

# COPEPODS AND SCOMBRID FISHES: A STUDY IN HOST-PARASITE RELATIONSHIPS

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## ABSTRACT

Host specificity of the copepods parasitic on scombrid fishes is the basis for an analysis of the host-parasite relationship. A total of 46 different species of parasitic copepods were collected from 47 species of Scombrinae (the monotypic Gasterochismatinae is excluded). A revised host-parasite list is presented, including new data by R. F. Cressey and H. B. Cressey. Those copepod species present on more than one host species have preferred hosts, and indicate tendencies to being host specific. The copepods present an American species of *Scomberomorus* suggest evolutionary trends in that group. Two species (ancestral *S. cavalla* and ancestral *S. sierra*) were probably present prior to the separation of the Atlantic and Pacific Oceans. The present Atlantic *S. maculatus* and *S. brasiliensis* arose from a *S. sierra* ancestor. Copepod data suggest that the Indo-West Pacific *S. commerson* is the most primitive extant species, while *S. multiradiatus* is the most advanced. The copepods parasitic on *Sarda* species indicate the origin of that genus in Australasia, with the Atlantic *S. sarda* being the most advanced species. The genus *Allothunnus*, previously regarded as a member of the tribe Sardini, is shown to have affinities with the Thunnini and may be the most primitive member of that tribe. A cladistic analysis of the copepod genus *Unicolax* correlates well with current hypotheses of the phylogeny of scombrid genera. Host-parasite relationships of the Scombrinae are compared with those found in a previous study of host-parasite relationships in needlefishes (Belonidae). Parasite-based host phylogenies follow the methods of Brooks.

In this paper we test the validity and application of several parasitological theories regarding host-parasite relationships of copepods parasitic on scombrid fishes. As in our earlier joint effort (Cressey and Collette 1970), in which we treated the relationships of parasitic copepods and needlefishes, the analyses are enhanced by the collaboration of specialists representing each animal group (Cressey—parasitic copepods, Collette and Russo—scombrid fishes). Parasite taxonomy on which the present paper is based has been published separately (Cressey and Cressey 1980). Additional material collected since that publication and an updated list of hosts and copepods, because over 200 additional scombrids have been examined, are included in this paper. Examples of 10 genera of copepods are illustrated (Fig. 1) to indicate the kinds of copepods that parasitize scombrids.

Because many earlier reports on parasitic copepods contain misidentifications of both host and parasite, we rely on our own collections or direct examination of specimens used in published accounts.

The often repeated "Fahrenholz rule" (Noble and Noble 1973:548) suggests that related parasites

are found on related hosts, thus indicating host phylogeny. This generalization we now know is an oversimplification.

Hennig (1966:109-110) illustrated how it is possible to have the same parasite species on hosts of polyphyletic origin through incomplete parallelism. Cautions on the use of parasites as indicators of host phylogeny, echoed by Mayr (1957), Hennig (1966), Noble and Noble (1973), and others, are well-founded. We feel, however, that these problems can be minimized by studying comprehensive collections of both hosts and parasites, using the maximum number of parasite groups on the hosts. Presence of parasites on any host may reflect host ecology, chorology, or phylogeny. We believe that information on host-parasite phylogeny has increased validity as sample size, and the numbers of parasite species from different parasite groups (Crustacea, Trematoda, Protozoa, etc.) available for study increases.

When a parasite group is taxonomically well understood, it can be treated as a host character with as much validity as host morphology, serology, and ecology.

Objections or reservations regarding the parasite approach to host phylogeny raised by Mayr (1957) and Hennig (1966) are based on studies or examples, using a relatively small number of parasite species, usually within one parasite taxon (genus or family). If, however, one repeats the analysis of the same hosts

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using numerous parasite groups, the parasite taxa that do not parallel the host phylogeny are likely to become apparent.

Another parasitological theory we have tested is "Szidat's rule," which suggests that primitive (generalized) parasites are found on primitive hosts and that advanced (specialized) parasites are found on advanced hosts. We provide an example supporting this concept when we consider the scombrid host preferences of the copepod genus *Unicolax* on scombrid hosts (p. 254).

## SAMPLING ADEQUACY AND HOST SIZE

Before considering host specificity, it is necessary to know whether enough hosts were examined to provide samples of all species of the usual parasite fauna. Individual collections of copepods from each scombrid species were recorded on cards sequentially, enabling us to consider the question: "How many specimens of a host species should be examined before all parasitic copepod species are likely to have been collected?" Examples are given in Table 1.

TABLE 1.—Number of specimens that had to be examined in order to find all known copepod species.

Species	Total specimens examined	Specimens examined until all collected	No. of copepod spp.
<i>Scomberomorus commerson</i>	130	53	9
<i>Scomberomorus sierra</i>	116	12	3
<i>Sarda sarda</i>	106	35	4
<i>Euthynnus affinis</i>	74	44	8
<i>Auxis</i> spp.	68	60	6
<i>Scomberomorus concolor</i>	47	2	3

Of the six species presented in Table 1, the two species of *Scomberomorus* endemic to the eastern Pacific (*S. sierra* and *S. concolor*) required a relatively small number of individuals to be examined (2-12 specimens), until all parasitic copepods were collected. Wider ranging species (*S. commerson*, *Sarda sarda*, *Euthynnus affinis*, and *Auxis* spp.) required

FIGURE 1.—Examples of copepods parasitic on scombrids: a) *Unicolax anonymous*, female; b) *Holobomolochus asperatus*, female; c) *Shiinoa inauris*, female and males; d) *Caligus bonito*, female; e) *Elytrophora brachyptera*, female; f) *Gloiopotes hygomianus*, female; g) *Tuxophorus cybii*, female; h) *Pseudocycnus appendiculatus*, female; i) *Pseudocycnoides armatus*, female; j) *Brachiella thynni*, female and dwarf male attached.

examination of a greater number of specimens (35-60) before we collected all of their copepod species. The two endemic species have fewer species of parasitic copepods than the nonendemic species. Other scombrids with restricted distributions (*Scomberomorus multiradiatus*, *S. sinensis*, and *S. munroi*) also have fewer parasitic copepod species than related species with wider distributions.

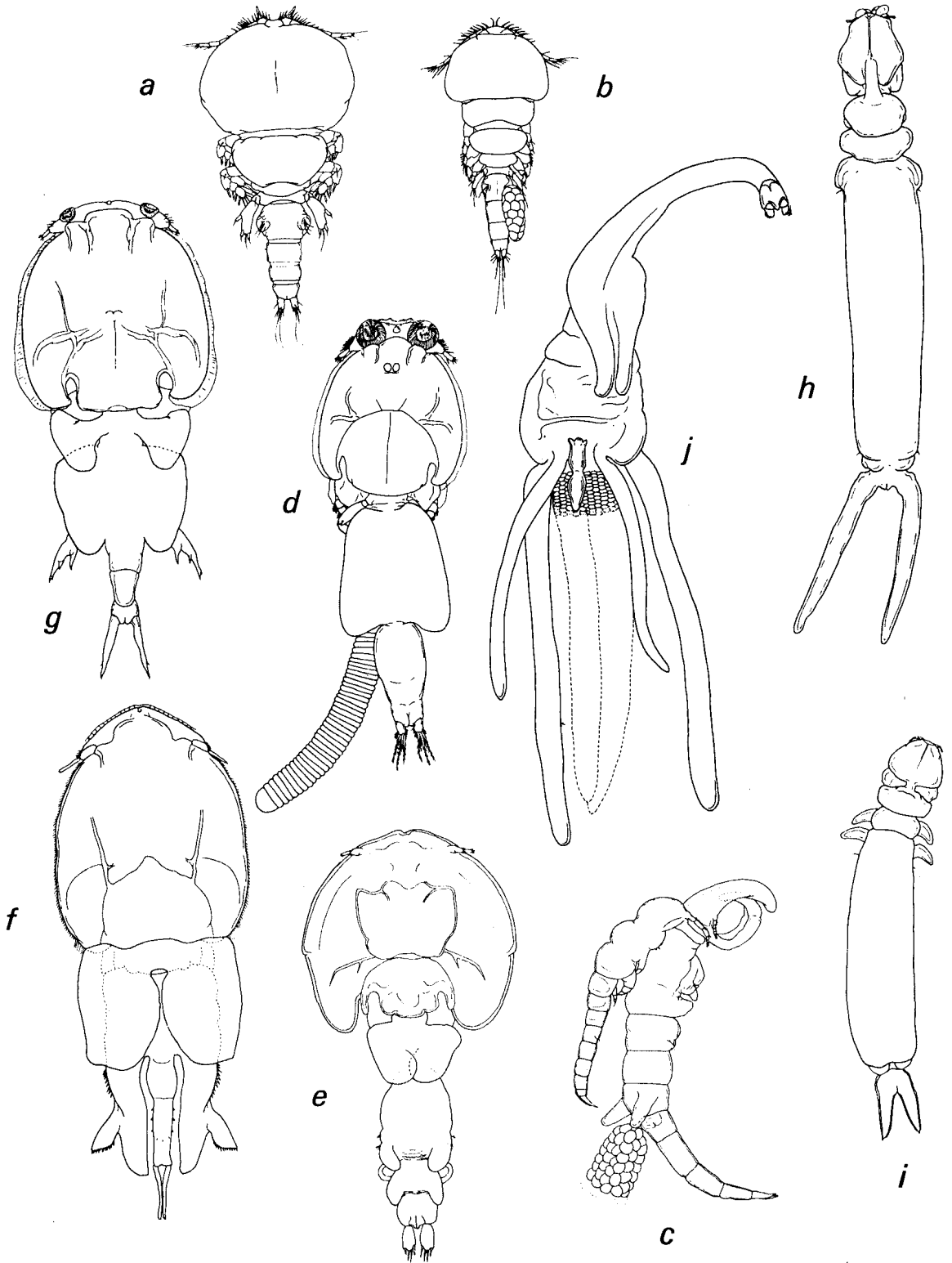
When collecting parasitic copepods from hosts with wide distributions, specimens must be examined from throughout the range. We found that the number of parasite species is usually less at the periphery of the host's range, so that conclusions relative to total parasite fauna for a species cannot be based on geographically limited collections.

We also examined the relationship between host size and infestation density in order to determine its importance in sampling adequacy. It is generally accepted that larger individuals of host species usually support a greater parasite fauna, both in number of species and individuals. Although little work has been done on the ectoparasite fauna in relation to host size (age), Dogiel et al. (1961:9) noted an increase in the numbers of *Ergasilus* sp. on the gills of *Esox lucius* on larger fish. Cressey and Collette (1970) found that specialized copepods (those possessing holdfasts or that are very host specific) are found mainly on larger needlefish, while generalized copepods (less host specific and not highly modified) are found most often on smaller needlefish individuals.

In the present study, copepods of the families Pseudocycnidae, Bomolochidae, and Shiinoidea parasitic on three species of *Scomberomorus* were considered (Table 2). We chose these copepod species for the study because they remain attached in preserved specimens. Pseudocycnids (Fig. 1h, i) are firmly attached to gill filaments; bomolochids (Fig.

TABLE 2.—Infestation densities of *Scomberomorus commerson*, *S. maculatus*, and *S. brasiliensis* for three copepod groups, *Pseudocycnoides*, Bomolochidae, and *Shiinoa*.

Range of hosts (mm FL)	No. of hosts	<i>Pseudocycnoides</i>		Bomolochidae		<i>Shiinoa</i>	
		No. of parasites	% density	No. of parasites	% density	No. of parasites	% density
100-200	32	64	2.0	31	1.0	0	0
201-300	47	202	4.3	89	1.9	1	0.02
301-400	17	35	2.1	11	0.7	5	0.3
401+	16	34	2.1	8	0.5	25	1.6



1a, b) are in the nasal sinuses and can only be collected by cutting open the nares; shiinooids (Fig. 1c) are firmly attached to lamellae of the nasal rosettes. Other copepods, such as caligids, are not as firmly attached, and many specimens are undoubtedly lost during handling and preservation of the hosts. The *Scomberomorus* species were represented by a reasonable number of specimens with adequate size-range coverage.

The apparent optimum size for infestation by the two species of pseudocycnids and the two bomolochids is between 201 and 300 mm FL (fork length). Infestations of *Pseudocycnoides armatus* and *P. bucata* seem to remain at the same levels (about 2 per fish) in groups with smaller and larger size individuals with about twice that infestation rate in the optimum size range. Infestations of the bomolochids *Unicolax ciliatus* (from *S. commerson*) and *Holobomolochus divaricatus* (from *S. maculatus* and *S. brasiliensis*) apparently decrease with increased host size after 300 mm FL; no *Scomberomorus* over 500 mm FL examined was parasitized by bomolochids. The two species of *Shiinoa* (*S. inauris* from *Scomberomorus brasiliensis* and *S. maculatus* and *Shiinoa oclusa* from *Scomberomorus commerson*), on the other hand, are not found on smaller fish, and the greatest infestation rate occurs on fish over 400 mm FL.

The change in infestation rate with host size in some of these parasite species may be due primarily to mechanical factors. In order for female pseudocycnids to remain attached to the gill filaments, the lateral lobes of the cephalon must partially encircle the filament. Until a prospective host reaches an optimum size, the filament may be too small for the adult copepod to secure itself. As the host fish grows, the filaments may become too large for the parasite to remain attached. Two very large *S. commerson* (1,115 and 1,150 mm FL) from New South Wales, Australia, were parasitized by several *P. armatus*. These copepods were considerably longer than average for the species (8.1 vs. 4.9 mm), which may account for their ability to infest a larger size host. *Shiinoa* attaches to its host by piercing a nasal lamella with its recurved second antennae which are opposed by an elongate and recurved rostrum. The combination results in a ring through the lamella, with the rest of the parasite hanging free. It may be necessary for the host to attain a minimum size (275 mm FL in our data) before the lamella is large enough to accommodate the parasite. (*Shiinoa* males attach to female copepods rather than the host.)

The presence of bomolochid species on 100-200 mm hosts cannot be as easily correlated with mechanical

factors. Bomolochids are not firmly attached to their hosts. Those species considered here are found loose within the nasal sinuses and are capable of moving about possibly as scavengers more than as true parasites. Possibly the reduction in infestation of bomolochids in larger fish is associated with the increased presence of *Shiinoa* in the nasal sinuses of hosts larger than 300 mm.

## ECOLOGICAL RELATIONSHIPS

To determine the influence of ecological relationships as opposed to phylogenetic host specificity of parasitic copepods found on scombrids, we examined the literature records of parasitic copepods from fishes with habits similar to those of scombrids (large size, open ocean, fast swimming, predatory, etc.). We compiled data for the following fish groups: Billfishes (Istiophoridae and Xiphiidae), sharks, *Alepisaurus*, *Lampris*, *Coryphaena*, several genera of Carangidae, *Rachycentron*, *Pomatomus*, and the gempylids, *Ruvettus* and *Thyrsites*.

We have tried to use discretion in evaluating the reliability of literature records. For example, Bere (1936) reported *Caligus bonito* from *Pomatomus saltatrix*, *Lutjanus griseus*, *Mugil cephalus*, *Oligoplites saurus*, *Scomberomorus maculatus*, and *S. cavalla*. She indicated in her report that the copepod material was identified by C. B. Wilson. The first author of this paper examined the specimens, deposited in the Smithsonian (USNM 79090), in order to verify the *Pomatomus* record. Bere presumably sent Wilson the material separated by host. Wilson apparently put together all specimens that he identified as a single species. The collection contains about 15 *Caligus* specimens with no host names and represents three species—*Caligus bonito*, *C. mutabilis*, and males of a third species. It is impossible to verify the occurrence of *C. bonito* on *Pomatomus*, and the record must be ignored. Another record (Capart 1959) of *C. pelamydis* from *Pomatomus* is questionable because Capart's illustration does not appear to be of *C. pelamydis*. Eliminating unreliable reports leaves *C. coryphaenae*, a relatively distinct species, as the only copepod common on scombrids which also occurs on many ecologically similar species. It has been recorded from the following nonscombrid genera: *Caranx*, *Elagatis*, *Coryphaena*, *Xiphias*, *Squalus*, *Seriola*, *Isurus*, *Echeneis*, and *Sphaeroides*. There have been a few reports of *Caligus productus* and *C. pelamydis* from nonscombrid hosts, but both of these copepods have been often confused with closely related species. Rohde (1980) reported *C. pelamydis* from 3 of 88 specimens of *Trachurus trachurus* and 22 of 122

specimens of *Scomber scombrus* with *C. pelamydis* from Helgoland (these copepod identifications were verified by G. Boxshall of the British Museum (Natural History)).

As the record shows, most species of copepods common on scombrid hosts are restricted to scombrids. *Caligus coryphaenae* apparently is the only common scombrid parasitic copepod whose host choice is influenced by ecological rather than phylogenetic factors.

There is evidence that in some cases the presence of a species of parasitic copepod on two or more host species which are not closely related may be the result of an association between the hosts. The parasitic copepod *Pumiliopes jonesi* (= *P. capitulatus*) is common on the eyes of scombrids of the tribe Scombrini (*Rastrelliger* and *Scomber*) and on the clupeids *Clupanodon punctatus* and *Herklotsichthys dispilonotus*. Both groups are filter-feeding schooling fishes.

Another example is *Caligus macarovi* (= *C. fulvipurpureus*) common on the Pacific saury, *Cololabis saira* (Hotta 1962), but reported on *Auxis* as well by Gussev (1951). *Cololabis* feeds primarily on planktonic crustaceans with eggs and larvae of fishes forming secondary diet items (Hotta and Odate 1956; Taka et al. 1980). *Auxis* feeds on a wide variety of small fishes, cephalopods, and planktonic crustaceans (Uchida 1981). We are unaware of any records of *Auxis* preying on *Cololabis*, but sauries are common food items of billfishes.

### HOST SPECIFICITY

Host specificity is concerned with the predilection of a parasite species for one or a few species of host or hosts. The comprehensive data on which this study is based demonstrate host specificity.

The occurrence of a species of parasite in a variety of host species does not necessarily imply a lack of host specificity. Careful analysis of collection data with reference to percent of host individuals parasitized by a particular parasite species will usually show that one or a few host species are heavily infested, some occasionally infested, and some rarely infested with the parasite species. Dogiel et al. (1961) referred to these groups as main, secondary, and accidental hosts. Holmes (1979) referred to the three groups as required hosts, suitable hosts, and unsuitable hosts. Holmes considered required and suitable hosts as those with which the parasite can develop to maturity (or to an infective stage in intermediate hosts), and unsuitable hosts as those with which the parasite cannot develop, but may be transported to a

suitable or required host. Not enough is known of the life histories of most parasitic copepods to evaluate their state of "well being" on respective hosts. Collection data, however, indicate that species found on several host species vary in infestation rate in ways suggesting the host categories of Dogiel et al. and Holmes. In addition, unpublished data based on parasitic copepod collections by the first author from fishes of the Gulf of Mexico indicate the same categories of infestation.

The recently published revised data on the parasitic copepods of scombrids (Cressey and Cressey 1980) enable us to compare data based on a synoptic review of literature records of copepods parasitic on scombrids (Silas and Ummerkutty 1967) with a survey based solely on verified host and parasite identifications (Cressey and Cressey 1980). We have used the same format as that of Holmes and Price (1980) except we have considered specificity at the generic level rather than the family level (our data are based only on the Scombridae).

Comparisons of the two analyses (Tables 3, 4) point out the inadequacies of an unverified data base. Data based on the literature survey of Silas and Ummerkutty (1967) indicate that 60% of the copepod species parasitic on scombrids are specific to 1 genus, 5% to 2 genera, 11% to 3 or 4 genera, 2% to 5 or more genera, and 23% were also recorded from nonscombrid hosts. The data based on Cressey and Cressey (1980) and additional records in this paper indicate 54% specific to 1 genus, 18% to 2 genera, 9% to 3 or 4 genera, 9% to 5 or more genera, and only 9% are also found on nonscombrids. Clearly, the latter is a better

TABLE 3.—Host specificity of scombrid copepods based on data from Silas and Ummerkutty (1967).

No. of genera infested	Number of host species infested				Scombrid and nonscombrid
	1	2	3-4	5-8	
1	28	3	3		
2		2	1		
3-4			3	3	
5+				1	
Nonscombrids					13

TABLE 4.—Host specificity of scombrid copepods based on data from Cressey and Cressey (1980) and later.

No. of genera infested	Number of host species infested					Scombrid and nonscombrid
	1	2	3-4	5-8	9+	
1	11	6	2	4	1	
2		3	2	3		
3-4			2	1	1	
5+					4	
Nonscombrids						4

index to host specificity at the generic level than that based solely on literature. The Silas and Ummerkutty data indicate a higher specificity at the level of 1 genus of host; they also indicate a higher percentage of "generalists" (36% with 3 or more genera plus nonscombrids). Furthermore, the Cressey and Cressey and later data indicate a gradual transition from greater to lesser host specificity, whereas the data based on Silas and Ummerkutty do not.

Comparison of percent specificity (percent species with only one host, see Price 1980:123) shows a wide range of specificity per genus of scombrid copepod parasites (Table 5). Specificity to a genus of hosts seems more meaningful to us, so we have also calculated these figures. Six of the seven families that contain scombrid copepod parasites show relatively high percent specificity at the generic level (50-75%) while the Caligidae is distinctly lower (35%).

## Scombrinae

The subfamily Scombrinae is composed of two groups of two tribes. The more primitive mackerels (Scombrini) and Spanish mackerels (Scomberomirini) have a distinct notch in the hypural plate, lack any bony support for the median fleshy caudal peduncle keels, and do not have the penultimate vertebral centra greatly shortened.

### Scombrini

The tribe Scombrini contains the two genera of mackerels, *Scomber* and *Rastrelliger*. Mackerels have small conical teeth and a large number of gill rakers. Characters differentiating the two genera have been given by Matsui (1967:table 4).

Copepod fauna: 9 species in 7 genera. Bomolochid copepods can be separated into two subgroups based on the presence of one or two major setae (in addition to the remainder of the normal complement) on each caudal ramus. The genera found on *Scomber* and *R. brachysoma* (*Pumilopes*, *Orbitacolax*, and *Nothobomolochus*) are members of the group with one major terminal seta. Although members of this same copepod subgroup are found on other fish families, none are found on other scombrids. This host specificity of some members of that subgroup to the Scombrini distinguishes the true mackerels from the other scombrid tribes. *Pumilopes jonesi* is the only copepod found in both genera of Scombrini and nowhere else, occurring in the orbits of two species of each genus. The infestation rate in *Rastrelliger* was 13%, in *Scomber* only 2%.

TABLE 5.—Percent specificity (percent species with only one host) and percent generic specificity (percent species with hosts only in one genus) in genera of copepod parasites of scombrid fishes.

Copepod genus	No. of species	Percent specificity	Percent generic specificity
Bomolochidae	(12)	(33)	(58)
<i>Holobomolochus</i>	3	33	100
<i>Unicolax</i>	5	20	75
<i>Ceratacolax</i>	1	0	0
<i>Nothobomolochus</i>	1	0	100
<i>Orbitacolax</i>	1	100	100
<i>Pumilopes</i>	1	0	0
Shiinoidea	(2)	(0)	(50)
<i>Shiinoa</i>	2	0	50
Caligidae	(12)	(17)	(35)
<i>Caligus</i>	12	17	35
Euryphoridae	(4)	(75)	(75)
<i>Elytrophora</i>	2	50	50
<i>Gloioptates</i>	1	100	100
<i>Caligulus</i>	1	100	100
Tuxophoridae	(3)	(67)	(67)
<i>Tuxaphorus</i>	3	67	67
Pseudocycnidae	(4)	(25)	(75)
<i>Pseudocycnus</i>	1	0	0
<i>Pseudocycnoides</i>	3	33	100
Lerneopodidae	(4)	(25)	(75)
<i>Brachiella</i>	2	0	0
<i>Clavellisa</i>	1	100	100
<i>Clevellopsis</i>	1	100	100

### *Scomber* Linnaeus

We follow most recent authors (Fraser-Brunner 1950; Collette and Gibbs 1963; Matsui 1967) in considering *Pneumatophorus* a synonym of *Scomber*. *Scomber* differs from *Rastrelliger* in a number of anatomical characters which have been summarized by Matsui (1967:table 4). Copepod fauna: 5 species in 4 genera. Only the lerneopodid *Clavellisa scombri* is restricted to *Scomber*, occurring on gills of *Scomber japonicus* and *S. australasicus* in our material. It was originally described from a host identified as *S. scombrus* from Trieste, but we failed to find it in 97 specimens of that species.

Matsui (1967) recognized three species of *Scomber*: *S. scombrus* Linnaeus in the North Atlantic and Mediterranean; *S. australasicus* Cuvier in the western Pacific from Japan to southern Australia east to the Hawaiian Islands, and across the eastern Pacific barrier to Socorro Island off Mexico; and *S. japonicus* Houttuyn, a worldwide antitropical species. All the copepod species known from the three species have been found on *S. japonicus*, of which we have examined about 500 specimens.

### *Rastrelliger* Jordan and Starks

Matsui (1967:table 4) summarized the diagnostic characters of *Rastrelliger*. Copepod fauna: 5 species in 5 genera. *Pumilopes jonesi* and two other bomo-

lochids were found in two species of *Rastrelliger*, *O. aculeatus* in the orbits, and *N. kanagurta* on the gills.

Matsui (1967) recognized three species of *Rastrelliger*: *R. faughni* Matsui from Taiwan, the Philippine Islands, Indonesia, and western India; *R. brachysoma* (Bleeker) in the same general area of the western Pacific as *R. faughni* but extending east to Fiji; and *R. kanagurta* (Cuvier) which is widespread throughout the Indo-West Pacific from Taiwan, the Philippines, Samoa, and Australia east throughout the Indian Ocean to Madagascar and the Red Sea. At least one individual has gone through the Suez Canal into the eastern Mediterranean Sea (Collette 1970). All but one of our copepod records are from *R. kanagurta* and *R. faughni*. Our only lernanthropid was a female *Lernanthropus kanagurta* from a Bornean specimen of *R. brachysoma*. This is probably not a usual scombrid parasite (Cressey and Cressey 1980:45).

## Scomberomorini

This is the most speciose tribe in the family, containing 20 of the 48 species. Most of these (18 species) belong to *Scomberomorus*, the Spanish mackerels and seerfishes; the other 2 species belong to the monotypic genera *Acanthocybium* and *Grammatorcynus*. Copepod fauna: 25 species in 8 genera. The copepod genus most characteristic of the Scomberomorini is *Shiinoa*, found attached to the nasal rosettes of *Acanthocybium*, *Grammatorcynus*, and 10 species of *Scomberomorus*. (*Shiinoa* was also found on one specimen of *Gymnosarda*, but we do not believe *Gymnosarda* is a usual host for this copepod.)

### *Scomberomorus* Lacepède

*Scomberomorus* differs from the other two genera in the tribe, *Acanthocybium* and *Grammatorcynus*, by usually lacking a swim bladder. The genus is composed of 18 species (Collette and Russo 1980). There is one species in the Gulf of Guinea and Mediterranean Sea—*S. tritor* (Cuvier); four in the western Atlantic—*cavalla* (Cuvier), *regalis* (Bloch), *maculatus* (Mitchill), and *brasiliensis* Collette, Russo, and Zavalla-Camin; and two in the eastern Pacific—*concolor* Lockington and *sierra* Jordan and Starks. The remaining 11 species are in the Indo-West Pacific: *guttatus* (Bloch and Schneider); *koreanus* (Kishinouye); *lineolatus* (Cuvier); *plurilineatus* Fourmanoir; *commerson* (Lacepède); *sinesis* (Lacepède); *semifasciatus* (Macleay); *queenslandicus* Munro; *niphonius* (Cuvier); *munroi* Collette and Russo; and

*multiradiatus* Munro. Copepod fauna: 23 species in 7 genera. In addition to two species of *Shiinoa*, *Scomberomorus* is commonly parasitized by the pseudocycnid genus *Pseudocycnoides* (*buccata*, *armatus*, *scomberomori*), the bomolochid genera *Holobomolochus* (*divaricatus*, *asperatus*, *nudiusculus*), and *Unicolax* (*U. ciliatus*), and several species of *Caligus* (especially *C. biserioidentatus*, *C. infestans*, and *C. cybii* in the Indo-West Pacific, *C. mutabilis* and *C. productus* in the western Atlantic, and *C. omissus* in the eastern Pacific). The speciose nature of *Scomberomorus* and its copepod parasites requires further discussion, by regions.

ORIGINS AND EVOLUTION OF AMERICAN *SCOMBEROMORUS*.—Six species of *Scomberomorus* occur in American waters. (Figs. 2, 3). Two of these, *S. sierra* and *S. concolor*, are restricted to the eastern Pacific from about lat. 10° to 40°N. *Scomberomorus concolor* presently occurs only in the Gulf of California. The four Atlantic species are *S. cavalla*, found from about lat. 30°S to 45°N; *S. brasiliensis*, a southern coastal species (Belize to southern Brazil); *S. maculatus*, a northern coastal species (Yucatan to Massachusetts); and *S. regalis*, a largely insular species (most abundant in the Bahamas and West Indies).

The six species of American *Scomberomorus* are parasitized as a group by the following species of copepods: *H. asperatus* (*S. cavalla*), *H. nudiusculus* (*S. sierra*, *S. concolor*), *H. divaricatus* (*S. brasiliensis*, *S. maculatus*, *S. regalis*), *Shiinoa inauris* (*Scomberomorus maculatus*, *S. brasiliensis*, *S. regalis*), *C. mutabilis* (*S. cavalla*, *S. brasiliensis*, *S. maculatus*), *C. omissus* (*S. sierra*, *S. concolor*), and *P. buccata* (all species mentioned in this paragraph).

To use parasitic copepods as indicators of host phylogeny we determined the pleisiomorphy-apomorphy of certain taxonomic characters. This is possible within a closely related group of parasites based on reduction and modification of characters for parasitism. It seems reasonable to assume that, as species of a parasite group evolve, the later (more recent) species are more specialized or reduced than the older species. If we assume that hosts and parasites evolve together, the information on the evolution of one group should provide evolutionary information about the other group. Four genera of copepods parasitic on *Scomberomorus* lend themselves to analysis and are discussed below.

Three species of *Holobomolochus* parasitic on American species of *Scomberomorus* and a fourth species from *Caranx hippos* form a subgroup of the genus (see Cressey and Cressey 1980:8). In these species,

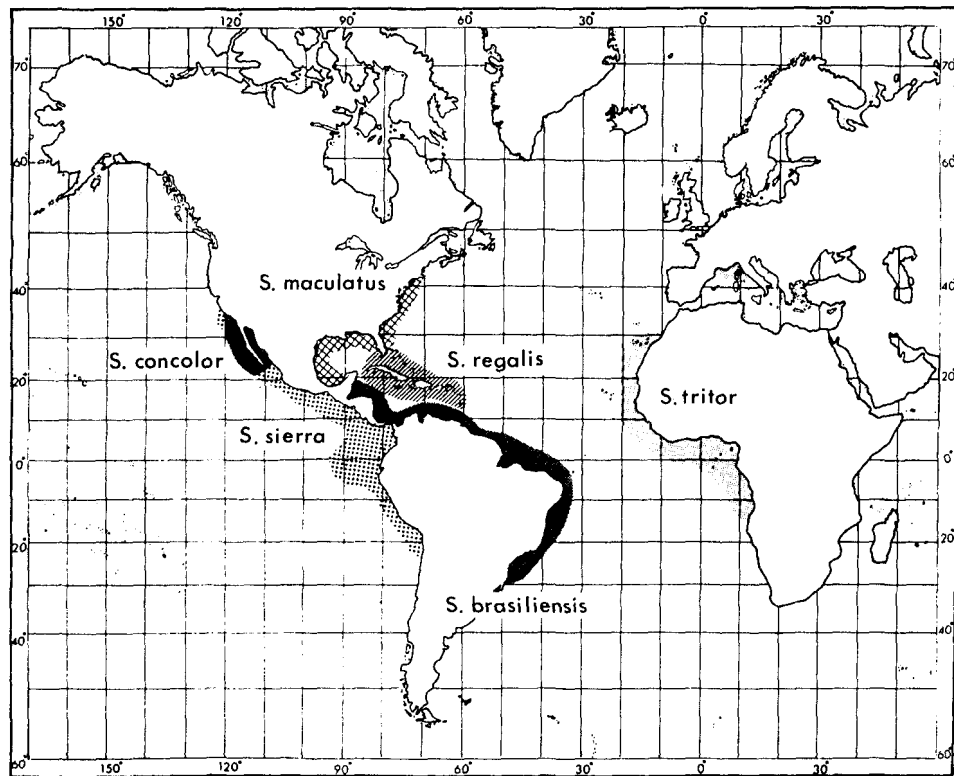


FIGURE 2.—Distribution of Atlantic and eastern Pacific species of *Scomberomorus*.

the last exopod segments of legs 2-4 bear a number of plumose setae, heavily sclerotized spines, and shorter nonplumose setae with armature intermediate to that on spines and setae. Long plumose setae (adaptations for free swimming) are primitive, whereas heavily sclerotized spines (adaptations for attachment) are advanced characters. The three *Holobomolochus* from *Scomberomorus* show a transition in the numbers of each of these character states. *Holobomolochus asperatus* (parasite of *S. cavalla*) bears 18 long plumose setae and 7 sclerotized spines on the last exopod segments of legs 2-4. The same appendages of *H. nudiusculus* (on eastern Pacific *Scomberomorus*) bear 16 plumose setae, 2 intermediate setae/spines, and 7 spines. The same appendages of *H. divaricatus* (on all western Atlantic *Scomberomorus* except *cavalla*) bear 14 setae, 4 intermediate setae/spines, and 7 spines. This transition in decreased numbers of long plumose setae and increase in intermediate setae/spines within these three parasite species suggests *H. asperatus* to be the most primitive, *H. nudiusculus* intermediate, and *H. divaricatus* to be most advanced. If the hosts reflect the phylogeny of the parasites, then this suggests that *S. cavalla* is the most primitive; the two eastern Pacific

species—*S. sierra* and *S. concolor*—are intermediate; and the three western Atlantic species—*S. regalis*, *S. maculatus*, and *S. brasiliensis*—are the most advanced of the American species of *Scomberomorus*.

*Holobomolochus* has 23 currently recognized species in the western Atlantic and eastern Pacific and 1 species from the eastern Atlantic (a species from India is not a *Holobomolochus*, as reported by Pillai 1973). *Unicolax ciliatus*, a species of another homolochid genus, is found on 9 species of *Scomberomorus* in the Indo-West Pacific and on *S. tritor* in the eastern Atlantic. Four remaining species of *Unicolax*, including Atlantic and eastern Pacific species, are found only on non-*Scomberomorus* scombrids. This parasite distribution and host affiliation suggest that *Holobomolochus* was already well established on American *Scomberomorus* before the appearance of *Unicolax* in this area. Based on the evidence that *U. ciliatus* has not undergone further speciation on 10 *Scomberomorus* species despite the geographic isolation of one of those species (*S. tritor* from the eastern Atlantic) and the presence of *Holobomolochus* on the American *Scomberomorus*, it can be assumed that *Holobomolochus* is older than *Unicolax*.



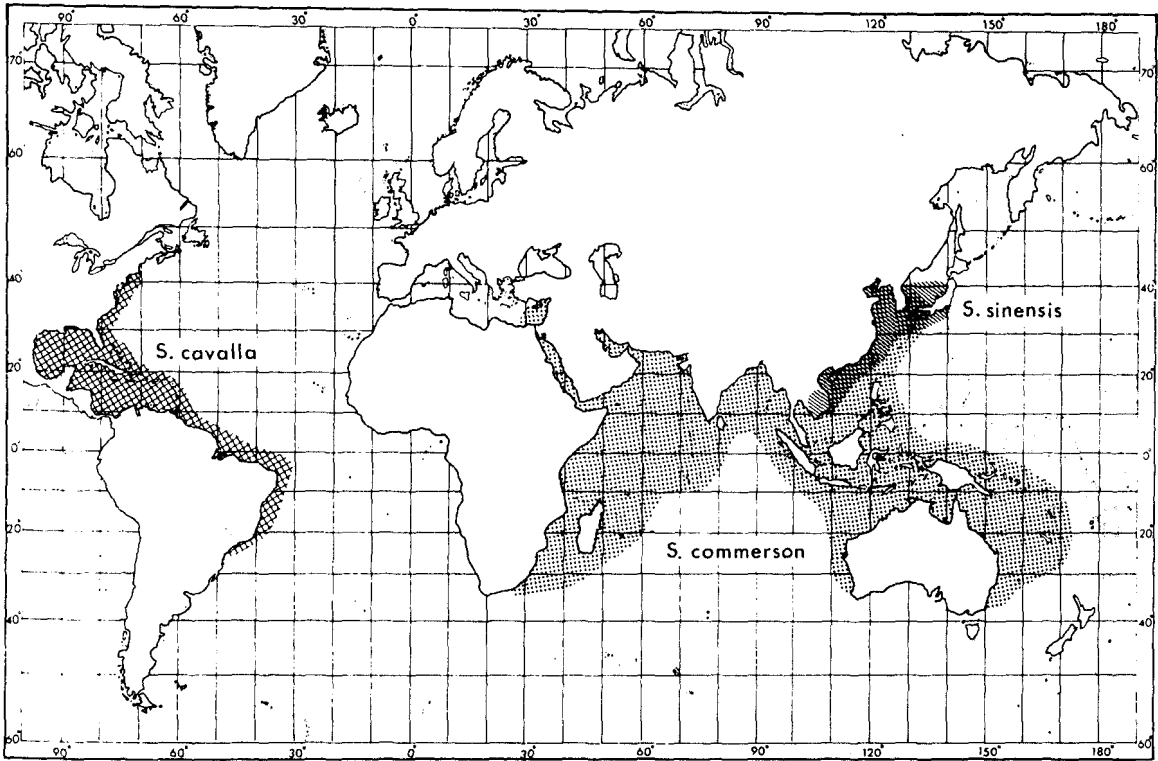


FIGURE 3.—Distribution of *Scomberomorus cavalla*, *S. commerson*, and *S. sinensis*.

*Uicolax* appears to be more advanced than *Holobomolochus* by possessing a heavily sclerotized modified seta on the first antenna and having 1 seta rather than 2 setae on the mid-endopod segment of leg 3.

The highly modified copepod genus *Shiinoa* (Shiinoidea) is comprised of three species: *Shiinoa oclusa* from Indo-West Pacific *Acanthocybium*, *Grammatorcynus*, *Scomberomorus*, and *Gymnosarda* and the eastern Atlantic *S. tritor*; *Shiinoa inauris* from western Atlantic *Scomberomorus* (except *S. cavalla*); and *Shiinoa elagatis* from Indo-Pacific *Elagatis* (Carangidae). The first author is describing a fourth species from the Indian Ocean jack, *Caranx malabaricus*. Of the three described species *S. elagatis* with 3-segmented rami of legs 1 and 2 is the most primitive. *Shiinoa oclusa* from Indo-West Pacific scombrids is intermediate with 3-segmented rami of legs 2 and 3 but with fewer spines and setae and reduced body segmentation compared with *S. elagatis*. *Shiinoa inauris* from three of the four western Atlantic *Scomberomorus* (all except *S. cavalla*) is most advanced with only 2 segments in the exopods of legs 2 and 3 of the females and 2 segments in both rami of legs 2 and 3 of the males.

Infestations by the western Atlantic *S. inauris* and

its speciation probably did not occur until after the last geologic separation of the eastern Pacific. On scombrids, *Shiinoa* has differentiated into only two species. Although this genus is recorded from 10 species of *Scomberomorus*, the highest rates of infestation among scombrid hosts are in *Grammatorcynus* and *Gymnosarda*. *Shiinoa oclusa*, from Indo-West Pacific scombrids, is more primitive than the western Atlantic *S. inauris*, indicating the latter's probable derivation from Indo-Pacific stock.

The presence of the highly specialized siphonostome copepod parasite, *P. buccata*, on all species of American *Scomberomorus* with relatively high infestation rates (30-63%) indicates that this parasite was present before the separation of Atlantic and eastern Pacific Oceans, but, in spite of the present isolation, the two populations have not differentiated (unlike the three *Holobomolochus* species).

From this it appears that dispersal and some speciation of American *Scomberomorus* occurred prior to their being parasitized by bomolochid and shiinoic copepods.

The evidence derived from an analysis of the copepods parasitic on the six American *Scomberomorus* species suggests the following sequence of events:

1. During the period when the eastern Pacific and Atlantic Oceans were continuous, two species of *Scomberomorus* were probably present, an ancestral *S. cavalla* and an ancestral *S. sierra*. Both of these were infested with species of *Holobomolochus* and *P. buccata*.

2. As the land mass of Central America separated the Atlantic from the Pacific, the two ancestral forms were divided into four populations. The Atlantic population of *S. cavalla* persisted while the Pacific population disappeared. The Pacific *S. sierra* population persisted and gave rise to *S. concolor*, while the Atlantic population subsequently divided into a southern species, *S. brasiliensis*, and a northern species, *S. maculatus*. The derivation of *S. regalis* was also probably from a *sierra* ancestor. The origin of pre-*cavalla* and pre-*sierra* populations was probably derived from the Indo-Pacific *S. commerson* line and the *S. tritor* line, respectively (Fig. 4).

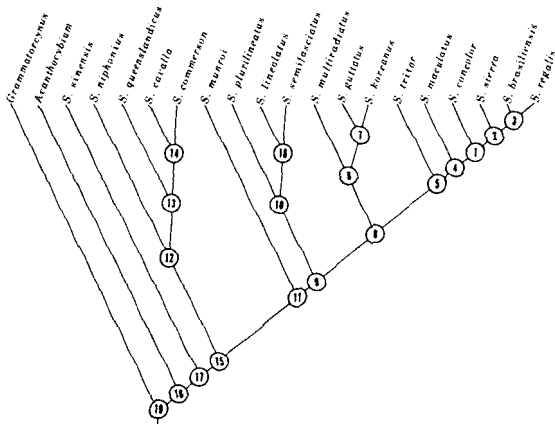


FIGURE 4.—Tentative cladogram of the Scomberomorini. Numbers refer to morphological characters from Collette and Russo (text footnote 3).

3. The population of ancestral *S. sierra* in the Atlantic differentiated to produce ultimately the northern coastal species *S. maculatus* and the southern coastal species *S. brasiliensis* and insular *S. regalis*.

4. Some species of copepods differentiated as either new host species were formed, or populations of related hosts were isolated.

5. An additional genus (*Shiinoa*) of parasitic copepod became established on three of the Atlantic species of *Scomberomorus* (*brasiliensis*, *maculatus*, and *regalis*) after the formation of a land barrier separating the eastern Pacific from the Atlantic. The absence of *Shiinoa* on *Scomberomorus cavalla* may

indicate that *S. cavalla*, derived from the *S. commerson* line, may have occupied the Atlantic prior to the parasitization of scombrids by *Shiinoa*. The later infestations of *Shiinoa* in the western Atlantic may have been derived from *Scomberomorus tritor* and consequently occur only on the three western Atlantic species of *Scomberomorus* derived from the *tritor* line.

Based on the anatomy of *Scomberomorus*, the American species belong to different species groups. *Scomberomorus cavalla* is the western Atlantic replacement for *S. commerson*, which is widespread in the Indo-West Pacific. The other five American species, plus *S. tritor* from the eastern Atlantic, form the *S. regalis* species group (Fig. 4), defined by the presence of nasal denticles (Collette and Russo manuscr. in prep.<sup>3</sup>). These five American species share a unique specialization of the fourth left epi-branchial artery (Collette and Russo footnote 3), which indicates that these species were derived from an *S. tritor* ancestor. This pattern of relationships is fully compatible with that derived from the copepod data.

**INDO-WEST PACIFIC SCOMBEROMORUS.**—There are 11 recognized species of Indo-West Pacific *Scomberomorus* (Collette and Russo 1980; Figs. 3, 5, 6). Four genera of parasitic copepods are common on Indo-West Pacific species of *Scomberomorus* (Table 6): *Unicolax*, parasitic in the nasal sinuses; *Shiinoa*, attached to the nasal lamellae; *Pseudocycnooides*, at-

<sup>3</sup>Bruce C. Collette and Joseph L. Russo. Systematics and morphology of the Spanish mackerels (*Scomberomorus*). Manuscr. in prep., 400 p. Systematics Laboratory, National Marine Fisheries Service, NOAA, Smithsonian Institution, Washington, DC 20560.

TABLE 6.—Infestation of Indo-West Pacific species of *Scomberomorus* with parasitic copepods. Host species arranged from most infested (most primitive?) to least infested (most specialized?). The eastern Atlantic *S. tritor* is included for comparison.

Species	n	Total copepod species	Total genera	Common genera <sup>1</sup>
<i>commerson</i>	130	9	6	4
<i>semifasciatus</i>	26	5	4	4
<i>queenslandicus</i>	39	5	4	4
<i>guttatus</i>	58	4	4	4
<i>plurilineatus</i>	14	5	5	4
<i>nipponicus</i>	19	4	4	4
<i>munroi</i>	19	3	3	3
<i>koreanus</i>	6	4	2	2
<i>lineolatus</i>	14	3	3	3
<i>sinensis</i>	10	3	2	1
<i>multiradiatus</i>	29	2	2	2
<i>tritor</i>	21	4	3	3

<sup>1</sup>*Unicolax*, *Pseudocycnooides*, *Shiinoa*, *Caligus*.

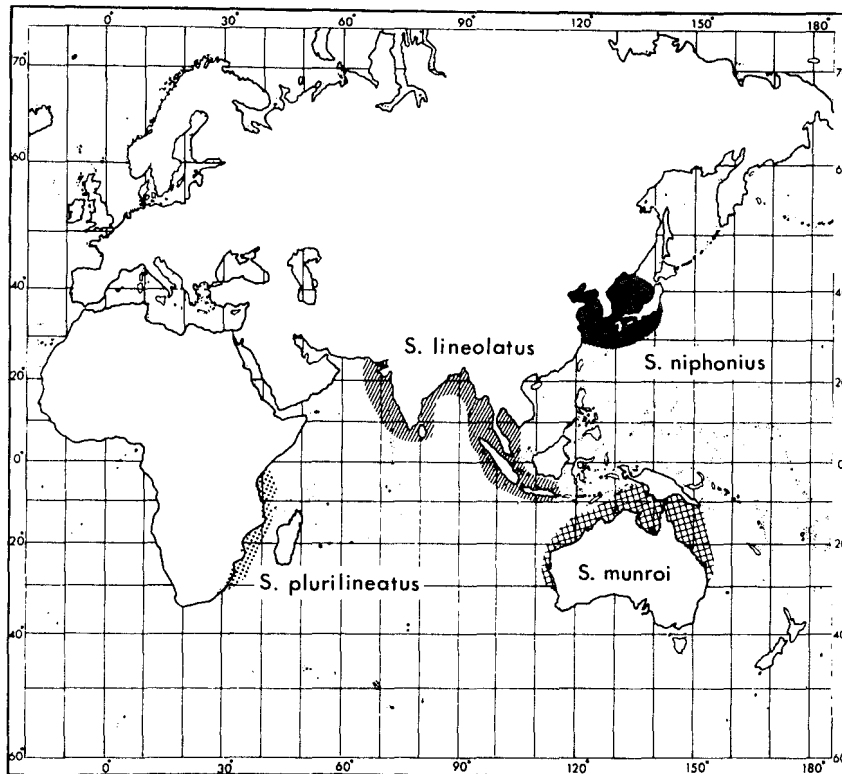


FIGURE 5.—Distribution of *Scomberomorus lineolatus*, *S. plurilineatus*, *S. munroi*, and *S. niphonius*.

tached to the gill filaments; and several species of *Caligus*, found in the gill area, mouth, and on the body surface.

The generally accepted theory that the more primitive members of a host group usually harbor more species of parasites than those that evolved later indicates the following. *Scomberomorus commerson* is the most widespread species occurring from the eastern Mediterranean (recent Suez migrant) eastward throughout the Indian Ocean into the western Pacific Ocean (see Figure 3). Nine species of copepods, from four genera cited above plus two additional genera (*Tuxophorus* and *Brachiella*), have been collected from *S. commerson*. No other species of *Scomberomorus* harbors more than seven species and six genera of copepods. Thus, the parasite data indicate *S. commerson* to be the most primitive member of the Indo-West Pacific *Scomberomorus*. If the converse is true, the data suggest that *S. multiradiatus* with only two copepod species is the most advanced (specialized).

The data further suggest that the origin of *S. commerson* was in the Indo-Australian Archipelago, because all nine species of copepods are reported from specimens in that area with a decrease in the num-

ber of parasite species to the north and west (Fig. 7).

*Scomberomorus niphonius* is unusual among the Indo-West Pacific members of the genus in its copepod parasites. Most Indo-West Pacific *Scomberomorus* are parasitized by *P. armatus*. *Scomberomorus niphonius* is commonly parasitized by a closely related species, *P. scomberomori*, which has more primitive characters than *P. armatus*, and is apparently specific to *S. niphonius*. This suggests that *S. niphonius* may be primitive compared with the other Indo-West Pacific species. *Scomberomorus niphonius* might also be considered primitive based on one of its morphological characters (Fig. 4). It is the only species in the genus to have a straight intestine. Most other species of *Scomberomorus* have two bends (and three sections) to the intestine. One species, *S. koreanus*, has three bends (and five sections), presumably a specialized condition.

Two of the 19 specimens of *S. niphonius* were parasitized by *C. pelamydis* (the only *Caligus* so far reported from it) which is found on several other scombrids, most commonly on species of *Sarda*. *Caligus cybii*, closely related to *C. pelamydis*, has been reported from six Indo-West Pacific species of

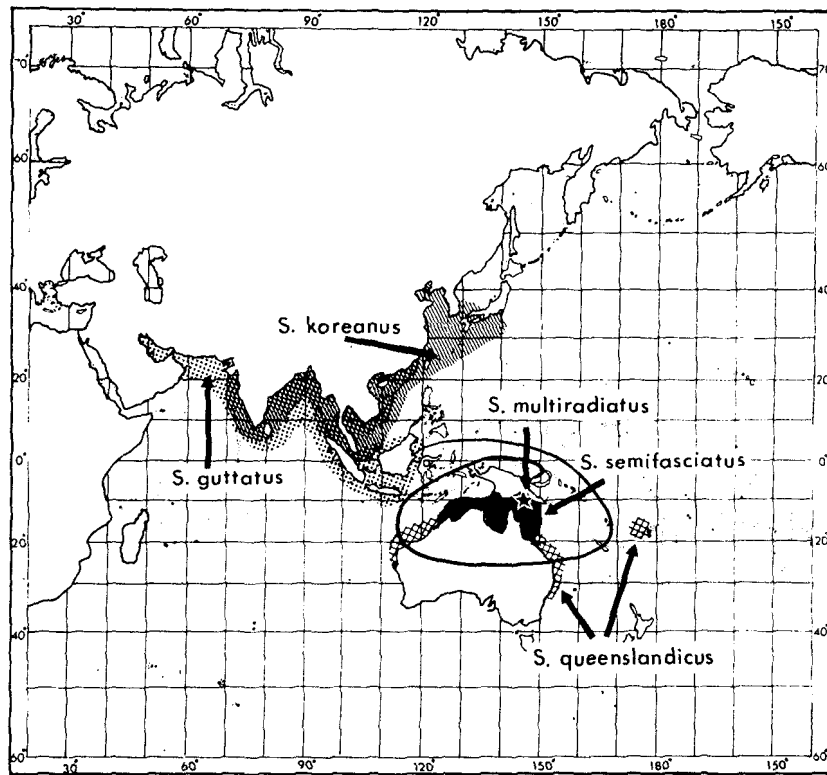


FIGURE 6.—Distribution of *Scomberomorus guttatus*, *S. koreanus*, *S. multiradiatus*, *S. semifasciatus*, and *S. queenslandicus*.

*Scomberomorus*, including species whose ranges overlap those of *S. niphonius*, *S. koreanus*, and *S. sinensis*. The first author cannot ascertain with certainty which of these two copepods, based on their morphology, may be the more primitive, but the reduced specificity of *C. pelamydis* and the apparent restriction of *C. cybii* to Indo-West Pacific *Scomberomorus* suggest *C. pelamydis* to be more primitive. If true, this supports the indication of the primitive nature of *S. niphonius* provided by the two species of *Pseudocycnoides*.

A single specimen of *C. pelamydis* has also been collected by us from *S. sinensis*. This might be used to argue that *S. commerson* and *S. niphonius* arose from a common ancestor, with *S. niphonius* now restricted to the northwest Pacific (colder water) and *S. commerson*, together with other species, occupying the more temperate and tropical waters. *Scomberomorus commerson* and *S. sinensis* both have prominent dips in the lateral line, but the dip is under the second dorsal finlets in the former species and under the first dorsal fin in the latter species; this similarity may be due to convergence rather than close relationships. These three species (*S. commerson*, *S. niphonius*, and

*S. sinensis*), *S. cavalla*, and *S. queenslandicus* all appear to be relatively primitive (Fig. 4).

#### *Grammatorcynus* Gill

Although included in the *Scomberomorini* by recent works such as Collette (1979), the exact systematic position of this monotypic genus is in doubt (Collette and Russo 1979), because it also shares some characters with the *Scomberini*. It has the same number of vertebrae as do the *Scomberini* (31), usually 13 precaudal plus 18 caudal. Its possession of an extra, ventral lateral line is unique in the family. The double-lined mackerel, *G. bicarinatus* (Quoy and Gaimard) is known from much of the tropical Indo-West Pacific, particularly near coral reefs from the Marshalls and Carolines, Philippine Islands, Australia, and the East Indies east to the Red Sea. Copepod fauna: 5 species in 2 genera, *Shiinoa* and *Caligus*. Only one species of *Caligus*, *C. asymmetricus*, is at all common on *Grammatorcynus* (14.9%). This copepod has been found on nine scombrids in the Indo-West Pacific and is perhaps more characteristic of the Sardini (*Cybiosarda elegans*, *Sarda*

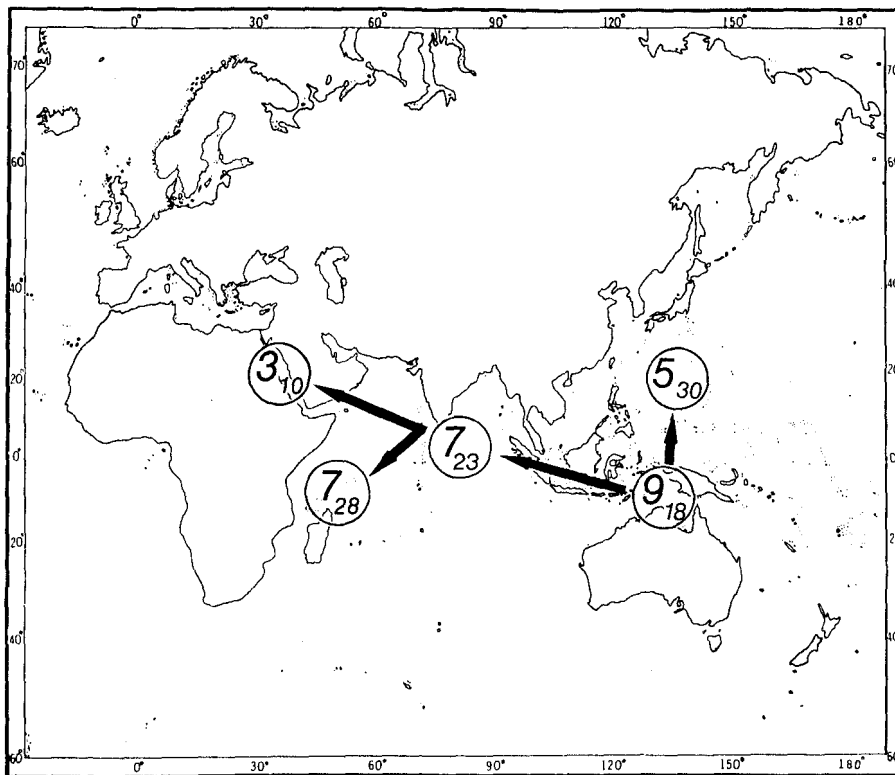


FIGURE 7.—Numbers of copepod species on *Scomberomorus commerson* in different areas of its distribution (large numbers represent number of copepod species; small numbers represent number of hosts examined).

*orientalis*, *S. australis*) with infestations of 8-12%.

**Acanthocybium Gill**

This monotypic genus appears to be a specialized offshoot of *Scomberomorus* and does not merit placement in its own subfamily or tribe as has been advocated by some previous authors (e.g., Starks 1910). It is closest to the *Cybium* group of *Scomberomorus* (*S. cavalla* and *S. commerson*), according to Conrad (1938) and Mago Leccia (1958). The wahoo, *A. solandri* (Cuvier), is a large species (reaching over 1,500 mm SL) and has a well-developed swim bladder. It is a high-seas epipelagic species found round the world in tropical and subtropical waters. Copepod fauna: 6 species in 5 genera. *Acanthocybium* is similar to the other *Scomberomorini* in being parasitized by *Shiinoa* and *Tuxophorus*, but the rate of infestation is very low. The most common two copepods are the euryphorid *Gloiopotes hygomianus* (infestation rate of 42% of our 64 specimens, 54% of the 100 fish from the Line Islands examined by Iverson and Yoshida 1957) and the lerneopodid *Brachiella thynni* (61% of our specimens, 98% of those examined by Iverson

and Yoshida). The other four species of *Gloiopotes* are parasites of billfishes (Istiophoridae).

Some workers in the past (e.g., Lütken 1880) and the present (G. David Johnson, pers. commun.<sup>4</sup>) believe that *Acanthocybium* is closely related to the billfishes. We feel that the parasite data are best interpreted as evidence of ecological similarity between the groups (fast swimming, high-seas species) rather than as evidence of phylogenetic relationships. *Brachiella thynni* was also found on three species of *Thunnus* (*T. obesus*, *T. albacares*, and *T. thynnus*) and two of *Scomberomorus* (*S. regalis* and *S. plurilineatus*). This species has been reported from a variety of hosts, usually attached in the axil of the pectoral fin. A second species of *Brachiella* is known only from two western Pacific species of *Scomberomorus*. There seems little ecological or phylogenetic information that can be drawn from parasitism by *Brachiella*.

Parasitic copepods of the genera *Tuxophorus* and *Gloiopotes* suggest relationships between *Scomberomorus* and *Acanthocybium* of the *Scomberomorini*

<sup>4</sup>G. David Johnson, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412.

and the Istiophoridae (Table 7). Three species of the copepod genus *Tuxophorus* are parasitic on the body surface of species of *Scomberomorus* and *Acanthocybium* in the Atlantic and Indo-West Pacific Oceans. When the paper by Cressey and Cressey (1980) went to press, these three species, *T. cybii*, *T. cervicornis*, and *T. collettei*, were retained in *Tuxophorus* because they conformed to the diagnosis of that genus. Subsequent considerations by the first author lead to the conclusion that they are not members of *Tuxophorus* but represent a new genus closely related to *Gloiopotes* or are possibly members of *Gloiopotes*. The presence of frontal lunules on these three species is the only character separating them from *Gloiopotes*, as it is presently defined. An earlier work on the parasitic copepods of lizardfishes (Cressey and Cressey 1979) gave an example of a caligid genus (*Abasia*), which showed a transition series of six species with a gradual reduction in the frontal lunule from well developed to absent. This indicates the possibility that the presence or absence of the frontal lunule is not always a valid generic character. The genus *Tuxophorus* was described by Wilson (1908) for *T. caligodes*, based on material collected from Atlantic *Rachycentron canadus* and *Echeneis naucrates*. The second species, *T. wilsoni*, was described by Kirtisinghe (1937) from the carangid, *Chorinemus*, from Sri Lanka.

Four of the five species of *Gloiopotes* are found on the body surface of various species of istiophorids; the fifth, *G. hygomanus*, is restricted to *A. solandri*. The occurrence of *Gloiopotes* on *Acanthocybium* and istiophorids might be used as evidence to support relationships between the two groups. The question is:

TABLE 7.—Host-parasite records for *Tuxophorus cybii*, *T. collettei*, *T. cervicornis*, and *Gloiopotes* spp.

Host-parasite	Area
<i>Tuxophorus cybii</i>	
<i>Acanthocybium solandri</i>	Indian Ocean
<i>Tuxophorus cervicornis</i>	
<i>Scomberomorus commerson</i>	Indo-Pacific
<i>Tuxophorus collettei</i>	
<i>Scomberomorus regalis</i>	Atlantic
<i>Gloiopotes hygomanus</i>	
<i>Acanthocybium solandri</i>	Cosmopolitan
<i>Gloiopotes americanus</i>	
<i>Istiophorus americanus</i>	Atlantic
<i>Gloiopotes ornatus</i>	
<i>Tetrapterus albidus</i>	Atlantic
<i>Makaira nigricans</i>	Atlantic
<i>Gloiopotes huttoni</i>	
<i>Tetrapterus audax</i>	Indo-Pacific
<i>Makaira indicus</i>	Indo-Pacific
<i>Istiophorus platypterus</i>	Indo-Pacific
<i>Gloiopotes watsoni</i>	
<i>Tetrapterus audax</i>	Indian Ocean
<i>Makaira nigricans</i>	Indo-Pacific
<i>Makaira indicus</i>	Indian Ocean
<i>Istiophorus platypterus</i>	Indo-Pacific

“Are these relationships ecological or phylogenetic?” The morphological similarities between *Acanthocybium* and the Istiophoridae seem best explained as convergences; those between *Acanthocybium* and *Scomberomorus* indicate that *Acanthocybium* is the specialized sister-group of *Scomberomorus* (Fig. 4). Thus, we argue that the presence of *Gloiopotes* on *Acanthocybium* and istiophorids is an ecological relationship, but that the occurrence of three species of *Tuxophorus* on *Acanthocybium* and *Scomberomorus* reflects shared phylogeny. Support for this argument could come from the presence of *Gloiopotes* on some open ocean, fast-swimming host but we have no such data. The explanation for the occurrence of species of *Gloiopotes* only on *Acanthocybium* and istiophorids must remain uncertain for the present.

## Sardini

The bonitos consist of eight species placed in five genera (Collette and Chao 1975). Except for *Allothunnus*, the Sardini differ from the Thunnini in lacking prominent prootic pits on the ventral surface of the cranium. Collette and Chao (1975:table 14) summarized the characters distinguishing the five genera of Sardini. Copepod fauna: 11 species in 5 genera. *Caligus bonito* has been found on all. *Unicolax collateralis* was found in *Orcynopsis*, *Cybiosarda*, and two species of *Sarda*.

## Orcynopsis Gill

The monotypic *Orcynopsis* and *Cybiosarda* show several characters that distinguish them from *Sarda* and *Gymnosarda* (Collette and Chao 1975). *Orcynopsis* is a short-bodied and short-headed bonito. *Orcynopsis unicolor* (Geoffrey St. Hilaire) is an eastern Atlantic endemic whose range is centered in the Mediterranean Sea but extends south to Dakar, Senegal, and north to Oslo, Norway (Collette and Chao 1975: fig. 69). Copepod fauna: 1 specimen of *U. collateralis* and 1 specimen of *Caligus bonito*.

## Cybiosarda Whitley

As noted above, the monotypic genera *Cybiosarda* and *Orcynopsis* share a suite of characters that differentiate them from *Sarda* and *Gymnosarda* (Collette and Chao 1975). *Cybiosarda elegans* (Whitley) is virtually an Australian endemic; is found along the northern three-quarters of the continent from Perth, Western Australia, to Sydney, New South Wales (Collette and Chao 1975:fig. 69); and occurs along the south coast of Papua New Guinea (Collette

1979). Copepod fauna: 3 species in 2 genera, the same species as in *Orcynopsis* plus *Caligus asymmetricus*, which is found on various species in three of the four tribes.

**Sarda Cuvier**

The four species of *Sarda* all have several dorsal stripes, ranging from horizontal to oblique in orientation. *Sarda* and *Gymnosarda* share a number of characters that distinguish them from *Orcynopsis* and *Cybiosarda* (Collette and Chao 1975).

Collette and Chao (1975) recognized four species of *Sarda* (Fig. 8): *Sarda australis* (Macleay) is restricted to the east coast of Australia, Norfolk Island, and New Zealand; *S. chiliensis* inhabits the eastern Pacific where it is divisible into two subspecies, *S. c. chiliensis* (Cuvier) from Peru and Chile and *S. c. lineolata* (Girard) from Alaska to Baja California; *S. orientalis* (Temminck and Schlegel) is widespread in the Indo-Pacific from South Africa and the Red Sea east to Japan, China, the Philippine Islands, the Hawaiian Islands, and across into the eastern Pacific from Baja California to Peru; and *S. sarda* (Bloch) is found throughout tropical and temperate waters of the Atlantic Ocean including the Gulf of Mexico and the Mediterranean and Black Seas (Collette and Chao 1975; Fig. 8).

A summary of the 26 most important characters used in distinguishing the species of *Sarda* was presented by Collette and Chao (1975:table 17).

Copepod fauna: 9 species in 3 genera. In addition to the two widespread bonito parasites, *U. collateralis* and *Caligus bonito*, three other copepods are common on species of *Sarda*; *Ceratocolax euthynni*, *Caligus pelamydis*, and *C. asymmetricus*. The presence of five common copepods on species of *Sarda* presents an opportunity for further analysis.

Over 200 specimens of the four species of *Sarda* were examined with an overall infestation rate of 75% (156 of 206 specimens examined). It is thought that as a host species or related group of host species disperses from its place of origin it loses parasites in the process (see discussion of *Scomberomorus commerson* above). When one examines the infestation rates

of the individual *Sarda* species, first with all of its copepod parasites and secondly each species with its individual parasite species, the change in infestation rates from one *Sarda* species to another may reflect the speciation of *Sarda* species away from the center of origin of the genus.

An analysis of these data (Table 8) indicates an origin of the genus in Australasia (*S. australis*, *S. orientalis*, or an ancestor of theirs) with the eastern Pacific *S. chiliensis* derived from *S. australis* and the Atlantic *S. sarda* from *S. chiliensis*. The infestation rates of *C. bonito*, *C. asymmetricus*, and *U. collateralis* suggest that the copepod parasites of *S. sarda* could have been derived from those of *S. orientalis*. The occurrence of *C. pelamydis* on *S. sarda*, however, and its absence on *S. orientalis* reinforce the idea that *S. sarda* may have been derived, along with its parasites, from *S. australis* or *S. chiliensis* but not from *S. orientalis*. *Sarda sarda* has the lowest overall infestation rate (68%) and has lost one *Caligus* species (*asymmetricus*) and replaced *U. collateralis* with the Atlantic scombrid bomolochid copepod *Ceratocolax euthynni*.

The overall infestation rates of the four species of *Sarda* are *S. australis*, 90%; *S. orientalis*, 82%; *S. chiliensis*, 76%; and *S. sarda*, 68%. These data support the proposal that species radiation progressed from Indo-West Pacific to eastern Pacific to Atlantic within the genus.

The 26 morphological characters used by Collette and Chao (1975:table 14) to distinguish the species of *Sarda* tend to support the evolutionary hypothesis deduced from the copepod data. *Sarda sarda* is the most specialized of the four species in its increased numbers of vertebrae and other correlated meristic characters. *Sarda australis* appears most primitive in such characters as number of dorsal and anal finlets. It shares some primitive characters, such as the occasional presence of vomerine teeth, with *S. sarda*. If other similarities between these two species (location of first closed haemal arch, length of haemal pre- and postzygapophyses, shape of vertical wing of pelvic girdle, etc.) can also be considered primitive, then *S. chiliensis* and *S. orientalis* are in a relatively intermediate evolutionary position. In some cases,

TABLE 8.—Infestation rates by four species of copepods on the four species of *Sarda* (arrows indicate direction of decrease).

Copepod species	<i>Sarda</i> species			
	<i>orientalis</i>	<i>australis</i>	<i>chiliensis</i>	<i>sarda</i>
<i>Caligus bonito</i>	36.4 ←	59.1 →	55.6 →	31.1
<i>Caligus pelamydis</i>	— ←	50.0 →	8.9 →	7.5
<i>Caligus asymmetricus</i>	12.1 →	9.1 →	— →	—
<i>Unicolax collateralis</i>	36.4 →	9.1 →	— →	—

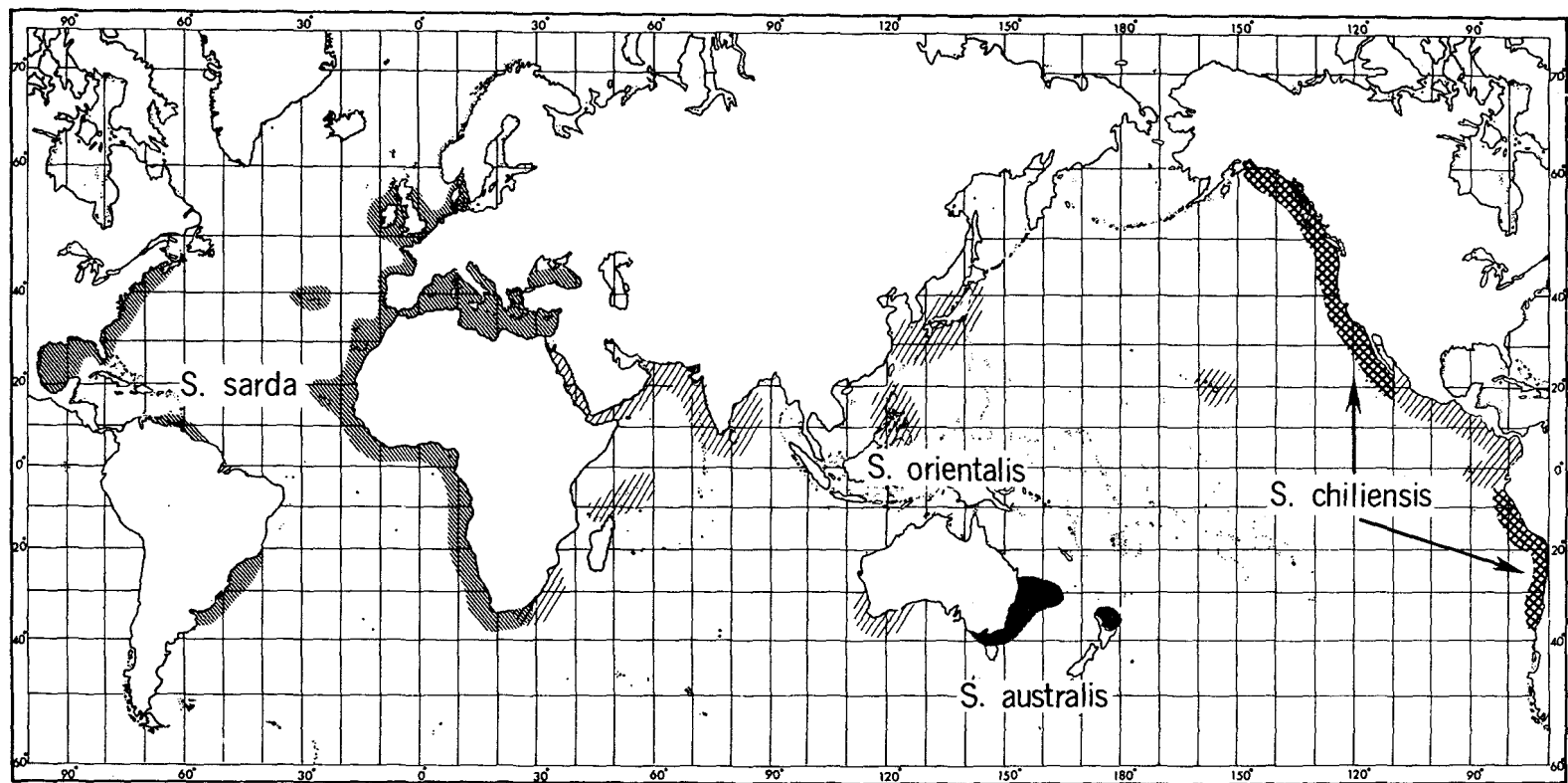


FIGURE 8.—Distribution of the four species of *Sarda*.



such as complete loss of vomerine teeth, these species have diverged from the primitive condition.

### *Gymnosarda* Gill

The monotypic genus *Gymnosarda* differs from other bonitos in a series of characters (Collette and Chao 1975). The dogtooth tuna, *G. unicolor* (Rüppell), is a coral reef species of the tropical Indo-West Pacific (Collette and Chao 1975:fig. 69). Its large eyes and teeth, numerous olfactory lamellae, and well-developed swim bladder indicate that it is more of a lurking predator on larger fishes than are the other bonitos. Copepod fauna: 3 species in 2 genera. Each copepod species was found only once, so it is difficult to draw any conclusions from the data. One species, *C. bonito*, is characteristic of the Sardini. *Caligus productus* is known from a wide variety of hosts, both scombrid (14 species from all tribes except Scombrini) and nonscombrid. *Shiinoa occlusa* is otherwise restricted to Indo-West Pacific species of Scomberomorini.

### *Allothunnus* Serventy

The systematic position of this monotypic genus is still in some doubt. It was included in the Sardini by Collette and Chao (1975) because it lacked the specializations considered diagnostic of the Thunnini and showed similarities to the bonitos in characters such as the otoliths. It differs from all other scombrids in having the prootic bones remarkably extended laterally as wings that frame the posterior margin of the orbit and in having a very large number of gill rakers. *Allothunnus* resembles the Thunnini and differs from other Sardini in having a prootic pit in the ventral surface of the skull. The pineal window is large and oval in *Allothunnus*, elongate and slit-shaped in the Thunnini and all other Sardini. The liver has three subequal lobes as in the bluefin tuna species group of *Thunnus*. *Allothunnus fallai* Serventy is found around the world in the Southern Ocean south of lat. 35°S (Collette and Chao 1975:fig. 69) with one highly unusual record from the Los Angeles-Long Beach harbor complex (Fitch and Craig 1964).

Copepod fauna: *Elytrophora brachyptera* was present in all 5 Pacific specimens that we examined and was also reported by Webb (1976) in 45 of 47 specimens that they examined from Tasmania. This copepod is otherwise known only from the tuna genus *Thunnus* where we have found it in six of seven species (all but *T. tonggol*). These copepod data support a closer phylogenetic relationship between *Allothun-*

*nus* and *Thunnus* than was indicated by Collette and Chao (1975). Two specimens from off the tip of South Africa, however, carried the copepod *C. bonito*, a common parasite of Sardini species. Infestation by *C. bonito* can be viewed as primitive in *Allothunnus*; infestation by *Elytrophora* advanced. Sharing specialized morphological characters and copepod parasites suggests that serious consideration must be given to transferring *Allothunnus* from the Sardini to a position as the most primitive member of the Thunnini. This issue will be considered further by Collette.

## Thunnini

The four genera of tunas are unique among bony fishes in having countercurrent heat exchanger systems of rete mirabilia in the circulatory system. These systems allow tunas to retain metabolic heat so that the fish is warmer than the surrounding water. The three more primitive genera (*Auxis*, *Euthynnus*, and *Katsuwonus*) and the yellowfin tuna group of *Thunnus* have central and lateral heat exchangers; the specialized bluefin tuna group of *Thunnus* has lost the central heat exchanger and has evolved well-developed lateral heat exchangers (Carey et al. 1971; Graham 1973, 1975). Copepod fauna: 17 species in 7 genera. *Caligus coryphaenae*, *C. asymmetricus*, and *C. productus* were found on species in all four genera of Thunnini. *Caligus coryphaenae* is common on the body surface of seven species of *Euthynnus*, *Katsuwonus*, and *Thunnus*, and we have one record from *Auxis* sp. (and one record from *Acanthocybium*). It is also common on species of the dolphin genus *Coryphaena*, a similarity we believe due to similarity of epipelagic habits. *Caligus productus* was found on 20 species of scombrids, from all tribes except the Scombrini. It occurred on 9 of the 13 species of Thunnini but was common (infestation 28-92%) on *Katsuwonus* and 3 species of *Thunnus*. *Caligus asymmetricus* was also found on scombrids from all tribes except the Scombrini, on a total of nine host species. It appears to be more characteristic of the Sardini, occurring commonly (infestation 8-12%) in *Cybiosarda* and two species of *Sarda*, than of the Thunnini (found in four species, infestation 1-7%). One additional copepod, *Pseudocycnus appendiculatus*, is characteristic of Thunnini and occurs on 9 of 13 species, in all genera except *Auxis*. However, it is common (infestation 14-27%) in only three species of *Thunnus*: *T. tonggol*, *T. albacares*, and *T. maccoyii*.

### *Auxis* Cuvier

This is the most primitive genus of the Thunnini.

Differences from the more advanced three genera of Thunnini were summarized by Collette (1979). Copepod fauna: 6 species in 2 genera, *Unicolax* and *Caligus*. The two species of *Unicolax* are shared with several species of Sardini and with species of *Euthynnus* in the Thunnini. *Euthynnus* is the genus most closely related to *Auxis*. Three of the species of *Caligus* are also found in the other three genera of Thunnini. The fourth, *C. pelamydis*, is shared only with *Euthynnus* among the Thunnini, but parasitizes scombrids in the other three tribes, particularly the Sardini. We have not found *P. appendiculatus* on *Auxis*, but it is known from species in the other three genera of Thunnini. Thus, infestation of copepods clearly relates *Auxis* to the other Thunnini, particularly *Euthynnus*.

There are two species of frigate mackerels (Fitch and Roedel 1963): The narrow-corseleted *A. thazard* (Lacepède) and the wide-corseleted *A. rochei* (Risso). The two species have been clearly distinguished in the Pacific by Kishinouye (1923), Wade (1949), and Matsumoto (1960) under a variety of names. Both species are widely distributed in tropical and subtropical waters of the Indo-Pacific, and both species apparently also occur in the Atlantic (Richards and Randall 1967). Confusion in identification of many specimens dictates that we refer all our copepod records for the genus to *Auxis* sp. Frigate mackerels are the smallest of the tunas, *A. rochei* reaching 600 mm FL and *A. thazard* at least 420 mm.

#### ***Euthynnus* Lütken in Jordan and Gilbert**

*Euthynnus* is closely related to both the more primitive *Auxis* and the more advanced *Katsuwonus*. Some workers (Fraser-Brunner 1950; Collette and Gibbs 1963) have placed the monotypic *Katsuwonus* in synonymy with *Euthynnus*, but this obscures the relationships of *Euthynnus* sensu stricto with *Auxis* and of *Katsuwonus* with *Thunnus*. *Euthynnus* differs from *Auxis* in having a common trunk for the dorsal and ventral branches of the cutaneous artery. It is less advanced than *Katsuwonus* because the ventral branch of the cutaneous artery is short and dendritic (Godsil 1954), much less developed than the dorsal branch. The dorsal cutaneous artery lies dorsal to the corresponding vein in *Euthynnus*, not ventral as in *Auxis*. Collette (1979) has summarized the generic differences along the genera of Thunnini. Copepod fauna: 11 species in 4 genera. Three species of *Caligus* (*asymmetricus*, *pelamydis*, *productus*) and *P. appendiculatus* are widespread among the Thunnini. Two species of *Unicolax* (*collateralis* and *myc-*

*terobius*) are shared only with *Auxis* in the Thunnini but also with species of Sardini. *Caligus bonito* was found on all three species of *Euthynnus* but is most commonly found on members of the tribe Sardini.

There are three allopatric species of *Euthynnus*: *E. alletteratus* (Rafinesque) in the Atlantic; *E. affinis* (Cantor) throughout the Indo-West Pacific; and *E. lineatus* Kishinouye in the eastern Pacific. There is a valid record of *E. affinis* from the eastern Pacific (Godsil 1954:139) and two of *E. lineatus* from the Hawaiian Islands (Matsumoto and Kang 1967; Matsumoto 1967). Godsil (1954: table 17) has summarized the characters that differentiate the species (with *E. affinis* as *E. yaito*). Two bomolochid and one caligid copepod parasites of *Euthynnus* apparently show host specificity within the genus. *Unicolax anonymous* is known only from the nasal sinuses of *E. alletteratus* in both the eastern and western Atlantic. *Ceratocolax euthynni* is also restricted to the Atlantic, but occurs on *Sarda sarda* as well. *Caligus regalis* is restricted to *E. affinis* (and *Grammatorcynus* in the Scomberomorini) and may replace the closely related, more widespread *C. coryphaenae* on this host.

#### ***Katsuwonus* Kishinouye**

This monotypic genus is related to both *Euthynnus* and *Thunnus*, and is more advanced than *Euthynnus*. The generic characters of *Katsuwonus* are summarized by Collette (1979). The skipjack tuna, *Katsuwonus pelamis* (Linnaeus), is a moderate-sized tuna, about a meter long and weighs 18 kg, rarely more than 23 kg. It has the highest number of gill rakers of any of the Thunnini, 53-63 on the first arch. It is cosmopolitan in tropical and subtropical seas. Copepod fauna: 6 species in 3 genera. The three species of *Caligus* and *P. appendiculatus* are widespread among species of Thunnini. The fifth copepod, *U. reductus*, is a highly specialized species restricted to *Katsuwonus*. It appears to replace the more primitive *U. collateralis*, *U. mycterobius*, and *U. anonymous*, which are common in the nasal sinuses of the two more primitive genera of Thunnini, *Auxis* and *Euthynnus*. This copepod evidence tends to support recognition of *Katsuwonus* as a separate genus.

#### ***Thunnus* South**

This, the most advanced genus of Scombridae, contains seven species. Posterior to the corselet, the body is covered with small scales but is naked in other genera of Thunnini. A swim bladder is present in all the species except *T. tonggol*. Vertebral trellis-

work (containing the central heat exchanger; Graham 1975, 1979) is present in *Euthynnus* and *Katsuwonus*, and is reduced (yellowfin tuna species group) or absent (bluefin tuna group) in *Thunnus*. Collette (1979) concluded that it was useful to utilize subgenera in *Thunnus* to reflect the adaptive significance of the difference in heat exchangers between the two groups of species, the subgenus *Thunnus* for the bluefin tuna group of species including *T. obesus*, *Neothunnus* for the yellowfin tuna group. Copepod fauna: 10 species in 5 genera. Three species of *Caligus* and *P. appendiculatus* are widespread among species of Thunnini. The lerneopodid *Brachiella thynni* occurs, usually in the axil of the pectoral fin, on a wide variety of hosts both scombrid and nonscombrid. In the Scombridae, it is most common on *Acanthocybium* and was also present on three species of *Thunnus* (*T. obesus*, 24%; *T. albacares*, 7%; *T. thynnus*, 4%). Occurrence of the euryphorid *Elytrophora* is of particular interest. Six species of *Thunnus* (all but *T. tonggol*) share *E. brachyptera* with *Allothunnus fallai*. As noted under the discussion of the latter, this indicates that the systematic position of *Allothunnus* within the tribe Sardini needs to be reconsidered.

#### Subgenus *Neothunnus* Kishinouye

This subgenus contains the three tropical species of *Thunnus* which have central heat exchangers, as do the three less advanced genera of Thunnini. Gibbs and Collette (1967:99) found that these three species were similar to each other in 15 or 16 of 18 characters. The three species are the blackfin tuna, *Thunnus atlanticus* (Lesson), of the western Atlantic, Martha's Vineyard, Mass., to Rio de Janeiro; the longtail tuna, *T. tonggol* (Bleeker), of the Indo-West Pacific, Japan to Australia west through the Indo-Australian Archipelago to Somalia and the Red Sea; and the yellowfin tuna, *T. albacares* (Bonnaterre), a pantropical species. Differences between the species were treated in detail by Gibbs and Collette (1967).

Copepod fauna: 7 species in 4 genera. Differences in copepod infestation in *Thunnus* appear to reflect species differences rather than subgeneric differences. *Caligus asymmetricus*, a copepod common on the three more primitive genera of Thunnini, was found on *T. albacares*, which tends to confirm closer relationships between the three primitive genera and *Neothunnus* than with *Thunnus*. However, the copepod was found only on one specimen of *T. albacares*, so this is only weak confirmatory evidence. We found the most common copepods on *T. albacares* worldwide to be *C. productus* (46%), *E. brachyptera* (35%),

*C. coryphaenae* (29%), *P. appendiculatus* (19%), and *B. thynni* (7%). In an intensive study of 200 *T. albacares* from the Gulf of Guinea, Baudin Laurencin (1971) found three of the five copepods in similar rates of infestation: *Caligus productus*, 64%; *P. appendiculatus*, 27%; and *B. thynni*, 7%. He did not report either *E. brachyptera* or *C. coryphaenae*, although both occur in the eastern Atlantic, and we have the latter from *T. albacares* in the Gulf of Guinea.

#### Subgenus *Thunnus* South

This subgenus contains the four larger species of tunas which have invaded cooler waters owing to their possession of effective lateral heat exchangers. Gibbs and Collette (1967:99) showed that three species of this group resembled each other in 14-16 of 18 characters. Striations caused by blood vessels are present on the ventral surface of the liver, and vascular cones are associated with the dorsal surface of the liver, indicating the presence of a visceral heat exchanger. Three species clearly belong to this subgenus: the Atlantic and Pacific bluefin tunas, *Thunnus thunnus thynnus* (Linnaeus) and *T. t. orientalis* (Temminck and Schlegel); the southern bluefin tuna, *T. maccoyii* (Castelnau); and the albacore, *T. alalunga* (Bonnaterre). The fourth species, the bigeye tuna, *T. obesus* (Lowe), is intermediate between the subgenera, sharing 12 characters with *T. maccoyii* and 10 with *T. albacares* (Gibbs and Collette 1967:99). Because it has lost the central heat exchanger, Collette (1979) believed that it belongs to the subgenus *Thunnus*, although it is the most different of the four species in the subgenus. The characters that distinguish the species of the subgenus *Thunnus* and the distributions of the species are treated in detail by Gibbs and Collette. All four species are found worldwide. The bluefin tuna extend into temperate waters of the North Atlantic (*T. t. thynnus*) and the North Pacific (*T. t. orientalis*). The southern bluefin, *T. maccoyii*, has a distribution pattern similar to those of *Gasterochisma* and *Allothunnus* in the Southern Ocean. *Thunnus alalunga* is found from lat. 42°N to 32°S in the Atlantic, lat. 10°N to 30°S in the Indian Ocean, and lat. 50°N to 45°S in the Pacific; however, most of the albacore fisheries are concentrated in temperate waters. *Thunnus obesus* has much the same latitudinal distribution as *T. albacares*, but it is usually found in deeper and cooler waters than *T. albacares*.

Copepod fauna: 8 species in 5 genera. *Thunnus obesus* differs in infestation from the other three species of the subgenus in lacking *C. productus*, in

having the highest infestation by *B. thynni* (24%), and in having a second species of *Elytrophora*, *E. indica*, which was found only on Indo-Pacific specimens of *T. obesus*. *Elytrophora indica* frequently occurs with *E. brachyptera*, but we lack data on possible microhabitat differences between the two copepods.

## HOST SPECIFICITY AND TAXONOMIC RELATIONSHIPS OF CALIGUS PARASITIC ON SCOMBRIDS

The genus *Caligus*, with over 200 recognized species, has been reported from species of marine fishes of several diverse higher taxa. Most species do not exhibit strict host specificity; those which have been commonly reported are known from more than one host species. Adults of *Caligus* species are occasionally found in plankton samples, indicating that species of *Caligus* may easily transfer from one host individual to another. Many, however, seem to be restricted to a genus or family of fishes. Furthermore, if one analyzes the data from comprehensive collections, it becomes clear that although a parasite may be present on several host species, it is consistently more common on some than others, which we interpret as a trend toward specificity. The first author has never found an equal rate of infestation of any *Caligus* species among its hosts in any large collections examined. There have always been one or two host species with significantly higher infestation rates, when as many as 10 host species are involved (unpubl. data). We have analyzed the data for *Caligus* most common on scombrids, and the results are consistent with this concept.

Ten most common of the 16 species of *Caligus* reported by Cressey and Cressey (1980) were chosen for study. These 10 *Caligus* species can be divided into 5 subgroups, based on the segmentation and number of setae on the fourth leg exopod, the presence or absence of a posterior process on the base of the second antenna, and the presence or absence of the postantennal spine. These groups are 1) *productus*, *asymmetricus*; 2) *bonito*, *omissus*, *mutabilis*; 3) *infestans*; 4) *pelamydis*, *cybii*; and 5) *coryphaenae*, *regalis*. All of the 10 species are found on more than one species of host (scombrid or otherwise). Frequency of their occurrences, however, indicates definite host preferences.

The distribution of infestation rates and host specificity indices (based on Rohde 1980) for *C. productus* and *C. asymmetricus* are given in Table 9. Neither of these two species are found on species of Scom-

brini. *Caligus productus* is most common on the closely related genera *Katsuwonus* and *Thunnus* and to a lesser extent on *Scomberomorus*, *Acanthocybium*, and *Gymnosarda*. Five of the six records of *C. productus* on species of *Scomberomorus* are from the Atlantic. *Caligus asymmetricus* complements *C. productus* in host distribution. It is common on hosts where *C. productus* is absent or rare, and uncommon or absent on those where *C. productus* is most common. The only genera of the three tribes infested, which so far are negative for either of these two copepods, are *Orcynopsis* and *Allothunnus*. This is due probably to the few specimens (seven) of each that we have examined.

Two species of *Caligus* (*cybii* and *infestans*) are apparently specific to Indo-West Pacific *Scomberomorus*, whereas there is apparently no *Caligus* species-specific to Atlantic *Scomberomorus*.

The next group of *Caligus* species are *bonito*, *mutabilis*, and *omissus*. *Caligus bonito* is circumglobal whereas *C. mutabilis* is restricted to the western Atlantic and *C. omissus* is, so far, only known from the eastern Pacific. The latter two species are very similar. In 1960, Causey reported *C. mutabilis* from several species of fishes, including *Scomberomorus sierra* from the Gulf of California and the Pacific coast of Mexico. The material from *S. sierra* was undoubtedly *C. omissus*, and it is likely that the rest was also. Wilson (1937) also reported *C. mutabilis* from *S. maculatus* (presumably *sierra*) from Pacific Mexico, which was probably *C. omissus*. None of these collections are available for verification, but we feel that these Pacific records of *C. mutabilis* should be discounted. The first author has collected *C. mutabilis* from two species of *Lutjanus* from the west coast of Florida, and it is apparent from the literature that all three of these

TABLE 9.—Infestation rates and host specificity indices of *Caligus productus* and *C. asymmetricus* on genera of Scombrinae (specificity indices in parentheses).

	<i>C. productus</i>	<i>C. asymmetricus</i>
Scombrini	—	—
<i>Restrelliger</i>	—	—
<i>Scomber</i>	—	—
Scomberomorini		
<i>Grammatorcynus</i>	2 (0.14)	14.9 (1.0)
<i>Scomberomorus</i>	1 (0.11)	1 (0.33)
<i>Acanthocybium</i>	17 (0.34)	—
Sardini		
<i>Orcynopsis</i>	—	—
<i>Cybiosarda</i>	—	8 (0.5)
<i>Sarda</i>	1.5 (0.32)	2.8 (0.2)
<i>Gymnosarda</i>	14.3 (0.26)	—
<i>Allothunnus</i>	—	—
Thunnini	3 (0.17)	1.3 (0.16)
<i>Auxis</i>	—	—
<i>Euthynnus</i>	1.3 (0.2)	3.3 (0.25)
<i>Katsuwonus</i>	38.6 (0.5)	1 (0.16)
<i>Thunnus</i>	41.4 (1.0)	1 (0.12)

copepod species are occasional parasites of non-scombrid hosts.

The distribution of infestation rates on scombrid hosts for these three species is summarized below. *Caligus bonito* is apparently most common on species of Sardinia and is only an occasional parasite of Atlantic *Scomberomorus* and *Grammatorcynus* and with scattered records from Thunnini (mostly western Atlantic and eastern Pacific).

*Caligus mutabilis* is apparently restricted to the western Atlantic, and its most common scombrid hosts are species of *Scomberomorus*. As in the case of *C. productus* in the Atlantic, this copepod probably replaces the Indo-Pacific species of *Caligus*, more host-specific to Indo-Pacific *Scomberomorus*.

*Caligus infestans* has been recorded primarily from *S. commerson* from the Indian Ocean and eastward as far as Indonesia. Although its preferred host ranges north to Japan and east to Fiji, *C. infestans* apparently is replaced in these areas by *C. cybii*, host-specific to Indo-West Pacific *Scomberomorus*. Kabata (1965) reported *C. infestans* from *Euthynnus alletteratus* (= *affinis*) from Queensland, and Heller (1865) originally described this species from *Scomber* from Java. The second author believes the latter host to be incorrect and the host was probably *Rastrelliger*. Four literature records and five additional collections reported by Cressey and Cressey (1980) indicate that *S. commerson* is undoubtedly its preferred scombrid host.

*Caligus pelamydis* and *C. cybii* are, together with *C. coryphaenae* and *C. regalis*, the most primitive of the 10 species considered here (assuming a 3-segmented fourth leg exopod is primitive to a 2-segmented one). *Caligus pelamydis* has been reported many times (Margolis et al. 1975; Cressey and Cressey 1980) primarily from *Sarda sarda* (usually reported as *Pelamys sarda* or *Gymnosarda pelamys*) and *Scomber scombrus*. Although our recent collections indicate *Sarda* species as a frequent host, several other literature records from *Scomber scombrus* may indicate that this fish is a more common host than our collections indicate. Most literature records are from European waters, whereas most of the *S. scombrus* we examined were from the western Atlantic. Possibly this copepod is more common on European *S. scombrus* than on American specimens. In addition, *C. pelamydis* has been reported from *Euthynnus*, *Auxis*, and *Scomberomorus nipponius*.

It is interesting to note that *C. pelamydis* is a common parasite of *S. nipponius*, whereas its close relative, *C. cybii*, is reported from six other Indo-West Pacific species of *Scomberomorus*. It seems likely that *C. pelamydis* is more primitive than *C. cybii*. This

suggests that *S. nipponius* is the most primitive species of Indo-West Pacific *Scomberomorus*. The ranges of both *C. cybii* and *C. pelamydis* overlap in Japan (*C. cybii* from *S. koreanus*, 11 of 19 fish infested). *Caligus cybii* apparently evolved parasitizing species of Indo-West Pacific *Scomberomorus* other than *S. nipponius*.

The closely related *C. coryphaenae* and *C. regalis* are both found on the body surface of their hosts. Consequently, the data may be biased because much of the host material used for this study is preserved in museum collections, and body-surface copepods, for the most part, are no longer present. Most of the specimens of Thunnini, however, were examined in the field, and infestation rate data are more reliable. Because *C. coryphaenae* is ubiquitous (circumglobal distribution and on many different species of hosts), it can be presumed to be more primitive than *C. regalis* (restricted to the Indian Ocean and southwestern Pacific and found only on *E. affinis* and *Grammatorcynus*). *Caligus coryphaenae* is also common on *Coryphaena hippurus* and *C. equiselis*. Within the Scombridae, both species are primarily parasites of the Thunnini with scattered records on Scomberomorini (*Acanthocybium* and *Grammatorcynus*). *Caligus regalis*, previously known only from *E. affinis*, has recently been collected by the first author from three specimens of *G. bicarinatus* from Australia. This is within the known geographic range of the parasite, but is another example of copepod parasites shared by the Scomberomorini and the Thunnini.

Within each of the four groups of *Caligus* with more than one species discussed here, one species of *Caligus* is widely distributed (circumglobal in three cases) and the remaining species are much more restricted in distribution (Figs. 9-12).

In conclusion, analysis of the collection data for the 10 species of *Caligus* considered here suggest the following:

1. Although *Caligus* species are generally not restricted to one host, they are often confined to a genus, tribe, or family and, in all cases considered here, they show strong host preferences at a generic or specific level. For example, although *C. productus* is found on three of the four tribes of Scombridae, it has significantly higher rates of infestation on *Katsuwonus* and *Thunnus* within the Thunnini. *Caligus bonito* is recorded from three tribes of scombrids but is much more common on the tribe Sardinia.
2. Within each group of related *Caligus* parasitic on scombrids, one species is either circumglobal or is significantly more widespread than any others.

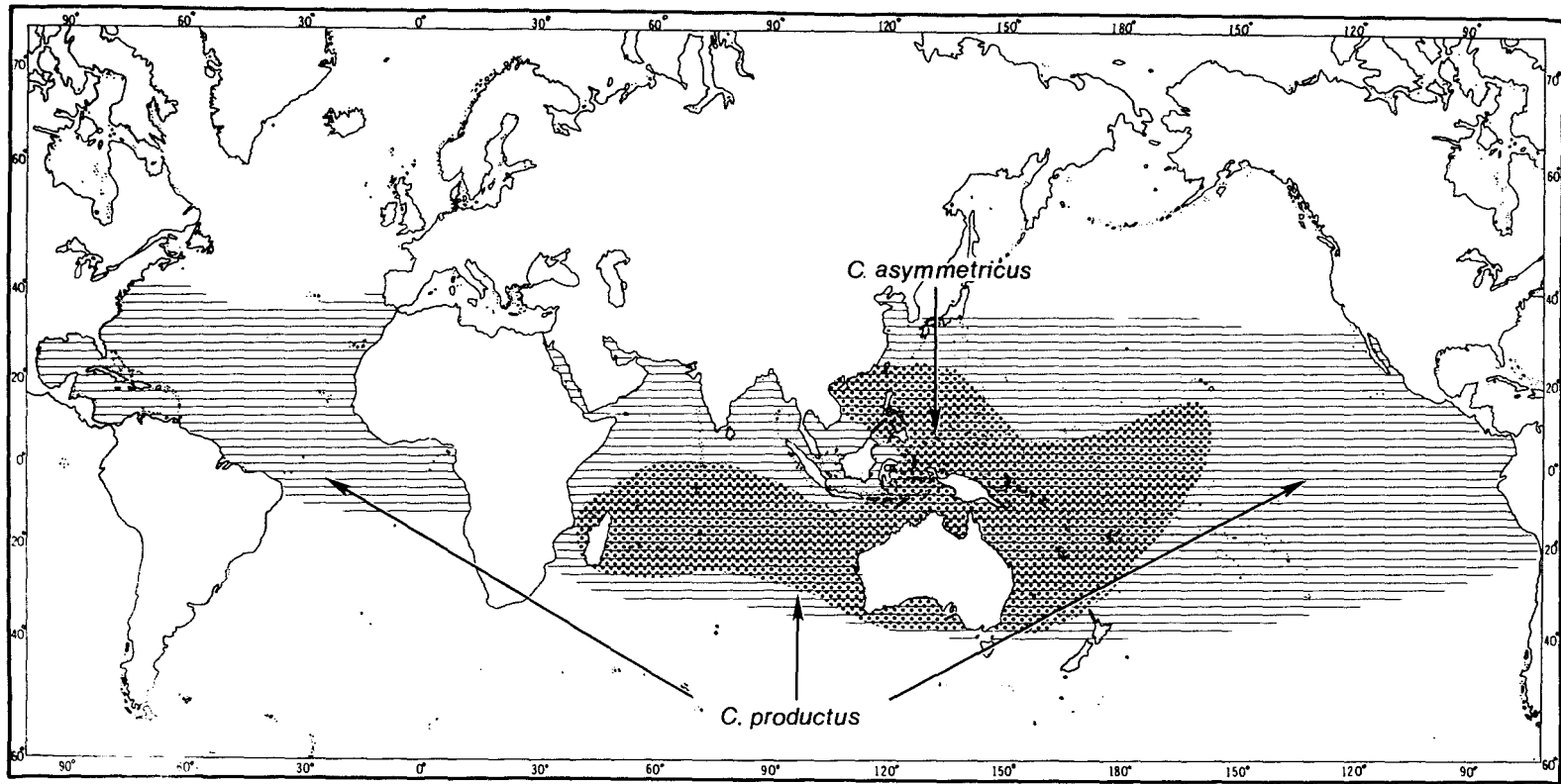


FIGURE 9—Distribution of *Caligus productus* and *C. asymmetricus*.

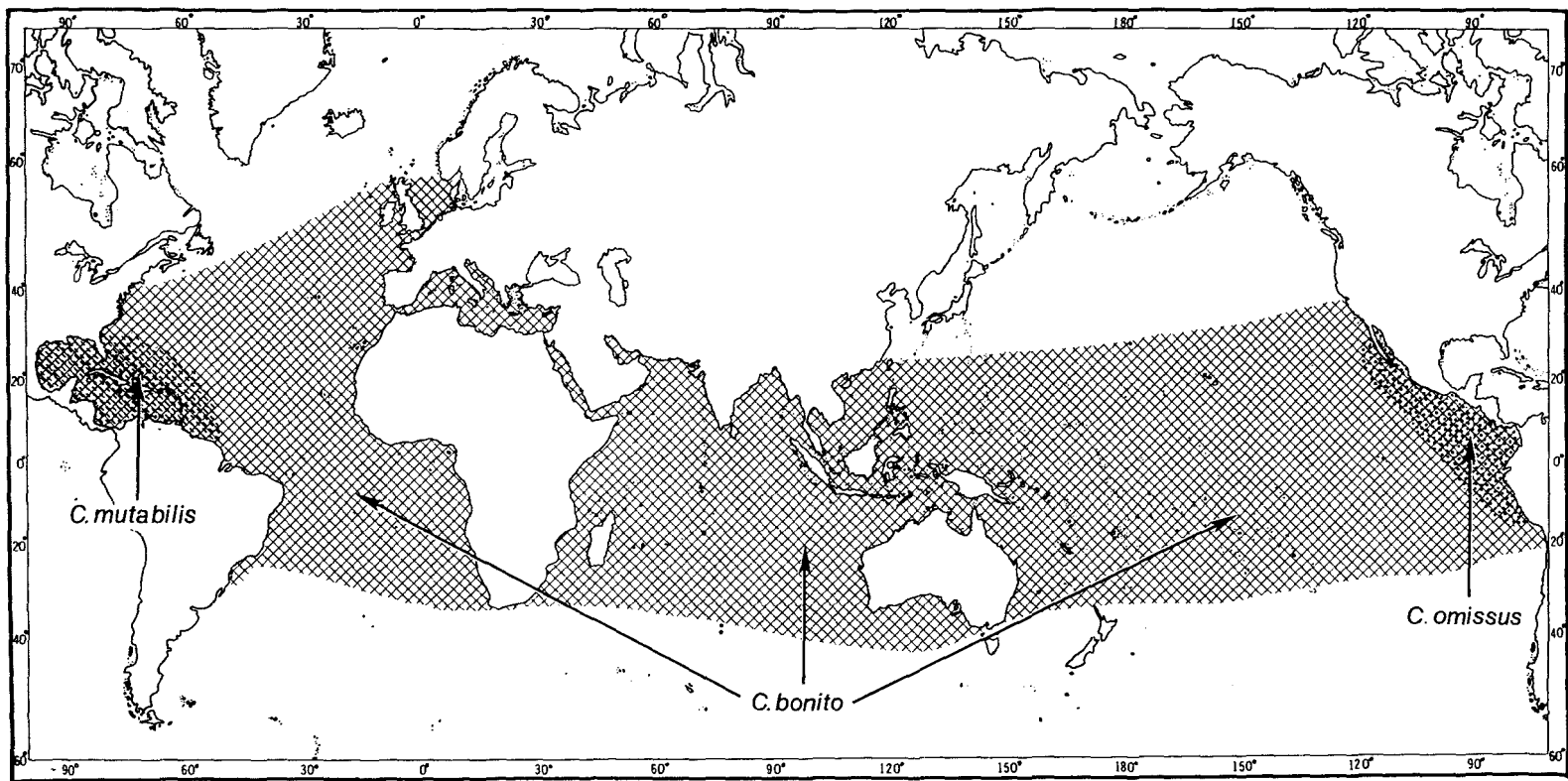


FIGURE 10.—Distribution of *Caligus mutabilis*, *C. bonito*, and *C. omissus*.

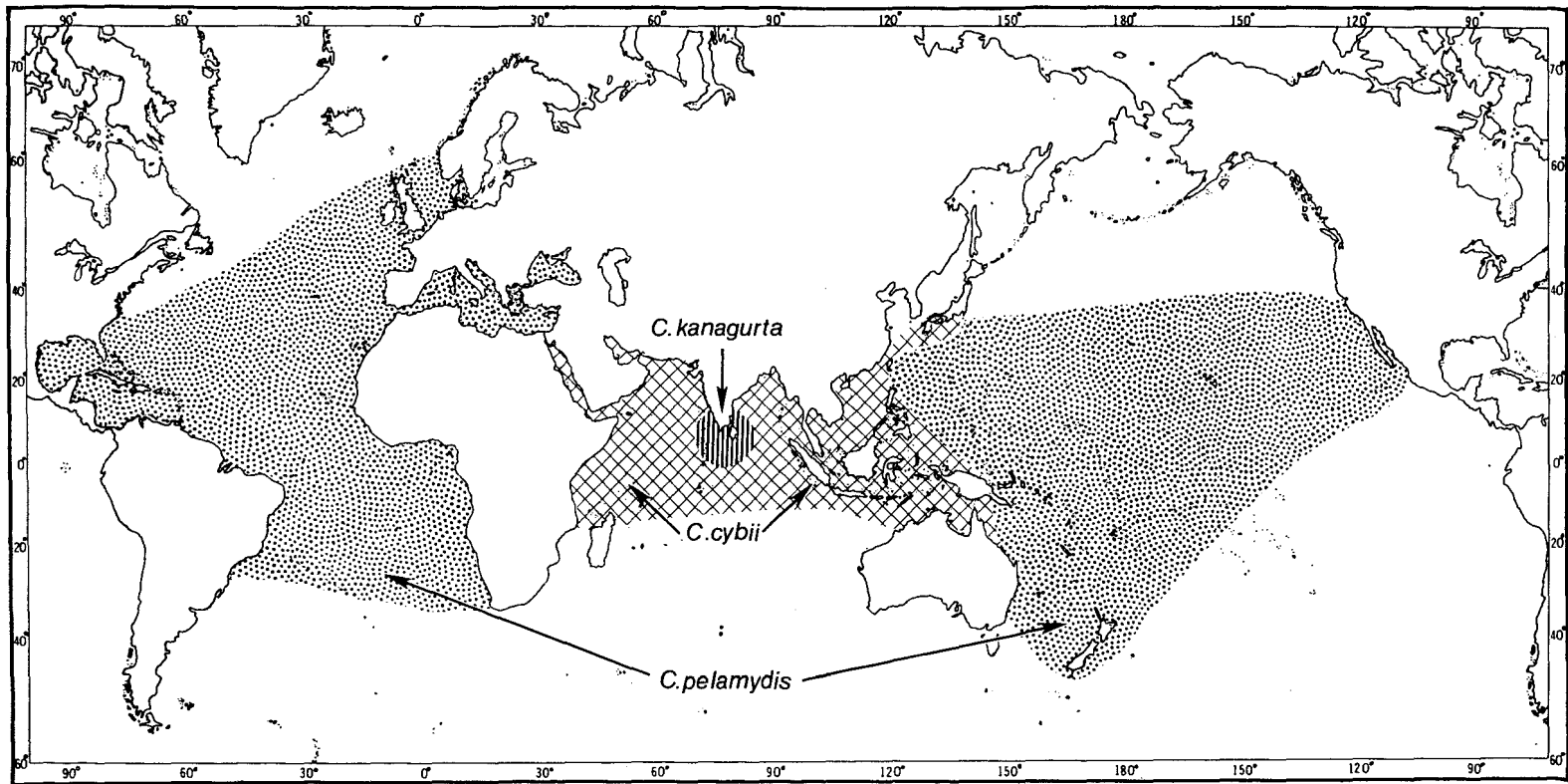


FIGURE 11.—Distribution of *Caligus pelamydis*, *C. cybii*, and *C. kanagurta*.



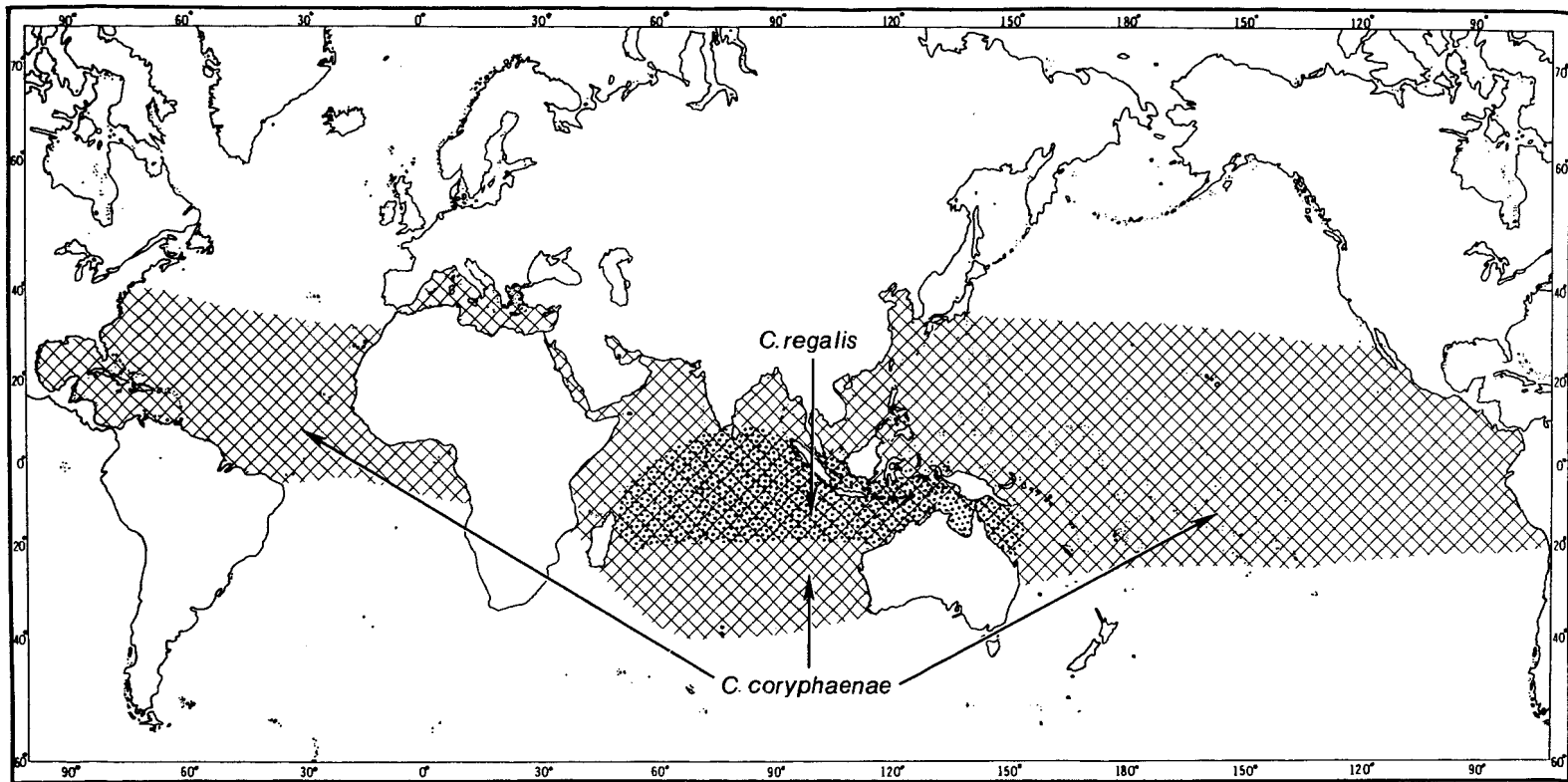


FIGURE 12.—Distribution of *Caligus coryphaenae* and *C. regalis*.

3. *Scomberomorus niphonius* is possibly the most primitive species of the genus based on *Caligus* and other copepod parasites (*Pseudocycnoides scomberomori*, a copepod specific to *S. niphonius*, is more primitive than *P. armatus* found on several other Indo-West Pacific *Scomberomorus*).

## Scomid Phylogeny

### Historic

Many workers have arranged the scombrids according to their ideas of relationships within the group. In this section we present a brief history of scombrid classifications, culminating in the most recently published article by Collette and Russo (1979). Then we present a classification derived from infestation by parasitic copepods and discuss differences between the two classifications.

Modern attempts at classification of the scombrid fishes date from Regan (1909), who placed the family Scombridae as the sole member of a division Scombriformes in the suborder Scombroidei of the order Percomorphi. Starks (1910) was the first to define subdivisions within the family recognizing five subfamilies: Scombrinae, Scomberomorinae, Acanthocybinae, Sardinae, and Thunninae (Fig. 13). Starks based his classification on osteology. Characters from soft anatomy, particularly the viscera and the circulatory system, were added by Kishinouye (in particular, his classic 1923 monograph). Kishinouye

was so impressed by the differences that he separated the most advanced scombrids as a separate order, Plecostei, with two families, the Thunidae (*Thunnus*) and the Katsuwonidae (*Auxis*, *Euthynnus*, and *Katsuwonus*). Rather illogically, he left the other scombrids as two families, Scombridae (*Scomber* and *Rastrelliger*) and Cybiidae (all the bonitos and seerfishes) of the Teleostei, suborder Acanthopterygii (Fig. 14). The next revisor of the family, Fraser-Brunner (1950) overreacted to this splitting of the scombrids into four families in two orders by ignoring the anatomical data in constructing his classification (Fig. 15). The most recent classification of the scombrids (Collette and Russo 1979) has been slightly revised for presentation here (Fig. 16).

### Parasite Based

Once a host-parasite relationship has been established, several events can occur with respect to the evolution of this relationship. Assuming the host will evolve and allowing for speciation, the parasite may gradually change maintaining compatibility with its changing host or the parasite may be divided into separate populations because of a speciation event in the host. In the former case, there is no speciation event in the host, thus a single parasite population would remain sympatric. In the latter case, the speciation event in the host would divide the parasite population into two allopatric populations and act as a vicariant event with respect to the parasites. The

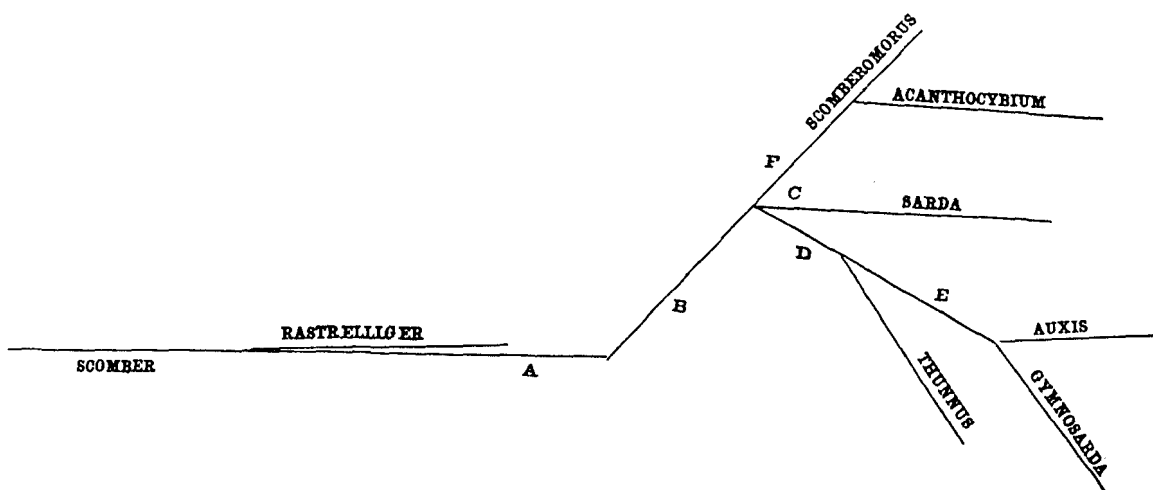


FIGURE 13.—Diagram of relationships of the Scombridae from Starks (1910). A) Characters of *Scomber*. B) Acquisition of interposed opisthotics. C) *Thunnus* type of cranial crests, and the inferior cranial pit indicated, with the *Scomberomorus* type of ethmoid and nasals. D) The inferior cranial pit excluding the pterotic from the brain cavity, and the condition of the ethmoid and nasals of *Scomber*. E) The condition of the infravertebral processes from which *Auxis* and *Euthynnus* (given as *Gymnosarda* by Starks 1910) have diverged. F) The *Scomberomorus* type of cranial crests, elongate form, concave ethmoid, and nonprojecting nasals.

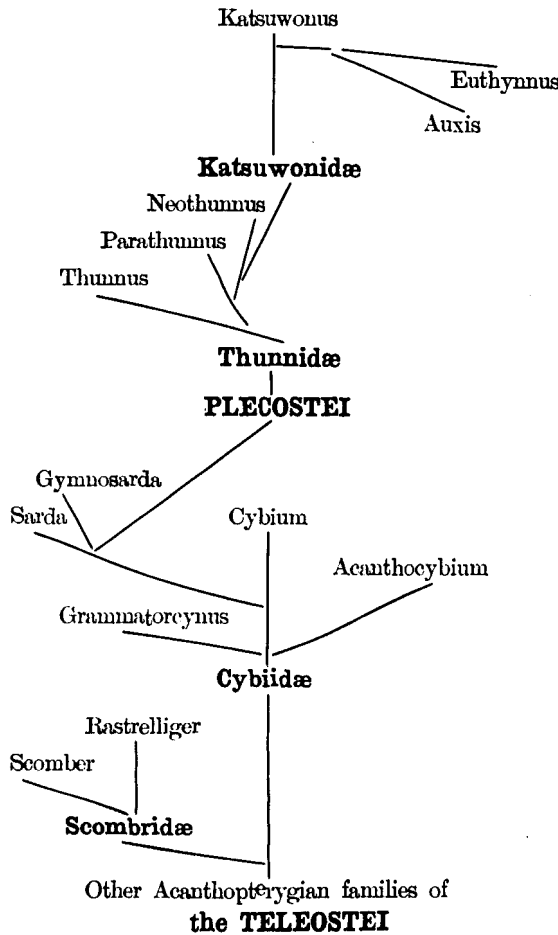


FIGURE 14.—Diagram showing classification of scombrid fishes adopted by Kishinouye (1923).

isolated parasite populations may remain the same, speciate, or one or both may become extinct. Morphological data from hosts or parasites may be used to reconstruct or estimate phylogenetic relationships. If questions regarding coevolutionary events are asked, however, information concerning the phylogeny of both hosts and parasites is necessary. Brooks (1979) discussed types of host-parasite relationships and outlined parasitic distributions on hosts and the coevolutionary implications of such distributions. Brooks (1981) provided a method for testing coevolutionary hypotheses.

Cladistic analysis of hosts and parasites, using morphological characters, will provide information concerning the phylogeny of both hosts and parasites. If host and parasite phylogenies are concordant, the distribution of parasites on hosts can be explained by cospeciation events. If, on the other hand, host-parasite relationships are convergent, they indicate host transfer or broadening coaccommodation (Brooks 1981). Using the additive binary coding method presented by Brooks to generate character state trees for host or parasite phyletic relationships, it is possible through character analysis to generate host trees based on parasite phyletic relationships and parasite trees based on host phyletic relationships. By direct comparison of these trees with each other it is possible to test hypotheses of coevolution.

In an attempt to utilize parasite data and to objectively resolve the problem of phyletic relationships among the genera of Scombridae, the first author coded our copepod infestation data and the third author subjected the data to a cladistic analysis, using a computer program (WAGNER 78) written by J.

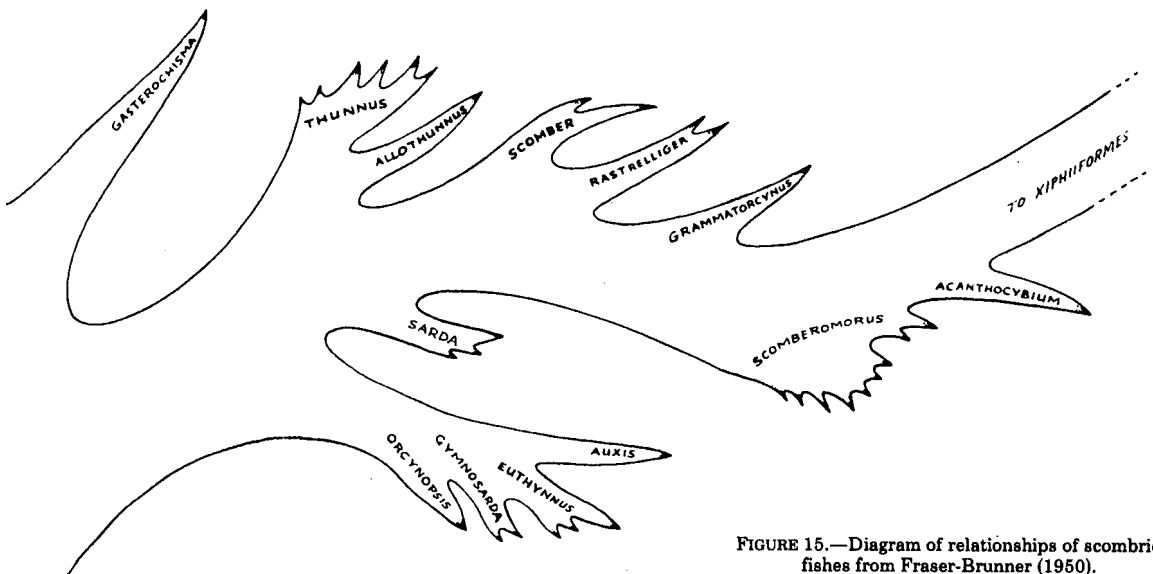


FIGURE 15.—Diagram of relationships of scombrid fishes from Fraser-Brunner (1950).

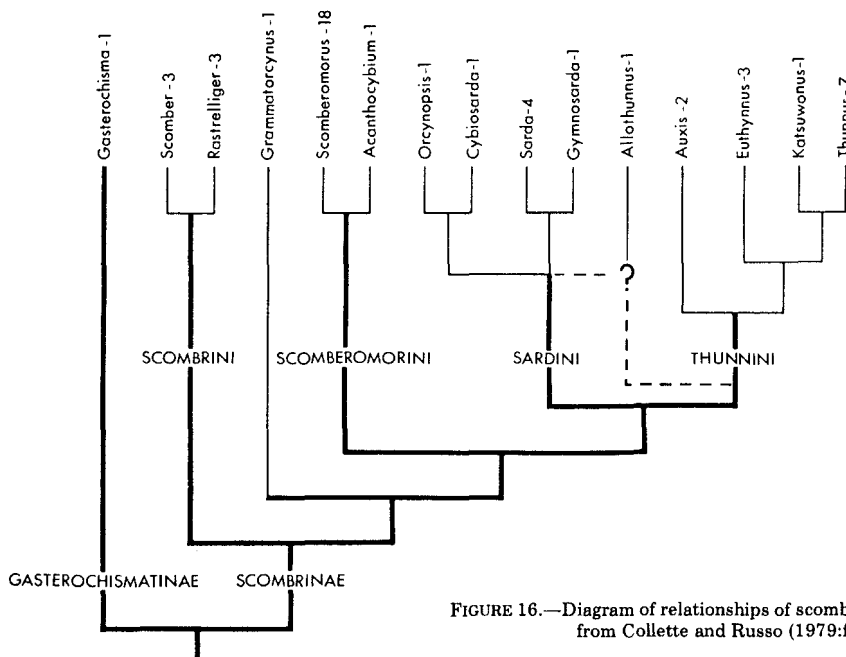


FIGURE 16.—Diagram of relationships of scombrid fishes modified from Collette and Russo (1979:fig. 1).

S. Farris (following Farris 1970 and Farris et al. 1970). Infestation by a given copepod species was, somewhat arbitrarily, considered primitive; absence, specialized. A transformation series was used to indicate decreasing amounts of parasitism by a given copepod species across a matrix of scombrid genera. The Wagner tree was rooted at *Rastrelliger*, one of the most primitive members of the Scombrinae. The resulting Wagner tree (Fig. 17) shows major differences from the diagram of relationships based on host morphology (Fig. 16). The only concordant sister groups produced in this tree are *Acanthocybium* and *Scomberomorus*.

There are at least two problems with coding the infestation data in this manner. Use of copepod species ignores information concerning the relationships of the species. Another difficulty is coding copepod infestation as a two-state character (present or absent in a host species), when *Caligus* infestation data can only be interpreted as host preference (relative percent of infestation) rather than as host specificity (see previous section on *Caligus*). The program was rerun using infestation by genera of copepods and defining *Caligus* presence as more than 5% infestation to correct for this problem. This Wagner tree (Fig. 18) is much closer to the diagram based on host morphology. Several concordant sister groups are present: *Scomberomorus-Acanthocybium* defined by the acquisition of *Tuxophorus* at node (5), *Grammatorcynus-Scomberomorus + Acanthocybium* defined by

the acquisition of *Caligus* at node (4); *Katsuwonus-Thunnus*, loss of *Ceratocolax* at node (9); and *Euthynnus-Katsuwonus + Thunnus*, acquisition of *Pseudocycnus* at node (8).

There are also several differences between this Wagner tree and the diagram of relationships based on host morphology. *Gymnosarda* is associated with *Grammatorcynus-Acanthocybium* group based on the presence of *Shiinoa* in all four genera. However, we found *Shiinoa* in only one specimen of *Gymnosarda*, so not much reliance can be placed on this association. We found only two other copepods on *Gymnosarda*, single occurrences of *C. bonito* and *C. productus*, which were omitted in this run of the program. There was only one common copepod on *Allothunnus* (*Elytrophora*), but there were also records of the same two species of *Caligus* as in *Gymnosarda*. Perhaps examining more specimens of *Gymnosarda* and *Allothunnus* (we examined only seven of each) would yield more copepods that would cluster these two genera with the natural group of the Sardini plus Thunnini.

We turned from attempts at producing a cladistic classification of all scombrids, using the infestation data, and decided to use only a portion of the data, infestation by the nasal bomolochids of the genus *Unicolax*. The five known species of *Unicolax* are all parasites in the nasal sinuses of scombrid fishes. The first author compared characters within the species of *Unicolax* with those in the related outgroup genus

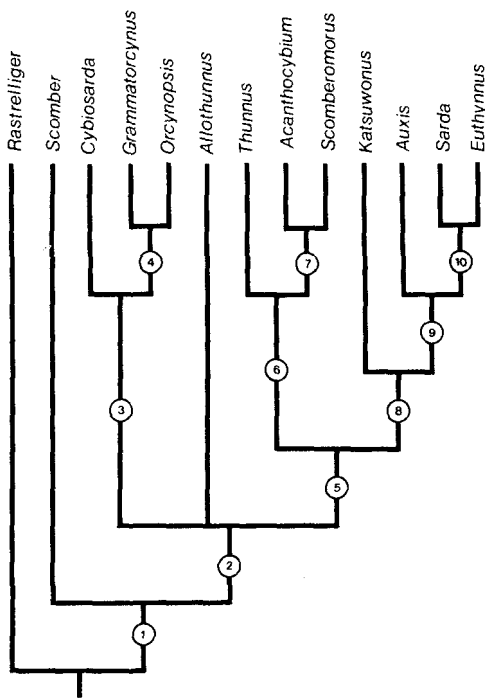


FIGURE 17.—Wagner tree of scombrid hosts based on infestation by copepod species. Synapomorphies (gain, loss, or reduction in infestation rate of copepod species) occurred at the following nodes: 1) loss of *Lernanthropus kanagurta*, *Orbitacolax aculeatus*, and *Nothobomolochus kanagurta*; 2) loss of *Pumilioes jonesi*; 3) gain of *Caligus asymmetricus* and *Unicolax collateralis*; 4) gain of *Caligus bonito*; 5) gain of *Caligus productus* and *C. coryphaenae*; 6) gain of *Brachiella thynni*; 7) gain of *Shiinoa oclusa* and reduction of infestation of *Caligus productus*; 8) reduction of infestation of *Caligus asymmetricus*; 9) gain of *Caligus pelamydis*, *Unicolax mycterobius*, *U. collateralis*, and reduction of infestation of *C. productus* and *C. coryphaenae*; 10) gain of *Caligus bonito*, *Ceratocolax euthynni*, and reduction of infestation of *Unicolax mycterobius*.

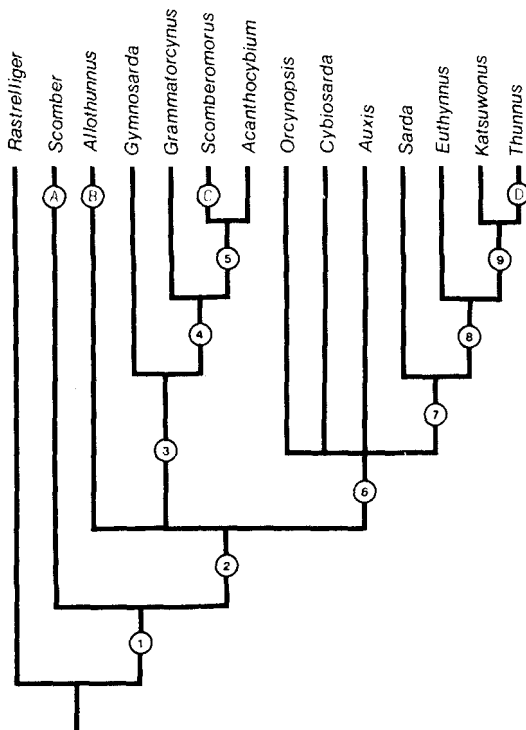


FIGURE 18.—Wagner tree of scombrid hosts based on infestation by copepod genera. Synapomorphies (gain or loss of copepod genera) occurred at the following nodes: 1) *Orbitacolax*, *Nothobomolochus*, and *Lernanthropus*; 2) loss of *Pumilioes*; 3) gain of *Shiinoa*; 4) gain of *Caligus*; 5) gain of *Tuxophorus*; 6) gain of *Unicolax*; 7) gain of *Ceratocolax* and *Caligus*; 8) gain of *Pseudocycnoides*; 9) loss of *Ceratocolax*. Autapomorphies are A) gain of *Clavellisa*; B) gain of *Elytrophora*; C) gain of *Homobomolochus*, *Unicolax*, and *Pseudocycnoides*; D) loss of *Unicolax* and gain of *Elytrophora*.

*Bomolochus*. The eight characters used are as follows: Number of setae on the exopod of leg 4 (many = plesiomorphic, few = apomorphic); presence or absence of surface ornamentation on the abdomen and caudal rami (presence = plesiomorphic, absence = apomorphic); first exopod segment of leg 2 with long hairs or short spinules (hairs = plesiomorphic, spinules = apomorphic); number of setae on the first maxilla (4 = plesiomorphic, 3 = apomorphic); number of setae on exopod last segment of leg 2 (5 = plesiomorphic, 4 = apomorphic); number of segments in first antenna (7 = plesiomorphic, 6 = apomorphic); endopod segments with a row of short hairs (plesiomorphic) or patch of fine spinules (apomorphic); exopod spines of leg 2 with fine hairs (plesiomorphic) or mostly toothed (apomorphic).

Phylogenetic relationships of the copepod parasites of the genus *Unicolax* are represented in the branching diagram (Fig. 19), generated with the

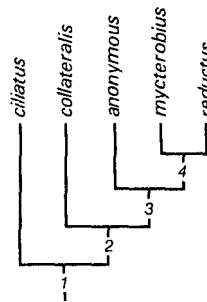


FIGURE 19.—Cladogram showing relationships of *Unicolax* species. The nodes (1-4) represent the following: 1 = species of *Unicolax*; 2 = teeth on leg 2 exopod spines; 3 = endopod segments with patches of spinules; 4 = fewer than 5 setae on fourth leg exopod.

WAGNER 78 program using characters of copepod morphology. The additive binary matrix of this tree is presented in Figure 20. Phylogenetic relationships of the scombrid hosts (Fig. 21) are adapted from Collette and Russo (1979) and represent a monophyletic sub-

	1	2	3	4	5	6	7	8	9
1									
2									
3									
4									
5									
6									
7									
8									
9									

FIGURE 20.—Additive binary matrix based on relationships of *Unicolax* parasites.

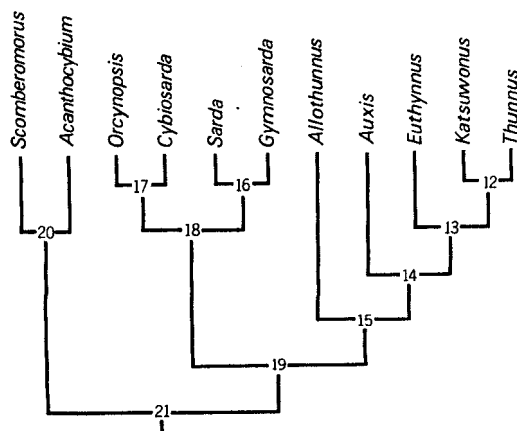


FIGURE 21.—Cladogram of scombrid hosts based on host morphology. Nodes 12-21 represent hypothetical ancestors.

set of the Scombridae. The additive binary matrix of this tree is presented in Figure 22.

In Figure 23 we have indicated the scombrid genera in the tribes Scomberomorini, Sardini, and Thunnini parasitized by *Unicolax*, based on the phylogeny of the Scombrinae proposed by Collette and Russo (1979). The copepod species are ranked from the most plesiomorphic (generalized) to the most apomorphic (specialized), based on the Wagner tree of *Unicolax* (Fig. 19).

As stated earlier, parasite phylogenies can be coded as characters and used to generate host trees; conversely, host phylogenies can be coded as characters and used to generate parasite trees (Brooks 1981). In

cases where a host has more than one parasite or a parasite has more than one host the character states for the two series are inclusively OR'd (Copi 1972) and a single series is used. By logically OR'ing two characters, a character state is said to be present in the union of two groups, if and only if it is present in one or both groups. For example, in Figure 20, *Auxis* harbors *U. collateralis* (2) and *U. mycterobius* (4). The character states for a host bearing *U. collateralis* can be determined by reading across line 2 of the additive character matrix, that is a one or logical true for states 2, 8, and 9 and not true for the others. The character states for a host bearing *U. mycterobius* can be determined by reading across line 4, that is a one or logical true for states 4, 6, 7, 8, and 9 and not true for the others. Logically OR'ing the two rows of the matrix results in the character states 2, 4, 6, 7, 8, and 9 being true and the others being not true. Referring to the parasite tree (Fig. 19), these character states represent the host, *Auxis*, as having or having had during the course of its evolution (sensu lato) parasitic taxa (2) *U. collateralis*, (4) *U. mycterobius*, and hypothetical ancestors (1), (2), (3), and (4).

Proceeding in this manner for each host, a parasite (parasite ancestor) by host matrix is constructed. This matrix was subjected to cladistic character analysis using the WAGNER 78 program for optimization. The resulting Wagner tree (Fig. 24) is rooted at a hypothetical host ancestor without *Unicolax* parasites. According to Brooks' (1981) methodology, this tree is an estimate of host phylogeny in lieu of host morphological data. It estimates host phylogeny based on phylogenetic events of their parasites. Because we have a host phylogeny based on morphological data, a direct comparison between the two trees is possible. We attempt to explain the source of differences between the estimate of host phylogeny based on parasites and a cladogram based on host morphology.

The most notable difference is that the base, node (5) of the host by parasite tree (Fig. 24), is formed by an unresolved multicotomy. This has resulted because it is more parsimonious to assume that the four scombrid taxa, which lack *Unicolax*, never had them than to assume they were first acquired then lost. Node (4) is a subset of node (21) on the host phylogeny (Fig. 21) and is based on a common *Unicolax* ancestor [node 1, (Fig. 19)]. Node (3) is a subset of node (19) on the host phylogeny and is based on the presence of ancestor (2) and parasite (2), *U. collateralis*. An unresolved tricotomy is present at node (3) because the only parasite shared by the hosts *Cybiosarda* and *Orcynopsis* is *U. collateralis*, which is present below node (3) and is therefore treated as

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
1																						
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FIGURE 22.—Additive binary matrix based on scombrid relationships. Numbers 1-11 are host taxa and 12-21 are hypothetical ancestors represented in Figure 21.

synplesiomorphous. Node (2) is based on ancestors (2) and (4). Node (1) is an unresolved tricotomy and does not represent a subset of the host phylogeny because it includes *Sarda*. This node is based on the presence of parasite (4), *U. mycterobius*. Events which are not shared (autopomorphous) include the acquisition of (1), *Unicolax ciliatus* in *Scomberomorus*; the acquisition of (5), *U. reductus* and the loss of (2); *U. collateralis*, in *Katsuwonus*; and the acquisition of (3), *U. anonymous*, in *Euthynnus*. The loss of the parasite *U. collateralis* in *Katsuwonus* is the only homoplasy in the host by parasite tree.

The above procedure can also be used to generate a parasite phylogeny by using a data matrix construct-

ed from information concerning host phylogeny. The parasite host tree (Fig. 25) is rooted at a nonscombrid ancestor based on the assumption that the common ancestor of *Unicolax* was from a nonscombrid. This tree (Fig. 25) can be compared with the tree representing parasite phylogeny, which is based on an analysis of parasite morphological characters (Fig. 19). Node (4) on the parasite by host tree (Fig. 25) is comparable with node (1) on the parasite phylogeny (Fig. 19). *Unicolax ciliatus* is the sister group of all other parasitic taxa in both trees. Node (3) of the parasite by host tree contains all elements of node (2) on the parasite phylogeny; however, *U. reductus* is removed as the sister group of other taxa on the

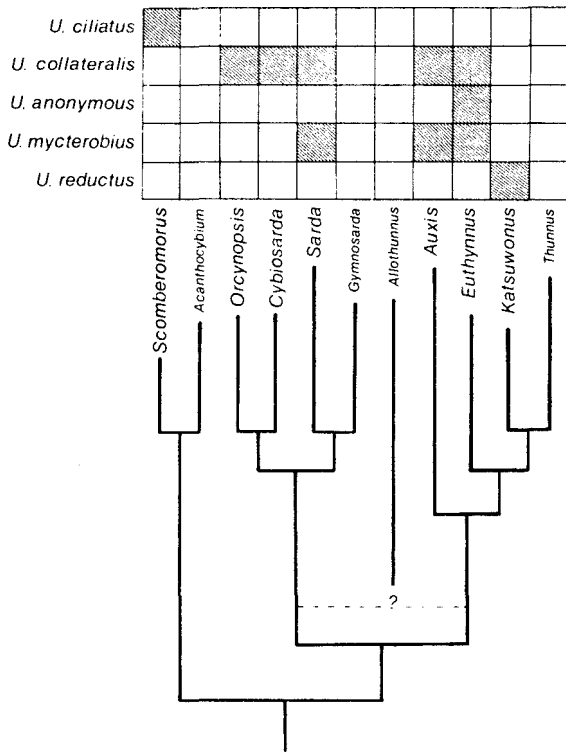


FIGURE 23.—Occurrence of species of *Uicolax* on scombrids in the tribes Scomberomorini, Sardini, and Thunnini. Copepods are ranked from most plesiomorphic (top) to most apomorphic (bottom). Scombrids are arranged to depict hypothesized phylogenetic relationships.

parasite by host tree whereas *U. collateralis* occupies this position on the parasite phylogeny. This discrepancy occurs because parasites *U. anonymous*, *U. collateralis*, and *U. mycterobius* are all found on the host *Euthynnus* (9), at node (2) on the parasite by host tree (Fig. 25). *Uicolax collateralis* and *U. mycterobius* are then grouped because they co-occur on host taxa 5 (*Sarda*) and 8 (*Auxis*) as well as nodes (16) and (18) of the host phylogeny (Fig. 21). Hypothesized hosts, which are not shared (autapomorphies), include *Scomberomorus* and host node (20) for *U. ciliatus*, *Katsuwonus* and host node (12) for *U. reductus*, and *Orcynopsis*, *Cybiosarda*, and host node (17) for *U. collateralis*. The parasite by host tree (Fig. 25) presents no homoplasy.

If we make the assumption that the host and parasite phylogenies, which are based on morphological data, are both true, how do we explain the current distribution of parasites on hosts? This question is analogous to questions of biogeography. We know by generating a host tree from parasitic phylogenetic information and by generating a parasite tree from host phylogenetic information that the two data sets are

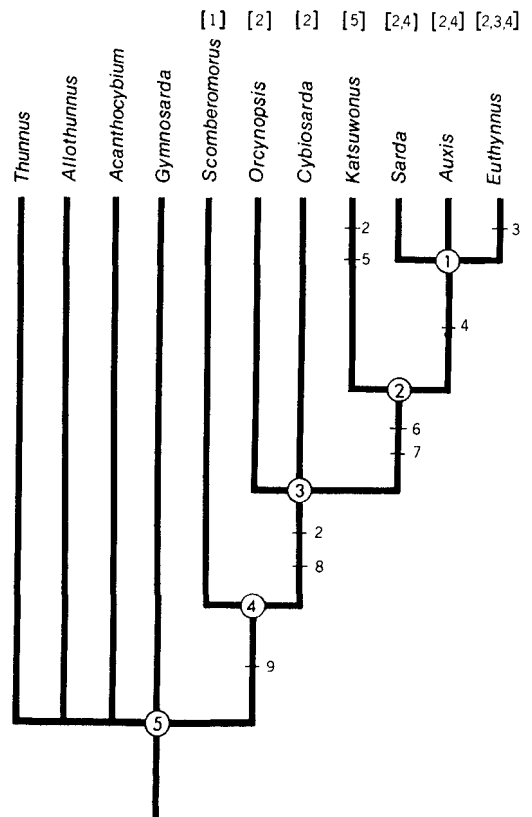


FIGURE 24.—Host tree based on parasitic phylogenetic information. Numbers in brackets at top of figure represent infestation by 1) *Uicolax ciliatus*, 2) *U. collateralis*, 3) *U. anonymous*, 4) *U. mycterobius*, and 5) *U. reductus*. Numbers crossing branches on tree represent acquisitions of parasites or parasite ancestors, except for number 2 leading to *Katsuwonus* which indicates a loss.

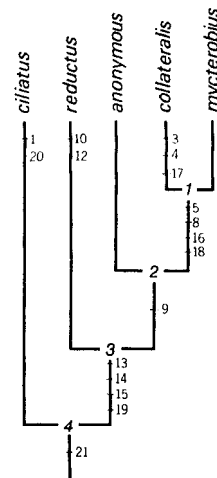


FIGURE 25.—Parasite tree of *Uicolax* species based on host phylogenetic information. Numbers crossing branches on tree represent historic infestations of hosts or host ancestors by parasites or parasite ancestors.



not concordant. We also know that several parts of these data sets are in agreement, that is to say, some evolutionary events in *Unicolax* are correlated with speciation (vicariant) events in the Scombridae. These events are easily explained by models of allopatric speciation and hypotheses of dispersal are unnecessary. Before we can suggest a dispersal event, we must first factor out host-parasite relationships which are due to cospeciation events. They may be done by overlaying parasitic phylogenetic data in the form of a character state tree on the host phylogeny. This procedure is similar to the generation of the host by parasite tree (Fig. 24), with the exception that the parasite phylogenetic information is forced onto the host cladogram.

In our example the scombrid host tree was coded as a character state tree. A character by scombrid taxon matrix was constructed so that each character was repeated a number of times. To this we added the characters from the parasite phylogeny by host data matrix used to generate the host by parasite tree. The repetition of the character by scombrid taxa matrix has the effect of forcing the tree into a particular shape, in our case, the original host cladogram. The number of replicates is large enough so the parasite phylogeny data does not alter the outcome of the tree. This combined data matrix was submitted to the WAGNER 78 program and a most parsimonious tree was generated. This tree (Fig. 26) is the same shape as the original host phylogeny, and characters relating to historical events of the parasites are overlaid or forced onto the tree in a parsimonious configuration.

The overlay presented in Figure 26 indicates that parasite evolutionary events (-2), (17), (-8), and (-9) (indicated as characters circled in broken lines) were reversed or lost in several host taxa or lineages. This indicates the loss of a parasite or a hypothetical ancestral parasite. The only independent acquisition of parasites or hypothetical ancestral parasites occurred between *Sarda*, node (8), and *Auxis* on the cladogram. In both cases parasite 4, *U. mycterobius*, and its hypothetical ancestors (6) and (7) not only were independently acquired but also must have been independently evolved. In this case it is more reasonable to invoke an hypothesis of dispersal and to explain the infestation of *Sarda* by *U. mycterobius* by dispersal from another scombrid host. This hypothesis is more parsimonious than the coevolutionary hypothesis in that it requires one dispersal event rather than a series of independent identical evolutionary events (having serious taxonomic implications for parasitic taxa, i.e., if two taxa evolve in independent lineages they must be considered sepa-

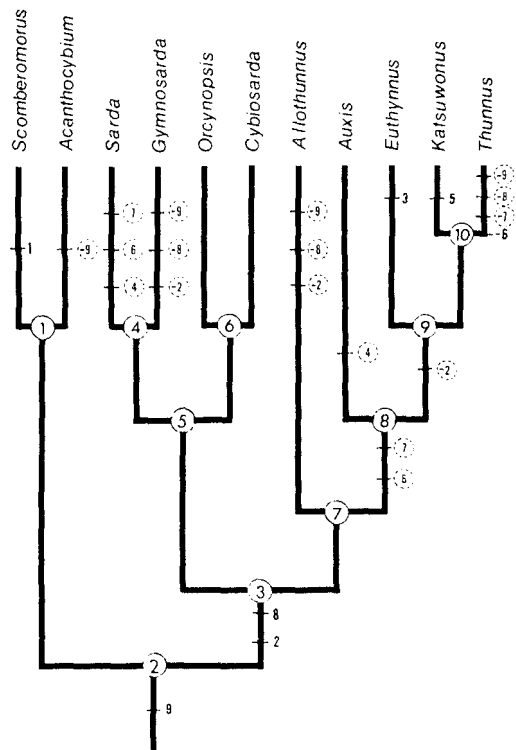


FIGURE 26.—Overlay of historical parasite information on host phylogeny. Negative numbers indicate losses and numbers circled in broken lines indicate independent acquisitions or losses of parasites or parasite ancestors.

rate, possibly sibling species). It must be noted that an hypothesis of independent evolutionary events leading to the establishment of *U. mycterobius* on *Sarda* may in itself require a dispersal event earlier in its evolutionary history.

The coevolution of *Unicolax* and its scombrid hosts can be reconstructed as follows. The three higher tribes of the Scombrinae (Scomberomorini, Sardini, and Thunnini) share *Unicolax*, indicating that this genus arose from a more primitive bomolochid after the ancestors of these three tribes evolved from the Scombrini. *Unicolax ciliatus*, the most primitive species of *Unicolax*, is present only in the most primitive of the three tribes, the Scomberomorini. *Unicolax collateralis* is found on members of the tribes Sardini and Thunnini. Infestation by *U. anonymous* yields little information because it is restricted to *Euthynnus alletteratus* from both sides of the Atlantic. It is apparently a more recently derived species that has not spread far geographically or host-wise. *Unicolax mycterobius* is restricted to the two most primitive genera of the Thunnini (*Auxis* and *Euthynnus*) except for its presence on two specimens of *Sarda orientalis* from Japan. This seems best explained as

dispersal from its usual host. It may be an example of a parasite species utilizing an alternate host in the absence of its preferred host. Finally, *U. reductus*, the most specialized species of *Unicolax*, has been found only on a highly specialized host, *Katsuwonus*. This indicates that *Katsuwonus* evolved from the *Euthynnus* stock, and *U. reductus* evolved from the ancestor of *U. mycterobius*.

It should be noted that, in each of the three tribes, *Unicolax* was not found in the most specialized scombrid genus. In *Thunnus* this may be the result of competition resulting from heavy infestations of the monogenetic trematode, *Nasicola klawei* (Stunkard), in the nasal sinuses of the host fish. There is no evidence, however, that parasite competition is a factor in *Acanthocybium*, *Gymnosarda*, and *Allothunnus*. It may be that as each of the tribes evolve, the most specialized members lose parasites. This concept is consistent with other data presented elsewhere in this paper (see *Scomberomorus* infestation data in Table 6 and *Sarda* parasite discussions).

## COMPARISON OF COPEPOD PARASITES IN SCOMBRIDAE AND BELONIDAE

After completing the analysis of the parasitic copepods of the Scombridae, it seemed instructive to make comparisons with those of the Belonidae, the only other family of fishes that has been studied in a similar manner (Cressey and Collette 1970). The Scombridae (48 species) is a larger family than the Belonidae (32 species). All scombrids are marine species, although several enter estuaries and only *Scomberomorus sinensis* is found far up the Mekong River. Four genera of Belonidae (*Belonion*, *Potomor-*

*rhapsis*, *Pseudotylorus*, and *Xenentodon*) plus three species of *Strongylura* are restricted to freshwater, and populations of several other species of *Strongylura* invade freshwater long enough to acquire freshwater parasites. Thus, parasites of the family Ergasilidae (nine species) must be omitted in any comparisons because they are restricted to hosts in freshwater. Several other families of copepods cannot be used because their habitat does not occur in the host group. Species of Shiinoidea live inside the nasal cavities of their host, attached to the lamellae of the nasal rosettes. Belonidae have an open nasal pit with no place for a *Shiinoa* to attach. Scombrid species breathe largely by ram-jet ventilation of the gills and so have small oral valves in the upper and lower jaws, apparently too small to house the caligid copepod *Caligodes* which was found on seven species of Belonidae. Several species of the caligid genus *Caligus* were found on needlefishes but all in small numbers, partially because Cressey and Collette's study used mostly preserved specimens that were prone to lose parasites like *Caligus*, which are mostly external.

Two ecological habitats, parasitized by three families of copepods in the two families of fishes, seem comparable—gills and oropharyngeal cavity. Bomolochid copepods are found in the oropharyngeal cavity of both host families (and also in the nasal cavities of the Scombridae). Species of the closely related families Lernanthropidae and Pseudocycnidae attach permanently to the gills of belonids and scombrids, respectively (Table 10).

Comparison of the parasitic copepod fauna of the most speciose genera of each family, *Strongylura* and *Scomberomorus*, reveals some interesting distributional patterns. *Bomolochus bellones*, the common bomolochid of *Strongylura*, extends from the

TABLE 10.—Comparison of parasitic copepod fauna on gills (Lernanthropidae and Pseudocycnidae) and oropharyngeal cavities (Bomolochidae) in genera from the Belonidae (*Strongylura*) and Scombridae (*Scomberomorus*).

<i>Strongylura</i>		<i>Scomberomorus</i>
5 species	Indo-West Pacific	10 species
<i>Bomolochus bellones</i> (5/5)		<i>Unicolax ciliatus</i> (9/10)
<i>Bomolochus sinensis</i> (1/5)		<i>Pseudocycnoides argatus</i> (8/10)
<i>Nothobomolochus digitatus</i> (1/5)		<i>Pseudocycnoides scomberomori</i> (1/10)
<i>Lernanthropus belones</i> (3/5)		
<i>Lernanthropus tylosuri</i> (5/5)		
<i>S. senegalensis</i>	Eastern Atlantic	<i>S. tritor</i>
<i>Bomolochus bellones</i>		<i>Unicolax ciliatus</i>
3 species	Western Atlantic	4 species
<i>Bomolochus bellones</i> (3/3)		<i>Halobomolochus divaricatus</i> (3/4)
<i>Lernanthropus belones</i> (3/3)		<i>Halobomolochus asperatus</i> (1/4)
<i>Lernanthropus tylosuri</i> (2/3)		<i>Pseudocycnoides buccata</i> (4/4)
2 species	Eastern Pacific	2 species
<i>Bomolochus constrictus</i> (2/2)		<i>Halobomolochus nudiusculus</i> (2/2)
<i>Bomolochus ensiculus</i> (2/2)		<i>Pseudocycnoides buccata</i> (2/2)
<i>Lernanthropus belones</i> (2/2)		
<i>Lernanthropus tylosuri</i> (1/2)		

Indo-West Pacific through the eastern Atlantic to the western Atlantic Ocean. It is replaced by two species of bomolochids in the eastern Pacific—*B. constrictus* and *B. ensiculus*. *Unicolax ciliatus*, the common bomolochid of *Scomberomorus*, extends from the Indo-West Pacific to the eastern Atlantic. It is replaced in the western Atlantic by *H. divaricatus* and *H. asperatus* and in the eastern Pacific by *H. nudiusculus*.

The gill parasites, *Lernanthropus* and *Pseudocycnoides*, show a similar pattern. The two species of *Lernanthropus*, being circumglobal, extend farther than *Bomolochus* does. *Pseudocycnoides armatus* is found on species of *Scomberomorus* in the Indo-West Pacific. It is replaced in the western Atlantic and eastern Pacific by *P. buccata*. No *Lernanthropus* or *Pseudocycnoides* were found on the single host species of *Strongylura* and *Scomberomorus* in the eastern Atlantic.

Host specificity at the generic level depends on factors such as the number of species in a given host genus, maximum body size of the host species, and distribution of the host species. The most speciose genera in each family (*Scomberomorus* with 18 of 47 species in the Scombrinae and *Strongylura* with 14 of 32 species in the Belonidae) have the most copepod species, 50 and 85%, respectively, of the total parasite fauna recorded for these two families (Table 11). However, if one calculates a mean number of copepod species per host species, a different picture emerges. In both fish families, monotypic genera, including large pantropical species, contain the most copepod species per host species, *Acanthocybium* and *Katsuwonus* in the Scombridae with 6 of 46 species of copepods and *Ablennes* in the Belonidae with 9 of 21.

The genera with the next highest number of cope-

pod species per host species are moderate-sized species, *Euthynnus* (three species) with 3.7 copepod species per host species in the Scombridae and *Platybelone* (monotypic) with 7 of 21 in the Belonidae. The three genera with the lowest number of parasitic copepods per host species in the Belonidae (0-0.5) are a special case, without parallel in the Scombridae, small (4-28 cm body length) freshwater South American species. No copepods were found on the South African monotypic *Petalichthys* but only a few host specimens were examined.

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TABLE 11.—Number of parasitic copepod species per genus and maximum size of Belonidae and Scombridae. (Maximum size of belonid species given in cm body length and of scombrid species in cm fork length.)

Belonidae				Scombridae					
Genus	No. spp.	Max. size (cm BL)	No. spp. copepods	$\bar{x}$ no. copepod spp./host spp.	Genus	No. spp.	Max. size (cm FL)	No. spp. copepods	$\bar{x}$ copepod spp./host spp.
<i>Ablennes</i>	1	73	9	9	<i>Acanthocybium</i>	1	183	6	6
<i>Belone</i>	2	32-53	3	1.5	<i>Allothunnus</i>	1	96	3	3
<i>Belonion</i>	2	4	0	0	<i>Auxis</i>	2	40-50	6	3
<i>Petalichthys</i>	1	21	0	0	<i>Cybiosarda</i>	1	42	3	3
<i>Platybelone</i>	1	30	7	7	<i>Euthynnus</i>	3	64-100	11	3.7
<i>Potamorhaphis</i>	3	10-16	1	0.5	<i>Grammatocynus</i>	1	100	5	5
<i>Pseudotylosurus</i>	2	20-28	1	0.5	<i>Gymnosarda</i>	1	108	3	3
<i>Strongylura</i>	14	23-59	18	1.3	<i>Katsuwonus</i>	1	100	6	6
<i>Tylosurus</i>	5	39-130	11	2.2	<i>Orcynopsis</i>	1	130	2	2
<i>Xenentodon</i>	1	17	2	2.0	<i>Rastrelliger</i>	3	20-35	5	0.7
					<i>Sarda</i>	4	50-85	9	2.3
					<i>Scomber</i>	3	40-50	6	2.0
					<i>Scomberomorus</i>	18	30-220	23	1.3
					<i>Thunnus</i>	7	90-300	10	1.4
Totals	32		21	0.68		47		46	0.98

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## APPENDIX

Below is a list of scombrid hosts and their parasitic copepods. Numbers after fish names indicate the number of fish examined. Numbers after copepod names indicate number of fish infested. Asterisks indicate new record since Cressey and Cressey (1980).

## SCOMBRINI

- |                                      |   |  |
|--------------------------------------|---|--|
| <i>Rastrelliger brachysoma</i> (33)  | <i>Shiinoa inauris</i> (3)              | <i>Caligus biseriodentatus</i> (7)*      |
| <i>Lernanthropus kanagurta</i> (1)   | <i>Scomberomorus cavalla</i> (36)       | <i>Scomberomorus niphonius</i> (19)      |
| <i>Rastrelliger faughni</i> (14)     | <i>Pseudocycnoides buccata</i> (18)     | <i>Pseudocycnoides scomberomori</i> (6)  |
| <i>Pumiliopes jonesi</i> (2)         | <i>Holobomolochus asperatus</i> (10)    | <i>Unicolax ciliatus</i> (3)             |
| <i>Nothobomolochus kanagurta</i> (2) | <i>Caligus mutabilis</i> (2)            | <i>Caligus pelamydis</i> (2)             |
| <i>Orbitacolax aculeatus</i> (2)     | <i>Caligus productus</i> (1)            | <i>Shiinoa occlusa</i> (1)               |
| <i>Rastrelliger kanagurta</i> (124)  | <i>Scomberomorus commerson</i> (130)    | <i>Scomberomorus plurilineatus</i> (14)  |
| <i>Pumiliopes jonesi</i> (20)        | <i>Pseudocycnoides armatus</i> (25)     | <i>Pseudocycnoides armatus</i> (12)      |
| <i>Nothobomolochus kanagurta</i> (7) | <i>Unicolax ciliatus</i> (23)           | <i>Unicolax ciliatus</i> (4)*            |
| <i>Caligus kanagurta</i> (2)*        | <i>Caligus cybii</i> (16)               | <i>Brachiella thynni</i> (1)*            |
| <i>Orbitacolax aculeatus</i> (2)*    | <i>Shiinoa occlusa</i> (15)             | <i>Caligus asymmetricus</i> (1)*         |
| <i>Scomber australasicus</i> (55)    | <i>Caligus biseriodentatus</i> (12)     | <i>Shiinoa occlusa</i> (1)*              |
| <i>Pumiliopes jonesi</i> (5)*        | <i>Caligus infestans</i> (7)            | <i>Scomberomorus queenslandicus</i> (39) |
| <i>Clavellisa scombri</i> (4)        | <i>Tuxophorus cervicornis</i> (3)       | <i>Caligus biseriodentatus</i> (12)      |
| <i>Scomber japonicus</i> (500)       | <i>Brachiella magna</i> (2)             | <i>Unicolax ciliatus</i> (3)             |
| <i>Clavellisa scombri</i> (9)        | <i>Caligus asymmetricus</i> (2)         | <i>Pseudocycnoides armatus</i> (2)       |
| <i>Pumiliopes jonesi</i> (8)         | <i>Tuxophorus cybii</i> (1)             | <i>Caligus cybii</i> (1)*                |
| <i>Caligus pelamydis</i> (1)         | <i>Scomberomorus concolor</i> (47)      | <i>Shiinoa occlusa</i> (1)               |
| <i>Caligus mutabilis</i> (1)         | <i>Pseudocycnoides buccata</i> (14)     | <i>Scomberomorus regalis</i> (38)        |
| <i>Clavelopsis saba</i> (1)          | <i>Holobomolochus nudiusculus</i> (13)  | <i>Pseudocycnoides buccata</i> (12)      |
| <i>Scomber scombrus</i> (97)         | <i>Caligus omisus</i> (7)               | <i>Holobomolochus divaricatus</i> (11)   |
| <i>Caligus pelamydis</i> (1)         | <i>Scomberomorus guttatus</i> (58)      | <i>Shiinoa inauris</i> (5)               |
|                                      | <i>Caligus biseriodentatus</i> (17)     | <i>Caligus productus</i> (3)             |
|                                      | <i>Unicolax ciliatus</i> (14)           | <i>Caligus bonito</i> (1)                |
|                                      | <i>Pseudocycnoides armatus</i> (3)      | <i>Brachiella thynni</i> (1)             |
|                                      | <i>Shiinoa occlusa</i> (1)              | <i>Tuxophorus collettei</i> (1)          |
|                                      | <i>Scomberomorus koreanus</i> (19)      | <i>Scomberomorus semifasciatus</i> (26)  |
|                                      | <i>Caligus cybii</i> (11)               | <i>Pseudocycnoides armatus</i> (5)       |
|                                      | <i>Pseudocycnoides armatus</i> (4)      | <i>Unicolax ciliatus</i> (4)             |
|                                      | <i>Unicolax ciliatus</i> (1)*           | <i>Caligus cybii</i> (3)                 |
|                                      | <i>Scomberomorus lineolatus</i> (14)    | <i>Shiinoa occlusa</i> (2)*              |
|                                      | <i>Unicolax ciliatus</i> (3)            | <i>Caligus biseriodentatus</i> (1)*      |
|                                      | <i>Caligus biseriodentatus</i> (1)      | <i>Scomberomorus sierra</i> (116)        |
|                                      | <i>Pseudocycnoides armatus</i> (1)      | <i>Pseudocycnoides buccata</i> (48)      |
|                                      | <i>Scomberomorus maculatus</i> (77)     | <i>Caligus omisus</i> (39)               |
|                                      | <i>Pseudocycnoides buccata</i> (27)     | <i>Holobomolochus nudiusculus</i> (28)   |
|                                      | <i>Holobomolochus divaricatus</i> (25)  | <i>Scomberomorus sinensis</i> (10)       |
|                                      | <i>Shiinoa inauris</i> (7)              | <i>Caligus cybii</i> (2)                 |
|                                      | <i>Caligus mutabilis</i> (2)            | <i>Brachiella magna</i> (1)              |
|                                      | <i>Scomberomorus munroi</i> (6)         | <i>Caligus pelamydis</i> (1)*            |
|                                      | <i>Caligus cybii</i> (3)                | <i>Scomberomorus tritor</i> (21)         |
|                                      | <i>Unicolax ciliatus</i> (2)            | <i>Unicolax ciliatus</i> (4)             |
|                                      | <i>Caligus biseriodentatus</i> (1)*     | <i>Shiinoa occlusa</i> (1)               |
|                                      | <i>Caligus productus</i> (1)            | <i>Caligus productus</i> (1)             |
|                                      | <i>Scomberomorus multiradiatus</i> (29) | <i>Caligus diaphanus</i> (1)             |
|                                      | <i>Pseudocycnoides armatus</i> (8)      |  |

## SCOMBEROMORINI

- |  |  |  |
|--|--|--|
| <i>Acanthocybium solandri</i> (64)     |  |  |
| <i>Brachiella thynni</i> (39)          |  |  |
| <i>Gloiopotes hygomanus</i> (27)       |  |  |
| <i>Caligus productus</i> (11)          |  |  |
| <i>Shiinoa occlusa</i> (2)             |  |  |
| <i>Caligus coryphaenae</i> (1)         |  |  |
| <i>Pennella species</i> (1)            |  |  |
| <i>Tuxophorus cybii</i> (1)            |  |  |
| <i>Grammatorcynus bicarinatus</i> (47) |  |  |
| <i>Shiinoa occlusa</i> (9)             |  |  |
| <i>Caligus asymmetricus</i> (7)        |  |  |
| <i>Caligus regalis</i> (4)*            |  |  |
| <i>Caligus bonito</i> (1)*             |  |  |
| <i>Caligus pelamydis</i> (1)*          |  |  |
| <i>Caligus productus</i> (1)*          |  |  |
| <i>Scomberomorus brasiliensis</i> (62) |  |  |
| <i>Pseudocycnoides buccata</i> (39)    |  |  |
| <i>Holobomolochus divaricatus</i> (14) |  |  |
| <i>Caligus mutabilis</i> (4)           |  |  |

SARDINI

*Sarda sarda* (106)  
*Caligus bonito* (33)  
*Ceratocolax euthynni* (21)  
*Caligus pelamydis* (8)  
*Caligus productus* (1)  
*Sarda australis* (22)  
*Caligus bonito* (13)  
*Caligus pelamydis* (11)  
*Caligus asymmetricus* (2)  
*Unicolax collateralis* (2)  
*Sarda chiliensis* (45)  
*Caligus bonito* (25)  
*Caligus pelamydis* (4)  
*Caligus productus* (1)  
*Sarda orientalis* (33)  
*Unicolax collateralis* (12)  
*Caligus bonito* (12)  
*Caligus asymmetricus* (4)  
*Caligus kanagurta* (2)\*  
*Caligus productus* (1)  
*Caligus coryphaenae* (1)\*  
*Unicolax mycterobius* (1)\*  
*Gymnosarda unicolor* (7)  
*Caligus bonito* (1)  
*Caligus productus* (1)  
*Shiinoa occlusa* (1)  
*Cybiosarda elegans* (38)  
*Unicolax collateralis* (16)  
*Caligus asymmetricus* (3)  
*Caligus bonito* (1)\*  
*Orcynopsis unicolor* (7)  
*Unicolax collateralis* (1)  
*Caligus bonito* (1)\*  
*Allothunnus fallai* (7)  
*Elytrophora brachyptera* (5)  
*Caligus bonito* (2)\*  
*Caligus productus* (1)\*

THUNNINI

*Auxis species* (68)  
*Unicolax collateralis* (19)  
*Unicolax mycterobius* (9)  
*Caligus productus* (2)  
*Caligus asymmetricus* (1)  
*Caligus coryphaenae* (1)  
*Caligus pelamydis* (1)  
*Euthynnus affinis* (74)  
*Unicolax collateralis* (32)  
*Caligus asymmetricus* (5)  
*Caligus regalis* (5)

*Pseudocycnus appendiculatus* (4)  
*Unicolax mycterobius* (3)  
*Caligus pelamydis* (2)  
*Caligus productus* (1)  
*Caligus bonito* (1)  
*Euthynnus alletteratus* (64)  
*Caligus coryphaenae* (9)  
*Unicolax collateralis* (8)  
*Ceratocolax euthynni* (7)  
*Caligus productus* (5)  
*Caligus bonito* (4)  
*Pseudocycnus appendiculatus* (3)  
*Unicolax mycterobius* (3)  
*Unicolax anonymous* (2)  
*Caligus pelamydis* (1)  
*Euthynnus lineatus* (15)  
*Unicolax collateralis* (4)  
*Caligus bonito* (3)  
*Katsuwonus pelamis* (135)  
*Caligus productus* (54)  
*Caligus coryphaenae* (51)  
*Pseudocycnus appendiculatus* (8)  
*Unicolax reductus* (3)  
*Caligus bonito* (2)\*  
*Caligus asymmetricus* (1)  
*Thunnus alalunga* (13)  
*Elytrophora brachyptera* (8)  
*Caligus coryphaenae* (1)  
*Caligus productus* (1)  
*Pseudocycnus appendiculatus* (1)  
*Thunnus albacares* (112)  
*Caligus productus* (51)  
*Elytrophora brachyptera* (39)  
*Caligus coryphaenae* (32)  
*Pseudocycnus appendiculatus* (21)  
*Brachiella thynni* (8)  
*Caligus asymmetricus* (1)  
*Thunnus atlanticus* (76)  
*Caligus productus* (70)  
*Caligus coryphaenae* (9)  
*Elytrophora brachyptera* (1)  
*Thunnus maccoyii* (7)  
*Elytrophora brachyptera* (5)  
*Caligus productus* (1)\*  
*Pseudocycnus appendiculatus* (1)\*  
*Thunnus obesus* (42)  
*Elytrophora brachyptera* (20)  
*Caligus coryphaenae* (18)  
*Brachiella thynni* (10)  
*Elytrophora indica* (11)  
*Pseudocycnus appendiculatus* (3)  
*Thunnus thynnus* (57)  
*Caligus coryphaenae* (16)

*Caligus productus* (16)  
*Elytrophora brachyptera* (11)  
*Pennella species* (3)  
*Brachiella thynni* (2)  
*Caligus bonito* (1)  
*Pseudocycnus appendiculatus* (1)  
*Thunnus tonggol* (29)  
*Pseudocycnus appendiculatus* (7)  
*Caligus kanagurta* (1)\*