbor	Hatch 1947
A. pugettensis Dana	Puget Sound	Hatch 1947
Crago sp. Lamarck	Central Calif.	Light 1957
C. alascensis (Lockington)	Alaska	Richardson 1905
	Brit. Columbia	Richardson 1905
	Puget Sound	Richardson 1905
	Columbia River	Richardson 1905
C. a. variety *elongata* (Rathbun)	Columbia River	Richardson 1905
C. alba (Holmes)	Brit. Columbia	Richardson 1905
C. communis (Rathbun)	Alaska	Richardson 1905
	Brit. Columbia	Richardson 1905
	Puget Sound	Richardson 1905 Dunn 1949
	Gray's Harbor	Richardson 1905
	Columbia River	Richardson 1905
	Point Arena	Richardson 1905
	San Luis Obispo	Richardson 1905
	S. of San Diego	Richardson 1905
C. dalli (Rathbun)	Alaska	Richardson 1905
C. franciscorum angustimana (Rathbun)	Brit. Columbia	Richardson 1905
	Puget Sound	Richardson 1905
C. munita (Dana)	Brit. Columbia	Richardson 1905
	Puget Sound	Richardson 1905
C. munitella Walker	Puget Sound	Hatch 1947
C. nigricauda (Stimpson)	Puget Sound	Dunn 1949
	Cape Johnson	Richardson 1905
	Coos Bay	Shearer 1942
C. nigromaculata (Lockington)	Cape Johnson	Richardson 1905
	Tillamook	Richardson 1905
	Farallones	Richardson 1905
	Monterey	Richardson 1905
	S. of San Diego	Richardson 1905
C. stylirostris (Holmes)	Brit. Columbia	Hatch 1947

Crangon sp. Fabricius	La Jolla	Nierstrasz and Brender à Brandis 1929
C. affinis De Haan	Puget Sound	Calman 1898
C. alaskensis Lockington	Alaska	Richardson 1904
	Brit. Columbia	Richardson 1904
	Puget Sound	Richardson 1904
		Holthuis 1952
	Columbia River	Richardson 1904
C. a. elongata Rathbun	Columbia River	Richardson 1904
C. alba Holmes	S. of San Diego	Richardson 1904
C. communis Rathbun	Alaska	Richardson 1904
	Puget Sound	Holthuis 1952
	Gray's Harbor	Richardson 1904
	Columbia River	Richardson 1904
	Point Arena	Richardson 1904
	San Luis Obispo	Richardson 1904
	S. of San Diego	Richardson 1904
C. dalli Rathbun	Alaska	Richardson 1904
C. franciscorum Stimpson	Puget Sound	Holthuis 1952
C. f. angustimana Rathbun	Brit. Columbia	Richardson 1904
	Puget Sound	Richardson 1904
C. munita (*us*) Dana	Brit. Columbia	Richardson 1904
		Fee 1926
	Puget Sound	Dana 1853
		Stimpson 1857
		Richardson 1904
C. nigromaculata Lockington	Alaska	Richardson 1904
	Cape Johnson	Richardson 1904
	Tillamook	Richardson 1904
	Farallones	Richardson 1904
	Monterey	Richardson 1904
C. resema (=*resima*) Rathbun	Puget Sound	Holthuis 1952
C. stylirostris Holmes	Brit. Columbia	Fee 1926
Nectocrangon alascensis Kingsley	Alaska	Richardson 1904
	Cape Johnson	Richardson 1904

	Gray's Harbor	Richardson 1904
	S. of San Diego	Richardson 1904
N. crassa Rathbun	Alaska	Richardson 1904
N. dentata Rathbun	Alaska	Richardson 1904
N. lar (Owen)	Alaska	Richardson 1904
	Puget Sound	Holthuis 1952
N. nigricauda Stimpson	Pt. Ano Nuevo	Richardson 1904
N. ovifer Rathbun	Alaska	Richardson 1904
Spirontocaris suckleyi (Stimpson)	Puget Sound	Hatch 1947

This is a very common branchial parasite. The head is large, the incubatory lamellae do not completely cover the marsupium, and the endopodites of all the pleopods are present. The first abdominal segment is without papillae, and thoracic processes are present on all segments. In the female, the pleopods have narrow and elongate exopodites, and small oval endopodites; and the posterior lateral lobes of the thoracic segments are produced. In the male, all 7 segments of the abdomen are fused. Adult female approximately 13 by 9 mm.

BATHYGYGE Hansen 1897 GRANDIS Hansen 1897. (Plate 5)

Glyphocrangon spinulosa Faxon	21°15' North, 106°23' West	Hansen 1897
	Acapulco	Richardson 1899

Only the above single record is known for this branchial parasite. This form is included here because the proximity of the collection site to the United States makes it likely that Bathygyge may be found off California. Apparently a complete female has not been found, although the male is well described. The abdomen of the female is turned to one side to a marked degree. Large oval lamellae, representing the epimeral plates, are much produced anteriorly. The abdomen is small, having distinct segments, each without lateral parts. There are 5 pairs of unequally branched lamellae comprising the pleopods. Uropods are double-branched. The male has an ovate abdomen, without pleopods or uropods, and lacking abdominal segmentation. An approximation of the size of the female gives a length of 7 mm, and a breadth of 2.3 mm.

BOPYRINA Kossmann 1881 STRIATA Nierstrasz et Brender à Brandis 1929. (Plate 5)

Host	Locality	Reference
Hippolyte californiensis Holmes	Puget Sound	Dunn 1949
	San Diego	Nierstrasz and Brender à Brandis 1929

A branchial parasite. This genus is unique because some of its members have the segments of the abdomen fused along the side (B. abbreviata) or just in the median line (B. urocaridis). The body of the adult female tends to be very asymmetrical. Fairly heavy pigmentation present on both male and female. Eyes present in both sexes. Although the cephalon is separate from the second thoracic segment in the female, the separation between the two is not complete in the male. The abdominal segments are fused along their midline, but show lateral divisions in the female. In the male, there is a small projection caudally on the abdomen, and the abdomen is fused. This parasite must be classed as rare on the West Coast, in view of there being only two records. Length of adult female about 3.25 mm, with a breadth of about 2 mm.

BOPYRISCUS Richardson 1905 CALMANI Richardson 1905. (Plate 6)

Host	Locality	Reference
No host indicated	Channel between San Nicolas and Santa Barbara Islands, Calif.	Richardson 1905

Presumably a branchial parasite. This is the only record in the literature, and in view of the research centers near the original site, it is indeed surprising that this form has not been found again. Since no host was indicated, any search for this isopod would be doubly difficult. Richardson describes this as "very close to Probopyrus" (57, p. 562, 563). The head of the female is deeply set into the thorax, which has 7 distinct segments. The lateral margins of the first thoracomere are bilobate, whereas those of the last three are straight. The last two abdominal segments are fused, and there are no uropods in the female. The pleopods of the female consist of five pairs of double-branched lamellae. In the male, the first three abdominal segments are separated, with the last three segments being fused into a trilobate mass. The male also has no uropods. Adult female, approximately

5 by 3 mm.

BOPYROIDES Stimpson 1864 ACUTIMARGINATUS Stimpson 1864.
Refer to B. hippolytes.

BOPYROIDES Stimpson 1864 HIPPOLYTES (Krøyer 1838).
(Plate 6)

Bopyrus hippolytes Krøyer 1838
Bopyroides acutimarginatus Stimpson 1864
Gyge hippolytes Bate and Westwood 1868
Bopyroides hippolytes G. O. Sars 1899
Bopyroides sarsi Bonnier 1900
Bopyroides sp. Bonnier 1900
Bopyroides hippolytes Richardson 1901

Eualus suckleyi (Stimpson)	Puget Sound	Holthuis 1952
Heptacarpus brevirostris Holmes	Puget Sound	Holthuis 1952
H. stimpsoni (author?)	Puget Sound	Holthuis 1952
Hippolyte brevirostris Dana	Puget Sound	Stimpson 1864
Pandalopsis dispar Rathbun	Puget Sound	Richardson 1905
Pandalus borealis Krøyer	Alaska	Richardson 1905
P. jordani Rathbun	Brit. Columbia	Richardson 1905
P. montagui Leach	Alaska	Richardson 1905
Spirontocaris arcuata Rathbun	Alaska	Richardson 1905
S. bispinosa Holmes	Heceta Bank	Richardson 1905
S. brevirostris (Dana)	Alaska	Richardson 1905
	Brit. Columbia	Fee 1926
	Puget Sound	Richardson 1905
S. herdmani Walker	Brit. Columbia	Richardson 1905
S. lamellicornis (Dana)	Puget Sound	Holthuis 1952
S. polaris (Sabine)	Alaska	Richardson 1905
S. spina (us) (Sowerby)	Alaska	Richardson 1905
	Puget Sound	Hatch 1947
S. suckleyi (Stimpson)	Alaska	Richardson 1905
	Puget Sound	Richardson 1905

A widespread branchial parasite. In the female, the eyes are absent, and the first pair of antennae is composed of three articles, whereas the second pair has 5 articles. The 7 thoracomeres are distinct. All 6 abdominal segments are distinct, and have straight lateral margins; although the sixth segment is quite tiny. The uropods are missing, and the pleopods are represented by fleshy ridges. There are 5 pairs of incubatory lamellae. In the male, the eyes are distinct, and there are neither uropods nor pleopods. Also for the male, all of the thoracomeres are clearly separated, but the pleomeres have fused to form a posteriorly tapering segment. The average size of the adult female is 8 by 7 mm.

<u>ENTOPHILUS</u> Richardson 1904 <u>OMNITECTUS</u> Richardson 1904. (Plate 7)

<u>Munida</u> <u>normani</u>

Henderson	Hawaii-Maui-Molokai Channels, Hawaiian Islands	Richardson 1904

A visceral parasite, with many specimens collected from only this one area. Causes a bulge or change of color on the mid-dorsal carapace of the host. The marsupium of the female is extremely large, and is completely enclosed by the incubatory lamellae. The dorsal thoracic region is colored orange, with the rest of the body white. The eyes are absent, and the head is distinctly lobed. The thoracic segments have marginal plates which overlap the dorsal surface of the thorax at the side and are free on their whole surface (being attached only at the extreme lateral margin to the legs). The abdominal segments have similar plates which extend around until they meet mid-ventrally; thus nearly forming a funnel. There are no uropods. The pleopods are 5 pairs of double-branched tapering appendages. For the male, there are no color markings, the head is large and eyeless, and both abdominal and thoracic segments are clearly defined. There are uropods, and 5 pairs of single-branched pleopods. The average size of the adult female is 9 by 5 mm.

<u>HEMIARTHRUS</u> Giard and Bonnier 1887 <u>ABDOMINALIS</u> (Krøyer 1840). (Plate 7)

<u>Bopyrus</u> <u>abdominalis</u> Krøyer 1840

<u>Phryxus</u> <u>hippolytes</u> Rathke 1843

Bopyrus abdominalis Krøyer 1849
Phryxus abdominalis Lilljeborg 1852
Hemiarthrus abdominalis Giard and Bonnier 1887
Phryxus abdominalis Walz 1890
Hemiarthrus abdominalis Stebbing 1893
Phryxus abdominalis Sars 1899
Anisarthrus abdominalis Giard 1907
Phryxus abdominalis Richardson 1909
Hemiarthrus abdominalis Stebbing 1914
Phryxus abdominalis Hansen 1916
Hemiarthrus abdominalis Barnard 1920
Phryxus abdominalis Nierstrasz and Brender à Brandis 1923
Hemiarthrus abdominalis Chopra 1923
Phryxus abdominalis Fee 1926
Hemiarthrus abdominalis Pike 1960

Eualus fabricii (Krøyer)	Puget Sound	Holthuis 1952
E. gaimardi (H. Milne Edwards)	Alaska	MacGinitie 1955
E. suckleyi (Stimpson)	Puget Sound	Holthuis 1952
Heptacarpus tridens (Rathbun)	Puget Sound	Holthuis 1952
"Hippolytids"	Puget Sound	Davis, P. 1960
Spirontocaris sp. Bate	Central Calif.	Light 1957 (no species given for parasite)
S. abdominalis Krøyer	Seattle	Hatch 1947
S. arcuata Rathbun	Alaska	Richardson 1905
S. barbata Rathbun	Brit. Columbia	Fee 1926
S. bispinosa Holmes	Brit. Columbia	Richardson 1905
S. biunguis Rathbun	Alaska	Richardson 1905
S. fabricii Krøyer	Alaska	Richardson 1905
S. gaimardi belcheri (Bell)	Alaska	Richardson 1905
S. groenlandica Fabricius	Puget Sound	Richardson 1905
S. macrophthalma Rathbun	Alaska	Richardson 1905
	Brit. Columbia	Richardson 1905
	Puget Sound	Richardson 1905
	Point Arena	Richardson 1905
S. phippsi Krøyer	Alaska	MacGinitie 1955
S. polaris (Sabine)	Alaska	Richardson 1905

S. prionata Stimpson	Brit. Columbia	Fee 1926
S. sica Richardson	San Simeon Bay	Richardson 1905
	San Luis Obispo	Richardson 1905
S. sitchensis Brandt	Seattle	Hatch 1947
S. suckleyi (Stimpson)	Alaska	Richardson 1905
	Puget Sound	Hatch 1947
S. townsendi Rathbun	Puget Sound	Richardson 1905
S. tridens Rathbun	Puget Sound	Richardson 1905

A widely distributed parasite of the ventral abdomen of the host. For the female, the left side of the body is much larger than the right. Eyes are absent. On the larger body side, the thoracic segments fuse with the incubatory pouch, and only the first thoracic leg is present on that side. On the other side, the thoracic segments are distinct, and all 7 legs are present. The 5 abdominal segments are distinct, with the fifth being slightly biramous. The first four segments of the abdomen each have a pair of double-branched pleopods. For the male, eyes are present, and the front of the head is widely rounded. Although the thoracic segments are distinct, the abdomen is fused and tapers to a point. Average measurements for the adult female are 5 by 4 mm.

HEPTALOBUS Nierstrasz and Brender à Brandis 1931 PARADOXUS Nierstrasz and Brender à Brandis 1931.

Spirontocaris biunguis Rathbun	Alaska	Nierstrasz and Brender à Brandis 1931
S. suckleyi (Stimpson)	Alaska	Nierstrasz and Brender à Brandis 1931

A branchial parasite, known only from the original report given above. As described (40), "The systematic position of this organism is quite unknown. Its characters furnish no clue as to its relationships." Only females have been found. Therefore, considerable reservation must be held in placing Heptalobus in the Bopyridae. The structureless, lobed appearance is relieved by a chitinous ventral ring. Since there may be teeth on this ring, it would be a reasonable assumption to consider the form as a member of the Cryptoniscidae, rather than as a bopyrid. The measurements are roughly 3.5 by 4 mm.

IONE Latreille 1817 BREVICAUDA Bonnier 1900. See I. cornuta.

IONE Latreille 1817 CORNUTA Spence Bate 1864. (Plate 8)
Ione cornuta Spence Bate 1864
Ione thoracica (part) Heller 1865
Ione cornuta Spence Bate and Westwood 1868
Ione brevicauda Bonnier 1900
Ione cornuta Richardson 1904

Host	Locality	Reference
No host given	Brit. Columbia	Nierstrasz and Brender à Brandis 1931
Callianassa sp. Leach	Brit. Columbia	Bonnier 1900
	Central Calif.	Bonnier 1900
		Light 1957 (no species given for parasite)
C. gigas Dana	Brit. Columbia	Hatch 1947
C. longimana Stimpson	Brit. Columbia	Bate 1864
		Fee 1926
	San Francisco	Richardson 1905

A relatively rare branchial parasite. In the female, the lateral parts of the abdominal segments are twice as long as are the uropods. The basal segment of the legs has an elevated eminence ("boss") with an irregular margin. The pleural lamellae of the abdomen are composed of distinct articles, and have arborescent branches on their posterior margins; the lamellae increasing in size posteriorly. The uropods are unbranched processes about 3 mm long, and curve outward at their extremities. The male has unbranched abdominal pleural lamellae, and all of the abdominal segments are fused. In comparison to males of other bopyrids, it is large, being about one-third the size of the female. Range of sizes of the adult female from 7 by 4 mm up to 18 by 12 mm; length to breadth.

MUNIDION Hansen 1897 PARVUM Richardson 1905. (Plate 8)
Munidion parva Richardson 1904
Munidion parvum Richardson 1905

Host	Locality	Reference
No host given	Brit. Columbia	Fee 1926
Munida quadrispina Benedict	Puget Sound	Richardson 1905
		Davis, P. 1960

Pagurus setosus
(Benedict) Puget Sound Davis, P. 1960

A relatively rare branchial parasite. For the female, there are ovarian bosses on all the thoracic segments, and there are lateral, leaf-like processes also on the thoracomeres. The epimeral plates of all the segments gradually increase in size towards the posterior. The terminal segment of the body is rounded and possesses a pair of biramous uropods which are branched in a similar fashion to the lateral branches of the anterior abdominal segments. The head is bilobed. For the male, there are distinct thoracic, but fused abdominal, segments. The abdomen is egg-shaped, with the large end forward. Eyes are present, but both uropods and pleopods are absent. The average dimensions of the adult female are 9 by 5 mm.

PARARGEIA Hansen 1897 ORNATA Hansen 1897. (Plate 9)

Sclerocrangon procax
Faxon Acapulco Hansen 1897
Richardson 1905

Only one record for this branchial parasite. It is included here because the proximity of Acapulco to the United States makes it likely that this form will be found off California. (Cryptione Hansen 1897 elongata Hansen 1897 was arbitrarily omitted because its discovery site -- the Galapagos -- seems too distant for possible spread to the United States.) For the female, the eyes are absent, and the front border of the head is anteriorly arcuate. The epimera of the first four segments of the thorax are placed on the anterior half of the lateral margin, lateral to the ovarian bosses (which are present on all thoracomeres). All 6 abdominal segments are distinct, serially decrease in size, and have no lateral parts. The uropods are simple and single-branched. There are 5 pairs of segments. The outer branches are large and look like the uropods; the inner branches are inconspicuous. The male is eyeless, and the body gets progressively larger towards the posterior, terminating in a spade-shaped fused abdomen. On the base of this abdomen is a prominent median tubercle dorsally. There are no pleopods or uropods. The dimensions of the female are 8 by 7 mm.

PHRYXUS Rathke 1843 ABDOMINALIS (Krøyer 1840). Refer to Hemiarthrus abdominalis.

PHYLLODURUS Stimpson 1857 ABDOMINALIS Stimpson 1857.
(Plate 9)

No host given	Brit. Columbia	Nierstrasz and Brender à Brandis 1931
	S. F. Bay	Richardson 1905
Gebia sp. Leach	Puget Sound	Stimpson 1857
	Tomales Bay	Stimpson 1857
G. pugettensis Dana	Tomales Bay	Lockington 1876
Upogebia sp. Leach	Puget Sound	Richardson 1905
		Davis, P. 1960
	Tomales Bay	Richardson 1899
	Central Calif.	Light 1957
U. pugettensis (Lockington)	Brit. Columbia	Fee 1926
	Puget Sound	Hatch 1947
	Tomales Bay	Richardson 1905
	S. F. Bay	Hatch 1947

A fairly common parasite of the ventral abdomen of the host. For the female, the eyes are absent, and the head is bilobate. There is a small amount of distortion of the body, but not nearly as much as found in other female bopyrids. The 7 distinct segments of the thorax have narrow epimeral plates, and the whole thorax is abruptly narrowed by the shortening of the last 3 segments. The 6 distinct abdominal segments rapidly narrow in a "V" pattern, with the first segment having 2 papillose processes. There are 2 double-branched pleopods on each of the first 5 abdominal segments, with the sixth segment having 2 single-branched uropods. For the male, eyes are present, and the thoracomeres are typical for a bopyrid, but the 6 distinct abdominal segments are unique. Each has a narrow, anterior point of attachment, and rapidly expands into a wide band. The first abdominal segment has 2 large dorsal rounded papillae, and the terminal segment has a caudally-produced process. Also unique for this genus and species is the fact that the male is reported to attach separately to the host (34). The average dimensions of the female are 14 by 10 mm.

PSEUDIONE Kossmann 1881 GALACANTHAE Hansen 1897.
(Plate 10)

Galacantha diomedeae var. parvispina Faxon	Gulf of Calif.	Hansen 1897
		Richardson 1905

Munida quadrispina Benedict	Brit. Columbia	Fee 1926
	Cape Flattery	Richardson 1905

A relatively rare branchial parasite. For the female, the eyes are absent, and the head is as long as it is broad. The thoracic segments are distinct, with the first four being notched unequally (the posterior lobe being the smaller). The pleural plates of the last three thoracomeres are developed as lamellae. The first 5 abdominal segments have double-branched pleopods as well as lateral lamellae. The uropods are single-branched. For the male, the eyes are present, and all of the thoracic and abdominal segments are distinct. The average measurements for the female are between 8 and 11 mm long, and 3 to 5 mm in breadth.

PSEUDIONE Kossmann 1881 GIARDI Calman 1898. (Plate 10)

Eupagurus ochotensis Brandt	Puget Sound	Calman 1898
Munida sp. Leach	Brit. Columbia	Nierstrasz and Brender à Brandis 1931
Pagurus sp. Fabricius	Puget Sound	Davis, P. 1960
	Central Calif.	Light 1957 (no species given for parasite)
P. aleuticus (Benedict)	Puget Sound	Holthuis 1952
P. hirsutiusculus (Stimpson)	Puget Sound	Holthuis 1952
P. ochotensis (Brandt)	Puget Sound	Richardson 1905

A common (in the colder waters) branchial parasite. Both the male and the female are similar to P. galacanthae, except that for the female, the pleural plates of the last three thoracomeres are not developed as lamellae. Also, the first incubatory lamellae process is a small, inwardly curved lobe; and the endopodite of the pleopods is much larger than the corresponding exopodite (they were only slightly larger in P. galacanthae). The average measurements for the female are 12 by 7 mm.

<u>SCYRACEPON</u> Tattersall 1904 <u>HAWAIIENSIS</u> Richardson 1911.
(Plate 14)

<u>Pilumnoplax</u> <u>cooki</u> Rathbun	Maui-Molokai Channel, Hawaii	Richardson 1911

A rare branchial parasite, found only once, and in only the one location. For the female, the body is distinctly oval in outline, and is colored light yellow. The head is very large, bilobed, and lacking eyes. Maxillipeds are very large, with the exopodite produced at the inner distal extremity into a long lamella-like process with many smaller lamellae along its inner margin. The 7 thoracomeres are distinct, with the last four having a dorsal boss in the midline. This is modified into an actual hook on the seventh segment. The 6 abdominal segments are distinct, and each of the first 5 has two elongate, fringed appendages on each side. These decrease in length posteriorly, and each segment has a pair of small sac-like bodies at the bases of the appendages. The uropods are a pair of appendages resembling those of the preceding segments. For the male, the thoracic segments are well defined, but the abdominal segments are fused into a diamond-shaped mass which has lateral indentations indicative of the segments. No dimensions were given.

<u>STEGOPHRYXUS</u> Thompson 1901 <u>SP</u>.

<u>Pagurus</u> <u>sp</u>. Fabricius	Central Calif.	Light 1957

As described for the Atlantic, this is a dorsal abdominal parasite of hermit crabs. The major characteristic is that the genus has triramous pleopods. Since neither the species of the bopyrid, nor the species of the host are given in the indicated reference, and there is no hint as to the collector or the collection site, this report should be strongly questioned. This (or any allied) form has not been reported for any part of western United States and therefore should not be considered as a valid record. No sizes can be estimated.

From the foregoing, it can be noted that there are four species from four genera of bopyrids from Alaska, and that one (<u>Heptalobus</u>) is unique (provided it is a bopyrid). There are 8 species from 7 genera reported from Canada, and none is unique. There are 12 species from 10 genera of bopyrids reported from western United States, and four (Argeia pauperata, Bopyrina, Bopyriscus and Stegophryxus) are unique. There are three species from three genera reported from Mexico, and two (Bathygyge and Parargeia) are unique. There are three species from three genera reported from Hawaii, and all three (Entophilus, Scyracepon, and an as yet unnamed form -- which is in neither of these genera) are unique.

If those which are not yet clearly verified for the eastern Pacific of the United States are discounted (Bathygyge, Heptalobus, Parargeia and Stegophryxus), there remain 14 species representing 11 genera for this area.

3. EXPERIMENTATION

Collecting Techniques and Areas. Since bopyrids have been reported from fresh water situations in North America, especially the semi-tropical areas (52) (57, p. 557-559), every opportunity was explored to check fresh-water arthropods such as crayfish. No isopod-infected forms were found. A similar lack of success was encountered regarding deep water hauls in Hawaii, to which the Fish and Game Commission and local fishermen permitted me access. Yet deep-water forms are recorded from this region (Plates 7, 14); and until recently, no bopyrid was known from the land or shoal waters, according to Edmondson (19, p. 239).

Collecting from rock, sand and mud shallow beaches was carried out in the three western states, Canada and Hawaii, with infected hosts found in all regions. In rocky areas, hand catching of crabs and hermit crabs was employed; in muddy flats, shoveling to uncover shrimp burrows proved to be most productive; and in sandy beaches, it was found that infected shrimp could be obtained by lightly dragging a flat-faced net at a good speed across the receding wave area at low tide. Bopyrid larval stages and copepods were sometimes collected by towing a very fine mesh net and collecting bottle behind a rowboat. The best collecting -- although very limited -- was on coral reefs, where almost any large chunk of coral would house many arthropods.

Offshore dredging was carried out in the San Juan Islands, near Dillon Beach, off Santa Monica, near La Jolla, and in Hawaii.

Augmenting the personally collected specimens were preserved bopyrids donated by the University of Washington Friday Harbor Laboratories, the U. S. Fish and Wildlife Service offices at La Jolla and Auke Bay, the Fish Commission of Oregon at Astoria, the Zoology Department at Oregon State University, the University of the Pacific Marine Station at Tomales Bay, a processing plant at Monterey, and the University of Hawaii. Lastly, I was permitted access to the arthropod collection of the Hancock Expedition at Los Angeles.

A New Bopyrid From Hawaii. In collecting from the aforementioned continental areas, no new types were encountered, and some that the literature indicated should be present were not found. *Argeia pauperata*, in any numbers, is apparently restricted to the San Francisco Bay region; Bopyrina striata is quite rare, judging from the records; Bopyriscus calmani has been recorded only once; and Pseudione giardi was not encountered (unless it was confused with P. galacanthae).

In Hawaii, a university zoology class collected a bopyrid-infected Xantho crassimanus A. Milne Edwards near Diamond Head, Oahu, in January 1962. The host's carapace was badly broken, and the parasite had subsequently gone unrecognized as to type. Upon receiving the specimen, I determined that there was a damaged bopyrid female and one male, together with many epicaridian larvae, in the left branchial chamber of the crab.

This was the first record of a member of the Bopyridae from the shores of any of the Hawaiian Islands (Scyracepon and Entophilus are from deep channels). It is hoped that other specimens will be found in the future, and thus permit the ascertaining of more details. A description is:

> For the female, the eyes are absent, the antennae are 4-jointed, and the cephalon is large. The head is sunken into the first of the 7 distinct thoracomeres. No median dorsal tubercles. Considerable overlapping of the oöstegites. Six distinct abdominal segments, each with digitate lamellae. The pleopods with large lateral leaf-like processes which superficially match the metasomal lamellae. Uropods smooth and evenly dichotomous.
> For the male, eyes are present, and there is some body pigmentation peripherally. Seven distinct

thoracomeres. Six distinct abdominal segments, all but the last having evident lateral plates. Five pairs of pronounced tubercles representing the pleopods. Uropods disc-like, notched. The measurements for the female are 9.7 by 8.1 mm.

Life Cycle Aspects for *Argeia pugettensis*. Since it was one of the aims of this research to determine a life cycle of a west coast bopyrid, *Argeia pugettensis* was selected because both it and a *Crago* host were common and widespread. The critical point was whether or not there was an intermediate host involved, since copepods had been indicated by many as filling this role, yet others had stated that a complete cycle was possible without alternate hosts. In particular, Gifford (24, p. 17) was unable to find copepod-parasitizing microniscan larvae for the closely related *Argeia pauperata*.

Several aquarium tanks were utilized in the life cycle study, and it was found that the hosts and parasites did well in thoroughly aerated ocean water, provided the temperature was held to 20 degrees Centigrade or less. Ordinary fine fish feed from pet shops proved to be adequate food, and the only precaution to be observed in general was the removal of hermit crabs from the tank, inasmuch as they would attack any vulnerable (weakened) shrimp.

Attempts to raise copepods as a pure colony were not satisfactory, so they were either obtained from other workers, or collected in a fine-mesh open-water net. Although some shrimp did develop in the tanks during the experiment, it was found easier to bring them in from the ocean as they were needed. This also insured a less artificial environment during their larval growth. If it was desired to isolate a host or to study the reactions of a bopyrid removed from its shrimp, the usual aquarium dip net served this purpose admirably.

When it was necessary to anesthetize a host, crystals of menthol, magnesium sulphate, or chloral hydrate were slowly added to a syracuse dish in which the animal had been isolated, until such time as the shrimp ceased flexing. For recovery of the host, it was placed into the aquarium immediately adjacent to the aerator. It was interesting to note that parasitic isopods did not react as quickly as did their hosts to the anesthetic.

Many techniques were attempted to ascertain the best procedure for killing, preserving and mounting the bopyrids. The best seemed to be a 10% formalin-sea water killing solution, followed as soon as possible by a preservative made up of one-fifth pure glycerine and four-fifths 70% ethyl alcohol. This preservative did not alter the animal's color, nor did it make the specimen as brittle as did Bouin's, formalin, or alcohol. Mounting could be done in Monk's fluid, glycerine jelly, or other standard media, but General Biological Supply House's "CMC-10" seemed to be best, provided care was taken to avoid the ubiquitous bubbles. Due to the thickness of the isopods, a circle or rectangle of thin plastic could be cemented to the slide with piccolyte cement, thus protecting the specimen.

The living female _Argeia pugettensis_ normally appeared to move little. However, close examination showed that oöstegite I on either side kept up a constant beating motion, thereby aerating the eggs or embryos. This beating was approximately 300 times per minute during periods when the female was apparently excited, such as times when it was under a warm lamp and separated from the host. At these times, she would also carry out rowing movements with the pereiopods, but extremely weakly. It was also noted that the genital aperture occasionally pulsated.

The male _Argeia pugettensis_ seemed to become quite agitated when the parasites were removed from the host and then subjected to the light and heat of a microscope lamp.

It would roam over the back and head of the female, but at the touch of a dissecting needle, it would immediately return to the posterior ventral region of the female. The pereipods enabled it to hold onto the female very strongly, but if it were forcibly freed, the male would extend its back until it became "U-shaped." If it were once again put into contact with the female, it would flex the back and regain a grip on adjacent tissues.

Since all experiments were carried out on _Argeia pugettensis_ Dana as the parasite, and on the shrimp _Crago nigromaculata_ (Lockington) as the host, subsequent comments about the parasitic bopyrid or the host shrimp will refer to these two. (Some experimentation was carried out with an alternate host -- _Crago alba_ (Holmes) -- but this gave results identical to those found for _C. nigromaculata_.)

A series of experiments indicated that the time of egg-laying until the release of the epicaridian larva usually amounted to three weeks. Since fertilization is external, all eggs developed at the same stage; however, discrepancies in the indicated laying-release time are undoubtedly due to inability to isolate the parasitized host and still keep conditions "normal" for the isopod. It is possible that in cooler off-shore waters, this period might amount to a month.

The epicaridian larvae are active swimmers, and tend to go towards the top of the aquarium. This positive phototropism creates a question, inasmuch as copepods tend to be negatively phototropic, and therefore contact between the two forms might be less than anticipated. The large number of larvae released by the female can be roughly followed by means of a "pseudo-" Tyndall effect, wherein a person viewing the aquarium in a dark room can see specks in the water if a strong light is placed at right angles to his line of vision.

After a day or so following their release, larvae could be found in many locations on other animals within the aquarium, such as on and under the carapace of arthropods, in the shell of hermit crabs, etc. When specific locations were checked, however, it was found that the larvae were no longer present after two or three weeks. On the whole, this parallels Gifford's findings (24, p. 12) wherein he could notice a darkening of the shrimp (Crago franciscorum) carapace if larvae entered the host, but 15 days seemed to be the limit of existence of the parasite, whether in Crago or free.

Although two instances were observed in one experiment and one in another of epicaridians attached diagonally across the back of a copepod with the parasite's head forward, no actual moment of attachment was ever observed. However, many copepods have been seen with subsequent larval stages upon them. Since so few of the isopods pass successfully through their life cycle under aquarium conditions, the larvae were left attached in the hope of obtaining the final bopyridium stages. Many different kinds of copepods were placed into the test aquaria as ocean collecting was done, and there seemed to be little selection of particular forms by the isopods. Subsequently, copepods which had been infected were sent to specialists for identification, and the two genera which seemed to have been especially parasitized were *Acartia* and *Calanus*. There are apparently many species of *Calanus*, but only a few of *Acartia* which would be found in the eastern Pacific, according to Davis (16, p. 3, 4).

An attempt was made to study the immediate post-epicaridian stage, but this (the microniscan larva) did not preserve well or was too soft-bodied to permit observation of much detail. Since there are several moults at this stage (42, p. 227), it may have been that my specimens were in a "soft-shelled" condition.

Approximately three weeks later, the parasite was obviously in a more firm, detailed form, and had a slimmer, tapered appearance. This was the cryptoniscan larval stage, and it was at this time that the bopyrid released its hold upon the copepod, and became free-swimming. Due to the similarity of the growth timing for each isopod larva, it might be expected that all of the forms which had survived and attached to copepods would therefore leave the intermediate hosts simultaneously. This was not the case. Since it was physically impossible to follow a single bopyrid under natural conditions, the foregoing results apparently indicate that the "3-weeks" on the copepod is subject to variation, or that some epicaridians did not anchor on the copepods as early as did others.

Those copepods which had been hosts to the bopyrid were not apparently injured. However, a small colored (red-orange) spot persisted at the point where the isopod's oral cone would have been placed.

The cryptoniscan larvae then seemed able to survive for long periods of time without having to metamorphose to the bopyridium stage. One was found two months after female isopods had been removed from the aquarium, attached to a pleopod of an adult female shrimp, and another was found in the branchial chamber of an adult shrimp by itself. This latter is interesting, because it raises the question of whether an adult host can be parasitized successfully, and more important, since the larva was in the correct location, why did it not change into a female bopyridium? Is it possible that sex in the Bopyridae is determined genetically, rather than by "site-priority" as discussed earlier?

Despite the large numbers of eggs and original larval stages, it was extremely difficult to obtain the last step in the life cycle -- namely the infection of a new host by one of the isopods that had been raised in the aquarium. Only two cases were provably complete, although several others were probably successful.

Just how this cycle correlates with that suggested by Gifford (24, p. 16) is questionable. Particularly so since he indicates that epicaridian larvae die within 15 days when in the _Crago_ gill chamber, yet he hypothecates that they change into a cryptoniscan larva (and then the bopyridium), in that same site. It would seem rather unusual to find that _Argeia pauperata_ had neither a copepod intermediate host nor a microniscan stage, whereas _Argeia_ pugettensis had both. In view of this discrepancy, it might be assumed that either life cycle was optional for the bopyrid. To test this, the following experiments were conducted.

Since many writers have assumed or stated that bopyrid infection of a decapod occurs only during the host's late larval stages (42, p. 227), and yet there are records available of immature bopyrids in adult hosts (8), it might be possible to obtain isopod growth by placing the parasites in their normal location on an unparasitized host. Accordingly, cryptoniscan larvae were placed into the aquarium with adult shrimp. No attachment was observed in the normal location, nor did the cryptoniscans become bopyridia. However, these larvae did fasten onto the pleopods and legs of the shrimp, and remained there for several weeks.

In another experiment, a small hole was cut in the carapace of an uninfected shrimp, and an adult male and female bopyrid transferred there from another host. (The reason for the hole was to prevent excessive pressure from the carapace -- pressure which is absent in parasitized hosts due to the branchial bulge.) Although this experiment was attempted several times, none of the parasites persisted intact more than three days. Naturally, it was necessary to be certain that the correctly twisted isopod ("dextral" or "sinistral") was employed.

In one series of tests, adult male bopyrids were placed in their normal location under the carapace of uninfected hosts, in the hope that direct feeding on the shrimp might cause some obvious change in the morphology. Here, the reaction was uniformly rapid. None stayed more than one day, and they were observed crawling to the carapace edge and then dropping off the host. This was true even when the males were placed into the youngest shrimp larval stages available. This seems to agree in general with aforementioned experiments in which scientists in the Naples area were unable to obtain sex reversal from male to female.

If it is correct to assume that the sex determination of Argeia pugettensis is a matter of "site-priority," and therefore related to food supply or type, then uniform feeding of cryptoniscan larvae should produce bopyridia of the same sex. To check this point, isopod larvae were isolated in a tank which was kept supplied with Crago extract (made by homogenizing many shrimp in a blender). Although most of the larvae remained alive and active, no discernible changes could be observed. Unfortunately, the extract was quite subject to decomposition, and therefore the experiment was not of long duration. Had sex been determined genetically, 50% of the larvae would have been female; but had sex been determined by nutrition, then one might have expected 100% to have become female.

Possibly a hormone is produced by the first parasite to occupy the gill chamber, and this might lead to the development of maleness on the part of any successive cryptoniscan larvae which "feed upon" the female. Certainly this would explain "supplemental males" which are often described as being present with a bopyrid couple. If techniques could be developed to insure accuracy, it would be of interest if a group of cryptoniscan larvae were released into a tank having larval Crago, and then each isopod dyed according to its location upon the host (red for the first in a definitive site, blue for the second). If the bopyrids were immediately removed from the shrimp larvae, and re-released, it could then be ascertained whether they selected exactly the same sequence and location -- and hence sex -- as they did before.

Since considerable reference has been made to the "castration effect" of bopyrids on their hosts, records were kept of the number of females "in berry" during the Crago nigromaculata breeding season. Of 214 infected shrimp examined -- all of which were carrying eggs -- most had a normal or nearly normal clutch. This certainly does not indicate that Argeia pugettensis inhibits egg production. However, it might be that non-egg-carrying Crago were not all males (as assumed), but temporarily sterilized females along with the males.

As far as could be ascertained by observation of the animals within the aquarium, infection of the shrimps occurred only in very young (larval, immediately post-larval) stages. This agreed with the findings of several investigators, but it does not rule out the possibility of occasional host infection at a more advanged age. Perhaps this latter would be an explanation for the unexpectedly higher rate of infection in second year Pandalus bonnieri by Pseudione affinis over that found for first year prawns (41, p. 245). Naturally, this supposition would have to be thoroughly checked, since collecting techniques, times or depths could turn out to be the selecting agent.

4. DISCUSSION

Evaluation of the Experiments. Even though very few specimens of *Argeia pugettensis* were completely carried through their life cycle from host *Crago nigromaculata* back to an uninfected host, the experiment serves to show agreement with what seems to be a consensus regarding life cycles in the Bopyridae. Several authors were mentioned as indicating that a copepod and/or a microniscan stage were not involved, but for *Argeia pugettensis*, both a microniscan larva and a copepod -- the most common being *Calanus finmarchicus*, *C. tenuicornis* -- were found to be part of the cycle. It is entirely possible (although improbable, as I evaluate it) that a bopyrid could have an option of either a direct cycle, or an indirect one, utilizing a copepod.

Many other experiments could be planned to check additional points on sex determination, hyperparasitism, and limits of host infectivity periods. In view of the paucity of knowledge of this family on the United States west coast, it might be more helpful to run life cycle studies on the other species and genera, rather than to concentrate on only one; at least at this time.

A Compiled Key for the West Coast Bopyridae. One of the purposes of this research was to provide a single source for information of a general nature concerning the bopyrids of the eastern Pacific of the United States. One facet of such data would be an identification key; accordingly, the following has been compiled from Fee (20, p. 23), Hatch (28, p. 222, 223), and Richardson (54, p. 868, 869), (56, p. 680, 681), (57, p. 498, 499), (59, p. 654-657).

KEY TO THE BOPYRIDAE OF THE EASTERN PACIFIC OF THE U.S.

Since all of these forms are isopods, they do not have a carapace; they do not have chela on the second thoracic appendage (first leg); they have the head fused with the first thoracic segment; and they carry out branchiation by means of pleopods.

Female: Body distinctly segmented, more or less asymmetrical, usually twisted to either the right or the left. Antennae with both parts rudimentary. Maxillipeds are lamellar and composed of two parts, frequently exhibiting a small terminal joint or palp; the two curved lanceolate appendages at the base representing epignaths. Coxal plates usually clearly defined. Legs usually in 7 pairs (sometimes all but the first leg may be missing on one side). All legs similar, short, prehensile. Five pairs of incubatory plates (the first pair composed of two segments), forming an arch over the ventral thoracic surface of the isopod. Abdomen relatively clearly defined. Pleopods with the same general structure; usually simple, biramous or triramous; rarely missing. Uropods, if present, simple or lanceolate.

Male: Body symmetrical. Head rounded in front. Much smaller than the female. All 7 thoracic segments sharply defined. Abdominal segments sometimes clearly delineated, but fused in some.

1 Body of female with one side greatly swollen and much longer than the other side. Only the first leg is present on the swollen side. Abdomen composed of 5 segments. Abdomen of male fused and pointed. Parasitic on the ventral abdomen of shrimp, particularly on Spirontocaris. . . . . Hemiarthrus

1' Body of female not greatly asymmetrical, but usually twisted. All legs present on both sides. Abdomen usually of 6 segments. . . . . (2)

2 Lateral parts of the abdominal segments elongate and digitate. . . . . (3)

2' Lateral parts of the abdominal segments not elongate and digitate. (4)

3 All 6 segments of the abdomen elongate and digitate. Abdomen of the male fused, having lateral elongations similar to those of the female. Branchial parasites found on Callianassa. . . . . Ione

3' Only the first 5 abdominal segments elongate and digitate. A mid-dorsal boss on the thoracomeres, becoming a hook on VII. Abdomen of male fused, but with lateral notches. A branchial parasite from deep Hawaiian waters. . . . . Scyracepon

4 Lateral parts of abdomen produced lamellarly. . (5)

4' Lateral parts of abdomen rudimentary or absent. (6)

5 Uropods in female double-branched. Head bilobed. Abdomen of the male is fused, with the largest part anteriorly. A branchial parasite of Pagurus, Munida. . . . . Munidion

5' Uropods in female single-branched. All segments of the male abdomen clearly evident. A branchial parasite of the hermit crab Pagurus, and Munida. Pseudione

a. Antennae 4-jointed. Maxillae present, normal. In the male, the eyes are absent, maxillae are present, and the last abdominal segment is entire. . . . . <u>P. galacanthae</u>

b. Antennae 5-jointed. First pair of maxillae absent. For the male, eyes are present, maxillae are absent, and the last abdominal segment is cordate. . . . . <u>P. giardi</u>

5" Uropods in female absent. Male abdomen segmented. Both sexes without eyes. A visceral parasite from deep Hawaiian waters, on <u>Munida</u>. . . . . <u>Entophilus</u>

6 Pleopods present in the female. . . . . (7)

6' Pleopods absent in the female. Uropods also missing. Male without pleopods or uropods, and with the abdomen fused. A common branchial parasite of many related forms, particularly <u>Pandalus</u> and <u>Spirontocaris</u>. . . . . <u>Bopyroides</u>

7 Pleopods of the female are biramous. . . . . . . (8)

7' Pleopods of female simple and single-branched. Eyes present in both sexes. The body suggests the fresh-water forms, since partial fusion of the abdominal segments occurs. The cephalon is separated from the second thoracic segment in the female, but partially fused in the male. A branchial parasite of <u>Hippolyte</u>. . . . . <u>Bopyrina</u>

8 Uropods present in the female. . . . . (9)

8' Uropods absent in the female, and the last two abdominal segments are fused. The last three abdominal segments of the male are fused into a tri-lobate mass. Probably a branchial parasite. No host known. . . . . <u>Bopyriscus</u>

9 Uropods simple and single-branched in female. . (10)

9' Uropods biramous in the female, and abdomen strongly twisted. The male has a fused abdomen, lacking pleopods and uropods. A branchial parasite of <u>Glyphocrangon</u>. . . . . <u>Bathygyge</u>

10 Branches of pleopods of female unlike: outer branch narrow and elongate; inner branch small and oval. Male has no uropods, no abdominal appendages, and no trace of abdominal segmentation. . . . . . . (11)

10' Branches of pleopods of female similar: narrow and elongate. Two dorsal papillae on first abdominal segment in both sexes. In the male, the abdominal segments are distinct, there are elongated appendages on the first 5 abdominal segments, and there are uropods. The male may be separated from the female on the host. A fairly common ventral abdominal parasite of Upogebia. . . . . Phyllodurus

11 Posterior lateral margins of each thoracic segment somewhat produced into processes. Male with narrow, tapering abdomen on which there is no dorsal tubercle. A very common branchial parasite on many forms (Crago, etc.). . . . . Argeia

a. Head bilobate. Anterior thoracic branchial and posterior abdominal appendages may be absent. Concentrated mainly at San Francisco Bay. . . . . A. pauperata

b. Head transverse. All thoracic branchial and abdominal appendages present. Incubatory plates leave much of the marsupium uncovered. . . . . A. pugettensis

11' Posterior lateral margins of each thoracic segment not produced into processes. Male with large, rounded abdomen on which there is a median dorsal tubercle near the base. A branchial parasite of Sclerocrangon. . . . . Parargeia

There are many inconsistencies in keys such as the foregoing, and it would be a boon if someone would collate the data on the world's Bopyridae so as to develop a standardized key and rid the records of overlapping or questionable forms. For instance, does "double-branching" mean with two or with four terminal branches? It is used both ways. Also, which genera and species are considered valid today? Perhaps Bopyrus could be combined into B. squillarum and B. stebbingi for the world, instead of the many different forms listed. Possibly Bopyrinella is actually Bopyrina; Synsynella might be Bopyrella; and there is even some disagreement about the separation of Palaegyge and Probopyrus. Certainly something should be done about the "incerta" species that appear in the appendices of many articles. For instance, Rhabdocheirus had been known and studied for two decades before Tattersall (67, Plate 11) so clearly pictured it, yet its taxonomic status is still in doubt. It appears to me to have the general features of a member of the Gnathiidae.

One of the difficulties in the taxonomy of the Bopyridae is the result of failure of scientists to follow rules of synonomy. The forms of abdominal parasites in the genus Phryxus should in actuality be in the genus Hemiarthrus, and several authors -- including this one -- do not consider Phryxus as valid. As related in Chopra (12, p. 429), Rathke's "Phryxus" (1843) was in reality two forms: Athelges and Phryxus. The latter was originally called Bopyrus by Krøyer in 1840; but more important than this was the fact that Phryxus livornica Pet. (lineata Fab.) had been used by Hubner in 1822 in "Verzeichniss," to designate a lepidopteran in the Deilephilidae tribe, Sphinx division. The genus Hemiarthrus was then used for the incorrect "Phryxus," and the matter was thoroughly covered by Giard (22). However, the generic status is still confused as shown by Nierstrasz and Brender à Brandis' (38, p. 112, 113) comment that although Hemiarthrus has priority over Phryxus, and Botryllofer has priority over Athelges, they would continue to employ the incorrect forms because of usage!

Hemiarthrus is used in this paper for two reasons: it is of little use to develop synonomy rules if they are not to be followed; and the Dajidae epicarideans have many genera that use "-phryxus" as a suffix, such as Arthro-, Aspido-, Branchio-, Hetero-, Holo-, Noto-, Pro-, and Zono-.

A Suggested Taxonomic Change. In view of the confusion in classification of the bopyrids -- a confusion which is understandable when it is realized that some authors combined groups on the basis of embryology, others on the basis of the hosts, others on the basis of the site on the host, etc. -- it might be well to establish a standardized system for the United States west coast. There is no assurance that this tabulation will be accurate on the basis of future work, but at least it can be a point of departure in research.

The general appearance, type of host, and life cycles (as far as they are known) are similar for the three proposed subfamilies of the Bopyridae; whereas all three differ from the choice of host, position on the host, and adult appearance of the parasites in the Dajidae. However, these variations are minor in comparison to drastic differences found in other epicarids with respect to adult parasite appearance, life cycles, hosts, and in position <u>within</u> the host. These differences would seem to justify completely separated Cryptoniscina and Entoniscina tribes. Therefore, the following taxonomy is suggested:

- Isopoda (order)
- Epicaridea (suborder)
  - Bopyrina (tribe)
    - Bopyridae (family)
      - Bopyrinae (subfamily)
      - Entophilinae
      - Phryxinae
    - Dajidae (family)
  - Cryptoniscina (tribe)
    - Asconiscidae (family)
    - Cabiropsidae
    - Crinoniscidae
    - Cyproniscidae
    - Hemioniscidae
    - Liriopsidae
    - Podasconidae
  - Entoniscina (tribe)
    - Entoniscidae (family)

As can be seen, the Entoniscidae has been removed from the Bopyridae and Bopyrina groups; thus an Entoniscina tribe was proposed. The added suggestion of Bopyrinae and

Phryxinae subfamilies of the Bopyridae is in line with the Entophilinae proposal of Richardson (56, p. 679).

Control Measures for the Bopyridae. It has been pointed out that decapod hosts often outlive their parasitic isopods, or are able to lose the bopyrids during changes in water salinity. It has not been fully proven that damage to the host gonads is present in every case during parasitization, whereas it has been shown that reproductive abilities return to "sterilized" hosts following the removal of the parasite.

The incidence of infection of decapods is relatively low; and from a commercial standpoint, the site of the parasite and the parasite itself are removed during preparation of the host for market.

Where there is proof that an intermediate host is utilized, it has always been a copepod. Therefore, it would seem that no control measures are needed, nor are they feasible. A method of controlling copepods would be impractical because of their use by other marine forms. Any chemical in the water to injure the parasitic isopods would most certainly injure their hosts. And there is no technique by which the larval bopyrid stages could be segregated from the rest of the plankton.

Therefore, no method of control of the Bopyridae seems to be either possible or desirable.

5. SUMMARY

The Epicaridea is a little studied suborder of isopods as far as the Eastern Pacific of the United States is concerned, and this lack of research extends particularly to the constituent Bopyridae. For this reason, the literature from many parts of the world was reviewed with respect to such items as isopod palaeontology, hosts of bopyrids, bopyrid genera and species, effects of parasitization upon the host, and forms known from western marine parts of the United States.

Collecting was accomplished in Hawaii, Canada, Washington, Oregon and California, and museum specimens of bopyrids were studied. A shore bopyrid was found in Hawaii, and represents the first record for the islands other than two types found in deep channels. The male was intact, but the female had been damaged; hence naming of the form will not be done until after further study.

The life cycle of Argeia pugettensis on the host Crago nigromaculata was determined to involve a copepod as an intermediate host. The apparently "preferred" copepod was Calanus. This bore out studies on bopyrid life cycles by many other research workers, but did not agree entirely

with one reported for Argeia pauperata.

An identification key was compiled from the literature. As part of the work needed to clarify the situation of west coast bopyrids, it was pointed out that synonomy demands that "Phryxus" be superceded by "Hemiarthrus"; and that clarification of the epicarid taxonomic situation could be aided by proposing an Entoniscina tribe, together with a Bopyrinae and Phryxinae subfamily.

Control measures for the Bopyridae were discussed.

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APPENDIX

Plate 1

Isopod Anatomy

Figure 1. Ventral aspect of a non-epicarid female (<u>Porcellio scaber</u>) which shows the basic isopod structures. (33, p. 138). No size given.

a. Peduncle
b. Flagellum
c. Antenna
d. Maxilliped
e. Oöstegites
f. Pereiopod
g. Pleopods 1-5
h. Uropod

Figure 2. Ventral aspect of a bopyrid female (<u>Probopyrus latilamellaris</u>). (38, Plate 6, Figure 19b). No size given.

a. Oöstegite
b. Pereiopod
c. Pleopod
d. Uropod

Figure 3. Dorsal aspect of a bopyrid female (<u>Probopyrus latilamellaris</u>). (38, Plate 6, Figure 19a). No size given.

a. Head
b. Pleural plate
c. Thorax
d. Abdomen

Figure 4. First thoracic appendage of adult male (<u>Argeia pauperata</u>). (24, Plate 4, Figure 2). X 139.

a. Dactylopodite
b. Propodite
c. Carpopodite
d. Meropodite
e. Ischiopodite
f. Basipodite

Plate 1

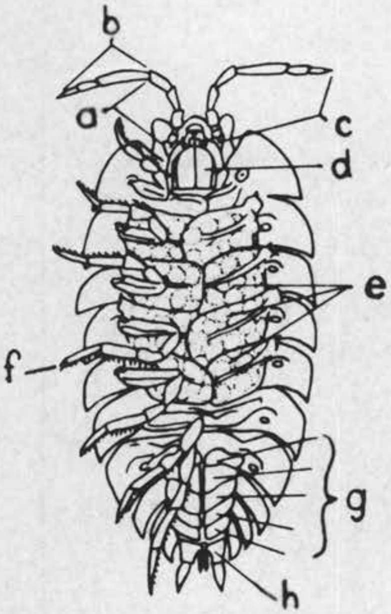


Figure 1

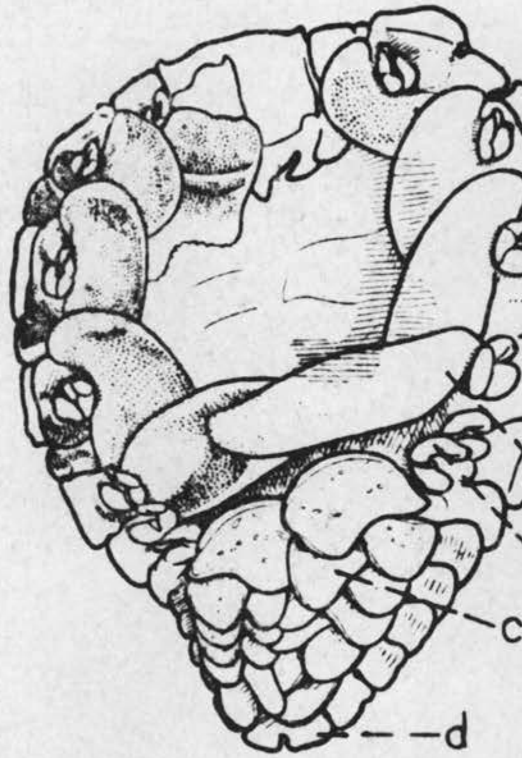
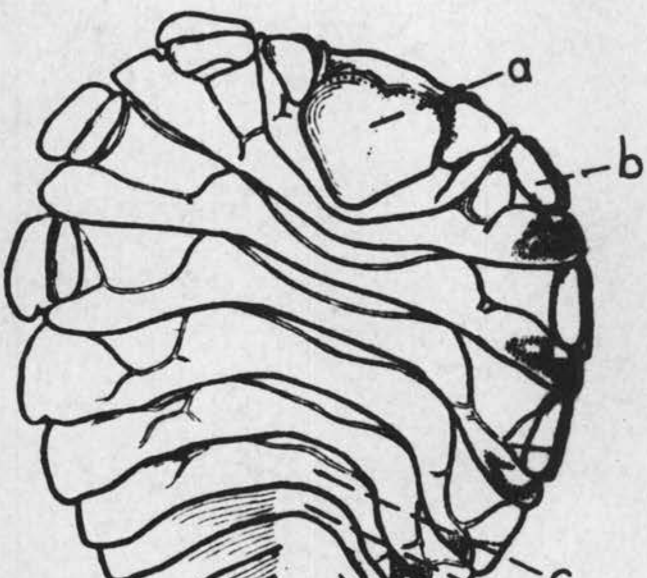


Figure 2



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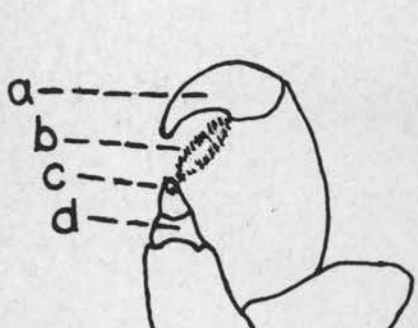


Figure 4

Plate 2

Bopyrid Larval Stages

Figure 1. Developing egg (<u>Argeia pugettensis</u>) showing embryo position. X 970.

Figure 2. Ventral aspect of an epicaridian (<u>Argeia pauperata</u>). (24, Plate 2). X 235.

a. Exopodite	i. Antenna
b. Endopodite	j. 1st pereiopod
c. Eye	k. 6th pereiopod
d. Superior maxilla	l. 1st pleopod
e. Cephalic segment	m. Uropod
f. Mandible	n. Telson
g. Inferior maxilla	o. Heart
h. Antennule	p. Intestine

Figure 3. Ventral aspect of a microniscan (unidentified). (53, Plate 92, Figure 1c). No size given.

Figure 4. Ventral aspect of a cryptoniscan (<u>Argeia pauperata</u>). (24, Plate 3, Figure 1). X 24.

a. Oral cone	f. 1st pleopod
b. Antennule	g. 5th pleopod
c. 1st pereiopod	h. Telson
d. Antenna	i. Uropod
e. 7th pereiopod	

Plate 2

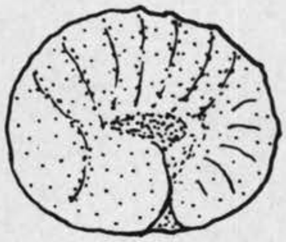


Figure 1

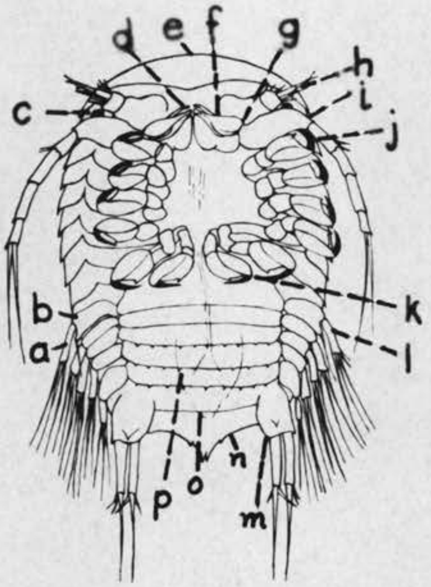


Figure 2

Figure 3

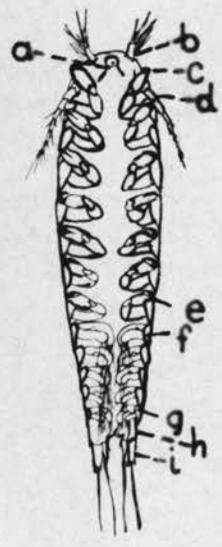


Figure 4

Plate 3

Infected Hosts

Figure 1. Dorsal aspect of the cephalothorax of *Spirontocaris polaris*, with a right branchial infection by *Bopyroides hippolytes*. (53, Plate 84, Figure 2). No size given.

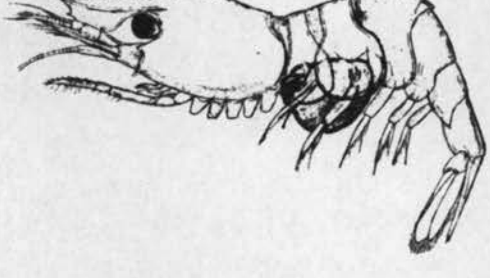
Figure 2. Lateral aspect of *Spirontocaris securifrons* with a ventral-abdominal infection by *Hemiarthrus* (*Phryxus*) *abdominalis*. (53, Plate 90). No size given.

Figure 3. Dorsal aspect of *Munida normani*, showing the site of the visceral bopyrid parasite *Entophilus omnitectus*. X 2.

Figure 4. Dorsal aspect of an intermediate-host copepod (*Pseudocalanus elongatus*), parasitized by two "micronisci" of different moult stages. (53, Plate 92, Figure 1). No size given.

Plate 3

Figure 1



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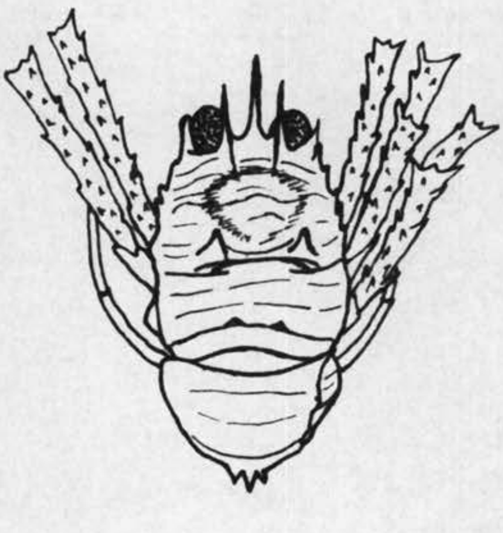


Figure 3

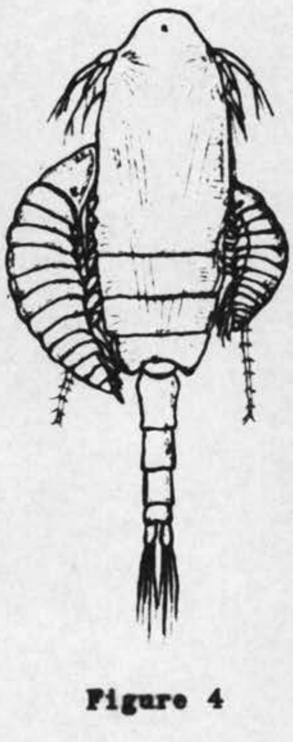


Figure 4

Plate 4

Figure 1. Dorsal aspect of female Argeia pauperata (24, Plate 5, Figure 2). X 7 1/3.

a. Cephalic segment
b. Antenna
c. 1st pereiopod
d. Coxopodite
e. 7th pereiopod
f. Uropod

Figure 2. Ventral aspect of male Argeia pauperata. (24, Plate 3, Figure 3). X 17 2/3.

a. Antennule
b. Antenna
c. 1st pereiopod
d. Hepatic caecum
e. Testis
f. 7th pereiopod

Figure 3. Ventral aspect of female Argeia pauperata. (24, Plate 5, Figure 1). X 7 1/3.

a. Incubatory pouch
b. 1st pereiopod
c. Rostrum
d. Palp
e. Antenna
f. Oöstegite
g. 7th pereiopod
h. 1st pleopod
i. Uropod

Figure 4. Dorsal aspect of female Argeia pugettensis. (57, p. 545). X 14 ½.

Figure 5. Dorsal aspect of male Argeia pugettensis. (57, p. 545). X 22.

Figure 6. Ventral aspect of female Argeia pugettensis. (57, p. 545). X 14 ½.

Plate 4

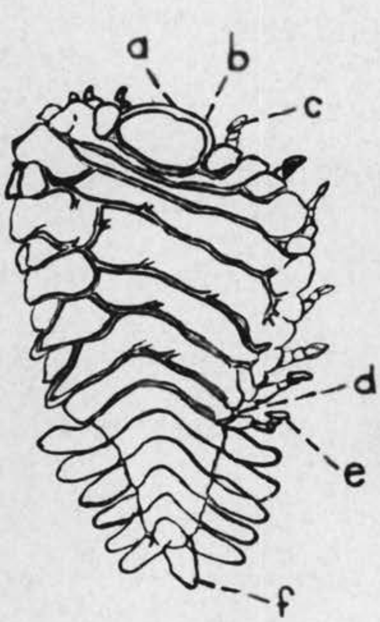
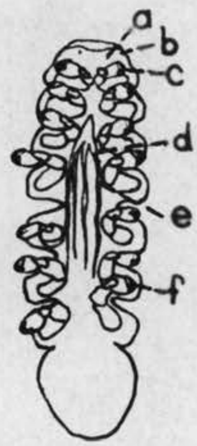


Figure 1



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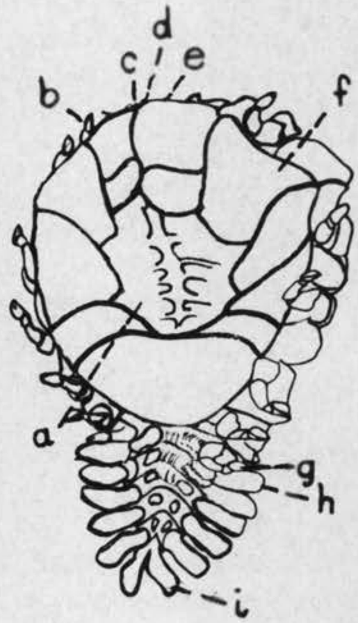

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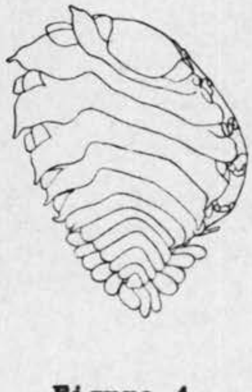


Figure 4

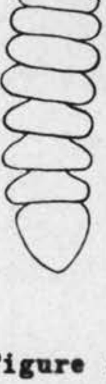


Figure 5

Figure 6

Plate 5

Figure 1. Dorsal aspect of male *Bathygyge grandis* (no female has been pictured). (26, Plate 6, Figure 2). X 6 ½.

Figure 2. Ventral head area of male *Bathygyge grandis*. (26, Plate 6, Figure 2a). X 26.

Figure 3. Dorsal aspect of female *Bopyrina striata*. (39, p. 41). X 19.

Figure 4. Dorsal aspect of male *Bopyrina striata*. (39, p. 41). No size given.

Figure 5. Ventral aspect of female *Bopyrina striata*. (39, p. 41). X 19.

Plate 5

Figure 1

Figure 2

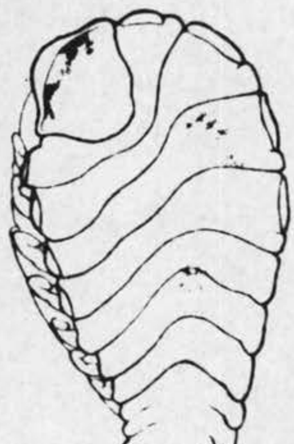


Figure 3

Figure 4

Figure 5

Plate 6

Figure 1. Dorsal aspect of female Bopyriscus calmani. (57, p. 562). X 11 3/5.

Figure 2. Dorsal aspect of male Bopyriscus calmani. (57, p. 562). X 39.

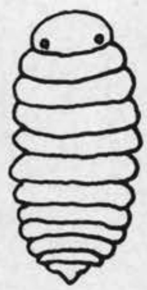
Figure 3. Dorsal aspect of female Bopyroides hippolytes. (53, Plate 84, Figure 2). X 7 ½.

Figure 4. Dorsal aspect of male Bopyroides hippolytes. (53, Plate 84, Figure 2). X 13.

Figure 5. Ventral aspect of female Bopyroides hippolytes. (53, Plate 84, Figure 2). X 7 ½.

Plate 6

Figure 1



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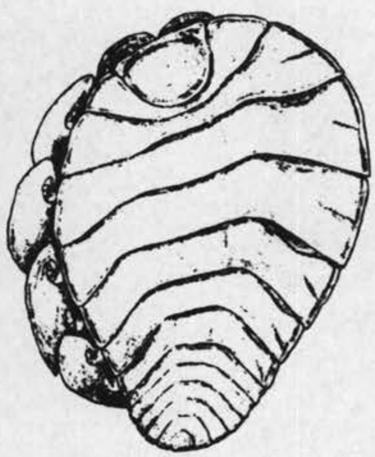

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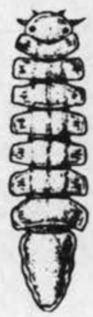

Figure 4

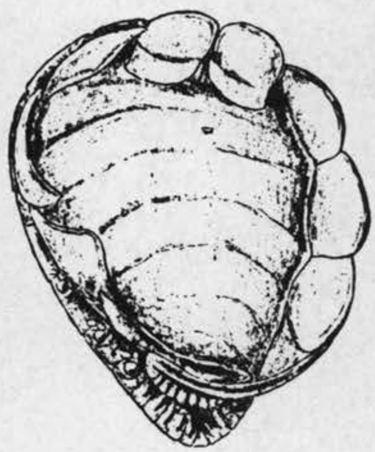

Figure 5

Plate 7

Figure 1. Dorsal aspect of female Entophilus omnitectus. (56, p. 680). X 5 ¼.

Figure 2. Dorsal aspect of male Entophilus omnitectus. (56, p. 681). X 14 ½.

Figure 3. Ventral aspect of female Entophilus omnitectus. (56, p. 680). X 5 ¼.

Figure 4. Dorsal aspect of female Hemiarthrus abdominalis. (53, Plate 90). X 8.

Figure 5. Dorsal aspect of male Hemiarthrus abdominalis. (53, Plate 90). X 20.

Figure 6. Ventral aspect of female Hemiarthrus abdominalis. (53, Plate 90). X 8.

Plate 7

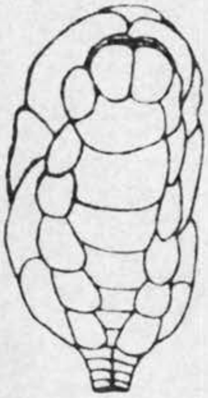

Figure 1

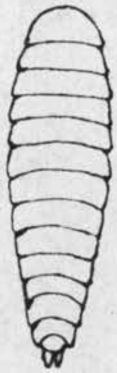

Figure 2

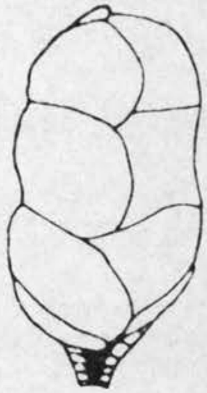

Figure 3

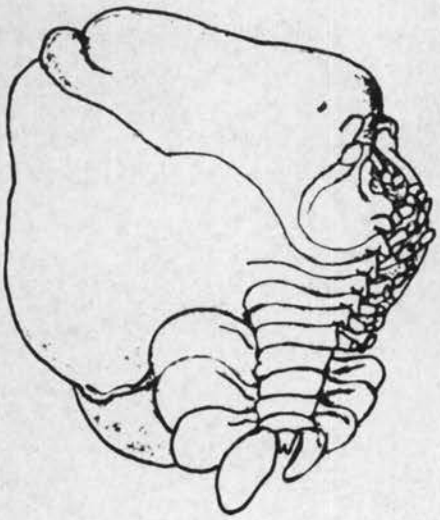

Figure 4

Figure 5

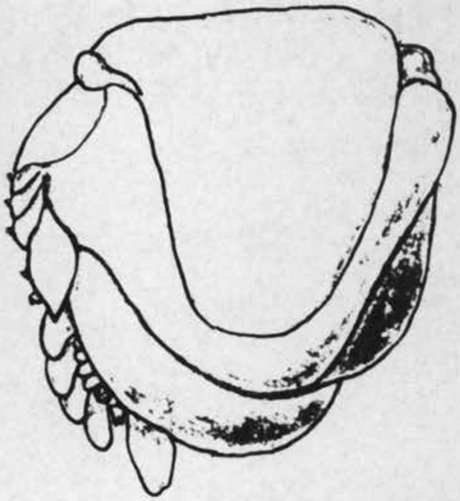

Figure 6

Plate 8

Figure 1. Dorsal aspect of female Ione cornuta. (57, p. 506). X 3.

Figure 2. Dorsal aspect of male Ione cornuta. (57, p. 506). X 7.

Figure 3. Ventral aspect of female Ione cornuta. (57, p. 506). X 3.

Figure 4. Dorsal aspect of female Munidion parvum. (55, p. 81). X 8.

Figure 5. Dorsal aspect of male Munidion parvum. (55, p. 82). X 23.

Figure 6. Ventral aspect of female Munidion parvum. (55, p. 81). X 8.

Plate 8

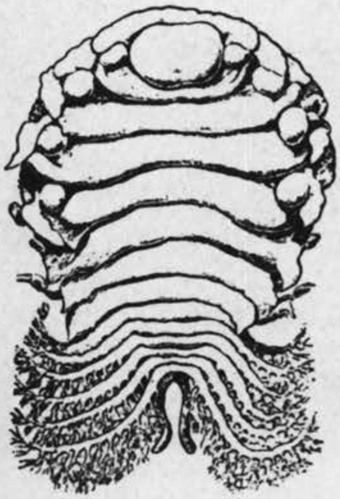

Figure 1

Figure 2

Figure 3

Figure 4

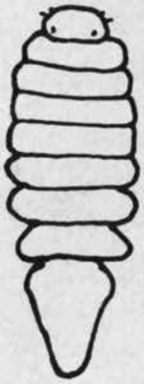

Figure 5

Figure 6

Plate 9

Figure 1. Dorsal aspect of female Parargeia ornata. (26, Plate 6, Figure 1). X 4 ½.

Figure 2. Dorsal aspect of male Parargeia ornata. (26, Plate 6, Figure 1f). X 8 ½.

Figure 3. Ventral aspect of female Parargeia ornata. (26, Plate 6, Figure 1a). X 4 ½.

Figure 4. Dorsal aspect of female Phyllodurus abdominalis. (57, p. 541). X 3 ½.

Figure 5. Dorsal aspect of male Phyllodurus abdominalis. (57, p. 542). X 7 ½.

Plate 9

Figure 1

Figure 2

Figure 3

Figure 4

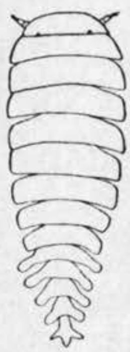

Figure 5

Plate 10

Figure 1. Dorsal aspect of female *Pseudione galacanthae*. (26, Plate 5, Figure 2). X 4 ½.

Figure 2. Dorsal aspect of male *Pseudione galacanthae*. (26, Plate 5, Figure 2f). X 10.

Figure 3. Ventral aspect of female *Pseudione galacanthae*. (26, Plate 5, Figure 2a). X 4 ½.

Figure 4. Dorsal aspect of female *Pseudione giardi*. (3, Plate 34, Figure 5). X 4.

Figure 5. Ventral aspect of male *Pseudione giardi*. (3, Plate 34, Figure 5). X 18.

Plate 10

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Plate 11

Dorsal aspect of female reef-crab bopyrid from Hawaii. X 17.

a. Cephalic segment
b. Pereiopod
c. Lamella of pleopod
d. Reconstructed area (damaged)

Plate 11

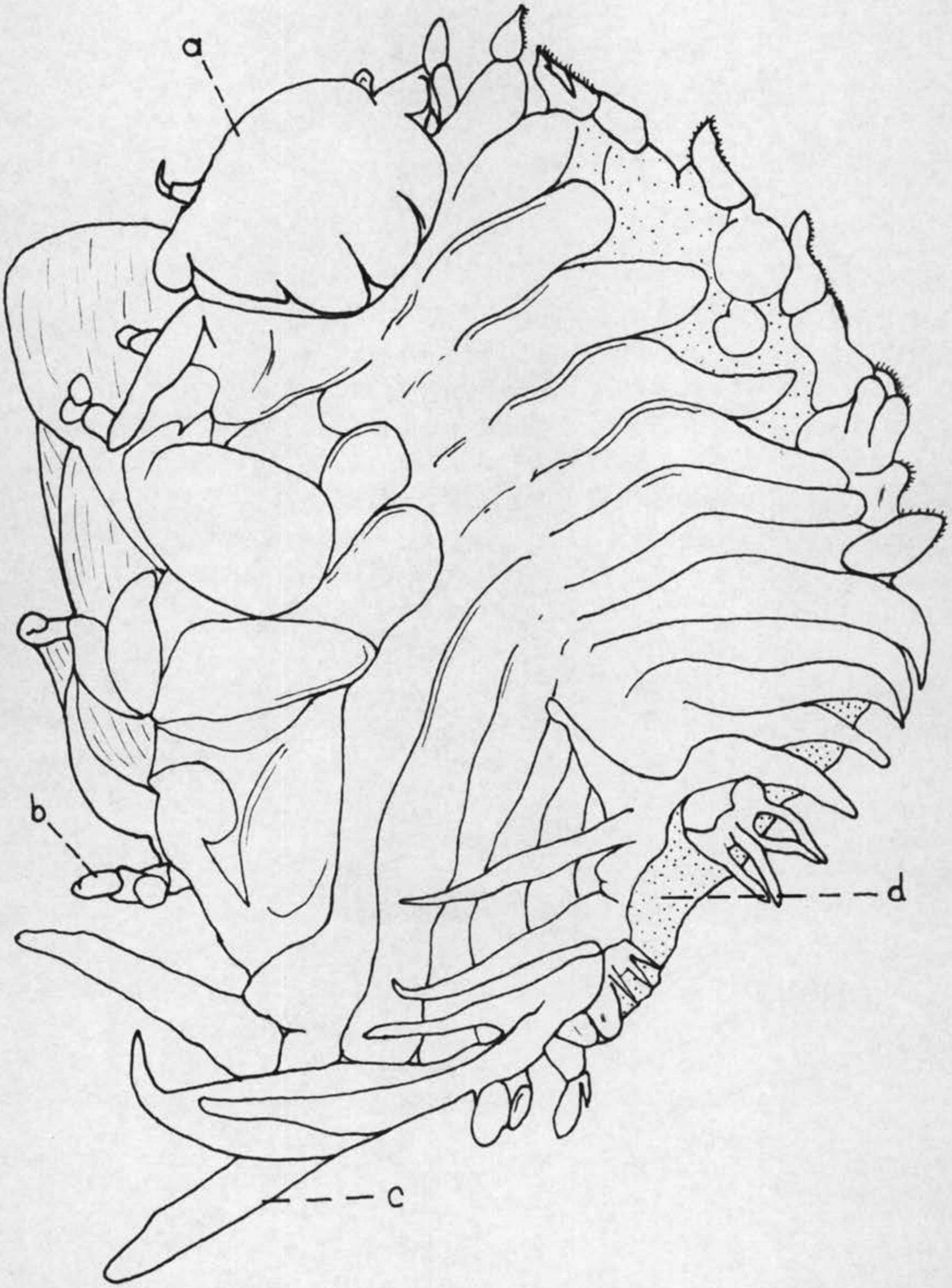

Plate 12

Ventral aspect of female reef-crab bopyrid from Hawaii. X 16.

a. Second pereiopod
b. Oöstegite
c. Lamella of pleopod
d. Reconstructed area (damaged)

Plate 12

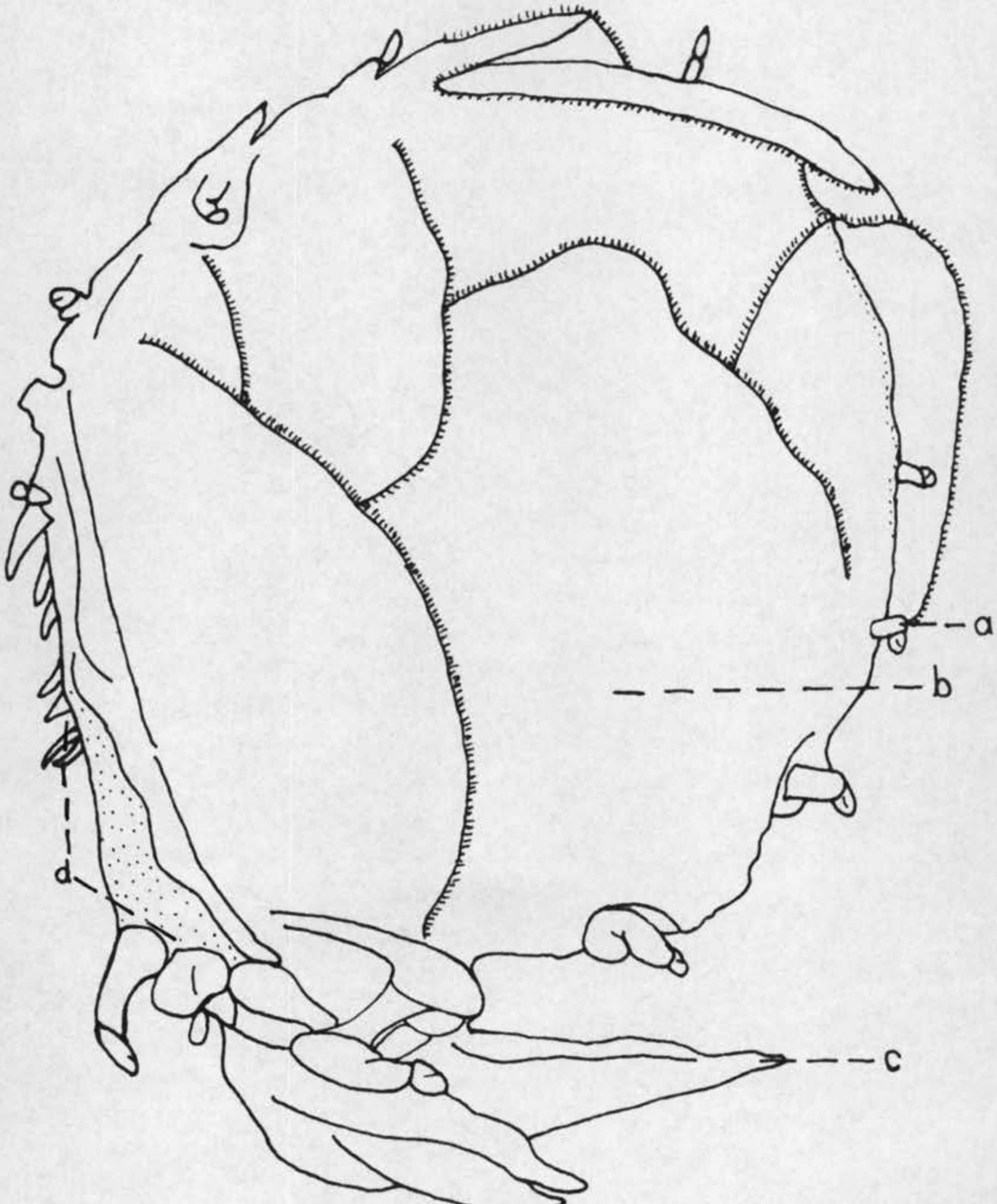

Plate 13

Figure 1. Third pleopod of female reef-crab bopyrid from Hawaii. X 40.

Figure 2. Dorsal aspect of epicaridian of reef-crab bopyrid from Hawaii. X 200.

Figure 3. Dorsal aspect of male reef-crab bopyrid from Hawaii. X 18.

Plate 13

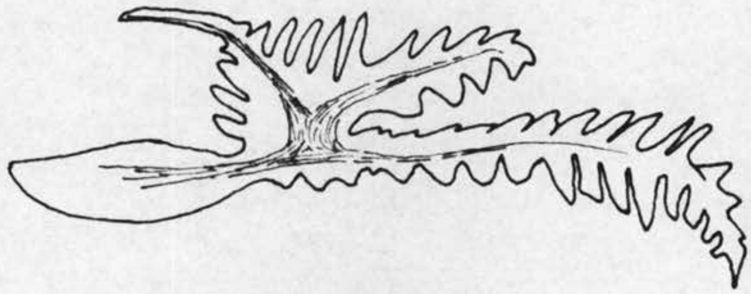

Figure 1

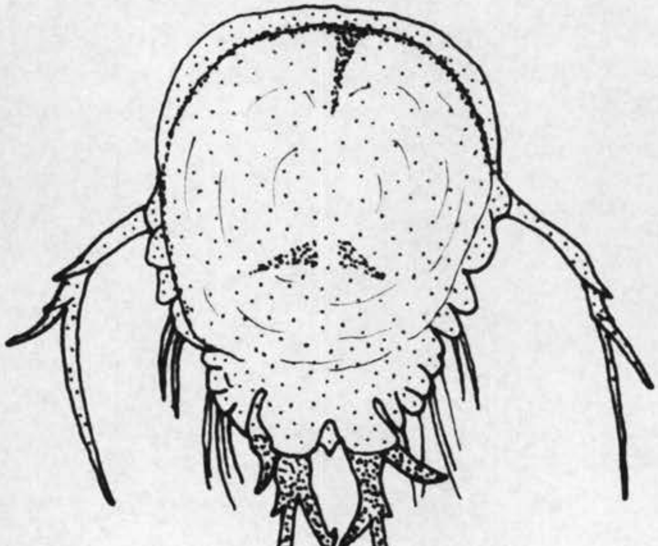

Figure 2

Figure 3

Plate 14

Figure 1. Dorsal aspect of female *Scyracepon hawaiiensis*. (59, p. 645). No size given.

Figure 2. Ventral aspect of female *Scyracepon hawaiiensis*. (59, p. 645). No size given.

Figure 3. Dorsal aspect of male *Scyracepon hawaiiensis*. (59, p. 647). No size given.

Plate 14

Figure 1

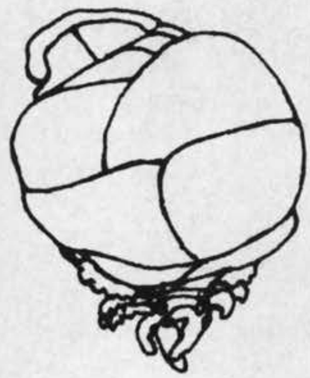

Figure 2

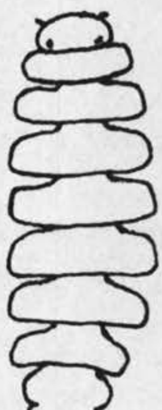

Figure 3